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TESIS

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PRESENTA

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A mis padres Ángela y Enrique†

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Contenido de la tesis

RESUMEN

Los objetivos de esta tesis fueron analizar los patrones en el desempeño demográfico de un conjunto de especies arbóreas del bosque mesófilo de montaña (BMM) y examinar su relación con los atributos morfo-funcionales de estas especies y con la heterogeneidad del ambiente lumínico. La investigación, desarrollada en la Estación Científica Las Joyas en la Reserva de la Biosfera Sierra de Manantlán (Jalisco), incluyó el estudio de estos atributos de las plantas como base para intentar identificar grupos funcionales (con 33 especies), y de sus desempeños en experimentos en casas de sombra y parcelas experimentales utilizando nueve y cuatro especies, respectivamente, con el fin de evaluar la respuesta de los atributos de las plántulas al ambiente lumínico. Para alcanzar los objetivos planteados y describir sus resultados se desarrollaron cinco capítulos. En el primer capítulo se presenta la introducción general del estudio y en él se plantea el marco de referencia, el problema de investigación, la justificación y los objetivos de la tesis. Este capítulo está seguido por tres capítulos donde de reportan los estudios particulares que se llevaron a cabo para obtener los resultados que permitieran analizar las preguntas de investigación específicas; estos tres capítulos representan una aproximación gradual en detalle y complejidad al problema. El primero de ellos (Capítulo II) se titula “Variation of functional traits in trees from a biogeographically complex Mexican cloud forest” y en él se examinó la variación de cuatro atributos (área foliar específica, biomasa de las semillas, altura máxima y densidad de la madera) con el fin de identificar grupos funcionales entre 33 especies de árboles de un bosque mesófilo de montaña con diferente afinidad biogeográfica; para ello se usó un árbol filogenético como hipótesis de trabajo para explorar los efectos de la filogenia en la correlación entre atributos morfológicos. Los análisis indicaron que en el sistema de estudio: (1) existe una variación continua de atributos, lo cual impide reconocer claramente grupos funcionales discretos, y (2) que es posible que diferentes linajes evolutivos (y de diferente origen biogeográfico) hayan convergido en atributos funcionales similares. En general, las correlaciones ecológicas y filogenéticas entre los atributos fueron débiles; las más significativas fueron entre la altura máxima y la biomasas de la semilla, y entre la altura máxima y la densidad de la madera. En ambos análisis el área foliar específica (AFE) no estuvo correlacionada con ningún atributo, a diferencia de muchos estudios que han demostrado lo contrario. En el siguiente capítulo (Capítulo III, “Seedling biomass allocation and vital rates of cloud forest tree species: responses to light variations in shade houses”, se compararon los patrones de asignación de biomasa a hojas, raíces

y tallos en plántulas de nueve especies arbóreas de BMM que crecían en condiciones controladas de luz en casas de sombra. Se analizaron las relaciones entre los atributos vitales (supervivencia y crecimiento) y los atributos morfológicos. La asignación de biomasa a tallos, raíces y hojas difirió significativamente para seis especies a los 225 días de iniciados los experimentos. Cinco especies tuvieron el AFE más grande en los niveles más bajos de luz, (*Citharexylum mocinnii*, *Dendropanax arboreus*, *Fraxinus uhdei*, *Magnolia iltisiana*, y *Quercus salicifolia*). La única especie que tuvo el AFE más grande en los niveles más altos de luz fue *Juglans major* (377.47 cm^2 g^{-1}). En general, todas las especies crecieron mejor en las casas de sombra con los niveles de luz más altos. Solamente la supervivencia de *Simplococarpon purpusii* mostró diferencias entre tratamientos y esta variable estuvo correlacionada con el AFE, y con la biomasa asignada a tallos, raíces y hojas. Sin embargo, cada especie tuvo una respuesta diferencial en la asignación de biomasa a los diferentes atributos evaluados. En el Capítulo IV (Relationships between leaf traits and vital rates of cloud forest tree seedlings: responses to light variations in field conditions) se compararon los patrones de asignación del AFE en plántulas de cuatro especies arbóreas comunes de bosque mesófilo de montaña (*Dendropanax arboreus*, *Fraxinus uhdei*, *Juglans major*, y *Magnolia iltisiana*) que crecieron en parcelas experimentales en ambientes heterogéneos de luz, y se analizaron las relaciones entre atributos vitales y el AFE. Se evaluó el porcentaje de apertura del dosel utilizando fotografías hemisféricas. El AFE difirió significativamente entre tratamientos en las cuatro especies; tres de ellas (*Dendropanax*, *Fraxinus* y *Magnolia*) tuvieron el AFE más grande en las parcelas con dosel más cerrado. No hubo relación entre las tasas de crecimiento en altura y el AFE para tres especies; sólo la tasa de crecimiento de *Juglans major* estuvo correlacionada con el AFE. La supervivencia de tres especies difirió significativamente entre tratamientos y estuvo correlacionada con el AFE. Todas las especies tuvieron un mayor número de plántulas vivas en las parcelas ubicadas en los rodales con el dosel más abierto. El último capítulo (Capítulo V) se presenta una discusión general que integra las conclusiones generales sobre los resultados y sus implicaciones para su aplicación al manejo de bosques en la RBSM, y en otros bosques mesófilos de México. El estudio permitió concluir que *Dendropanax arboreous*, *Fraxinus uhdei* y *Magnolia iltisiana* son especies viables para ser introducidas utilizando a los pinos como especies nodrizas. Por el contrario, los valores altos de supervivencia y crecimiento de *Juglans major* sugieren que sus plántulas tienen mayor potencial para ser introducidas en áreas abiertas.

ABSTRACT

The objectives of this thesis were to analyze the patterns of demographic performance of a group of cloud forest (CF) tree species and to examine their relationships with the morpho-functional traits of these species with light heterogeneity. The investigation, carried out at Las Joyas Scientific Station, located in the Sierra de Manantlan Biosphere Reserve (Jalisco), included the study of these plant traits as a basis to attempt the identification of functional groups (with 33 species); their performance was assessed in shade house and field experiments using eight and four species, respectively. The thesis was divided in five chapters. The first chapter provides a general introduction to the study, identifies the research problem, and provided the background and the objectives of the thesis. This is followed by three chapters that report the particular studies whose results allowed the analysis of the specific research questions; these three chapters represent a gradual approximation in detail and complexity to the problem. In the first one (Chapter II), entitled "Variation of functional traits in trees from a biogeographically complex Mexican cloud forest", the variation of four plant traits (specific leaf area, seed biomass, height at maturity, and wood density) is examined, and an attempt was made to identify functional groups among 33 tree species with different biogeographical affinities. We constructed a phylogenetic tree as a working hypothesis for examining the effects of phylogeny on the correlations between morphological attributes. The analyses showed that: (1) the studied traits show continuous variation, which prevents recognition of clearly discrete functional groups, and (2) it is possible that different evolutionary lineages (differing in biogeographic origin) converged to similar functional traits. Overall, cross-species and phylogenetic correlations between attributes were weak, the most obvious ones being between height at maturity (Hmax) and seed mass (SM), and between Hmax and wood density (WD). In both analyses specific leaf area (SLA) was unrelated to all other traits, contrary with reports in the literature. In the next chapter (Chapter III, "Seedling biomass allocation and vital rates of cloud forest tree species: responses to light shade houses conditions") we compared the patterns of above- and below-ground biomass allocation in seedlings of nine common CF tree species growing under varying controlled light conditions in shade houses. We analyzed the relationships between vital rates (growth rates and survival) and four morphological traits (SLA, biomass allocation to stems, leaves and roots); for six species,

biomass allocation to leaves, roots and stems differed within species at day 225 of the experiment. Five species had the largest SLA in the lowest light levels (*Citharexylum mocinnii*, *Dendropanax arboreus*, *Fraxinus uhdei*, *Magnolia iltisiana*, and *Quercus salicifolia*). *Juglans major* was the only species with a large SLA at the highest light level (377.47 cm^2 g^{-1}). Overall, all species grew better in the highest light levels. Only survival of *Simplococarpon purpusii* differed between treatments, and this variable was significantly correlated with all morphological variables. However, each species had an individual response regarding biomass allocation to the studied traits. In Chapter IV ("Relationships between leaf traits and vital rates of cloud forest tree seedlings: responses to light variations in field conditions"), patterns of SLA and the relationships between this leaf trait and the vital rates were compared between four common CF tree species grown in experimental plots under pine canopies and open areas, and the relationships between vital rates (survival an growth rates) and SLA were analyzed. Percent canopy openness was measured with hemispherical photographs. SLA differed significantly between treatments in the four species; three of them had the largest SLA in those plots with lowest canopy openness (*Dendropanax*, *Fraxinus* and *Magnolia*). None of the studied species differed significantly in their GR between treatments. Only for *Juglans* was this trait correlated with SLA. Survival of three species varied significantly between treatments and was correlated with SLA. All species had more surviving individuals at the plots located at the most open canopy stands. The last chapter (Chapter V) presents a general discussion in which the final conclusions about the main results and their implications for management purposes of CF tree species are integrated. Based on these results, it is suggested that reintroduction efforts in the field should mainly focus on *Dendropanax arboreous*, *Fraxinus uhdei* and *Magnolia iltisiana*, using pine species as nurse trees. Conversely, the high seedling survival of *Juglans major* implies a large potential of this species for introduction in open areas.

Capítulo I. Introducción general

Esta tesis se centra en el estudio de los atributos morfo-funcionales de las plantas relacionados particularmente con la fase de establecimiento, ya que éste es un proceso esencial para el manejo experimental de plantaciones de especies arbóreas del bosque mesófilo de montaña (BMM) en condiciones heterogéneas de luz (Ramírez-Bamonde et al., 2005). La investigación descansa en la premisa de que el binomio uso-conservación de especies arbóreas del BMM es una posibilidad real en el marco de las plantaciones mixtas de pino y de especies arbóreas de BMM, es decir, a través de la reforestación sucesional. Se entiende por reforestación sucesional el diseño de acciones de reforestación que imiten la sucesión natural (Herrera et al., 1990). Para avanzar en esta dirección, la identificación de grupos funcionales para la regeneración a partir de los atributos de las plantas y el conocimiento de la relación entre estos atributos y el desempeño demográfico de plántulas de árboles del BMM pueden ayudar a planear adecuadamente el manejo de los árboles propios de este tipo de bosque.

Fase de establecimiento

Una de las etapas más críticas en el ciclo de vida de una planta es el de establecimiento (Harper, 1977). Esta fase en el ciclo de vida es importante debido a que la mayoría de las plántulas mueren durante ella (Swaine, 1996). Entre otras cosas, este hecho puede tener una fuerte influencia en la composición y la diversidad futuras del bosque. En general, se considera que las plántulas están establecidas cuando las hojas cotiledonarias se tornan fisiológicamente inactivas, y las raíces y los tallos se incorporan a la estructura interna de soporte y de conducción de la planta (Harper, 1977; Fenner, 1987; Kitajima, 1996b; Lieberman, 1996; Gray y Spies, 1997; Clark et al., 1998; Leishman et al., 2000).

Las limitaciones en la fase de establecimiento constituyen un filtro importante para el reclutamiento de la mayoría de las especies. Entre los factores determinantes del para el establecimiento de plántulas se encuentran las deficiencias lumínicas, la temperatura y la disponibilidad de agua (Martínez-Ramos y Álvarez-Buylla, 1995; Bazzaz, 1996; Swaine, 1996; Whitmore, 1996; Clark et al., 1998), la herbivoría, la alelopatía y la heterogeneidad de micrositios (variaciones en el substrato, sombra, tamaño y edad del claro) (Gray y Spies, 1997); la pérdida de follaje, la ruptura de tallos y meristemos por la caída de ramas (Harper, 1977; Martínez-Ramos y Álvarez Buylla; 1995), y la biomasa de la semillas (Leishman et al., 1995; Bonfil, 1998; Kitajima, 2002; Paz y Martínez, 2003; Moles y Westoby, 2004; Paz et al., 2005).

La luz es un factor crítico para el establecimiento de las plántulas (Swaine, 1996; Kobe, 1999; Lusk y Piper, 2007), debido a que juega un papel muy importante en el crecimiento y la supervivencia de las plántulas y juveniles en el sotobosque (Kitajima, 1996b; Veneklass y Poorter, 1998; Bonfil y Soberón, 1999). Por lo tanto, la manipulación del dosel para crear artificialmente claros de diferentes formas y tamaños constituye un componente fundamental de la silvicultura, de esta manera se pueden favorecer o suprimir ciertas especies. Estudios realizados en ecosistemas forestales han mostrado que la sombra y la competencia a nivel de las raíces pueden suprimir el crecimiento de las plántulas en el sotobosque (Christy, 1986; Ashton et al., 1998; Peña-Claros et al., 2008). En poblaciones de árboles tropicales, Martínez-Ramos y Álvarez-Buylla (1995) encontraron que el riesgo de muerte tiende a disminuir a medida que los árboles crecen en altura y alcanzan mejores niveles de recursos lumínicos, y que las plántulas que crecen en sitios con niveles altos de luz pueden sobrevivir a la defoliación y al daño causado por hongos.

Asignación de biomasa y desempeño demográfico

Para entender la dinámica de los bosques es necesario contar con información morfológica, fisiológica y demográfica sobre las respuestas de las especies vegetales que los conforman a los diferentes ambientes de luz (Ramos y Grace, 1990; Pacala et al., 1996). Sin embargo, todavía son pocos los estudios que han examinado los requerimientos de luz para liberar el crecimiento en etapas juveniles, y que han investigado de qué manera la variación en la asignación de biomasa a diferentes órganos y su plasticidad afecta las tasas de crecimiento y de supervivencia de las plántulas y de individuos juveniles, y su relación con los gradientes ambientales (Whitmore, 1996; McGill et al., 2006; Ackerly, 2007). El crecimiento vertical de las plantas en claros del dosel es un componente esencial de la capacidad de regeneración de las especies arbóreas y constituye la única manera de que los juveniles alcancen el dosel, aunque las generalizaciones son limitadas debido a que cada árbol tiene características propias para su crecimiento desde la germinación de la semillas hasta el estado adulto (Takahashi et al., 2002; Poorter et al., 2005).

Una vez que las plántulas han agotado las reservas de las semillas, el mantenimiento de una ganancia positiva de carbono es fundamental para su supervivencia. La tasa relativa de crecimiento (RGR, tasa de producción de biomasas seca por unidad de biomasa seca) ha sido uno de los índices más ampliamente utilizados por lo ecólogos para estudiar el crecimiento (Hunt y Cornelissen, 1997). Uno de los principales indicadores de las estrategias adaptativas de las plantas, por su relación con las tasas de crecimiento y la supervivencia de las especies leñosas, es el mantenimiento de una mayor área foliar por unidad de biomasa (AFE, siglas de área foliar específica), variable que corresponde a la superficie foliar por unidad de biomasa de hojas (Lambers y Poorter, 1992; Westoby, 1998; Wright y Westoby, 2001; Westoby et al., 2002; Wright et al., 2007). Las características foliares juegan un papel fundamental en la asimilación de carbono, las relaciones hídricas y el balance de energía del individuo (Popma et al., 1992; Poorter et al., 1995; Reich et al., 1998a; Ackerly, 1999; Ackerly et al., 2002). Una alta AFE permite a la planta exponer una mayor área foliar a la luz y el CO_2 por unidad de biomasa invertida en las hojas. Es importante notar que los atributos de las hojas presentan una gama en la economía de las hojas (Wright et al., 2004), por ejemplo desde especies que poseen hojas con una mayor AFE (menor inversión en biomasa por área), con altas tasas fotosintéticas y de respiración, menos longevas, y con altas concentraciones de nutrientes, hasta especies con un AFE menor, las hojas tienden a ser más gruesas y por lo tanto son menos atractivas a los herbívoros (Coley, 1983; Lambers et al., 2000). Por consiguiente, las hojas con una menor AFE son más longevas y acumulan mayor cantidad de biomasa y son capaces de capturar mayor cantidad de luz durante su vida (Williams-Linera, 2000; Valladares et al., 2002). Las especies tolerantes a la sombra poseen hojas delgadas (mayor AFE) y una rápida producción de hojas nuevas durante los estadios tempranos de su vida que las especies intolerantes a la sombra con hojas más gruesas y menor AFE (Reich et al., 1992, 2003). No obstante, hay evidencias que refutan la idea generalizada de que las especies tolerantes producen siempre hojas con mayor AFE que las especies intolerantes. De hecho, las especies tolerantes a la sombra también pueden tener hojas con menor AFE que las especies intolerantes (Veneklass y Poorter, 1998 Reich et al., 2003). Por otro lado, se ha encontrado que el AFE disminuye conforme disminuye la humedad y la disponibilidad de recursos (Givnish, 1988), y que este atributo funcional está correlacionado negativamente con la longevidad de las hojas y sus tasas de asimilación (Reich et al., 1997). Estas diferencias dependen de las características morfológicas y fisiológicas de las especies, de la etapa de desarrollo de la planta y de sus respuestas fenotípicas al ambiente (Reich et al., 1998b; Sack y Grubb, 2002; Niinemets, 2006).

Las diferencias en el crecimiento y la supervivencia de las plántulas también están asociadas a la biomasa asignada a hojas, tallos y raíces. Aunque la importancia de estos atributos es indudable para el análisis del crecimiento de plántulas en ambientes heterogéneos de luz, es difícil tener una interpretación única porque las respuestas reportadas en la literatura son contrastantes. Por ejemplo, en ambientes oscuros Kitajima (1994) y Veenendaal et al. (1996) encontraron un aumento en el cociente raíz/ tallo en plántulas de especies arbóreas tropicales. En contraste, en otros estudios enfocados en este tipo de ambientes, todas las especies tuvieron cocientes raíz/ parte aérea menores que en ambientes con niveles altos de luz (Walters et al., 1993; Reich et al., 1998a). Hunt y Cornelissen (1997) analizaron la contribución la tasa de producción de biomasa seca por unidad de área foliar (ULR) en las tasas de crecimiento, y la asignación a raíces y tallos en especies de zonas templada en dos niveles de luz contrastantes. Sus resultados mostraron una tendencia marcada de las especies de rápido crecimiento hacia la producción de biomasa de raíces, mientras que para las especies de lento crecimiento la producción de raíces y tallos fue equivalente. En condiciones de poca luz, *Brosimum alicastrum* (especie tropical considerada tolerante a la sombra) presentó mayores tasas de crecimiento de raíces que de tallos (Montgomery y Chazdon, 2002).

Grupos funcionales

La cantidad de artículos relacionados con la clasificación funcional de plantas es extensa. Este tipo de clasificación persigue reducir la complejidad de la naturaleza a un nivel más fácilmente interpretable. Estos estudios han dado lugar al reconocimiento de gremios o grupos funcionales de especies de árboles (Vázquez-Yanes y Guevara, 1985; Martínez-Ramos y Álvarez-Buylla, 1986; Swaine y Whitmore, 1988;Whitmore, 1989; Clark y Clark, 1992; Lavorel y Garnier, 2002), que poseen un conjunto de atributos biológicos correlacionados con su comportamiento y que desempeñan papeles similares en los procesos de los ecosistemas (Gitay y Noble, 1997; Díaz y Cabido, 1997; Westoby y Leishman, 1997; Lavorel et al., 1998; Lavorel y Garnier, 2002). La utilidad de clasificar a las plantas en diferentes grupos funcionales, o de ubicarlas a lo largo de un espectro o ejes funcionales con base en uno o varios atributos, ha sido señalada por diversos autores (Grime 1979; Díaz et al., 1999; Reich et al., 2003). El reconocimiento de grupos funcionales y de sus atributos puede ayudar a entender la respuesta de la vegetación a la variabilidad ambiental debido al fuerte poder predictivo de la respuesta de las comunidades a los cambios ambientales, sin la necesidad de tener información detallada de cada una de las especies (Noble y Gitay, 1996; Garnier et al., 2001). Si bien en cada grupo funcional hay un amplio espectro de variación en los atributos continuos, a menudo existen diferencias en los promedios entre grupos (Díaz et al., 1999).

Otra manera de agrupar a las plantas es con base en los atributos que definen su respuesta a gradientes ambientales o por los atributos que definen su papel en los procesos de los ecosistemas (efecto en el ambiente; Lavorel et al., 1997; Lavorel y Garnier, 2002; Hooper et al., 2002). Esta manera de agrupar a las plantas incluye a la clasificación tradicional de las especies por su tolerancia a la sombra y a la sequía (Reich et al., 2003). Se pueden distinguir dos estrategias en los enfoques para clasificar especies en cuanto a su respuesta a la luz (Denslow, 1980; Leishman y Westoby, 1992; Boot, 1996; Kitajima, 2002; Ramírez- Marcial et al., 2008). La primera consiste en dividir a las especies en grupos funcionales utilizando un enfoque de arriba a abajo (“top-down”). Este procedimiento define a priori a los atributos y divide a las especies en grupos discretos (e.g. Swaine y Whitmore, 1988; Whitmore, 1989). La segunda utiliza un enfoque de abajo a arriba (“bottom-up”), el cual consiste en examinar un número de atributos que influyen en el crecimiento y en la regeneración de las plantas (e.g. ganancia de carbono, tamaño de la semilla), y que este conjunto de atributos defina los principales ejes de variación (Reich et al., 1997; Westoby et al., 2002; Ackerly, 2004). En el presente estudio se utilizó el segundo enfoque para definir grupos funcionales de árboles a partir de cuatro atributos cuya variación es continua y que han sido ampliamente estudiados (área foliar específica, biomasa de la semillas, densidad de la madera y altura máxima).

Una forma de abordar la cuestión de la clasificación funcional de plantas es la elaboración de esquemas de sus estrategias ecológicas. Dichos esquemas agrupan a las especies en categorías de acuerdo con sus atributos ecológicos y varían en el número de atributos usados y en el número de grupos generados (Raunkaier, 1934; Drury y Nisbet, 1973; Grime, 1977, 1979; Noble y Slatyer, 1980). Esto ha permitido identificar atributos de fácil medición y que se han evaluado de manera consistente para un gran número de especies de plantas y de comunidades diferentes, relacionados con la adaptación a un ambiente en particular, lo que ha contribuido a simplificar la clasificación funcional (Shipley et al., 1989; Oldeman y van Dijk, 1991; Leishman y Westoby, 1992; Cornelissen et al., 1996; Reich et al., 1999).

Diversos estudios han coincidido en una propuesta que reconoce un grupo de cuatro atributos morfológicos, los cuales consistentemente han sido reportados como importantes por su fácil medición e interpretación: (a) el AFE, que es el área de captura de luz por unidad de biomasa seca, (b) la biomasa de la semilla (BS), (c) la altura máxima (Hmax), y la densidad de la madera (DM).

El AFE es un atributo crucial para la etapa de plántula y un determinante de las tasas de crecimiento (Lambers y Poorter,1992; Cornelissen et al., 1996; Wright et al., 2005). Estudios basados en protocolos controlados, con un conocimiento amplio del sistema de estudio, han encontrado relaciones del AFE con otros atributos, por ejemplo, con la densidad de la madera y el tamaño de la hoja (e.g. Wright et al., 2007).

La biomasa de las semillas es un atributo relacionado con la regeneración, juega un papel central en la reproducción y en la fase de establecimiento de las plántulas, porque determina la cantidad de recursos disponibles para las etapas tempranas de su desarrollo (Swanborough y Westoby, 1996; Bonfil, 1998; Ibarra-Manríquez et al., 2001; Dalling y Hubbell, 2002; Moles y Westoby, 2004; Paz et al., 2005). Se ha demostrado que la BS está correlacionada positivamente con la forma y capacidad de dispersión, el tamaño de las hojas y el tipo funcional de las plántulas (Leishman et al., 1995; Kitajima, 1996a; Falster y Westoby, 2005a). La altura máxima de las plantas es un atributo que está asociado con el vigor competitivo, la fecundidad y con el tiempo que tienen para crecer entre dos disturbios subsecuentes (Westoby et al., 2002), así como con las estrategias para asegurar la ganancia de carbono a través de la captura de luz (Givnish, 1995; Falster y Westoby, 2005b). Finalmente, la densidad de la madera es un atributo de los tallos que ha sido utilizado como un indicador del estatus sucesional de las plantas, así como de las estrategias de historia de vida de las especies arbóreas (Ter Steege y Hammond, 2001; King et al., 2006). Por razones mecánicas e hidráulicas, la Hmax de los árboles está fuertemente asociada con DM (Lawton, 1984; Muller-Landau, 2004; King et al., 2005); la DM y el reforzamiento de las paredes del xilema están correlacionadas con la resistencia contra de la cavitación del xilema (Hacke et al., 2001). Al parecer, al incrementarse la proporción de las paredes gruesas en el xilema (mayor DM) se reduce el riesgo de colapso en los vasos por tensión en el xilema (Cavender-Bares y Holbrook, 2001; Maherali et al., 2004; Falster y Westoby, 2005b). Asimismo, una DM alta puede estar inversamente correlacionada con las tasas de crecimiento, pero positivamente con la supervivencia de las especies tolerantes a la sombra al proporcionar a los árboles una mayor resistencia de los tallos contra herbívoros y patógenos (Lawton, 1984; Coley, 1988; Poorter et al., 1995; Sterck y Bongers, 2001; Muller-Landau, 2004; King et al., 2006).

Correlaciones evolutivas entre los atributos morfo-funcionales

Recientemente, las diferencias y semejanzas entre las especies que coexisten en una comunidad ecológica han sido explicadas más en términos de ancestrías comunes que por causas adaptativas que pudieran haber actuado de manera independiente en los atributos de las especies (Webb et al., 2002; Hardy y Senterre, 2007). Los estudios evolutivos se han enfocado al análisis de la correlación entre atributos con el fin de identificar asociaciones adaptativas entre atributos, o entre atributos y condiciones ambientales (Ackerly, 1999; Ackerly et al., 2000). Los métodos comparativos evolutivos que incorporan un enfoque filogenético han sido muy útiles para contestar preguntas sobre el significado ecológico de la variación funcional entre las especies de plantas (Saverimutu y Westoby, 1996). Por ejemplo, se han utilizado para analizar si la biomasa de las semillas está asociada con la supervivencia de las plántulas en la sombra o después de un evento de defoliación (Armstrong y Westoby, 1993; Rees y Westoby, 1997; Coomes y Grubb, 2003). En una parte inicial de esta tesis incluimos el análisis filogenético y utilizamos el método de contrastes independientes (CI) (Felsenstein, 1985). Los CI son una herramienta ampliamente utilizada que permite incorporar información filogenética en estudios basados en atributos continuos, particularmente para el análisis de correlaciones evolutivas de los atributos de las plantas (Pagel, 1993; Reich et al., 1997; Ackerly, 2000). Los CI son útiles para responder preguntas ecológicas porque incorporan las relaciones filogenéticos entre las especies para evaluar los patrones evolutivos (o la historia evolutiva compartida) que fundamentan la distribución de los atributos actuales (Ackerly y Donoghue, 1998; Ackerly y Reich, 1999; Zanne et al., 2005). De este modo, el examen de la estructura filogenética de las comunidades puede otorgar ideas útiles para entender los factores históricos y ecológicos que determinan el ensamblaje de especies (Webb et al., 2002; Cavender-Bares et al., 2004).

Presentación del problema

Este estudio tiene como base un conjunto de trabajos previos que se vienen llevando a cabo desde hace más de 20 años en la Reserva de la Biosfera Sierra de Manantlán (RBSM). Éstos han abarcado cuestiones generales, como la descripción de la vegetación en la Estación Científica Las Joyas (ECLJ) (Santiago y Jardel, 1993; Sánchez-Velásquez et al., 1996), hasta otras más particulares, como el análisis de la dinámica del banco de semillas en bosque mesófilo de montaña (BMM) (Ortiz-Arrona, 1993). Algunos trabajos ya habían analizado las respuestas funcionales de un grupo de especies a distintas condiciones ambientales del dosel y el suelo (Ortíz-Arrona, 1999; Saldaña-Acosta, 2001), incluyendo la descripción de los tipos de germinación de 40 especies arbóreas de BMM y de sus mecanismos de propagación (Saldaña-Acosta et al., 2001). Algunos de estos estudios fueron realizados en parcelas permanentes que cuentan ya con más de quince años de observaciones sobre la supervivencia, el crecimiento de tallos y la incorporación de especies arbóreas del BMM. Además, Jardel (1991) analizó el historial de manejo de los sitios que han estado sujetos a distintos tipos de disturbios, incluyendo los incendios forestales.

En el marco de estos estudios, Saldaña-Acosta (2001) propuso una clasificación funcional preliminar de especies arbóreas y arbustivas presentes en el BMM de la ECLJ basada en la propuesta de van der Pijl (1972), organizando los síndromes de regeneración en cuatro grupos funcionales. Sin embargo, todavía se desconocen aspectos relacionados con la fase de establecimiento de las especies arbóreas del BMM, en particular sobre la ecofisiología de sus plántulas, las características morfológicas y fisiológicas de sus hojas, tallos y raíces, y sus respuestas a diferentes ambientes de luz, la demografía de las especies desde su establecimiento hasta la liberación de su crecimiento a etapas juveniles, las respuestas en el crecimiento y la supervivencia de las diferentes especies a diferentes ambientes de luz (Ortiz-Arrona, 1999).

Todas estas incógnitas son particularmente importantes en el caso de los bosques mesófilos de montaña de México, ya que conforman una comunidad muy compleja desde el punto de vista biogeográfico, porque están compuestos de una mezcla de elementos laurásicos, tanto tropicales como templados, junto con taxa tropicales y templados de origen gondwánico (Wendt, 1998). Por ello, es una comunidad en donde no es fácil interpretar patrones, y no es obvio cuáles correlaciones entre atributos funcionales sean similares para aquellas descritas para otros tipos de bosques (e.g. Wright et al., 2007). Por ello, este sistema fue usado para entender aspectos relacionados con el funcionamiento de especies arbóreas, en particular, si: (1) atributos morfo-funcionales simples como el AFE, el tamaño de la semilla, la altura máxima y la densidad de la madera pueden expresar dimensiones ecológicas útiles en la detección de grupos funcionales de árboles en un bosque compuesto por especies con diferente origen biogeográfico, y (2) si estos atributos pueden ayudar a identificar especies útiles en actividades de restauración ecológica.

La identificación de patrones generales a nivel de comunidad para efectos de manejo forestal y su estudio brindarán información aplicable para el manejo de comunidades diversas en la Sierra de Manantlán (Jardel, 2008). La restauración del BMM es una de las prioridades de manejo y un componente esencial de las estrategias de conservación en la RBSM (Jardel, 1992; INE, 2000). La restauración se define como una actividad intencional y es considerada como un proceso de manejo de los ecosistemas forestales con el fin de recuperar sus componentes, patrones y procesos alterados por las acciones humanas, mitigar los impactos ambientales de éstas y restablecer su capacidad de mantener a largo plazo un flujo continuo de bienes y servicios hacia la sociedad (SER, 2002; Hilderbrand et al., 2005). En última instancia, esta actividad tiene el propósito de devolver a los sitios degradados a un estado lo más natural posible, lo cual implica, entre otras cosas, la reintroducción de especies nativas. Este proceso, aunado a un enfoque experimental, en el que se pongan a prueba los conceptos teóricos de la ecología de comunidades y de poblaciones (Jordan, 1988; Lugo, 1988; Sánchez-Velásquez et al., 2004; Martínez-Garza et al., 2005), permite tanto avanzar en el conocimiento de la ecología de especies y comunidades, como brindar bases sólidas para el manejo. El proceso sucesional puede ser utilizado en el manejo de plantaciones forestales utilizando la técnica de reforestación sucesional, como lo han demostrado algunas experiencia sobre manejo de bosques (Herrera et al., 1990; Pompeia, 1990). Otro método de regeneración artificial son las plantaciones de enriquecimiento, que complementan la regeneración natural, utilizando en muchos casos especies nodrizas (Piggot, 1990; Evans, 1992; Shropshire et al., 2001; Ramírez-Bamonde et al., 2005; Ramírez-Marcial et al., 2008). En ambos casos, la selección cuidadosa de una combinación de especies pertenecientes a diferentes grupos funcionales y con una amplia gama de atributos es fundamental para el reestablecimiento de los procesos que tienen lugar en los ecosistemas forestales (Kageyama, 1992; Ashton et al., 1997; Parrota y Knowles, 1999; Standley y Montagnini, 1999; Hooper et al., 2002).

Con base en estas consideraciones, en esta tesis se pretende contestar la siguiente pregunta central: ¿cómo se relaciona el desempeño demográfico de especies arbóreas del bosque mesófilo de montaña con sus atributos morfológicos y con la heterogeneidad del ambiente lumínico? La hipótesis de este trabajo es que si en el BMM de Manantlán ha habido convergencias en grupos de árboles suficientemente fuertes como para permitir el reconocimiento de grupos funcionales entre ellos, estos patrones tendrían que estar reflejados tanto en sus atributos morfológicos, y en el desempeño demográfico de plántulas desarrolladas en condiciones heterogéneas de luz.

Los estudios de regeneración natural de bosques que se han hecho en la ECLJ han demostrado la presencia de regeneración de avanzada de especies arbóreas típicas de BMM, en particular de *Carpinus tropicales* (Donn. Sm.) Lundell, *Magnolia iltisiana* A. Vázquez y *Persea hintonii* C.K. Allen bajo el dosel de pino en suelos fértiles y húmedos (Anaya, 1989; Saldaña-Acosta y Jardel, 1992; Sánchez-Velásquez y García-Moya, 1993; Ortiz-Arrona, 1999; Saldaña-Acosta, 2001). Así mismo, han demostrado que *Pinus douglasiana* Martínez facilita el establecimiento en el sotobosque de especies arbóreas de BMM. Se considera que este tipo de vegetación está amenazado, ya que históricamente ha sido afectado por la explotación maderera y por la presencia de incendios forestales, lo que ha reducido las poblaciones que lo componen, y la calidad y cantidad de madera (Jardel, 1991; Hernández, 1996). Estos estudios también han señalado que en ausencia de nuevos disturbios, los rodales de pino tienden a ser reemplazados por especies arbóreas del BMM durante el proceso sucesional (Saldaña-Acosta y Jardel, 1992; Pineda y Sánchez- Velásquez, 1992; Sánchez-Velásquez y García-Moya, 1993; Ortíz-Arrona, 1999; Saldaña-Acosta, 2001). Recientemente se iniciaron estudios experimentales sobre la restauración de áreas afectadas por incendios forestales en la RBSM, como parte del Programa de Manejo del Fuego coordinado por la Dirección de RBSM (SEMARNAT).

El conjunto de especies arbóreas del BMM utilizado en este estudio fue seleccionado debido a la información que se ha generado sobre su fenología, biología reproductiva, tamaño de semilla, tipo de germinación y posibilidades de establecimiento bajo condiciones controladas. Además, representa un gradiente en su comportamiento ecológico en la invasión de bosques de *Pinus* (Saldaña-Acosta, 2001). La mayoría de las especies tiene madera de buena calidad que se ha utilizado para construcción y la elaboración de muebles finos (Ortega y Castillo, 1996; Cuevas et al., 1995).

Para contestar la pregunta central de esta investigación, los resultados de este estudio se organizan en cuatro capítulos. El Capítulo II explora la posibilidad de identificar conjuntos naturales entre un grupo de 33 especies arbóreas de BMM que pudieran ser interpretados como grupos funcionales con base en un conjunto de atributos ampliamente estudiados y de fácil medición con un enfoque “bottom-up”. Asimismo, se construyó un árbol filogenético que se considera como una hipótesis de trabajo para la exploración de los efectos de la filogenia en la correlación entre atributos morfológicos.

En el Capítulo III seleccionamos, de este conjunto, nueve especies para llevar a cabo experimentos controlados (casas de sombra en invernadero) en donde examinamos su respuesta en la asignación de biomasa, utilizando cuatro atributos y su relación con en el desempeño demográfico (supervivencia y tasa de crecimiento). Cuatro especies se usaron para examinar la variación del AFE y su relación con el desempeño demográfico en condiciones naturales de campo (parcelas experimentales), también en áreas abiertas como en el sotobosque de bosques de pino con diferente edad (Capítulo IV). En el Capítulo V se presenta una discusión general en donde se integran las conclusiones generales sobre los resultados y sus implicaciones para su aplicación al manejo del BMM en la RBSM.

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Original article

Variation of functional traits in trees from a biogeographically complex Mexican cloud forest

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ABSTRACT

Several studies have proposed a group of morpho-functional traits as determinants of the ecological strategy of species. Among these, four morpho-functional traits are considered to be relevant in determining a plant's ecological strategy: specific leaf area (SLA), height at maturity (Hmax), wood density (WD), and seed mass (SM). We examined the variation of these traits and attempted to identify functional groups among 33 tree species with different biogeographical affinities from a montane cloud forest. Covariation among the four traits was examined using Principal Component Analysis (PCA) and species clustering. Bivariate trait relationships were evaluated through two methods: cross-species correlations, and evolutionary divergence correlations using phylogenetically independent contrasts (PICs). Correlations between attributes were overall weak, the most obvious ones being between Hmax and SM, and between Hmax and WD; this latter trait pair was also correlated in PICs. In both analyses SLA was unrelated to all other traits. In the PCA ordination the first two axes explained 66.9% of the between-species variation. Despite a largely continuous between-species variation, species clustering allowed differentiation of two main groups. Observed trait correlations were consistent with those reported for other floras, with the important exception of the independent behaviour of SLA. This study indicates a variety of comparable successful life history strategies among the studied species. The effect of phylogeny in trait covariation was unimportant, in fact, a mixture of clades was represented in several groups among the species they contained, suggesting among-lineage convergence.

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1. Introduction

The quantitative study of plant traits has revealed the existence of an extremely large across-species variation, some of which seems to reflect the occurrence of trade-offs in plant life histories (Wright et al., 2004); therefore plant traits provide a useful base for the classification of plants in functional groups (Díaz and Cabido, 1997). Functional groups have been defined as sets of species sharing biological traits and playing similar roles in ecosystem processes (Gitay and Noble, 1997; Lavorel et al., 1998). The benefits of classifying plants in functional groups have been recognized by many authors (Lavorel et al., 1997; Díaz et al., 1999); for example, such groups may be viewed as plant life strategies, inasmuch as they represent different ways in which plants secure carbon profit during vegetative growth, and acquire, use, and conserve resources (Westoby et al., 2002). A fruitful approach in developing functional classifications of plants is represented by ecological strategies schemes, which consists in grouping species in categories, according to a varying number of ecological traits (Raunkiaer, 1934; Drury and Nisbet, 1973; Grime, 1977; Noble and Slatyer, 1980).

Several studies have proposed a group of morpho-functional traits that have proven to be appropriate, independent predictors of a species ecological behaviour (Westoby, 1998; Westoby et al., 2002; Wright et al., 2006b). Among these, four have received much attention because of their ease of measurement and interpretation: (a) specific leaf area (SLA); (b) maximum height (Hmax); (c) wood density (WD); and (d) seed mass (SM). SLA is an important determinant of growth rate because the larger SLA, the larger the area for capturing light per unit of previously captured mass (Lambers and Poorter, 1992).

There is empirical evidence that SLA is weakly related with plant height and seed size, and that it often shows no relationship with WD and leaf size across many species and community types (Díaz et al., 2004; Wright et al., 2006b). However, site-specific studies based on controlled protocols and on an ample knowledge of the system's ecology have succeeded in finding relationships of SLA with other traits, e.g. with WD and leaf size (Wright et al., 2006b). These contrasting results imply a lack of a strong basis to support the existence of significant correlations between SLA and other traits. In turn, Hmax is linked to strategies that ensure carbon gain through light interception, e.g. slow growth in low light levels vs. fast growth in gap conditions (a trade-off between height gain and shade tolerance) (Falster and Westoby, 2005b). Apparently due to mechanical reasons, Hmax is tightly associated to WD (Lawton, 1984; Muller-Landau, 2004; King et al., 2005); a higher WD provides more resistance against xylem cavitation (Cavender-Bares and Holbrook, 2001; Maherali et al., 2004) and pathogens (Coley, 1988). WD is positively correlated with tree height along successional gradients, with the opposite being true along light-availability gradients (Falster and Westoby, 2005a), and in general, negatively correlated with leaf size across different vegetation types (Cavender-Bares et al., 2004; Wright et al., 2006a). Also, a trend has been reported for bigger plants to bear bigger seeds (Moles et al., 2004).

Finally, SM is a regenerative trait playing a central role for reproduction and the seedling establishment phase because it determines the amount of resources available for seedlings' early growth (Paz and Martínez-Ramos, 2003; Moles and Westoby, 2004b; Paz et al., 2005). SM has been shown to be positively correlated with dispersal mode, leaf size, seedling functional type and plant height (Leishman et al., 1995; Kitajima, 1996; Falster and Westoby, 2005b).

The occurrence of multiple trade-offs involving these attributes allows visualization of a gradient of ecological strategies, ranging from fast-growing, short-lived pioneer species on one extreme, to slow-growing, long-lived, late successional species, associated with increased shade tolerance, on the other (Muller-Landau, 2004). According to existing theory and available empirical information, often contradictory as shown above, it is difficult to propose specific hypotheses establishing a definite directionality for the relationships between the four attributes. However, based on the results of the majority of studies analysing between-trait correlations, it is reasonable to state that most small-seeded trees are fast growing species, while the opposite will be true for large seeded trees. Because growth rate of a tree is usually positively associated to a larger light interception area per leaf and negatively to WD, we predict here that species with small seeds should tend to have high SLA, relatively low WD and a wide variation in total height, whereas species bearing large seeds should tend to have medium to high WD, low SLA, and a large Hmax.

It has been demonstrated that patterns of species distribution and functional covariation in an ecological community can reflect both species' inherited traits from a common ancestor (phylogenetic effect) and adaptive convergences among distantly related species (Webb et al., 2002; Ackerly, 2003; Chazdon et al., 2003). The evolutionary comparative methods that incorporate a phylogenetic approach have proven useful in solving questions about ecological significance of functional variation among plant species (Ackerly, 1999). For example, the question whether the trend toward a shorter leaf life-span and a high SLA in more recent cloud forest taxa reflects ecological variation, or if it is rather related with the phylogenetic relationships among species (Williams-Linera, 2000). In general, more related taxa tend to be more similar, which implies a lower level of evolutionary divergence between related taxa (Ackerly, 2000).

An underlying assumption of the general relationships discussed above is that they derive from the evolution of many species in common communities, and that strategies have emerged through the appearance of different trade-offs (Westoby et al., 2002; Wright et al., 2006a). However, the possibility of generalizing trait correlations may be limited; for example, the significant correlation between SLA and WD observed in tropical rain forests may not be valid for other forest types (Wright et al., 2006b). This uncertainty is particularly relevant for cloud forests (CF) of the mountains of southern/central Mexico, which is a highly complex community from a biogeographical point of view, as it is composed of a mixture of both tropical and temperate Laurasian elements, together with tropical and temperate taxa of Gondwanic origin (Wendt, 1998). In addition to this particular concoction, these are not post-glacial communities, since they have existed since at least 20 Ma ago (Miranda and Sharp, 1950; Axelrod, 1975; Rzedowski, 1991), so that the appearance of the different lineages may not be synchronic. Therefore, these forests may be regarded as an excellent system for investigating the role of the phylogenetic loading and the ecological constraints in the determination of functional properties of trees.

In Mexican CF, studies on patterns of forest regeneration have shown that the pioneer species of *Pinus* form almost pure stands shortly after disturbances, subsequently facilitating the establishment of a second wave of non-pioneer, typical CF tree species; with time, the latter replace the pines, forming mature cloud forests (González-Espinosa et al., 1991; Sánchez-Velásquez and García-Moya, 1993; Saldaña-Acosta, 2001). Although the establishment of the second group appears to be relatively homogeneous at first sight, field observations including density variation and microsite selection suggest that each of these species may actually be finely adapted to particular environmental conditions, especially but not only to light environment (Ortíz-Arrona, 1999). This suggests that life-history traits are important in species regeneration strategies in Mexican CF, as they are in tropical forests in general. Management of forests for biodiversity, conservation or economic activities such as carbon offset trading requires understanding of trait-environment relationships. For this purpose we sought to determine functional groups for regeneration.

In this study we constructed a phylogenetic tree as a working hypothesis for examining the effects of phylogeny on the correlations between morphological attributes in a Mexican CF. Specifically, we addressed the following questions: are there patterns of functional covariation in the cloud forest, and if so, are they similar to those described in other forest types? Based on this variation, is it possible to recognize natural groups of cloud forest species based on morpho-functional traits? Finally, are groups made up primarily of single clades or do members of the same clade present different combinations of traits belonging to several different groups?

2. Materials and methods

2.1. *Study area and stand selection*

Fieldwork was conducted at Las Joyas Scientific Station located in the Sierra de Manantlán Biosphere Reserve (hereafter referred to as Manantlán), Jalisco State, Mexico (19° 35′ N; 104° 17′ W). Vegetation cover comprises pine, pine-oak, and cloud forests, as well as scrub and secondary grasslands (Sánchez-Velásquez et al., 1996). Cloud forests (CF; known in Mexico as bosque mesófilo de montaña), grow along ravines and protected slopes, or in the higher parts of the mountains of tropical and subtropical regions, where fog is frequent (Rzedowski, 1978).

Four CF stands were established for the selection of individuals using the belt transect method (five by stand, 50 m × 1 m each) located at random distances from each other. The four stands were located in an altitudinal range between 1800 and 2100 m. At random intervals, points were determined for measurements and/or sample collections; at each one, we selected individuals falling on the transect for the sampling of leaves, seeds, and wood core, and for the measurement of height.

2.2. *Species and traits*

Thirty-three of the most common canopy tree species of the regional CF (Vázquez et al., 1995) were selected for the study. SLA was determined in fully expanded, healthy leaves collected from the highest parts of the crowns. Any petiole or rachis in the case of compound leaves, and all veins were considered (Westoby, 1998). We took five leaves from 15 individuals per species (75 leaves in total). To determine leaf area we scanned leaves to create digital images and measured their area by using the SigmaScan PRO 5, SPSS Inc. Finally, leaves were oven dried at 80 °C for at least 48 h and their dry mass was determined.

For determination of SM we collected five seeds from each of 25 mature and healthy trees, giving a total of 125 seeds, for each of the 33 species that had been selected. Trees were chosen at random along the transects. Seeds were dried at 80 °C for 48 h and weighed.

Tree height and WD were measured on the same randomly chosen 25 individuals per species with a Haga clinometer. The closest tree height value to the 95th percentile was defined as Hmax. For WD (oven dry mass/fresh wood volume) 15–50 cm long cores that included heartwood were taken from these trees with a Pressler increment borer. Volume of fresh wood was determined with the volume replacement method, after which samples were oven-dried at 70 °C and weighed and expressed in mg mm^{-3}.

2.3. *Data analysis*

Two of the four traits were $\log_{10}$ transformed before analysis because they showed right skewed distributions (SLA and SM). In order to explore patterns of multiple covariation among SLA, Hmax, SM and WD, we used Principal Component Analysis (PCA). We then constructed a dendrogram by using Ward's grouping linkage method and Euclidian distances, in PC-ORD Ver. 4.10 (McCune and Mefford, 1999). This clustering method, based on an analysis of variance approach to measure distance between clusters, is considered to be very robust and to yield readily interpretable results (Cao et al., 1997).

We used two methods to evaluate bivariate trait relationships: (1) cross-species correlation (among attribute Pearson product-moment correlations); and (2) evolutionary divergence correlations analysis using phylogenetically independent contrasts (PICs) to test for correlations among evolutionary trait-divergences. Phylogenetic relationships between the 33 studied species were constructed by using the Phylomatic database V.3.22 (Webb and Donoghue, 2002). This software uses a backbone family-level tree of angiosperms, based on recent family level phylogenies from published molecular studies (e.g. Soltis et al., 2000). An online program (http://www.phylodiversity.net/phylomatic) translates the input list of taxa into a phylogeny for those taxa, and the genera are attached as polytomies within families, and species as polytomies within genera. Generic polytomies could be resolved for those groups for which more detailed phylogenies were available (Fig. 1). More detailed information is given in the figure legend.

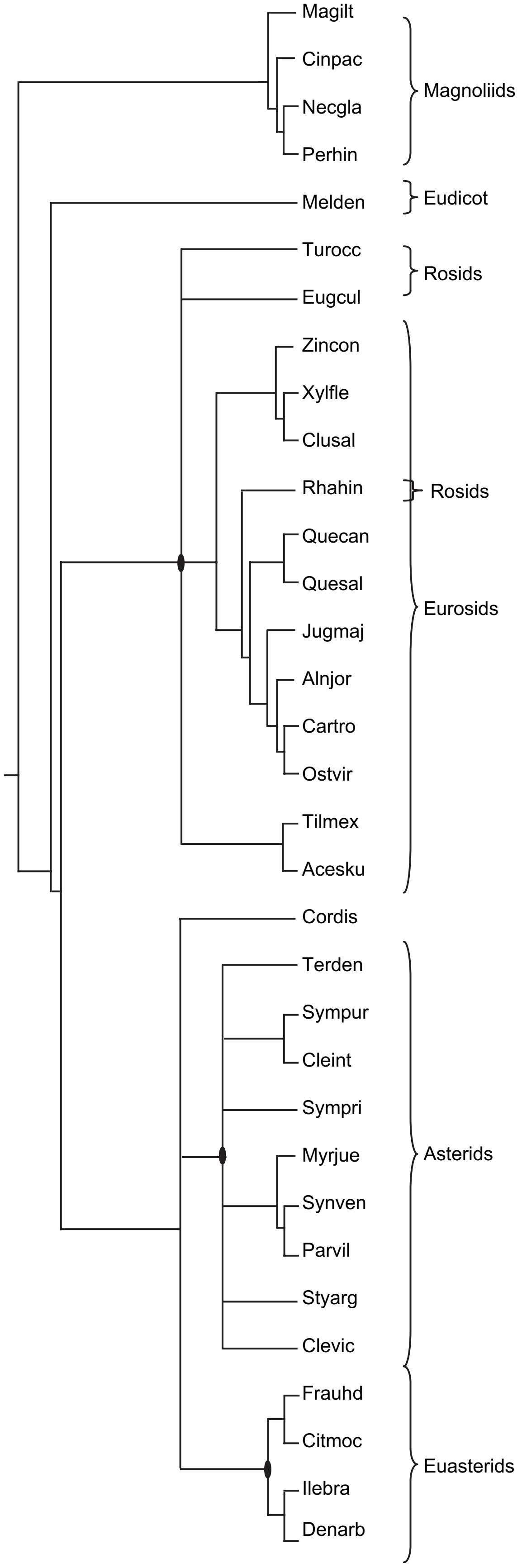

Fig. 1 – Phylogenetic relationships among 33 cloud forest species from Manantlán, Jalisco, Mexico. Circles indicate those divergences that were the most important contributors to PICs correlations (see text for further explanation). The phylogeny for the 33 cloud forest species is dominated by the Eurosids and Asterid clades (both with 14 species), although the minor clade of Magnoliid (four species) is also present. Phylomatic produced a large number of polytomies which were resolved in the following manner: the polytomy of *Cleyera*, *Ternstroemia* and *Symplococarpon* was resolved by using the phylogenetic relationships of Theaceae of Prince and Parks (2001). For the Betulaceae (*Alnus*, *Carpinus* and *Ostrya*), we used the study of Chen et al. (1999), and the study of Chanderbali et al. (2001) for the Lauraceae (*Persea*, *Cinnamomun* and *Nectandra*). For the Myrsinaceae (*Myrsine*, *Parathesis* and *Synardisia*), Ricketson and Pipoly (1997) and Stevens et al. (2001) locate *Parathesis* as a section of *Ardisia* sect. *Parathesis* A. DC, as well as *Synardisia* but as a subgenus (Ardisia subg. Synardisia Mez); *Myrsine* was considered as a synonym of *Rapanea* (*R. juergensenii* Mez).

The regressions based on PICs *sensu* Felsenstein (1985) are a very powerful statistical tool which is used to assess correlated evolutionary changes between variables; therefore they have been amply used to incorporate phylogenetic information in studies based on continuous attributes (Ackerly, 1999). This method permits statistically controlling for potential non-independence of species due to common ancestry. Contrasts are constructed from differences between the values of attributes in pairs of sister taxa along the phylogenetic tree, allowing contrasts at deep nodes. Each contrast represents an evolutionary divergent and independent event in the history of a particular trait. Standardized independent contrasts were obtained for all traits using CAIC Ver. 2.0 (Purvis and Rambault, 1995). Regression through zero was used to test for the hypothesis of evolutionary correlation between each pair of traits.

3. Results

3.1. *Character correlations*

Two correlations were significant based on cross-species analyses (Table 1). The strongest correlation was observed between Hmax and SM, followed by a less strong correlation among between Hmax and WD. Interestingly, the latter pair of characters was also correlated when phylogeny was taken into account; PICs of the former pair were not significantly correlated but showed a clear trend (Table 1; Fig. 2a,b). For PICs analyses, the most important contributors to the relationship between Hmax and WD were old divergences located specifically in the clade of the Eurosids I (which includes the orders Celastrales, Fagales, Malpighiales and Rosales), and the clade of the Eurosids II (comprising the orders Malvales and Sapindales), more recent ones in the clade of the Asterids (which encompasses the order Ericales), and very recent ones in the clades of the Euasterids I (with the Lamiales), and Euasterids II (Aquifoliales and Apiales) (Fig. 1; Table 2).

Table 1 – Between-trait correlations for species-based analysis (lower left triangle) and PICs analysis (upper right triangle) for cloud forest species from Manantlán, Jalisco, Mexico. SLA and SM were $\log_{10}$ transformed before analysis. Bivariate fit of SLA by SM is an artefact due to two points representing *Juglans major* and *Nectandra glabrescens*. Figures in bold indicate the strongest correlations

		Plant height	Wood density	Seed mass	SLA
Plant height	*r*		**0.18**	**0.12**	0.034
	n		25	25	25
	P		<0.05	0.082	0.366
Wood density	*r*	**0.29**		0.37	0.012
	n	33		25	25
	P	<0.05		0.762	0.587
Seed mass	*r*	**0.36**	0.11		0.09
	n	33	33		25
	P	<0.05	<0.05		0.116
SLA	*r*	0.11	−0.05	0.20	
	n	33	33	33	
	P	0.522	0.859	<0.05	

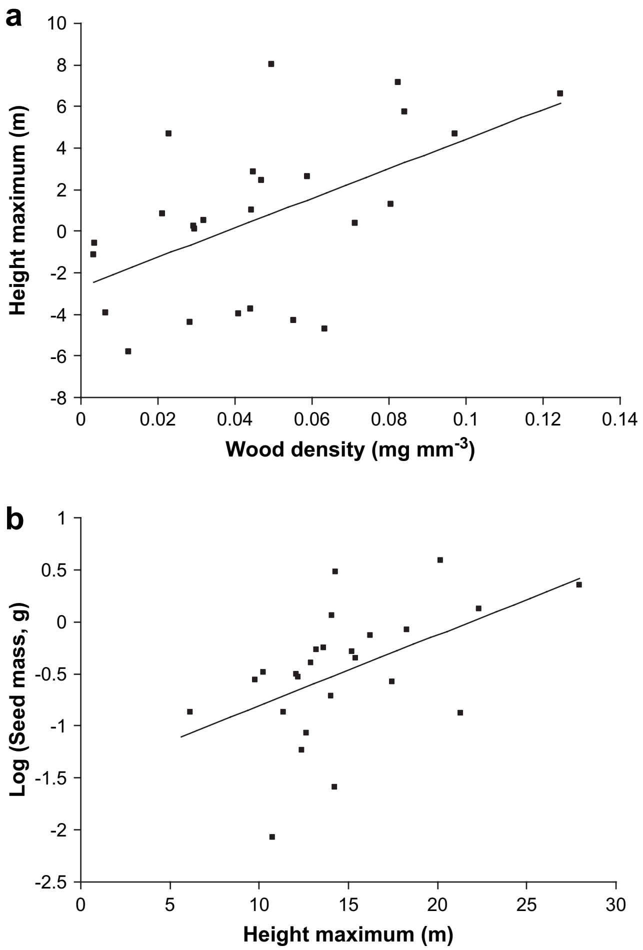

Fig. 2 – Correlations between (a) maximum height (Hmax, m) and wood density (WD, mg mm^{-3}), and (b) maximum height and seed mass (log SM, g), using phylogenetically independent contrasts as data points (PICs analysis). Correlation and *P* values as follows: Hmax and WD, *r* = 0.18; *P* = 0.030; log SM and Hmax (*r* = 0.12; *P* = 0.0821).

3.2. *Multivariate trait relationships*

In the PCA ordination the first two axes explained together 66.9% of the between-species variation (36.1% and 30.8%, respectively) (Fig. 3). Three traits were most strongly associated with axis 1, WD ($r = 0.712$), SM ($r = 0.790$) and Hmax ($r = 0.507$). In contrast, the second axis was more strongly correlated (albeit negatively) with SLA ($r = -0.855$). The loadings of each trait for axis 1, as assessed through the eigenvalues, showed that the ordination dimensions are related to three attributes. Only in the case of SLA a strong asymmetry was observed, as its eigenvalue for axis 2 (negative) was almost four-fold that of its corresponding value for axis 1 (also negative) (Table 3).

The distribution of the species in ordination space revealed continuous variation, with the majority of species (26) being concentrated in the upper central sector of the PCA plot. Seven species had positions relatively distant from this central species cloud (Fig. 3). On the far right end of the plot are located *Quercus salicifolia*, *Nectandra glabrescens* and *Juglans major*, characterized by intermediate to high SLA (183.43–284.67 cm^2 g^{-1}), very high SM (2.63–12.06 g), and high Hmax (19.7–35.15 m). In turn, in the left far end of the graph *Xylosma flexuosum* stands out as a quite distinct species, with an intermediate Hmax (16.6 m), but low SM (0.03 g) and the lowest SLA (22.75 cm^2 g^{-1}). Finally, *Rhamnus hintonii*, *Eugenia culminicola* and *Cinnamomum pachypodum* formed a loose cluster located towards the bottom of the ordination plot; these are short species (3.4–10.3 m), with high SLA (119.66–153.25 cm^2 g^{-1}) and intermediate SM (0.15–2.53 g).

The dendrogram obtained from the cluster analysis did not lead to a clear division into several groups. In fact, only two major groups could be distinguished at a cut-off distance of 18. One group was small and well defined, and comprised the nine species mentioned previously in the PCA (Group 1). The other one, named Group 2, encompassed all remaining 24 species and was very heterogeneous, and it could be divided into two subgroups at a cut-off Euclidean distance of 12. Subgroup 2a included five species and Subgroup 2b had 19 species (Fig. 4; Table 2). The nine species of Group 1 showed the largest mean values for all studied traits. The species of Subgroup 2a had smaller mean SM, SLA and Hmax, but a mean WD that was indistinguishable from that observed in the other group. Subgroup 2b comprised the smallest mean values for most traits except for SM, which was intermediate (Fig. 5). Some family level taxa were restricted to one group, as was the case of Betulaceae, all of the members formed part of Subgroup 2a, of Fagaceae, with its two species belonging to Group 1, and of Myrsinaceae, with three species in Subgroup 2b. Likewise, other species not belonging to the same family but that emerged as sister species in the phylogenetic reconstruction of the study species were grouped together (e.g. *Tilia americana* and *Acer skutchii* in Subgroup 2b). Such taxonomic homogeneity was not perfect, however, as illustrated by Lauraceae, with two species in Group 1, and a third one in Subgroup 2b. Also, it is noticeable that the

Table 2 – Species names with their family, order, biogeographical origin and abbreviation, for cloud forest tree species of Manantlán, Jalisco, Mexico. Specific leaf area (SLA, $cm^2\ g^{-1}$), seed mass (SM, g), wood density (WD, $mg\ mm^{-3}$), and maximum height (Hmax, m) organised by groups produced by hierarchical classification using Ward's method and Euclidean distances

Species	Family	Order	Origin	Abbreviation	SLA	SM	WD	Hmax
Group 1								
Cinnamomun pachypodum (Nees) Kosterm.	Lauraceae	Laurales	Boreotropical	Cinpac	153.25	2.539	0.5447	10.33
Cleyera integrifolia (Benth.) Choisy	Theaceae	Ericales	Boreotropical	Cleint	256.21	1.623	0.4665	12.8
Cornus disciflora Moc. et Sessé ex DC.	Cornaceae	Cornales	Holarctic	Cordis	183.77	0.892	0.5352	13.71
Ilex brandegeana Loes.	Aquifoliaceae	Aquifoliales	?	Ilebra	142.75	2.23	0.5831	20.07
Juglans major (Torr.) Heller	Juglandaceae	Fagales	Neotropical	Jugmaj	284.67	12.06	0.4818	19.7
Nectandra glabrescens Benth.	Lauraceae	Laurales	Holarctic	Necgla	183.43	8.45	0.4691	25.97
Quercus candicans Née	Fagaceae	Fagales	Holarctic	Quecan	79.39	1.948	0.4621	20.79
Q. salicifolia Née	Fagaceae	Fagales	Holarctic	Quesal	190.52	2.639	0.627	40.15
Ternstroemia dentisepala B.M. Barthol.	Ternstroemiaceae	Ericales	Pantropical	Terden	186.47	0.771	0.5201	11.5
Group 2								
Subgroup 2a								
Alnus jorullensis Kunth	Betulaceae	Fagales	Holarctic	Alnjor	228.65	0.004	0.4436	8.4
Carpinus tropicalis (Donn. Sm.) Lundell	Betulaceae	Fagales	Holarctic	Cartro	246.96	0.028	0.5459	14.0
Fraxinus uhdei (Wenz.) Lingelsh.	Oleaceae	Lamiales	Holarctic	Frauhd	103.77	0.037	0.5306	13.67
Ostrya virginiana (Mill.) K. Koch	Betulaceae	Fagales	Holarctic	Ostvir	49.04	0.024	0.6046	14.48
Zinowiewia concinna Lundell	Celastraceae	Celastrales	Neotropical	Zincon	172.68	0.033	0.4394	16.6
Subgroup 2b								
Acer skutchii Rehder	Sapindaceae	Sapindales	Boreotropical	Acesku	47.65	0.135	0.564	27.93
Citharexylum mocinnii D. Don	Verbenaceae	Lamiales	Neotropical	Citmoc	38.38	0.194	0.4495	11.6
Clethra vicentina Standl.	Clethraceae	Ericales	Neotropical	Cletvic	48.3	0.227	0.4126	17.34
Clusia salvinii Donn. Sm.	Clusiaceae	Malpighiales	Neotropical	Clusal	95.48	0.127	0.5401	10.1
Dendropanax arboreus (L.) Decne. et Planch.	Araliaceae	Apiales	Neotropical	Denarb	35.52	0.09	0.3887	10.72
Eugenia culminicola McVaugh	Myrtaceae	Myrtales	Neotropical	Eugcul	119.66	0.565	0.5306	3.89
Magnolia iltisiana A. Vázquez	Magnoliaceae	Magnoliales	Boreotropical	Magilt	129.68	0.38	0.6213	20.82
Meliosma dentate (Liebm.) Urb.	Sabiaceae	Ranunculales	Boreotropical	Melden	204.15	0.27	0.4355	11.65
Myrsine juergensenii (Mez) Lundell	Myrsinaceae	Ericales	Neotropical	Myrjue	43.21	0.254	0.6089	22.56
Parathesis villosa Lundell	Myrsinaceae	Ericales	Neotropical	Parvil	218.21	0.214	0.4651	6.0
Persea hintonii C.K. Allen	Lauraceae	Laurales	Boreotropical	Perhin	32.0	1.811	0.4938	14.33
Rhamnus hintonii M.C. Johnst. et L.A. Johnst.	Rhamnaceae	Rosales	Holarctic	Rhahin	142.87	0.148	0.4001	3.45
Styrax argenteus C. Presl	Styracaceae	Ericales	Neotropical	Styarg	60.99	0.68	0.4646	10.79
Symplococarpon purpusii (Brandegee) Kobuski	Theaceae	Ericales	Neotropical	Sympur	28.12	0.834	0.6276	15.35
Symplocos prionophylla Hemsl.	Symplocaceae	Ericales	Neotropical	Sympri	49.23	0.601	0.3536	10.59
Synardisia venosa (Mast.) Lundell	Myrsinaceae	Ericales	Neotropical	Synven	146.71	0.355	0.3769	13.52
Tilia mexicana Schldtl.	Malvaceae	Malvales	Holarctic	Tilmex	69.28	0.131	0.3151	14.71
Turpinia occidentalis (Sw.) G. Don	Staphylaceae	Crossosomatales	Boreotropical	Turocc	146.83	0.452	0.5846	13.7
Xylosma flexuosum (Kunth) Hemsl.	Salicaceae	Malpighiales	Pantropical	Xylfle	22.75	0.033	0.6221	16.6

groups and subgroups identified in the cluster analysis were not segregated on the PCA ordination plot.

4. Discussion

4.1. *Between-trait correlations*

The studied CF encompasses a biogeographical mixture of tree species that have evolved not only in different geographic regions, but also in quite different habitat types (i.e. tropical vs. temperate). At least three major sets are included in the studied flora: in addition to the typical temperate Laurasian (e.g. *Cornus disciflora*) and tropical Gondwanan (e.g. *Myrsine juergensenii*) elements (see Table 2), there also are tropical Laurasian taxa (e.g. *Magnolia iltisiana*), and at least one species without a clear biogeographical affinity (*Ilex brandegeana*). Despite this mixture of biogeographical histories, it must be stressed that the effect of phylogeny in the covariation of the functional attributes was rather unimportant. In fact, in several groups a mixture of clades was represented among the species they contained, suggesting the convergence of many lineages. Overall, our results showed that the relationships between the four traits studied are weak in Manantlán's cloud forest. The most obvious relationship was that between Hmax and SM, a pair of characters that were significantly correlated when using cross-species analyses, and nearly so in PICs. A loose relationship between Hmax and SM has been reported for several floras (r^2 ranging from 0.12 to 0.35; Rees, 1997; Westoby et al., 1997; Moles et al., 2004; Falster and Westoby, 2005a). The link between Hmax and SM has been proposed to reflect the association between two life

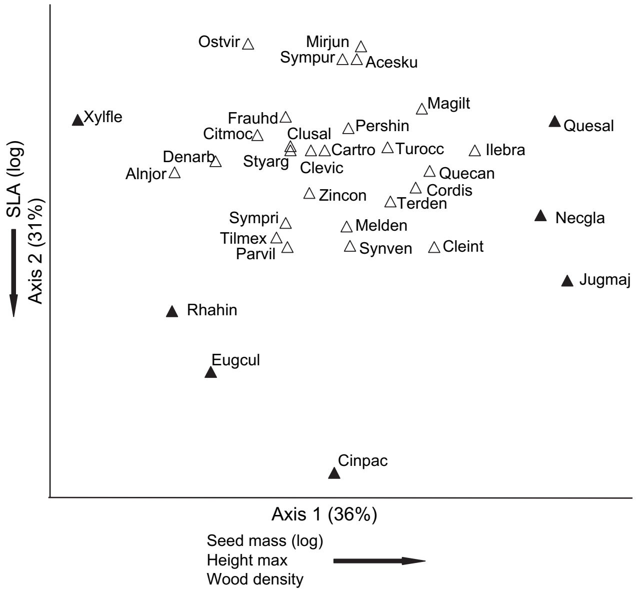

Fig. 3 – Ordination plot along two first principal components of 33 cloud forest species from Manantlán, Jalisco, W Mexico, based on the following traits: specific leaf area (SLA), seed mass (SM), wood density (WD) and maximum height (Hmax). Total variation explained by the first axis was 36.1%, and by the second was 30.8%. Black triangles distributed in the periphery of the ordination plot represent seven species and white triangles distributed in the central sector represent 26 species. Species abbreviations as in Table 2.

history components; big plants require longer periods before attaining adult size and reproductive maturity, and juvenile survivorship, an essential step in this process, is positively associated with seed size, especially in forests with a dense canopy and shaded understories (Moles and Westoby, 2004a; Wright et al., 2006b).

We expected that species with larger seeds would tend to have a large Hmax. In the case of Manantlán's cloud forest, taller trees tended to have larger SM, e.g. those species belonging to Group 1. This was well exemplified by *Juglans major* and *Quercus salicifolia*; however, there were important exceptions of taller trees having smaller SM, as illustrated by *Acer skutchii* and *Magnolia iltisiana*, both of which belong to groups with boreotropical affinities (see Table 2).

Table 3 – Loadings of traits that better explain between-species variation in the PCA ordination of 33 cloud forest tree species from Manantlán, Jalisco, Mexico

	Axis 1	Axis 2	Axis 3	Axis 4
Plant height	0.42 (+)	0.46 (−)	0.76 (+)	0.14 (−)
Seed mass	0.65 (+)	0.32 (+)	0.03 (−)	0.67 (+)
Wood density	0.59 (+)	0.28 (−)	0.58 (−)	0.46 (−)
SLA	0.19 (−)	0.77 (−)	0.26 (−)	0.54 (+)
Eigenvalue	1.44	1.23	0.79	0.52

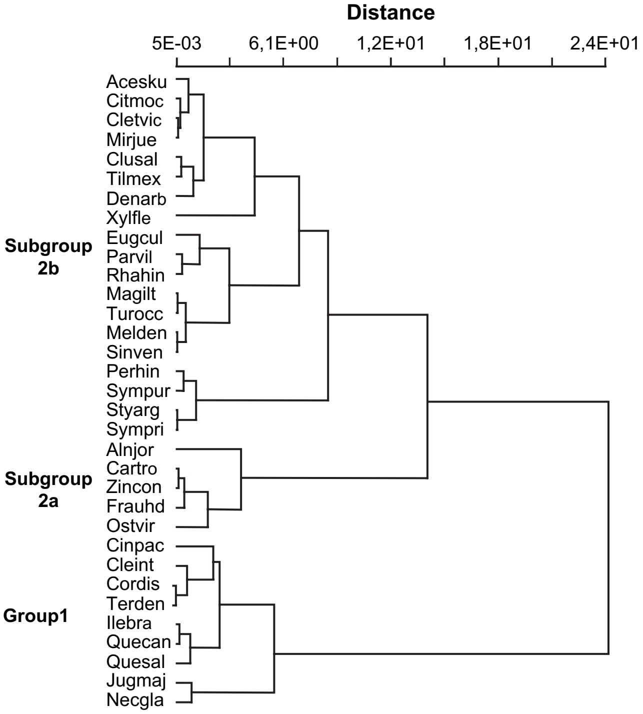

Fig. 4 – Species clustering for the cloud forest of Manantlán, Jalisco, W Mexico, based on Ward's grouping linkage method and Euclidian distances. Species abbreviations as in Table 2.

Hmax and WD also showed a significant positive correlation in the cross-species analysis, and this relationship was also significant in PICs. This frequently reported association has been interpreted as a pure mechanical relationship, as taller trees need more substantial investments in supporting structures to maintain a safety factor (Niklas, 1994; Sterck et al., 2006a). In this case, we expected a tight correlation between Hmax and WD; however, this relationship was very loose, suggesting that other factors may account for the positive relationship between Hmax and WD. Alternatively, Falster and Westoby (2005b) found that a positive Hmax vs. WD relationship can be expressed through a correlation with successional status; early successional plants have lower stature and softer wood than late successional ones. This possibility may apply to the species studied, but our field observations suggest that the range of successional status is rather narrow, with only a few species like *Nectandra glabrescens* and *Quercus salicifolia* being relatively more shade-tolerant. One must recall that pines, the true pioneers in this community (early fast colonizers with high growth rates and a short time to reproduction; Saldaña-Acosta, 2001) were not included in the study. Moreover, the relatively open canopy of this forest could prevent the existence of extremely shade tolerant species, as those described for lowland forests. In fact, all studied species may be clearly classified as mature forest components in Manantlán.

We hypothesized that species with medium to high WD would have a large Hmax, but that total height would be unrelated to a relatively low WD. In Manantlán, the variation

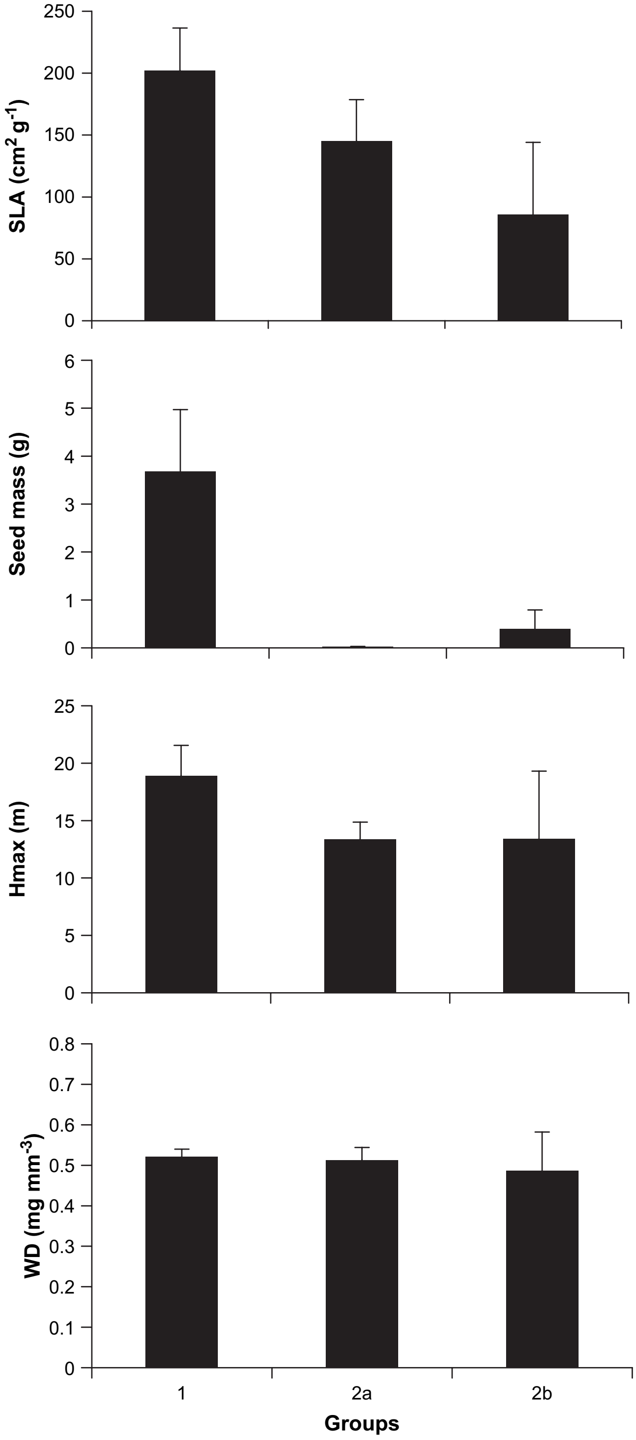

Fig. 5 – Mean values and ± SE of specific leaf area (SLA, cm^2 g^{-1}), seed mass (SM, g), wood density (WD, mg mm^{-3}) and maximum height (Hmax, m) for species forming the two different groups: Group 1 (1), and Group 2 (the latter with two Subgroups, 2a and 2b).

in WD observed across species was relatively small (range: 0.3–0.6 mg mm^{-3}), and there were no large differences in WD between short and tall plants, leading to the conclusion that this trait makes a very minor contribution to the multivariate between-species variation. Contrastingly, plant height in our cloud forest did vary across one order of magnitude (4–35 m). Consequently, there are both shorter species (e.g. *Ternstroemia dentisepala* and *Ostrya virginiana*), and tall species (e.g. *Quercus salicifolia* and *Magnolia iltisiana*) with similar WD. In fact, of the entire range of WD values reported in the literature, our set of cloud forest species is quite homogeneous (Lawton, 1984; King et al., 2005). In the case of lowland tropical trees, WD ranges from ca. 0.12 mg mm^{-3} for light-wooded species to ca. 1.15 mg mm^{-3} for the densest woods (Baker et al., 2004; Muller-Landau, 2004; King et al., 2006; Wright et al., 2006b). For temperate trees of higher latitudes this trait varies from 0.24 mg mm^{-3} for the light wooded species, to 0.77–0.98 mg mm^{-3} for the very heavy wood species (US Department of Agriculture, 1999; Woodcock and Shier, 2003). Finally, among tropical montane rain forest trees in sites other than Manantlán, WD ranges from 0.27 to 0.48 mg mm^{-3} for shade intolerant species, and from 0.39 to 0.58 for the shade tolerant ones (Lawton, 1984).

Unlike other forests, particularly lowland tropical ones, where vegetation structure is denser and the canopy is more closed (Sterck et al., 2006b), in Manantlán specialisation through WD differentiation for specific light environments appears to be less important. In this community, species differentiation along the vertical light gradient may derive from a trade-off between shade tolerance and growth in height, mediated by other traits such as the light capture architecture (see Poorter et al., 2005).

SLA showed the most independent behaviour among all traits, as it was unrelated to either Hmax, SM and WD in the cross-species and PICs analyses. This result is in partial disagreement with other studies that reported this trait to be related at times to other plant attributes such as SM, WD, Hmax and leaf size (Wright et al., 2006a,b; Falster and Westoby, 2005b; Poorter and Bongers, 2006), and to show phylogenetic correlations (Ackerly and Reich, 1999). The inconsistent correlations of SLA and Hmax, WD or SM found in the literature can be due to a variety of reasons related to the use of different protocols (collecting sun or shade leaves), to the particular community or site as they differ in nutrients or water or canopy openness, and even to the ontogenetic stage of sampled individuals (see Niinemets, 2006 for a discussion). Yet when comparing forests where sun leaves of adult trees were sampled, the direction of the SLA vs. Hmax correlation exhibited opposite directions between forests; positive for La Chonta, Bolivia, and negative for Los Tuxtlas, Mexico (Wright et al., 2006b). This result suggests that vertical variation in SLA is reflecting multiple correlations with life history as well as direct responses to environmental gradients, which need to be understood for each community. Perhaps the least generalised correlation of SLA is its proposed negative relationship with WD, which should reflect a trade-off between fast growth (high leaf return per mass invested) and survival in the shade (high resistance to losses of plant parts due to pathogens or physical damage). Again, in our study, the reduced variation in WD is likely to preclude the detection of such a functional relationship between SLA and WD.

In Manantlán we found a large among-species variation in SLA, ranging across one order of magnitude (22.3 cm^2 g^{-1} in *Xylosma flexuosum* to 284.6 cm^2 g^{-1} in *Juglans major*). Similar levels of variation have been found in other studies for lowland tropical and temperate forests, as well as for montane cloud forest communities (e.g. Reich et al., 1999; Williams-Linera, 2000; Wright et al., 2004; Pickup et al., 2005). We also found differences in SLA within taller and shorter species, i.e. there are both shorter and taller species with low and high SLA (Table 2). This kind of variation has been interpreted as an indication of a large plasticity of SLA, allowing plants to adjust continuously to the changing light environment experienced by trees during their ontogenetic development (Popma et al., 1992; Rozendaal et al., 2006). This is particularly relevant if one considers that there is a significant SLA reduction with tree age, suggesting ontogenetic changes in leaf traits (Niinemets, 2006). More studies are needed that analyze the variations of the four traits in response to changing conditions in different light levels and during ontogeny, as well as their relations with growth and mortality.

The lack of functional correlations in Manantlán may provide valuable insights as to which are the main axes of phenotypic variation in cloud forest trees. For instance, the fact that SLA represents an independent axis of niche differentiation and of evolutionary change (Ackerly, 2003) may be extremely useful in defining major functional strategies. Therefore, we may expect SLA to make a significant contribution to specialisation (through net carbon gain) to the heterogeneous light environments in CF, as previously demonstrated for tropical tree communities (Sterck et al., 2006a).

A particularly important goal of this study was to examine the possibility that correlations defining groups would still be present within particular clades, or whether they would reflect mainly between-clades differences. In our study we found a general concordance of functional correlations (Hmax vs. SM, and Hmax vs. WD) when evaluated based on cross-correlations or phylogenetic contrasts. This overall agreement suggests that a given functional relationship found among extant species has resulted from repeated divergence of the traits in different clades along the evolutionary history (Ackerly, 1999), and thus that common ancestry does not account fully for all potential variables affecting a given relationship (Paz et al., 2005). For example, for the relationship between Hmax and WD we detected several significant evolutionary divergences: the one corresponding to Eurosid trees took place at a very early stage of divergence. Thus it appears that these two attributes were acquired long ago and have been maintained since. Finally, the changes observed in the Asterid and Euasterid trees indicate that these attributes emerged as an adaptation in recent evolutionary stages of these two large groups.

4.2. *Species grouping*

Regarding our initial question about the possibility of morpho-functional traits indicating natural groups of cloud forest species, our results point out to a largely continuous among-species variation, as seen in the PCA plot (see Fig. 3). However, the trait-based classification allowed differentiating two main groups, whose distinction assisted in the effort to recognise a natural grouping among the studied species. The consistency of this distinction along a large range of linkage distance axis indicates that it is not completely artificial. Yet species classification in these groups is better justified from a practical perspective, i.e. for management purposes, than because of the existence of significant discontinuities between groups. In fact, the range of variation within groups, e.g. for SM and SLA, shows the large heterogeneity existing within the defined groups. According to dendrogram topology, Group 1 was better defined. Interestingly, the two main groups represented a combination of phylogenetic lineages, highlighting the role of ecological rather than phylogenetic constraints.

Cloud forest tree species of Manantlán do not form permanent seed banks so that a persistent seedling bank is the commonest regeneration strategy (Saldaña-Acosta, 2001). The diametric structures of some taxa (e.g. *Nectandra glabrescens*, *Magnolia iltisiana*, and *Myrsine juergensenii*) are characteristic of populations having advanced regeneration and probably a good response capacity when gaps open in the canopy. In contrast, other species like *Fraxinus uhdei* are large canopy trees, with their seedlings and saplings being scarce or absent in the understorey. This study suggests the existence of a variety of comparable, but by no means identical, successful life history strategies for Manantlán's cloud forest species, and reflects the coexistence of species with varying functional traits but living under similar conditions. As it happens in other montane forests, cloud forest tree species possess a set of traits that are linked to key aspects of the establishment phase of their life cycles.

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Capítulo III. Seedling biomass allocation and vital rates of cloud forest tree species: responses to light in shade house conditions

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Running title: Seedling responses to light variations

Abstract

The patterns of above- and below-ground biomass allocation in seedlings of nine common cloud forest (CF) tree species of western Mexico were evaluated under varying controlled light conditions using shade houses in nursery. We analysed the relationships between vital rates (growth rates and survival) and four morphological traits (SLA, biomass allocation to stems, leaves and roots). We hypothesised that these traits represent differentiation axes in the way seedlings face the heterogeneous light regime typical of the CF understorey. For all species traits between the different light levels, i.e. allocation to leaves, roots and stems differed among light levels. Five species had the largest SLA in the lowest light levels at the end of the experiment (*Citharexylum, Dendropanax, Fraxinu*s, *Quercus* and *Magnolia*). *Juglans* was the only species with a large SLA at the highest light level (377.47 $\text{cm}^2\ \text{g}^{-1}$). In contrast, light levels did not cause any significant variation in SLA of *Persea* and *Simplococarpon* at the end of the experiment. Growth rates of the seedlings of five species were significantly different between light levels ($P < 0.05$). Overall, all species grew better in the highest light levels. The relative height growth rates of three species were correlated positively with SLA. In turn, allocation to stem, leaves and root biomass were strongly correlated with the growth rates of five species (e.g. *Citharexylum, Dendropanax*, *Fraxinus*). Survival did not vary significantly between treatments in any species, only in the case of *Simplococarpon* ($P < 0.05$) and was correlated with all morphological variables. In this species Peto and Peto's test showed a significantly larger survival of seedlings in the highest light level. These results suggest that all the species display a wide range of resource allocation patterns when exposed to the varying light conditions that may be found in the forest understorey and highlight the role of morphological traits in this variation

Keywords: SLA, biomass allocation, shade houses, cloud forest, seedlings, survival, light levels.

1. Introduction

Acquisition and effective use of light are crucial for seedling establishment in the forest understorey. Light varies greatly both in time and space in this environment, and this phenomenon hampers or accelerates plant growth intermittently (Montgomery and Chazdon, 2002), as demonstrated by several experiments controlling light and canopy openness (Ashton et al., 1997; Baratolo et al., 2005; Beckage et al., 2005; Palomaky et al., 2006; Ramírez-Marcial et al., 2007).

A number of morpho-functional traits contribute to seedling persistence in the forest understorey (e.g seed biomass, leaf area; Kitajima, 1996; Valladares et al., 2002). Several studies have documented the large variation displayed by these traits under different light regimes, along with their effects on survival and plant growth (e.g. Kitajima, 1994; Veneklass and Poorter, 1998; Niinemets, 2006). An important practical implication of the analysis of this variability and its relationships with vital rates of plants (survival and growth rates), is that it allows to develop specific management practices for individual species, and to propose restoration practices based on them (Sánchez-Velásquez et al., 2004; Martínez-Garza et al., 2005).

The cloud forest (CF) of Mexico is an endangered ecosystem (Challenger, 1998). The natural fragmented distribution of this forest type has been exacerbated due to human activities, and only between 1993-2000 approximately 90% of its surface was cleared for agriculture, fires and cattle ranching (OCDE, 2003). Despite this situation, no reforestation programme in Mexico has ever included the massive production of CF tree species, which may be a result of an insufficient knowledge of various aspects related to their propagation, particularly those concerning the establishment phase (Ortíz-Arrona, 1999; Pedroza and Williams-Linera, 2003; Ramírez-Balmonde et al., 2005). Previous studies have shown that most CF tree species regenerate mainly in the shaded understoreys, although some appear to be capable of establishing also in small gaps or in forest edges (Saldaña-Acosta, 2001). However, there is a group of CF tree species that are considered to be pioneers, such as pine species, or *Liquidambar styraciflua* which is able to achieve high growth rates in open areas facilitating the establishment of other species (e.g. *Magnolia dealbata* and *Persea americana*) beneath their canopy (Ramírez-Bamonde et al., 2005; González-Espinosa et al., 2007; Sánchez-Velásquez et al., 2008). Adaptive successional reforestation for restoration purposes (Herrera et al., 1990; Jardel, 2008), must acknowledge the regenerative individual or collective behaviours of these species (Martínez-Garza and Howe, 2003). Investigating the responses of morphological attributes (e.g. leaf traits) of CF tree seedlings to different light conditions may provide a sound base for recommendations aimed at better management practices.

Shade tolerance is a key functional trait for seedling survival in low light, and thus it is capable of influencing forest composition, structure and dynamics (Baker, 1949; Lusk, 2002, 2004). This trait often varies greatly among coexisting species, showing a continuum of seedling performance strategies (Kobe et al., 1995; Poorter and Arets, 2003; Valladares, 2003). For instance, it determines not only the life history strategies of the species but also the position along the growth-survival trade-off in some species (DeLucia et al., 1998; De Walt et al., 2003; Capers et al., 2005; Myers and Kitajima, 2007).

Among those key traits proposed as drivers of the ecological strategy of plant species performance under different light environments, the ones that provide shade tolerance are the maintenance of a high leaf area for capturing light per unit of previously captured mass (i.e. high specific leaf area, SLA) and a low root/shoot mass ratio (Givnish, 1988; Reich et al., 1998; 2003; Niinemets and Valladares, 2006). However, recent studies with seedlings grown in controlled environments do not fully support this generalization, and in fact some of them lead to the conclusion that biomass allocation of shade tolerant species show the opposite trend. For example, when grown in low light some shade tolerant seedlings had smaller SLA and higher root/shoot ratios than intolerant ones (Veneklaas and Poorter, 1998; Poorter, 1999; Walters and Reich, 1999). Similarly, in controlled field experiments, Paz (2003) found that seedlings of shade tolerant species allocated more biomass to roots, and tended to have higher SLA in the understorey than intolerant species.

Such differences in biomass allocation may represent different strategies for the maintenance of the long-term carbon balance (Walters et al., 1993; Kitajima, 1994; Shipley and Meziane, 2002; Poorter et al., 2005). For example, a high SLA may increase the mortality risk in low light (Walters and Reich, 1999) whilst a larger allocation to leaves may reduce storing ability (e.g. roots), which is very important for survival during unfavourable periods and for recovery from herbivore damage (Lusk, 2002). Given the discrepancies discussed above, it is necessary to further study the combined responses of these traits, in order to gain a better insight on the functional significance of the variation in biomass allocation for seedling growth and survival (Poorter and Nagel, 2000).

In this study we contrast patterns of above- and below-ground biomass allocation in seedlings of nine common CF tree species of western Mexico grown under varying controlled light conditions. We analysed the relationships between vital rates and morphological traits, by examining differences in shade tolerance among these species and the optimal light levels for their growth and survival. This goal was achieved by using shade-house experiments, under relatively well-controlled, low light levels. We predicted that: (1) seedlings of the different species would allocate differentially biomass to stems, leaves and roots; (2) leaves of those seedlings growing in poorly-lit conditions would have a higher SLA, and a higher biomass allocation to stems and leaves relative to root allocation than those growing in less limited light conditions; (3) seedlings of the different species would show a differential response in their survival and growth rates; and (4) seedlings survival and relative height growth rates would be related to the differential biomass allocation to the four traits analyzed.

2. Methods

2.1. Study site

This study was conducted at the Las Joyas Scientific Station (LJ; 19º 35' N; 104º 17' W; elevation 1800-2100 m) located in the Sierra de Manantlán Biosphere Reserve, Jalisco State, western Mexico. Mean annual temperature is 17ºC and mean total annual precipitation is 1609 mm, most of which falls between June and October, with sporadic rain events from November to January; the dry season spans between February and May. Vegetation cover includes pine, pine-oak, and cloud forests, as well as secondary scrub and grassland (Sánchez-Velásquez et al., 1996). At LJ, cloud forest (known in Mexico as 'bosque mesófilo de montaña') grows in ravines and in shaded and humid slopes, where fog is frequent during the rainy season. According to the management history of the area before its legal protection, clearings for agriculture, livestock, logging, and forest fires played a major role in configurating the current forest mosaic (Jardel et al., 1993; Hernández-Vargas et al., 2000; Pineda-López et al., 2000). At the study site, CF was logged intensely in the second half of the 20th century, creating large canopy gaps and causing extensive structural changes (Jardel, 2008). Studies of forest regeneration patterns have shown that several pioneer *Pinus* species form almost pure stands shortly after disturbances, subsequently facilitating the establishment of a second wave of non-pioneer, CF representative tree species. With time, the latter replace the pines, forming mature cloud forests (Sánchez-

Velásquez and García-Moya, 1993; Saldaña-Acosta, 2001).

2.2. Species

We selected nine CF tree species whose seedlings and saplings are common in the understorey of the study site, but that differ in seed mass (SM) and cotyledon functional morphology (Saldaña-Acosta, 2001; Table 1). SM varied from 0.03 in *Fraxinus uhdei* (Wenz.) Lingelsh to 12.06 g dry mass in *Juglans major* (Torr.) Heller. (Saldaña-Acosta et al., 2008). For brevity, hereafter we refer to the study species by their generic names only.

Mature seeds of all species were collected from natural populations at LJ from a minimum of ten individuals each, and germinated under nursery conditions. Seed and germination characteristics of these species were described elsewhere (Saldaña-Acosta et al., 1998). We placed seeds in plastic trays filled with forest soil and maintained them in a nursery until seedlings were transplanted to polyethylene containers (30 cm height × 20 cm diameter) that were placed in the shade houses in nursery; seedlings were watered whenever necessary.

2.3. Shade house experiment

At the centre of the experimental nursery at LJ we constructed four 3 × 1.5 m shade houses with different light levels. These levels were selected based on data from field experiments conducted previously in the study site (Ortiz- Arrona, 1999; Saldaña-Acosta, 2001). Four levels of photosynthetically active radiation (PAR) were obtained and variations of irradiance in shade houses was achieved by varying the number of layers of shadow mesh: 3-5%, 8-10%, 18-20%, and 55-60%. PAR was recorded with a quantum sensor (LI-185a, LI-COR).

Shortly after full expansion of the first true leaves, we placed 50 individuals within each shade house for all species except for *Acer* and *Quercus* because of differences in seed and seedling availability (25 individuals each). In total, 400 individual were placed within each shade house. Initial seedling height did not differ significantly between the individuals of each species (in all cases $P > 0.05$). Within each shade house, seedlings were place randomly and tagged. Individual plants were taken as the experimental units, thus variables were determined for each plant measured and these values were averaged for each light × species treatment (the average leaf size for each individual plant was considered as one statistical observation for calculating mean and standard deviation). In turn, survivorship was calculated based on the total number of individuals by species that had survived at each sampling date. A very large initial mortality of individuals of *Juglans* and *Magnolia* required replacing individuals of these two species one month after the beginning of the experiment.

2.4. Traits and biomass measurements

To calculate biomass allocation, ten seedlings per species (five in *Acer* and *Quercus*) and light level were randomly harvested at 45 days intervals, and height (cm) was recorded and measured vertically from the forest floor to the stem apex for each seedling to calculate relative height growth rates (RGR). The experiment started on March 2004 and ran during 225 days. Seedlings were carefully washed to eliminate substrate and separated into three fractions: stems, leaves (with petioles), and roots.

We scanned all the leaves to create digital images and measured their area by using the SigmaScan Pro ® 5 software (SPSS Inc., 1999). All veins were included; if petioles or petiolules were lacking, leaves were carefully detached from branches and stems (e.g. *Fraxinus* and

Juglans). Plant material was then dried at 80°C for at least 48 h and weighed. SLA was determined by dividing the area of each leaf by its dry mass.

2.5. Data analysis

All four traits (SLA, root, stem and leaf biomass) were $\log_{10}$ transformed before analysis because their distributions were right skewed. The treatment effects were evaluated by split-plot ANOVAS through the Mixed procedure of SAS (Ver. 8, 2000), because it allows the statistical analysis of models with combinations of both random and fixed effects. Degrees of freedom were calculated with the Satterthwaite method. In those cases where the independent variables and interactions (time, light level, time × light level) were significant, they were compared with the least squares mean with the Bonferroni adjustment (Zar, 1999).

Relative height growth rates were analyzed by split-plot ANOVAS through the Mixed procedure of SAS. Growth rates were estimated with the following equation:

$$T_c = \frac{\ln C_2 - \ln C_1}{t}$$

where C_2 is final height, C_1 is initial height, and t is time in days.

We used the Kaplan-Meir method (Kaplan and Meir, 1958) to estimate the seven-month (225 days) survivorship curves for each species by light level by means of the survival analysis procedure (comparing multiple samples) of the Statistica ver. 6 software (StatSoft 2001). We compared survival curves through Peto and Peto Wilcoxon test. We then examined the correlations between the four traits and the species' survival and growth rates; we used cross-species correlations (between attribute Pearson product-moment correlations). The high mortality of *Acer* seedlings precluded further analysis of this species. In the case of *Simplococarpon,* its high seedling mortality in the 8-10% light level did not allow performing the analysis for this level. In some cases we observed a decrease in leaf mass at the end of the experiment; apparently this was due to the onset of the dry/cold season, which triggered leaf shedding in the case of the deciduous *Fraxinus* and *Juglans*, or to an excessively long duration of the experiment causing root suffering in the plastic containers, as inferred by final root morphology in *Magnolia, Persea,* and *Dendropanax* (Fig. 3). Therefore, for these species the analyses were performed with those data obtained at day 180. However, although leaf biomass also decreased in seedlings of *Quercus* and *Simplococarpon* in some light levels (e.g. in the 3-5 % and 18-20% light levels for *Quercus*), we decided to perform the analyses with the final data (225 days) because leaf biomass in seedlings in other light levels continued to increase until that date (Fig. 3).

3. Results

3.1. Biomass allocation

Substantial differences were found regarding the responses of the eight species studied to different light levels (Table 2). For six of them, the split-plot ANOVAS were significant for all traits between the different light levels, i.e. allocation to leaves, roots and stems differed within species at or the near the end of the experiment (i.e. 225 or 180 days). *Citharexylum* and *Magnolia* showed the clearest differences in root and stem biomass between the highest and lowest light levels (Figs. 1 and 2). Those species showing the clearest patterns of leaf biomass allocation were *Citharexylum*, *Magnolia*, *Fraxinus*, *Dendropanax*, and *Simplococarpon* at the higher light levels (Fig. 3).

Juglans had the largest biomass allocation to roots and stems (Fig. 5). Its seedlings allocated more leaf mass in the lowest light level (2.94 g) (< SLA), but they allocated a similar biomass to roots (3.1 g) and stems (2.58 g) in the 8-10% light level. *Citharexylum* and *Fraxinus* were the species that allocate more to leaf biomass at the highest light level. *Magnolia* allocated more biomass to roots and stems at the 55-60% light level.

For stem and root biomass, seedlings of *Dendropanax* allocated a higher proportion to roots (4.01 g) in the 8-10% light level, and a greater proportion to stems (2.65g) in the higher light level (Figs. 1 and 2). In the case of *Persea*, the allocation to stem biomass did not differ significantly between light levels (Fig. 2). The seedlings of *Persea*, *Dendropanax* and *Magnolia* had the greater leaf dry mass in the highest light levels (1.04, 1.07 and 1.4 respectively; Fig 3).

3.2. SLA

Among the studied species, five had the largest SLA in the lowest light levels at the end of the experiment: *Fraxinu*s (336.16 cm^2 g^{-1}), *Quercus* (340.02 cm^2 g^{-1}), *Dendropanax* (404.99 cm^2 g^{-1}), *Citharexylum* (314.94 cm^2 g^{-1}), and *Magnolia* (355.44 cm^2 g^{-1}). *Juglans* was the only species with a large SLA at the highest light level (377.47 cm^2 g^{-1}) (Fig. 4). In contrast, light level did not cause any significant variation in SLA of *Persea* at the end of the experiment.

In 45% of the cases there were significant interactions between time and light levels, which implied that in some cases significant between-treatment differences became apparent since day 180. For instance, in the case of *Juglans* there were marked differences between the 3-5% and the 18-20% light levels at that moment ($P < 0.0029$; Fig. 4). Yet, in other species, (e.g. *Magnolia*) it was only at the end of the experiment (225 days) when differences in SLA (and also in stem and root biomass) became clear. Significant interactions were not only observed for SLA, as for *Magnolia* a significant interaction was found for leaf biomass (Table 2, Fig. 3) and for *Persea,* in root biomass (Table 2; Fig. 2).

3.3. Seedling growth rates and survival

Five species differed significantly in their relative height growth rates between light levels during the experiment (Table 2). Overall, all species grew taller in the highest light levels. Only the seedlings of *Persea* showed a slightly higher growth rate in the 8-10% light level.

Survival at the end of the experiment (225 days) did not vary significantly between treatments in any species (in all cases $P > 0.05$) (Table 3). Only in the case of *Simplococarpon* survival differed between treatments and was greater in the highest light treatment ($P < 0.05$). In this species Peto and Peto's test showed a significantly larger survival at the highest light level (Fig. 6).

3.4. Relationships between morphological traits and vital rates

Relative height growth rate was correlated with almost all traits for five species (Table 4). RGR of *Fraxinus* was not correlated with SLA but was significantly and negatively correlated with leaf mass, and positively correlated with stem and root mass. The RGR of *Dendropanax, Juglans* and *Persea* were positively correlated with SLA; moreover, in the former species a significant correlation was found between growth rate and leaf mass, whereas in the latter growth rate was also correlated with stem and root biomass. In turn, allocation to stem and root biomass in *Citharexylum* were strongly correlated with its RGR, and for *Dendropanax* they were correlated with leaf and stem mass. We found that for almost all species studied (*Citharexymun*, *Dendropanax*, *Fraxinus*, and *Persea*) the strongest correlation was observed between growth rate and stem biomass (Table 4). Survival was generally unrelated to morphological attributes, with the only exception of *Simplococarpon*, in which survival was significantly correlated with all morphological variables ($P < 0.05$).

4. Discussion

4.1. Strategies related to biomass allocation

Although all studied species seem to have a generally similar ecological behaviour, as all of them are typical elements of the mature CF in Manantlán (Saldaña-Acosta et al., 2008), it is noteworthy that they display a wide range of resource allocation patterns when exposed to the different light conditions that may be found in the forest understorey. That is, each species allocates biomass preferentially to the plant part specialized in obtaining the resource that more strongly limits growth during the seedling stage (balanced growth; Poorter and Nagel, 2000).

Our findings suggest the existence of different life strategies in the understorey, driving the specific ways in which species face the conditions imposed by the shaded environments and emphasize the role of morphological traits in determining this variation (Lusk and Piper, 2007). For example, *Dendropanax*, *Magnolia* and *Persea* allocate more biomass to roots and leaves, but less to stems in the higher light level. Large root mass allocation has been reported for young seedlings of shade-tolerant species (Bonfil, 1998; Paz, 2003; Portsmuth and Niinemets, 2007), as their seedlings generally have a low biomass allocation to foliage (Kitajima, 1994; Walters and Reich, 1999); this early strategy of below-ground storage, which was observed in some CF tree species, may allow them to respond rapidly in growth height when light increases as a consequence of a canopy opening (DeLucia et al., 1998), even if they do not find optimal conditions for growth in the forest understorey. Conversely, *Juglans* allocated more biomass to leaf mass and stems, and less to roots in the lower light level; a larger allocation to leaves may possibly reduce the storage ability (e.g. roots), which is very important to low-light survival during periods of shortage and to recovery from herbivore damage (Coley et al., 1985; Kobe, 1997; Lusk, 2002).

4.2. SLA responses across species

Increasing SLA is a frequent phenotypic response to shade in seedlings grown in poorly-lit environments (Popma and Bongers, 1988; Walters et al., 1993). Most of our study species (*Citharexylum, Dendropanax*, *Fraxinu*s, *Magnolia*, and *Quercus*) had higher SLA in the lowest light level. However, *Juglans* had exactly the opposite response, i.e. its SLA was largest in the higher light levels; this behaviour is in agreement with the fact that this was the only species whose seedlings survived in open areas in the field experiments (A. Saldaña-Acosta, unpublished data), suggesting shade intolerance. It is also interesting that *Persea* and *Simplococarpon* did not show a clear trend for SLA in varying light conditions, similarly to the findings of DeLucia et al. (1998). Therefore, our results provide partial support to our second prediction that SLA would be inversely related to light intensity, even though all of these species are capable of growing and surviving in the forest understorey and most of them (with the noticeable exception of *Juglans*) do not survive in open sites (A. Saldaña-Acosta, pers. obs.).

The between-species differences in their individual responses to changes in light levels clearly indicate the existence of different strategies between species. This observation is consistent with the results of other studies involving the comparison of multiple species, as they have found reductions in SLA with increasing shade tolerance of the species. Such reductions are usually coupled with increments in leaf life span, resulting in a larger carbon gain per unit leaf mass (Kitajima 1996; Veneklass and Poorter, 1998; Lusk, 2002), and in smaller losses of productive tissue (Coley, 1988). Previous studies conducted at LJ had suggested that the range of successional status of CF tree species is relatively narrow, with some species as *Quercus* and *Juglans* being relatively more shade-tolerant, whereas others like *Magnolia* have an intermediate shade tolerance (Saldaña-Acosta, 2001). With the new information available, it is clear that this preliminary successional classification of the species must be revised; at least in the case of *Juglans* it is clear that it may be less shade tolerant that originally thought, and the same may be the case of *Persea* and *Simplococarpon*.

4.3. Relationships of traits and vital rates

It has been broadly recognized that interspecific variation in the performance of first-year seedlings is associated to variation in SLA (Lambers and Poorter, 1992; Cornelissen et al., 1996; Veneklass and Poorter, 1998; Westoby et al., 2002; Wright et al., 2004). However, the accumulation of information from a larger number of species has cast doubts on the strength of this correlation (Shipley, 2002, 2006). The five species that showed significant differences in their RGR between light levels (*Citharexylum, Dendropanax*, *Fraxinu*s, *Juglans*, and *Persea*) grew faster in the highest light levels, strongly suggesting that growth of these species ultimately require more open canopies. Interestingly, only in three of them (*Dendropanax*, *Juglans*, and *Persea*) was their RGR was associated to SLA, although we had anticipated growth to be positively correlated with SLA in all species. Indeed, in this study SLA was little informative on the performance of the majority of the examined CF tree seedlings. We must acknowledge that the lack of relationship between SLA and RGR in some species may be an artefact produced by the duration of the experiment, which may not be completely representative of seedling performance in the field over longer periods of time (Sack and Grubb, 2001).

In addition to the relationship between SLA and RGR discussed above, other ecological traits may be of great significance to the ecological performance of seedlings. A particularly important one is seed mass, as this trait is associated to major morphological adaptations (van der Pijl 1982; Saverimuttu and Westoby, 1996; Ibarra-Manríquez et al., 2001; Kitajima, 2002). This regenerative trait favours survival during seedling recruitment, and it is correlated to other traits (dispersability, growth rate, root mass, and seedling size) determining the life history strategy of plants (Swanborough and Westoby, 1996; Bonfil, 1998; Dalling and Hubbell, 2002; Westoby et al., 2002; Moles and Westoby, 2004; Paz et al., 2005). Thus, seed mass is associated to major morphological adaptations that allow species to cope with heterogeneous light conditions (van der Pijl 1982; Saverimuttu and Westoby, 1996; Ibarra-Manríquez et al., 2001; Kitajima, 2002).

4.4. Relative growth rates in height and *seedling survival*

With the exception of *Simplococarpon*, we did not find differences in low-light survival for most studied species. Unfortunately, this precluded ranking the other seven species based on shade tolerance. Again, this result may be due at least partially to the limitations imposed by the duration of this experiment (ca. seven months), which may be insufficient for seedlings to show the mortality associated with different light levels (Poorter et al., 2008). Nevertheless, it is clear that *Simplococarpon* seedlings had a lower mortality in the higher light level, suggesting that this species is more shade intolerant than the others (Poorter and Bongers, 2006), in coincidence with the significant correlations between survival and all traits examined for this species.

4.5. Final remarks

Our study supports our hypothesis that at the seedling stage the CF species studied at LJ display differential life strategies. However, there is no doubt that the complex linkages between seedling performance and morphological traits requires further study in order to gain a better understanding of these relationships; these studies should involve more species from a wide range of habitats (Cornelissen et al., 1996; Lin et al., 2001; Kneeshaw et al., 2006), and should be based on experiments of longer duration. Ultimately, patterns observed for CF species at the seedling stage will have to be integrated with their responses as juveniles and adults in order to gain a deeper insight of the ecological strategies of these species. However, knowing the individual behaviours in a set of species that otherwise would be simply classified as shade tolerant is of utmost importance in order to design specific management strategies that would allow promoting growth and survival of some species over others.

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Table 1. Study species, family, seed mass (SM, g), and cotyledon functional morphology (PE = photosynthetic, epigeal; SE = storage, epigeal; SH = storage, hypogeal) according to Garwood (1996).

Species	Family	Seed mass	Cotyledon morphology
Acer skutchii Rehder	Sapindaceae	0.135 ± 0.011	PE
Citharexylum mocinnii D. Don	Verbenaceae	0.194 ± 0.053	PE
Dendropanax arboreus (L.) Decne. et Planch.	Araliaceae	0.090 ± 0.012	PE
Fraxinus uhdei (Wenz.) Lingelsh.	Oleaceae	0.037 ± 0.005	PE
Juglans major (Torr.) Heller	Juglandaceae	12.06 ± 1.37	SH
Magnolia iltisiana A. Vázquez	Magnoliaceae	0.380 ± 0.041	SE
Persea hintonii C.K. Allen	Lauraceae	1.81 ± 0.442	SE
Quercus salicifolia Née	Fagaceae	1.95 ± 0.169	SH
Symplococarpon purpusii (Brandegee) Kobuski	Theaceae	0.083 ± 0.60	PE

Table 2. Summary of split-plot ANOVAS through the Mixed process to examine the influence of different light levels and time on specific leaf area (SLA), biomass allocation to roots, stems and roots, and relative height growth rate for eight cloud forest tree seedlings.

	log SLA		log root		log stem		log leaves		growth rate	
Species	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fraxinus udhei										
time	2.74	0.0309	56.81	0.0001	70.65	0.0001	51.87	0.0001	51.03	0.0001
light	4.12	0.0077	25.19	0.0001	17.28	0.0001	6.68	0.003	2.72	0.0464
time × light	3.21	0.0004	2.77	0.002	1.38	ns	2.19	0.015	1.46	ns
Quercus salicifolia										
time	5.45	0.007	3.8	0.0072	5.56	0.006	8.25	0.0001	15.14	0.0001
light	4.36	0.007	2.77	0.0475	2.33	0.0076	2.74	0.0017	0.29	ns
time × light	2.24	0.0206	1.38	ns	0.94	ns	0.94	ns	1.75	ns
Dendropanax arboreus										
time	9.37	0.0001	88.46	0.0001	79.25	0.0001	86.33	0.0001	86.4	0.0001
light	3.09	0.0289	4.18	0.007	5.63	0.0011	14.68	0.0001	8.41	0.0001
time × light	4.11	0.0001	1.2	ns	2.21	0.0137	14.98	0.0001	2.63	0.0032
Magnolia iltisiana										
time	1.61	ns	53.64	0.0001	47.03	0.0001	17.35	0.0001	53.35	0.0001
light	4.81	0.0081	11.82	0.0001	3.67	0.0137	26.31	0.0001	1.54	ns
time × light	0.99	ns	1	ns	1.12	ns	14.5	0.0001	1.32	ns
Citharexylum mocinnii										
time	3.89	0.0048	50.4	0.0001	61.44	0.0001	17.48	0.0001	10.2	0.0001
light	17.52	0.0001	6.71	0.0003	17.52	0.0001	17.52	0.0001	3.44	0.0184
time × light	1.61	ns	5.07	0.0001	2.84	0.0015	2.84	0.0015	2.69	0.0025
Juglans major										
time	23.55	0.0001	12.2	0.0001	15.32	0.0001	19.01	0.0001	6.43	0.0001
light	2.68	0.0489	6.33	0.0004	3.83	0.0109	7.2	0.0001	5.78	0.0009
time × light	6.13	0.0001	1.27	ns	1.19	ns	2.82	ns	1.33	ns
Persea hintonii										
time	3.17	0.0153	34.09	0.0001	18.24	0.0001	41.06	0.0001	28.41	0.0001
light	1.28	ns	6.36	0.0004	1.18	ns	4.79	0.0031	10.89	0.0001
time × light	0.54	ns	2.41	0.0067	0.87	ns	6.36	0.0001	2.04	0.0239
Simplococarpon purpusii										
time	3.25	0.0165	7.22	0.0001	11.35	0.0001	19.51	0.0001	9.63	0.0001
light	1.41	ns	4.88	0.0038	5.09	0.0028	13.82	0.0001	0.06	ns
time × light	2.72	0.0114	0.26	ns	1.13	ns	4.53	0.0002	1.15	ns

Table 3. Pearson's correlations between traits and relative height relative growth rates (cm) on five cloud forest tree species. Marked correlations are significant at $P < 0.05$).

Trait		*Citharexylum*	*Dendropanax*	*Fraxinus*	*Juglans*	*Persea*
log SLA	r	0.17	**0.28**	-0.038	**0.29**	**0.54**
log Leaf mass	r	**0.44**	**0.81**	**-0.49**	**0.22**	0.07
log Stem mass	r	**0.90**	**0.90**	**0.59**	0.15	**0.85**
log Root mass	r	**0.81**	0.07	**0.49**	0.10	**0.77**

Table 4. Comparison of the survival between four light levels for each species based on the Kaplan-Meir method through the survival analysis procedure (comparing multiple samples).

Species	χ^2	df	*P*
Citharexylum mocinnii	5.81	4	0.121
Dendropanax arboreus	3.44	4	0.328
Fraxinus uhdei	1.44	4	0.696
Juglans major	3.94	4	0.268
Magnolia iltisiana	5.81	4	0.121
Persea hintonii	5.33	4	0.149
Quercus salicifolia	6.97	4	0.728
Symplococarpon purpusii	9.46	4	0.0238

Legends to figures

Figure 1. Variation of root biomass between four light levels in eight cloud forest tree species. Means with the same letter are not different between light levels (Tukey HSD-test). Symbols for light levels are indicated as follow: solid squares for 3-5%, solid triangles for 8-10%, stars for 18-20% and for 55-60% open squares.

Figure 2. Variation of stem biomass between four light levels in eight cloud forest tree species. Means with the same letter are not different between light levels (Tukey HSD-test). Symbols for light levels are indicated as follow: solid squares for 3-5%, solid triangles for 8-10%, stars for 18-20% and for 55-60% open squares.

Figure 3. Variation of leaf biomass between four light levels in eight cloud forest tree species. Means with the same letter are not different between light levels (Tukey HSD-test). Symbols for light levels are indicated as follow: solid squares for 3-5%, solid triangles for 8-10%, stars for 18-20% and for 55-60% open squares. Note that we perform the analyses with the data at 180 days because leaf biomass decrease at the end of the experiment for *Fraxinus, Juglans*, *Magnolia*, *Persea* and *Dendropanax*.

Figure 4. Variation of SLA between four light levels in eight cloud forest tree species. Means with the same letter indicate that there is no significant difference (Tukey HSD-test). Symbols for light levels are indicated as follow: solid squares for 3-5%, solid triangles for 8-10%, stars for 18-20% and for 55-60% open squares.

Figure 5. Proportion allocation of biomass to roots, stems, and leaves of tree seedlings of *Citharexylum mocinnii* (Citmoc), *Dendropanax arboreus* (Denarb), *Fraxinus uhdei* (Frauhd), *Juglans major* (Jugmaj), *Magnolia iltisiana* (Magilt), *Persea hintonii* (Perhin), *Quercus salicifolia* (Quesal), and *Symplococarpon purpusii* (Sympur) growing in four different light levels: a) 3-5%, b) 8-10%, c) 18-20%, and d) 55-60%. Black color is for

roots, white color for stems, and crosshatched for leaves.

Figure 6. Comparison of the survival curves for seedlings of *Simplococarpon purpusii* in a cloud forest. Means with the same letter indicate that there is no significant difference. The differences between survival curves were evaluated through Peto and Peto Wilcoxon tests. Symbols for light levels are indicated as follow: solid squares for 3-5%, solid triangles for 8-10%, stars for 18-20% and for 55-60% open squares.

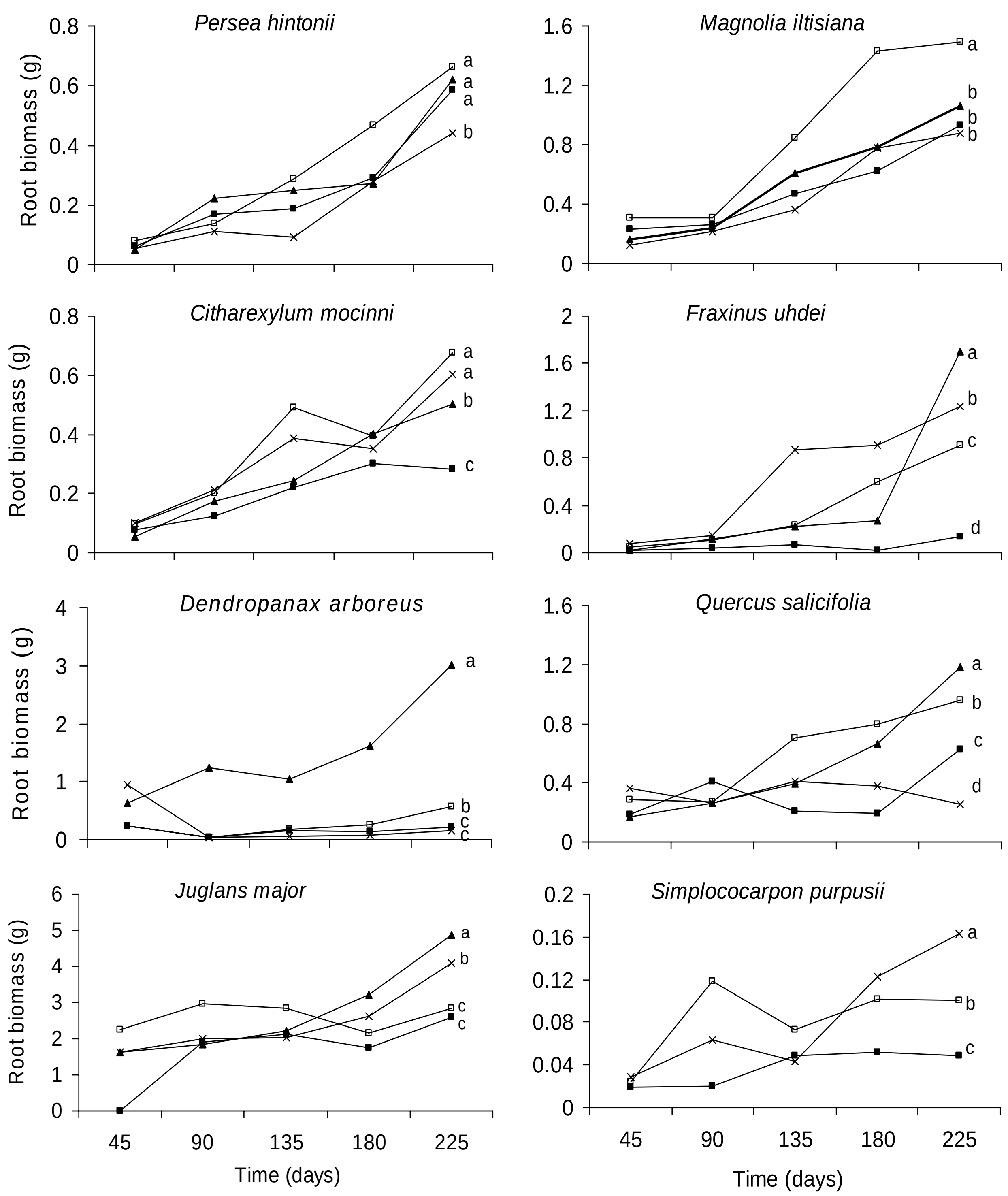

Persea hintonii
0.8
0.6
0.4
0.2
0
a
a
a
b
Magnolia iltisiana
1.6
1.2
0.8
0.4
0
a
b
b
b
Citharexylum mocinni
0.8
0.6
0.4
0.2
0
a
a
b
c
Fraxinus uhdei
2
1.6
1.2
0.8
0.4
0
a
b
c
d
Dendropanax arboreus
4
3
2
1
0
a
b
c
c
Quercus salicifolia
1.6
1.2
0.8
0.4
0
a
b
c
d
Juglans major
6
5
4
3
2
1
0
a
b
c
c
Simplococarpon purpusii
0.2
0.16
0.12
0.08
0.04
0
a
b
c
Root biomass (g)
45
90
135
180
225
Time (days)

Figure 1

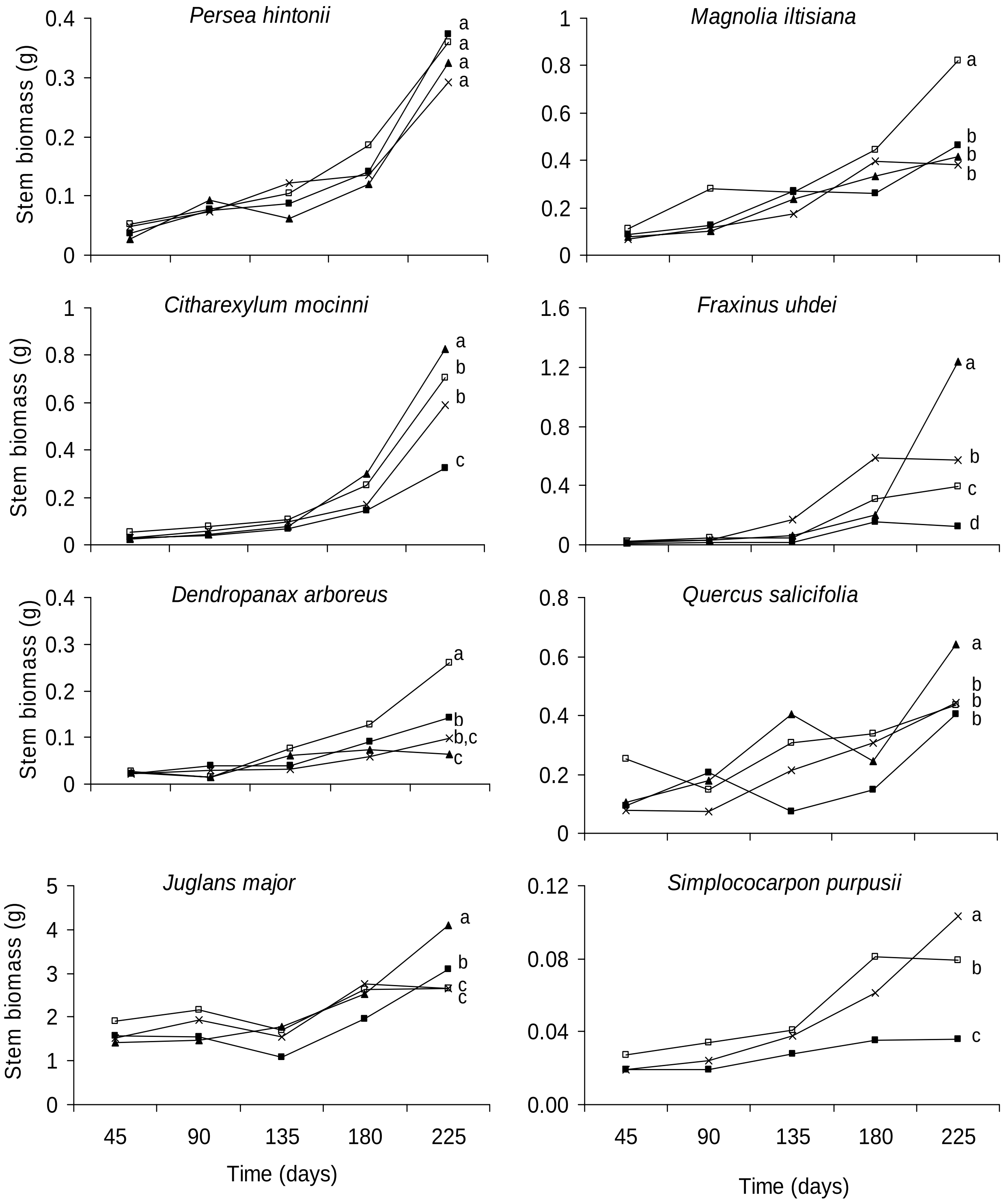

Persea hintonii
Magnolia iltisiana
Citharexylum mocinni
Fraxinus uhdei
Dendropanax arboreus
Quercus salicifolia
Juglans major
Simplococarpon purpusii
Stem biomass (g)
Time (days)
45
90
135
180
225
a
b
c
d
b,c

Figure 2

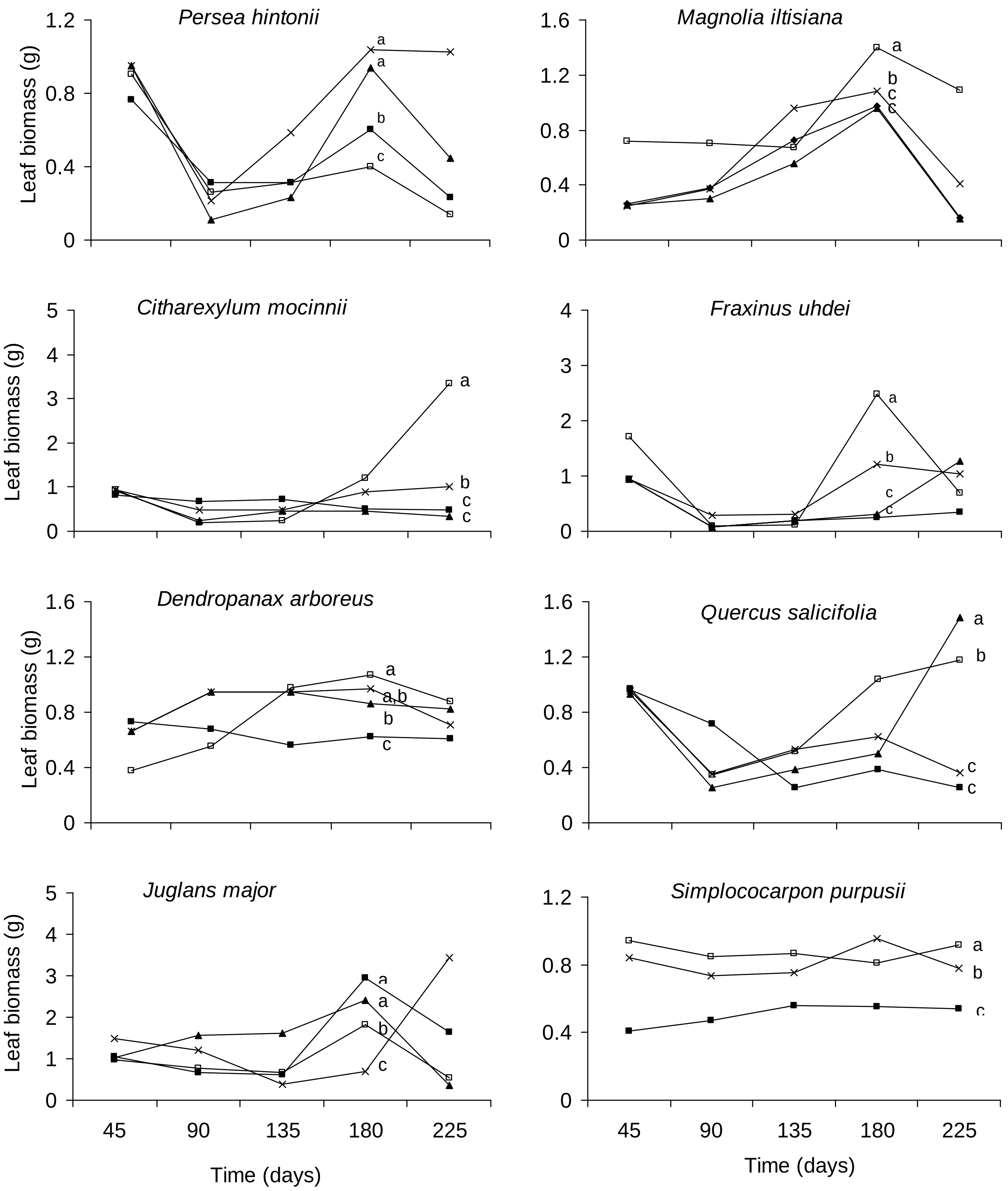

Persea hintonii
Magnolia iltisiana
Citharexylum mocinnii
Fraxinus uhdei
Dendropanax arboreus
Quercus salicifolia
Juglans major
Simplococarpon purpusii
Leaf biomass (g)
Time (days)
45
90
135
180
225
0
0.4
0.8
1.2
1.6
1
2
3
4
5
a
b
c
a,b

Figure 3

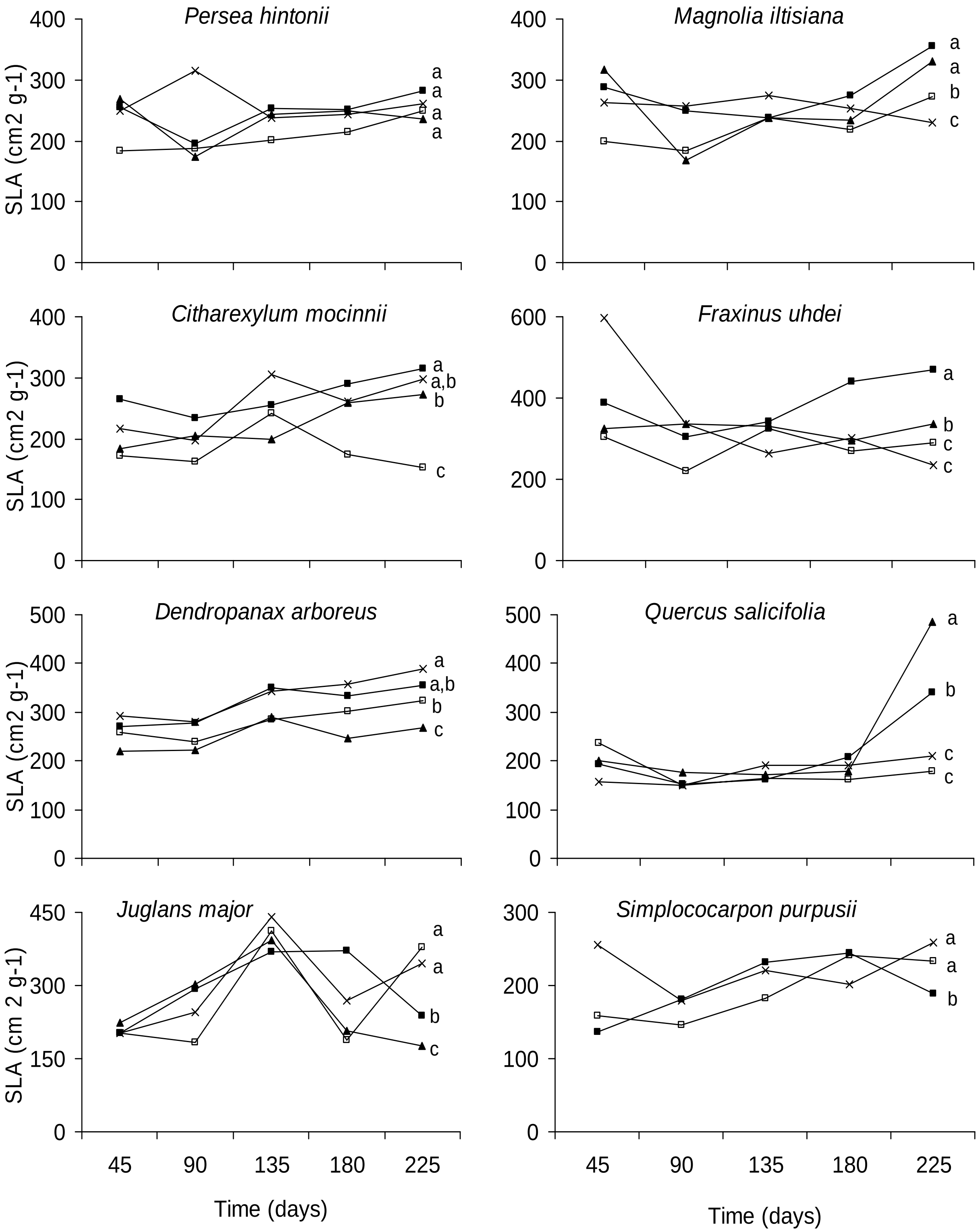
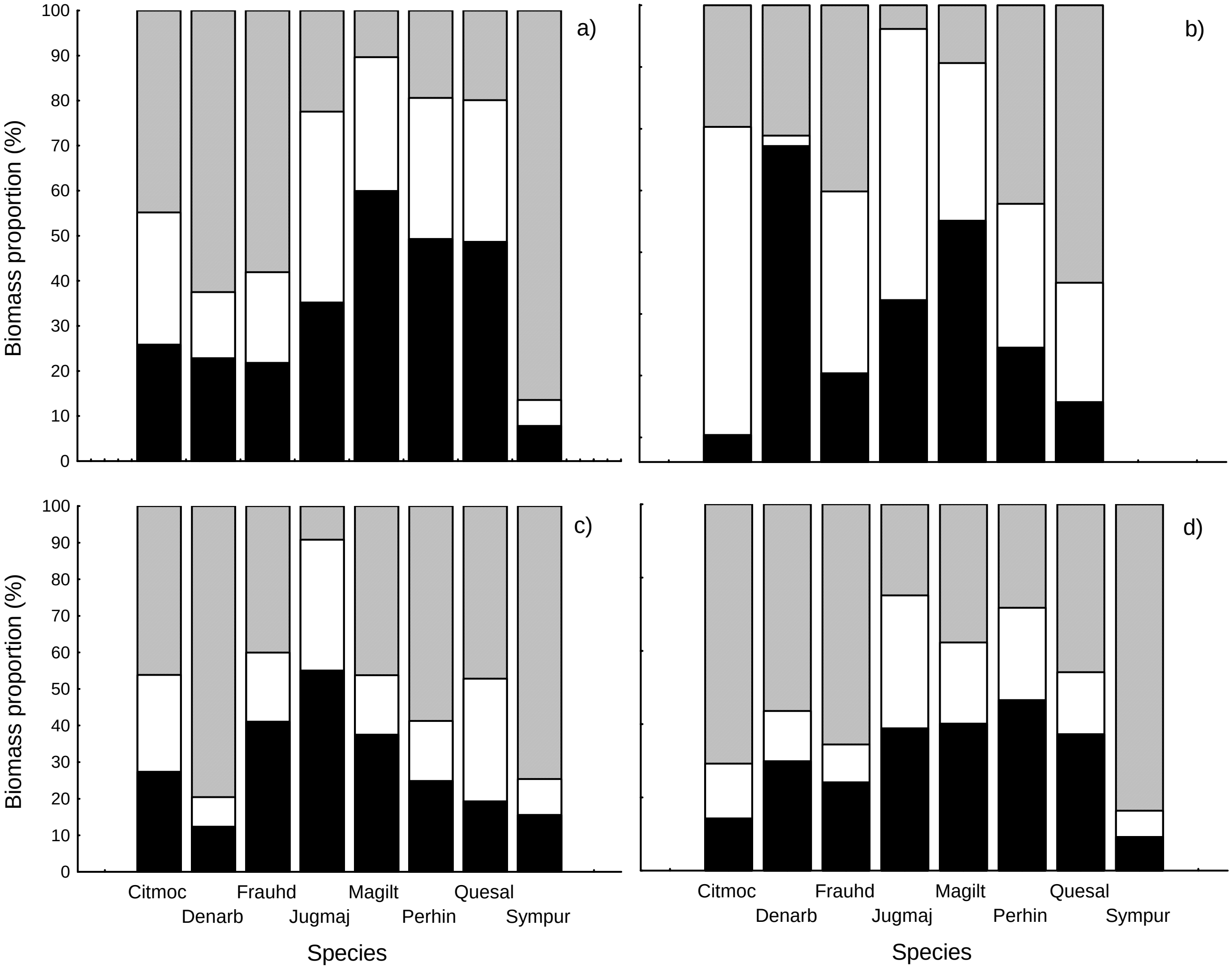
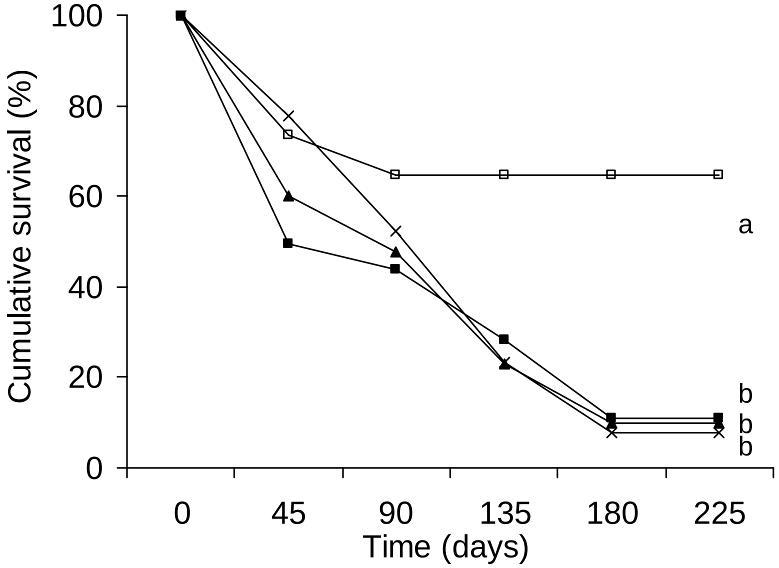

Persea hintonii
Magnolia iltisiana
Citharexylum mocinnii
Fraxinus uhdei
Dendropanax arboreus
Quercus salicifolia
Juglans major
Simplococarpon purpusii
SLA (cm2 g-1)
SLA (cm 2 g-1)
0
100
150
200
300
400
450
500
600
45
90
135
180
225
Time (days)
a
a,b
b
c

Figure 4



100
90
80
70
60
50
40
30
20
10
0
Biomass proportion (%)
a)
b)
c)
d)
Citmoc
Denarb
Frauhd
Jugmaj
Magilt
Perhin
Quesal
Sympur
Species

Figure 5


100
80
60
40
20
0
Cumulative survival (%)
0
45
90
135
180
225
Time (days)
a
b
b
b

1

2 Figure 6

Capítulo IV. Relationships between leaf traits and vital rates of cloud forest tree seedlings: responses to light variations in field conditions.

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Running title: Leaf traits and vital rates of cloud forest tree seedlings.

Abstract

The variation in SLA and the relationships between this leaf trait and vital rates (relative height growth rates and survival) of four common cloud forest (CF) tree species of western Mexico (*Dendropanax arboreus*, *Fraxinus uhdei, Juglans major* and *Magnolia iltisina*) were evaluated experimentally under three growing conditions: (1) under the canopy of 50-year-old *Pinus douglasiana* stands, (2) under the canopy of 40-year-old *P. douglasiana* stands, and (3) in15-year-old open areas (OA). We assessed the heterogeneity of light environment of seedlings under the pine canopy stands and open area using hemispherical photographs and a densiometer. For the statistical analysis in open areas, *Fraxinus, Dendropanax* and *Magnolia* were excluded because all seedlings died. We found the lowest values of canopy openness (%) in the younger stands (40 yr) followed by the older (50 yr) stands, and finally for OA. After 270 days SLA differed significantly between treatments in the four species. Three species had the largest SLA in the closed stands, whereas *Juglans* had the largest SLA in OA. No significant differences were found in the relative height growth rates (RGR) between conditions in the four species, while seedling survival was significantly different between treatments in all species ($P < 0.05$). The survival of three species was correlated with SLA, and only RGR of *Juglans* was correlated with SLA (r = 0.45, $P < 0.05$). These results suggest that a group of CF tree seedlings develop leaves adapted to differences within the different stands. The effect of SLA on RGR was very poor, but was positively related to survival. This allowed us to classify this group of species as mid-successional species based on their shade tolerance. We suggest that these species could be used for restoration.

Keywords: cloud forest, light heterogeneity, pine forest, SLA, seedlings, vital rates.

1. Introduction

Light availability plays an important role in the growth and survival of tree seedlings and saplings in the forest understorey (Kitajima, 1996; Veneklaas and Poorter 1998; Montgomery and Chazdon, 2002). Forest succession is often explained based on the light requirements of tree species for their establishment, survival and growth (Finegan, 1996). Some studies have examined the effect of light heterogeneity on seedling performance in two contrasting light levels - gaps and closed canopy -, leading to the classical classification of tree species into groups, according to their shade tolerance during their regeneration phase i.e. pioneer vs. shade tolerant species (Swaine and Whitmore, 1988). However, this practice overlooks the gap-understorey continuum of light levels beneath closed canopy and gaps (Nicotra et al., 1999; Portsmuth and Niinemets, 2007). Individual seedlings grow under a wide range of light environments (Bongers and Sterck, 1998; Poorter and Aerts, 2003), which has given place to the recognition of a broader gradient of species between this two extremes (Montgomery and Chazdon 2001, 2002; Saldaña-Acosta et al., 2008). For this reason, it is necessary to evaluate the light requirements and the differential response of tree species to the light heterogeneity typical of forest understories (Kobe et al., 1995; Kobe, 1999; Kitajima, 2002; Mejía-Domínguez, 2006)

The cloud forest (CF) of Mexico has a fragmented distribution, and covers less than 1% of Mexico's territory. This forest type has experienced very strong pressures because of land use changes and forest exploitation for their quality timber, such as *Fraxinus uhdei* (ash) and *Juglans major* (walnut). This forest type in now considered an endangered ecosystem (Rzedowski, 1991; Challenger, 1998). Despite this, little is known about the propagation, nursery production, silvicultural characteristics, and effective reproduction mechanisms of many species. Virtually no research has been conducted on their potential for cultivation under natural conditions or in plantations, which appears to result from an insufficient knowledge on various aspects related to their establishment (Butterfield and Fisher, 1994; Ortíz-Arrona, 1999; Pedroza and Williams-Linera, 2003; Ramírez-Balmonde et al., 2005; Rámirez-Marcial et al., 2008). Previous studies have shown that most CF tree species regenerate mainly in the shaded understorey, although some species appear to be capable of establishing also in small gaps or forest edges (Saldaña-Acosta, 2001). It has also been shown that some pine species behave as pioneers, dominating early stages of succession, and that in the absence of disturbances they are gradually replaced by other broadleaved CF tree seedlings. This circumstance has direct implications for designing reforestation activities following the successional trajectory of the community (Jardel and Sánchez-Velásquez, 1989), i.e. following the sequence of species replacement, which is the base of the successional reforestation concept (Luken, 1990). Thus, pines have been used as nurse plants to reintroduce other CF tree seedlings beneath pine forests (Saldaña-Acosta, 2001; Ramírez-Bamonde et al., 2005). The establishment of mixed plantations for successional reforestation activities has proved a successful strategy for restoration purposes (Herrera et al., 1990; Jardel, 2008). Yet, the regenerative individual or collective behaviours of tree species must be acknowledged (Martínez-Garza and Howe, 2003). Investigating the responses of morphological attributes (e.g. leaf traits) of CF tree seedlings to different light conditions in field conditions may provide a sound base for recommendations aimed at better restoration practices.

Seedlings responses to the light environment are achieved by adjusting morphology and physiology (Lusk and Piper 2007). Functional traits are morpho-functional attributes, which strongly influence fitness indirectly through their effects on growth, reproduction and survival of plant species (Ackerly, 2003; Violle et al., 2007). Leaf traits that change with environmental conditions are associated to tree growth rates and survival (Kitajima, 1996; Paz, 2003; Martínez-Garza, 2005). Specific leaf area (SLA), defined as the light-capturing foliar area per unit of previously captured mass, is considered a key-trait for plant performance (Lambers and Poorter 1992; Wright et al., 2004). Among plants is an extremely variable trait and currently its variation appears to be quite irregular regarding shade tolerance. For example, although shade tolerant taxa may produce leaves with lower SLA in shaded conditions (Veneklaas and Poorter, 1998; Reich et al., 2003), the shade tolerant *Rhamnus catharticus* had exactly the opposite behaviour in temperate forest understorey (Grubb et al., 1996). Additionally, in a study carried out with eight temperate rainforest species under different light conditions, light demanding taxa (e.g. *Embothrium coccineum*) tended to have higher SLA than shade tolerant species in all light environments (Lusk, 2002).

The aim of this study was to explore experimentally the variation in SLA of four common CF tree species of western Mexico grown under pine canopies and open areas. We analyzed the relationships between vital rates (relative height growth rates and survival) and SLA, in order to identify between-species differences in their abilities to adjust their performance to light heterogeneity. Differences in shade tolerance occurring in natural regeneration among these species and optimal habitats for their growth and survival for this group of species is still unknown. We predicted that: (1) leaves of seedlings of the different species growing in poorly-lit conditions would have higher SLA than those growing in the open; (2) seedlings of the different species would show differential responses in their survival and growth rates in different light environments; and (3) seedlings SLA would be related to survival and growth rates across light conditions.

2. Methods

2.1. Study area and species

The study was conducted at Las Joyas Scientific Station (LJ; 19º 35’ N; 104º 17’ W; elevation 1800-2100 m) located in the Sierra de Manantlán Biosphere Reserve, Jalisco State, western Mexico. Mean annual temperature is 17ºC and mean annual precipitation is 1600 mm, most of which falls between June and October, with sporadic rain events from November to January; the dry season spans between February and May. Vegetation comprises pine, pine-oak, and cloud forests, as well as secondary scrubs and grasslands (Sánchez-Velásquez et al., 1996). At LJ, cloud forest (known in Mexico as ‘bosque mesófilo de montaña’; Rzedowski, 1978) grows in ravines and in shaded and humid slopes, where fog is frequent during the rainy season.

Prior to the legal protection of the area, clearings for agriculture and livestock, together with logging and forest fires, played a major role in configurating the current forest mosaic (Jardel et al., 1993; Hernández-Vargas et al., 2000; Pineda-López et al., 2000). At the study site, CF was logged intensely in the second half of the 20th century, creating large canopy gaps and causing extensive structural changes (Jardel, 2008). Studies of forest regeneration patterns and succession in pine-oak forests and CF in the area have shown that pioneer species of *Pinus*, mostly *P. douglasiana*, can establish shortly after a disturbance, and in pine forest with deep, fertile and moist soils, and without the occurrence of forest fires since 15 to 20 years ago, there are abundant CF tree seedlings and small trees in the undestorey. These studies also suggests that *Pinus* trees facilitate the establishment of CF tree species, which in time replace the pines, forming mature cloud forests (Sánchez-

Velásquez and García-Moya, 1993; Saldaña-Acosta, 2001).

We selected four common broadleaved CF tree species (*Dendropanax arboreus, Fraxinus uhdei, Juglans major* and *Magnolia iltisiana*). These differ in seed mass (SM) and cotyledon functional morphology (Saldaña-Acosta, 2001; Table 1). SM varied from 0.03 in *Fraxinus uhdei* (Wenz.) Lingelsh. to 12.06 g dry mass in *Juglans major* (Torr.) Heller. (Saldaña-Acosta et al., 2008). For brevity, hereafter we refer to the study species by their generic names only.

Mature seeds of all species were collected from natural populations at LJ from a minimum of ten individuals each, and germinated under nursery conditions. Seed and germination characteristics of these species were described elsewhere (Saldaña-Acosta et al., 1998). We placed seeds in plastic trays filled with forest soil and kept them in a nursery until seedlings were transplanted to polyethylene containers (30 cm height × 20 cm diameter) and later planted in the experimental plots, when seedling age was approximately 1 yr.

2.2. Experimental design

Six *Pinus* stands were selected to establish the experimental plots (three treatments with two replicates): two approximately 50-year-old *Pinus douglasiana* Martínez stands, La Moza (LM) and Charco de los Perros (ChP), two 40-year-old *P. douglasiana* stands, Puerto del Escobedo (PE) and Cuchilla de la Tuna (CT), and two 15-year-old open areas (cleared by forest fires), Barbecho de las Burras (OAB) and Plaza de Gallos (OAG). The stands are referred to by the names used by local residents. All stands were located within the same slope, soil type (alfisoles) (see Martínez-Rivera et al., 1995), and elevation (1900 m).

During the dry season (April-May 2004) we established five 8.5 × 9.5 m plots in the lowest slope within each stand (30 plots in total). Initial seedling height did not differ significantly between the individuals of each species (in all cases $P > 0.05$). We transplanted the seedlings during the rainy season. In each plot, 12 seedlings of each species were randomly planted and tagged; sowing distance between individuals was 1 m. Individual plants were taken as the experimental units, thus traits were determined for each plant and these values were averaged for each light × species treatment (the average leaf size for each individual plant was considered as one statistical observation for calculating mean and standard deviation). In turn, survivorship was calculated based on the total number of individuals by species that had survived at each sampling date. A very large initial mortality of individuals of *Juglans* and *Magnolia* required replacing individuals of these two species one month after the beginning of the experiment.

To calculate SLA, two seedlings per species and plot randomly selected were harvested at 45 days intervals, and height (cm) was recorded and measured vertically from the forest floor to the stem apex for each seedling to calculate relative growth rates (RGR). The experiment started on July and ran during 270 days.

We scanned all the leaves of each seedling to create digital images and measured their area by using the SigmaScan PRO 5 software (SPSS Inc). All veins were included; if petioles were lacking, leaves were carefully detached from branches and stems (e.g. *Fraxinus* and *Juglans*). Plant material was then dried at 80°C for at least 48 h and weighed.

In order to evaluate the heterogeneity of the seedlings light environment under the pine canopy stands and open areas, we took hemispherical photographs at the centre of each plot with a fisheye lens located with a north orientation. Photographs were analyzed with the Gap Light Analyser (GLA) program Version 2.0 (Frazer et al., 1999). We analysed canopy openness (%), the amount of direct, diffuse and total incident radiation. In addition, we measured canopy openness with a densiometer in 12 randomly selected points within each plot.

2.3. Data analysis

SLA was $\log_{10}$ transformed before analysis because its distribution was right skewed. The treatment effects in SLA were evaluated by split-plot ANOVAS through the Mixed procedure of SAS (SAS Ver 8, 2000), because it allows the statistical analysis of models with combinations of random effects and fixed effects. Degrees of freedom were calculated with the Satterthwaite method. In those cases where the independent variables and interactions (time, light level, time × light level) were significant, they were compared with the last squares mean with the Bonferroni adjustment (Zar, 1999). Analyses were performed for each species separately.

Relative height growth rates (RGR) were analyzed by split-plot ANOVAS through the Mixed procedure of SAS. RGR were estimated with the following equation:

$$T_c = \frac{\ln C_2 - \ln C_1}{t}$$

where C_2 is final height, C_1 is initial height, and t is time in days.

We used the Kaplan-Meir method (Kaplan and Meir, 1958) to estimate the seven-month (270 days) survivorship curves for each species by light level by means of the survival analysis procedure (comparing multiple samples) of the Statistica ver. 6 software (StatSoft, 2001). We compared survival curves through the Peto and Peto Wilcoxon test.

We then examined the correlations between SLA and the species' survival and growth rates; we used cross-species correlations (between attribute Pearson product-moment correlations). The high mortality of the seedlings of *Dendropanax*, *Fraxinus* and *Magnolia* in the open areas precluded the analysis of these species for this treatment.

3. Results

3.1. Hemispherical photographs

Table 2 shows the values of percent canopy openness and of the amount of direct, diffuse and total incident radiation for each plot. The lowest values for the canopy openness were observed in the 40 year old stands, followed by the 50 year old stands, and finally for the open areas (OA). Canopy openness ranged from 11.69 to 13.28, 17.84 to 19.09, 58.23 to 62.04 for the younger and older stands, and for the OA, respectively. Ranges of total radiation transmitted by the canopy forest (relative to the amount of above-canopy radiation, 39.3 mol/m^2 day^{-1}) were 6.28 to 9.34 (40 yr old stands), 11.63 to 12.39 (50 yr old stands), and 32.56 to 33.69 in the OA.

3.2. SLA

The split-plot ANOVAS for SLA were significant for the four species, i.e. SLA differed within species at 270 days of the experiment (Table 3). Three species had the largest SLA in those stands with the lowest canopy openness (40 yr old stands) than in the stands with the highest canopy openness (50 yr old stands): *Dendropanax* (205.99 vs.

161.27 cm^2 g^{-1}), *Fraxinus* (301.94 vs. 212.3 cm^2 g^{-1}), and *Magnolia* (287.97 vs. 230.44 cm^2 g^{-1}). *Juglans* was the only species with the largest SLA at OA (347.76 cm^2 g^{-1}), followed by a larger SLA in the stands with the highest canopy openness (309.89 cm^2 g^{-1}), and the smallest one in the stand with the lowest canopy openness (276.82 cm^2 g^{-1}) (Fig. 1).

Only for *Juglans* were there significant interactions between time and treatments, with significant between-treatment differences (increase in SLA) becoming apparent since day 135 (Table 3). At this time there were marked differences between the treatment with the lowest canopy openness and the highest ones ($P < 0.05$; Fig. 1). In the other species, it was only at the end of the experiment (270 days) when differences in SLA became evident.

3.3. Seedling growth rates and survival

Except for *Juglans*, none of the other studied species differed significantly in their RGR between treatments (Table 3). Overall, all species had a small increase in height during the experiment. Survival at the end of the experiment (270 days) varied significantly between treatments in *Fraxinus*, *Juglans* and *Magnolia* (in all cases $P < 0.05$; Table 4). All three species had more individuals alive in the relatively open canopy stands (50 yr), compared to the closed canopy stands (40 yr). *Juglans* was the only species whose seedlings survived in open areas. In this species Peto and Peto's test showed a significantly larger survival with more open canopy sites for the three above-mentioned species (in all cases $P < 0.01$). Only the RGR of *Juglans* was correlated with SLA (r = 0.45, $P < 0.05$). Survival was significantly correlated with SLA in all studied species (*Dendropanax*, r = 0.10; *Fraxinus*, r = 0.35; *Juglans*, r = 0.44, and *Magnolia*, r = 0.48), but the Pearson correlation coefficients were not very high, particularly in the case of *Dendropanax*.

4. Discussion

4.1. SLA and light heterogeneity

SLA is an important leaf trait that provides information about the strategies of survival and growth of CF tree species (Saldaña-Acosta et al., 2008). Thus, understanding differences in SLA among CF species and their ecological implications should provide a better insight on the functional diversity of these forests for management purposes.

Leaf traits are expected to vary when individuals of the different species studied grow under different environmental conditions. In this study there was an overall increase in SLA, as three species (*Dendropanax*, *Fraxinus* and *Magnolia*) had a larger SLA beneath the closest canopy than in more open places. These data are consistent with a previous study carried out in shade houses, where these species showed a large SLA in lowest light conditions (A. Saldaña-Acosta et al., unpublished data). However, the fact that *Juglans* exhibited the opposite response, i.e. that its SLA was largest in the OA followed by the stands with an open canopy, cannot be overlooked. This is consistent with the fact that this was the only species whose seedlings survived in the open areas. In controlled experiments (shade houses) the seedlings of this species had the largest SLA in the highest light levels (A. Saldaña-Acosta et al., unpublished data), which suggests shade intolerance. Therefore, our results provide partial support to our first prediction that SLA would be inversely related to light intensity, because all of these species are capable of growing and surviving in the forest understorey and most of them (with the remarkable exception of *Juglans*) do not survive in open areas.

The hemispherical photographs showed the existence of a heterogeneous light environment beneath pine forests and that the relatively younger stands had lower canopy openness than the older ones, although the amount of total radiation transmitted by the pine canopy was very heterogeneous within stands, and greater in the OA. The range of variation of SLA found in this study beneath the pine canopy could have been a response to the light heterogeneity (Bongers and Popma, 1988; Popma et al., 1992; Bloor and Grubb, 2004; Portsmuth and Niinemets, 2007). This study allowed us to identify a group of CF tree seedlings that may have the ability to respond to such changing light availability and develop leaves adapted to differences in between stands of different age and canopy openness.

4.2. Seedling growth rates and survival

Three species did not show significant differences in growth rates between treatments beneath pine canopies. They showed low height growth rates beneath pine canopies, suggesting that the variation in the understorey light environment affects their growth rates. Thus, in order to achieve higher growth rates they require more open canopies, as shown in several studies in both temperate and tropical forests (Martínez-Ramos et al., 1989; Sipe and Bazzaz, 1995; Nicotra et al., 1999). We found differences in low-light survival for most species; all of them had more individuals alive at the end of the experiment in the more open canopies. Previous studies conducted at LJ suggested that the range of environmental conditions (an thus the successional status) of CF tree species was relatively narrow, with some species (e.g. *Juglans*) being relatively more shade-tolerant, whereas others (e.g. *Magnolia*) had an intermediate shade tolerance (Saldaña-Acosta, 2001). The results of this study call for a revision of this preliminary successional classification of the species; at least *Juglans* appears to be less shade tolerant, and *Fraxinus*, *Dendropanax* and *Magnolia* have a rather intermediate behaviour. This allowed us to rank this group of species as mid-successional, based on their shade tolerance.

4.3. Relationships between SLA and vital rates

Studies with seedlings under controlled light conditions show that SLA is a good predictor of interspecific variation in growth and survival (Walters et al., 1993; Kitajima, 1994; Bloor and Grubb, 2002; Poorter and Bongers, 2006), but in this study the relationships between SLA and growth rates were not significant, except for *Juglans*. We had anticipated that the seedlings SLA would be related to survival and growth rates because it is considered a key trait for plant performance (Lambers and Poorter, 1992; Wright et al., 2004), due to its importance for light interception (Popma and Bongers, 1988). Again, this is in partial agreement with the results from controlled experiments, in which SLA was not correlated with RGR in *Fraxinus* and *Magnolia,* but positively correlated in *Juglans*. Patterns of biomass allocation observed in the controlled experiments showed that the RGR was correlated with stem, leaf and root biomass. In this study we did not examine patterns of biomass allocation, it is likely that the strategy observed in this smaller group of species in shade houses also occurs in field conditions. It has been demonstrated that seedlings and saplings with high survival rates in the understorey exhibit low growth rates (Kitajima, 1994; Poorter et al., 2006); such growth-survival trade-off probably exists in our studied species, for which allocation to defence and storage over traits that maximize growth rates are important for their survival (Alvarez-Clare and Kitajima, 2007). The lack of relationship between SLA and RGR in almost all species may be due to the duration of the experiment; it is possible that the evaluation of seedling RGR in the field must be done over longer periods (Sack and Grubb, 2001).

In the case of survival, there seems to be a relationship between the variations in SLA and survival in this group of species. The conditions to which plants must respond change with ontogeny (Niinemets, 2006). Thus, this variation in SLA may be interpreted as an ability to withstand alternative suppression and release when growing to reach the canopy (Martínez-Garza et al., 2005). The present study points out the potential of using a group of CF tree species, i.e. mixed-species plantations, for management purposes. Our data reinforce the conclusion that the use of pine canopies is crucial for the regeneration of CF tree species (Ortíz-Arrona, 1999; Saldaña-Acosta, 2001), and that consequently it may be regarded as a tool for the rehabilitation of these forests (Ramírez-Bamonde et al., 2005).

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Table 1. Study species, family, seed mass (SM, g), and cotyledon types (PE = photosynthetic, epigeal; SE = storage epigeal; SH = storage, hypogeal) according to Garwood (1996).

Species	Family	Seed mass	Cotyledon morphology
Dendropanax arboreus (L.) Decne. et Planch.	Araliaceae	0.09 ± 0.012	PE
Fraxinus uhdei (Wenz.) Lingelsh.	Oleaceae	0.037 ± 0.005	PE
Juglans major (Torr.) Heller	Juglandaceae	12.06 ± 1.37	SH
Magnolia iltisiana A. Vázquez	Magnoliaceae	0.38 ± 0.041	SE

Table 2. Variables of the light environment for each site obtained from the analysis of the hemispherical photographs using the Gap Light Analyser (GLA) program.

Site	Canopy openness (%)	Transmitted direct	Transmitted diffuse	Transmitted total
OAB	58.23 ± 21.19	16.24 ± 3.76	15.91 ± 3.92	32.56 ± 7.65
OAG	62.04 ± 11.80	17.24 ± 2.91	16.44 ± 2.7	33.69 ± 5.44
PE	13.28 ± 5.45	5.03 ± 2.90	4.42 ± 2.04	9.34 ± 4.90
CT	11.69 ± 3.47	2.76 ± 0.61	3.52 ± 0.96	6.28 ± 1.14
LM	17.84 ± 4.92	5.99 ± 2.84	5.54 ± 1.95	11.63 ± 4.73
ChP	19.09 ± 7.76	6.58 ± 1.55	5.81 ± 2.16	12.39 ± 3.50

Table 3. Summary of the split plot ANOVAS through the Mixed procedure to examine the influence of different light levels and time on specific leaf area (SLA) and relative height growth rates of four species of seedlings.

	SLA		Growth rate	
Species	*F*	*P*	*F*	*P*
Dendropanax arboreus				
time	1.07	ns	1.61	ns
light	13.2	0.0001		ns
time x light	2.09	ns	2.41	ns
Fraxinus uhdei				
time	19.5	0.0001	2.85	ns
light	31.2	0.0006		ns
time x light	1.00	ns	2.19	ns
Juglans major				
time	16.48	0.0001	30.13	0.0001
light	18.06	0.0001	19.61	0.0001
time x light	11.13	0.0001		0.0001
Magnolia iltisiana				
time	1.14	ns	2.40	ns
light	9.1	0.0005		ns
time x light	1.06	ns	1.04	ns

Table 4. Survival between light levels for each cloud forest tree species based on the Kaplan-Meir method through the survival analysis procedure (comparing multiple samples).

Species	χ^2	df	P
Dendropanax arboreus	1.72	4	0.7864
Fraxinus uhdei	23.68	4	0.00003
Juglans major	46.80	6	0.00001
Magnolia iltisiana	40.56	4	0.00001

Legends to figures

Figure 1. Variation of SLA between different stands in four cloud forest tree species. Means with the same letter are not different between light levels (Tukey HSD-test). Symbols for different sites are indicated as follow: solid squares for the 40-year-old *Pinus* stands, solid triangles for the 50-year-old *Pinus* stands, and full circles for the 15-year-old open areas.

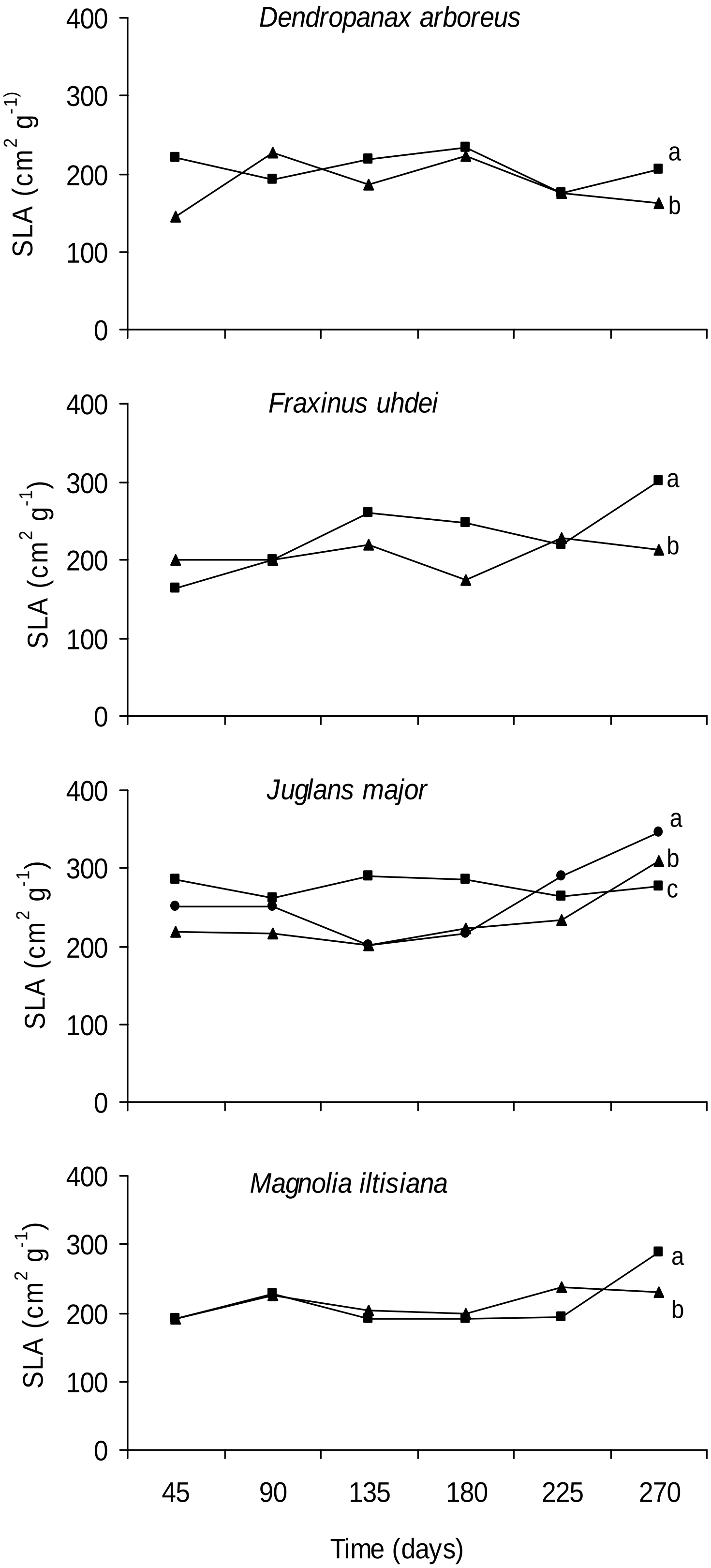
Dendropanax arboreus
Fraxinus uhdei
Juglans major
Magnolia iltisiana
SLA (cm^2 g^{-1})
400
300
200
100
0
a
b
c
45
90
135
180
225
270
Time (days)

Figure 1.

Capítulo V. Discusión general

La meta primordial de esta tesis fue analizar si el desempeño demográfico de plántulas de especies arbóreas de bosque mesófilo de montaña (BMM) está relacionado con sus atributos morfo-funcionales y con la heterogeneidad del ambiente lumínico. La motivación última de la investigación era obtener la información básica relevante para hacer propuestas para el manejo de estas especies. El trabajo tiene como antecedente los estudios sobre regeneración natural y sucesión ecológica que se han llevado a cabo en la Estación Científica las Joyas (ECLJ) y sus alrededores (Saldaña y Jardel, 1992; Sánchez-Velásquez y García-Moya, 1993; Pineda et al., 2000; Saldaña-Acosta, 2001). Partiendo de dichas experiencias, se había identificado la necesidad de seleccionar un grupo de especies arbóreas del BMM capaces de establecerse debajo del dosel del bosque de pino (e.g. *Magnolia iltisiana*, *Cornus disciflora* y *Juglans major*) para restaurar áreas que han sufrido incendios superficiales, y que de acuerdo con estudios previos, podrían establecerse con éxito en estas condiciones (Ortiz-Arrona, 1999; Saldaña-Acosta, 2001). En el área de estudio se habían hecho con anterioridad ensayos de propagación con el objeto de desarrollar prácticas de propagación de especies nativas utilizando ensayos experimentales de restauración (e.g. *Carpinus tropicalis, Cornus disciflora*, *Juglans major*, *Magnolia iltisiana* y *Tilia americana*). Además, esos mismos estudios evaluaron la respuesta de un grupo de especies a las variaciones ambientales (e.g. luz y disponibilidad de agua) asociados con la etapa de establecimiento de las plántulas. Este conjunto de investigaciones son de gran importancia para la planeación de estrategias de restauración del BMM en la ECLJ (Herrera et al., 1990; Saldaña-Acosta, 2001; Ramírez-Marcial et al., 2008).

Para tratar de alcanzar esta meta, en esta investigación decidimos utilizar de manera integral dos enfoques diferentes. En primer lugar, partimos del supuesto de que existen características morfológicas de las especies vegetales que pueden servir como indicadores de sus estrategias adaptativas, ya que muestran respuestas predecibles en diferentes ambientes (Westoby, 1998; Westoby et al., 2002; Reich et al., 2003). Para indagar esta cuestión, se examinó la posibilidad de identificar grupos funcionales (utilizando un conjunto de 33 especies de árboles del BMM), con base en sus atributos morfológicos (Capítulo 2; Saldaña-Acosta et al., 2008). Paralelamente, se hizo una evaluación por medio de ensayos experimentales (y utilizando un conjunto más pequeño de especies) con el fin de indagar la manera en que responden las especies a la heterogeneidad del ambiente lumínico (Capítulos 3 y 4).

Uno de los resultados principales obtenidos en el Capítulo 2 es que las especies arbóreas del BMM se distribuyen de manera continua a través de las dimensiones de los atributos estudiados. Esto significa que, a diferencia de nuestras expectativas iniciales, no se observó una tendencia clara a la formación de grupos funcionales. Si bien varios autores (e.g. Swaine y Whitmore, 1988) habían reconocido la existencia de al menos dos grandes grupos funcionales claramente distintos (especies pioneras y especies climax), otros autores habían identificado a estos grupos como los extremos de un *continuum* de grupos funcionales. Un ejemplo de esta visión es el trabajo de Oldeman y van Dijk (1991), quienes intentaron incorporar de manera integral un mayor número de atributos morfológicos. Los grupos identificados por ellos representan varias combinaciones entre especies competidoras muy fuertes (*strugglers*) y otras claramente oportunistas (*gamblers*); sin embargo, al ordenar las categorías sobre un gradiente entre ambos extremos, ellos reconocieron una categoría intermedia (*struggling gamblers*). Por lo general, se acepta que este tipo de agrupación para especies arbóreas está asociada principalmente con diferencias en el ambiente lumínico del bosque (Forcier, 1975; Clebsh y Busing, 1989; Martínez-Ramos et al., 1989; Oldeman y van Dijk, 1991; Everham III et al., 1996; Dalling et al., 2004; González-Espinosa et al., 2007). Sin embargo, en este estudio se encontró una gran variación al interior de cada grupo identificado, y esto probablemente esté reflejando, al menos en parte, su composición taxonómica compleja desde el punto de vista biogeográfico (Rzedowski, 1991; Wendt, 1998).

A partir de los estudios iniciales mencionados arriba, Saldaña-Acosta y Jardel (1992) y Saldaña-Acosta (2001) habían propuesto una clasificación preliminar de las especies de este bosque; en dicho esfuerzo se utilizaron muchas de las especies analizadas por nosotros en este estudio. Dicha agrupación preliminar se basó en la propuesta de van der Pijl (1972), y se obtuvo organizando los síndromes de regeneración en cuatro grupos funcionales discretos. En contraste, en esta investigación la clasificación de grupos funcionales no estaba forzada a ser discreta, ya que la mayoría de los atributos varían de manera continua a lo largo de las escalas de medición. De todas maneras, debe reconocerse que los grupos funcionales a menudo son utilizados, como la mayoría de las categorizaciones, como una forma de simplificar el mundo natural, y por ello pueden ser concebidos como divisiones arbitrarias a lo largo de un continuo de atributos (Díaz et al., 1999; Díaz y Cabido, 2001).

Entre los objetivos de esta tesis estaba averiguar si las características que definen estos extremos son las mismas que las identificadas en bosques de otros tipos. Por ejemplo, es frecuente que en los bosques tropicales de tierras bajas las especies pioneras tengan semillas pequeñas, un área foliar específica (AFE) grande, valores bajos de densidad de la madera y alturas que varían entre bajas e intermedias; en cambio, las especies tolerantes de esos bosques suelen tener semillas grandes, maderas con densidad media y alta, grandes alturas y AFE relativamente menor. Nuestro estudio reveló que los grupos ecológicos extremos del BMM estudiado no corresponden bien con los de los bosques tropicales de tierras bajas. Es decir, encontramos árboles altos con maderas duras y blandas, con semillas grandes y pequeñas, y una gran variación en el AFE. Estas combinaciones inusuales de rasgos podrían ser características de los BMM, ya que incluyen en su flora mezclas de especies con historias evolutivas diferentes, lo cual tendrá que ser confirmado por futuras investigaciones en otras comunidades.

Las correlaciones entre atributos pueden surgir no solamente como adaptaciones, sino también como resultado de convergencia en los atributos entre los principales linajes de las plantas (Felsenstein, 1985; Leishman et al., 1995; Lord et al., 1995, Westoby et al., 2002). En este trabajo se usó la reconstrucción de la filogenia como una herramienta para interpretar las correlaciones entre atributos morfológicos. De esta manera, fue posible confirmar la idea de que el BMM es un sistema especialmente interesante para explorar el peso relativo de la carga filogenética y las restricciones ecológicas, ya que en estos bosques persiste un conjunto de plantas que formaban parte de una vegetación que estuvo más extendida en el pasado geológico, específicamente en el Terciario (Sharp, 1951; Wolfe, 1985), y que poseen historias evolutivas desarrolladas en ambientes diferentes.

Las correlaciones entre atributos observadas en esta investigación fueron consistentes con lo reportado en otros estudios (e.g. Wright et al., 2007), excepto en el caso del AFE, ya que esta variable tuvo un comportamiento independiente en ambos análisis (Capítulo 2). Este resultado no coincide con los numerosos estudios que han reportado que este atributo está asociado con la densidad de la madera, la biomasa de la semilla, la altura y el tamaño de las hojas (Westoby et al., 1997; Reich et al., 1998; Díaz et al., 2004; Wright et al., 2006). Por otra parte, el AFE tuvo un intervalo muy amplio de variación (22.3—445.0 $cm^2 g^{-1}$), lo que coincide con lo descrito en otros trabajos realizados en bosques tropicales (Williams-Linera, 2000; Wright et al., 2004; Pickup et al., 2005). El hecho de que el AFE haya tenido un comportamiento independiente no permitió distinguir grupos funcionales y destaca su relevancia porque varía con cierta independencia de otros atributos y en la definición de las estrategias ecológicas para las especies arbóreas de BMM (Ackerly, 2004). Por ejemplo, Popma et al. (1992) agruparon a las especies de acuerdo con su dependencia a los claros para su regeneración y para ello se basaron de manera importante en atributos foliares de las especies, en particular su área foliar específica.

Al inicio de este estudio esperábamos que todos los atributos analizados contribuyeran de manera importante a la distinción de los grupos funcionales. Sin embargo, esto no fue así. En particular, es necesario mencionar que la pequeña variación detectada en la densidad de la madera no contribuyó casi en nada a la formación de grupos funcionales. En contraste, el AFE destacó como un atributo fundamental para definir grupos de especies arbóreas de BMM. Por lo tanto, podemos recomendar que futuras investigaciones se enfoquen en la evaluación de las correlaciones de este atributo con los factores ambientales, en particular con la luz. En claro contraste, el efecto de la filogenia en la covariación de los atributos no fue muy importante; como ya se ha dicho repetidamente, el BMM está formado por especies que poseen historias evolutivas muy diferentes, a pesar de lo cual parece que han convergido hacia soluciones funcionales semejantes.

El segundo enfoque integrado en esta investigación fue el análisis experimental de las respuestas de las plántulas de las especies arbóreas de BMM, con dos niveles de precisión experimental. En primer lugar, se utilizaron casas de sombra, donde el control de los niveles de luz fue relativamente preciso. Posteriormente se hicieron experimentos en parcelas ubicadas en el bosque, donde el control lumínico fue mucho menos preciso, pero donde las condiciones que experimentan las plántulas se asemejan mucho más a las naturales. En ambos casos, la meta era documentar el desempeño demográfico de las plántulas con respecto a la heterogeneidad del régimen lumínico. Los resultados de esta parte del estudio (Capítulos 3 y 4) confirmaron que el factor lumínico juega un papel determinante en la variación de los atributos morfo-funcionales analizados, así como en el desempeño de las plántulas. Un resultado particularmente interesante es que hubo congruencia en las respuestas del AFE obtenidas a través de la manipulación de la luz en las casas de sombra y los experimentos de campo.

Esta investigación permitió apreciar que la tasa de crecimiento es un atributo clave para el desempeño demográfico de cinco de las especies estudiadas en las casas de sombra, es decir, hubo diferencias significativas en sus tasas de crecimiento entre los diferentes niveles de luz, y éstas estuvieron correlacionadas con el AFE y con la biomasas asignada a tallos, raíces y hojas (Capítulo 3). Sin embargo, la asignación de biomasa a los diferentes órganos varió considerablemente en cada especie, lo cual sugiere que tienen diferentes estrategias de crecimiento en las condiciones del sotobosque (Lusk, 2002; Lusk y Piper, 2007). Por el contrario, la supervivencia de las especies no varió significativamente entre los diferentes niveles de luz (excepto en el caso de *Simplococarpon purpusii*). En contraste, los experimentos de campo, en donde las plántulas estuvieron sometidas a condiciones de vida más rigurosas, no mostraron diferencias significativas en las tasas de crecimiento de las mismas especies, pero sí en la supervivencia, la cual estuvo correlacionada con el AFE (Capítulo 4). Aunque en los experimentos de campo no se evaluó la asignación de biomasa a tallos, hojas y raíces, el AFE fue nuevamente un atributo indicador de las posibles estrategias de regeneración y de las historias de vida de las especies del BMM. En los experimentos de campo las cuatro especies sobrevivieron mejor en los rodales con el menor porcentaje de cobertura. Un caso notable de esta parte del estudio fue el de *Juglans major*, que a diferencia de las demás especies, tuvo un mayor número de plántulas vivas en las áreas abiertas. Esta especie pertenece al grupo de especies con el mayor AFE, biomasa de las semillas y altura máxima (Capítulo 1). Además de formar bancos de plántulas como estrategia de regeneración de avanzada, tuvo la mayor biomasa de semillas de todas las especies estudiadas, y una mayor AFE con los niveles más altos de luz en casas de sombra.

Una estrategia adaptativa debe, por definición, variar predeciblemente a lo largo de un gradiente ambiental (e.g. el tamaño de semilla y la tolerancia a la sombra) (Shipley et al.,1989;

Leishman y Westoby, 1992; Westoby et al., 2002). Por ejemplo, las especies tolerantes a la sombra tienden a tener semillas más grandes que las especies intolerantes (Foster y Janson, 1985; Grubb y Metcalfe, 1996). Sin embargo, en la última década varios autores han señalado la existencia de especies de bosques tropicales que poseen semillas muy pequeñas y que pueden establecerse y persistir en sitios con sombra profunda (Grubb, 1998; Metcalfe et al., 1998). En este estudio, encontramos que *Juglans major* tuvo las semillas más grandes de todas las especies estudiadas (12.06 g en promedio) y al mismo tiempo fue la única especie que tuvo individuos vivos en las áreas abiertas. Por el contrario, las plántulas de *Fraxinus uhdei*, que poseen semillas pequeñas y aladas (0.037 g), no sobrevivieron en las mismas condiciones. Esto sugiere que la capacidad predictiva de los atributos puede ser muy limitada y arroja serias dudas sobre las generalizaciones hechas a partir de estudios realizados en un ambiente particular hacia otros tipos de vegetación.

Nuestros resultados mostraron que las especies de BMM que se encuentran en el sotobosque del bosque de pino no conforman un grupo funcional homogéneo en términos de la supervivencia y del crecimiento de las plántulas. El hecho de que todas las especies hayan tenido un mayor número de individuos en los rodales con mayor apertura del dosel nos permitió clasificar a este grupo de especies como intermedias con base en su tolerancia a la sombra. Este grupo tuvo una gran variación de atributos morfológicos (Capítulo 2), lo que sugiere que se establecen y maduran en ambientes muy heterogéneos. Esto indica, a su vez, que parece existir un continuo de estrategias de las especies con respecto a la sucesión, incluso entre especies intermedias. Hacen falta datos para más especies en condiciones experimentales para poder proponer grupos de especies con respuestas similares al ambiente lumínico.

El número de especies utilizadas en cada experimento varió (nueve en las casas de sombra y cuatro en las parcelas experimentales) debido a la disponibilidad de semillas. Aunque sin duda este desequilibrio numérico necesariamente impone limitaciones a las conclusiones que se pueden derivar de este estudio, destaca su relevancia por tratarse de información generada con respecto al desempeño de un conjunto de especies en condiciones experimentales. El hecho de haber trabajado con un número más pequeño de especies, en comparación con las 33 especies que utilizamos para el Capítulo 2, indudablemente requirió reducir el estudio pero al mismo tiempo hizo posible conocer a las especies con mayor profundidad. En la fase de planeación de esta investigación se había planteado la necesidad de seleccionar a las especies para los experimentos con base en los resultados obtenidos en el segundo capítulo. Desafortunadamente, esto no fue posible debido a que no todas las especies producen las semillas al mismo tiempo, ya que ello hubiera retrasado la producción de las plántulas que se necesitaban para los experimentos. A pesar de que por esto no fue posible elegir a las especies para la fase experimental con anterioridad, parece que la selección de especies que se hizo fue adecuada, ya que se basó en la información generada en estudios previos sobre su biología reproductiva, métodos de propagación en vivero, tipos de germinación, formas de dispersión, y sobre el manejo experimental de plantaciones con especies arbóreas del BMM.

Muchos estudios han intentado encontrar grupos funcionales en conjuntos muy grandes de especies, por ejemplo en floras completas. Ese enfoque hace muy difícil someter a prueba experimental la asignación de las especies a los diferentes grupos. En este sentido, en la presente investigación se llevó esta búsqueda un paso más allá, al intentar integrar las respuestas experimentales de las plantas con la información basada en sus caracteres morfo-funcionales. Es obvio que el enfoque experimental enfrenta muchos problemas técnicos y logísticos, y eso resultó en un desbalance en el número de especies utilizadas en cada una de las tres partes del estudio. Por lo tanto, queda como una tarea pendiente el análisis experimental de un mayor número de especies, sobre todo en condiciones de campo, porque es allí donde el desempeño de las plántulas muestra más claramente qué papel juegan los atributos en su supervivencia y crecimiento. En última instancia, estas respuestas serán la mejor información que conduzca a proponer estrategias de manejo específicas para cada especie o para grupos de especies con un comportamiento semejante.

Es importante señalar que, además de la tolerancia a la sombra, hay otros ejes de variación de los atributos que se deberían estudiar en investigaciones posteriores, y que además son muy útiles cuando se intenta agrupar muchas especies (Condit et al., 1996; Denslow, 1996; Lavorel et al., 1998; Köhler et al., 2000). Además del ambiente lumínico, se ha demostrado que otros factores como los ataques de herbívoros y patógenos afectan el desempeño demográfico de las plántulas en ensayos de campo (Benítez-Malvido y Martínez-Ramos, 2003) Esto significa que en nuestros experimentos operaron muchos factores que no fueron controlados. Las observaciones de campo que se han realizado durante más de 15 años en la ECLJ sugieren, además, que la cantidad de mantillo, la depredación diferencial de semillas y la disponibilidad de agua afectan el establecimiento de las plántulas de especies arbóreas de BMM (Jardel, 2008).

No tenemos duda de que la información generada en esta investigación doctoral permitió fortalecer el conocimiento disponible sobre el funcionamiento del bosque que está protegido en la ECLJ, pues contribuyó con información valiosa para el diseño, la aplicación y la evaluación de prácticas de restauración, así como a incrementar el conocimiento de la autoecología de un grupo de especies. De todas formas, consideramos que la investigación a largo plazo y el monitoreo permanente deben ser elementos integrales de una estrategia de restauración de éste y otros sistemas forestales. A partir de nuestros resultados, podemos recomendar la selección y plantación de un grupo de especies siguiendo una secuencia que simule lo más cercanamente posible sus respuestas secuenciales al ambiente lumínico, ya que este procedimiento tiene un gran potencial de imitar la regeneración natural del bosque; éste es precisamente el proceso que se conoce como reforestación sucesional (Herrera et al., 1990). Los resultados de este estudio apoyan la idea de que las nueve especies estudiadas pueden ser utilizadas en actividades de reforestación sucesional. Específicamente, el grupo de especies conformado por *Dendropanax arboreous*, *Fraxinus uhdei*, y *Magnolia iltisiana*, las cuales fueron usadas en los experimentos de campo, tienen un potencial alto para ser reintroducidas en sitios que se quiere enriquecer, siempre y cuando se utilicen pinos como especies nodrizas. *Magnolia iltisiana* y *Fraxinus uhdei* tuvieron una mayor supervivencia al transplante, lo que sugiere que su capacidad de tolerancia a las condiciones iniciales en el campo (e.g. humedad del suelo) es relativamente mayor. Un caso especial de este grupo fue *Juglans major*, cuyo potencial para ser reintroducida en áreas abiertas debido a su mayor supervivencia es todavía mayor. Todas las especies estudiadas parecen requerir de doseles más abiertos para establecerse; por lo tanto, se debe tener precaución de no introducir a las plántulas de estas especies en sitios con doseles muy cerrados. Esta idea se refuerza con resultados de sitios permanentes en BMM maduro, en donde la supervivencia de estas especies fue muy baja (A. Saldaña, datos no publicados).

En última instancia, su éxito dependerá de los resultados de estudios como éste, además de la evaluación de otros atributos de las plantas como el tipo de germinación, y de la realización de más experimentos que permitan descubrir las respuestas de las especies a las exigencias y las limitaciones del mundo real en el que viven.

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