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PLASTICIDAD, DISPONIBILIDAD DE RECURSOS Y CRECIMIENTO EN PLANTULAS DE LA SELVA BAJA CADUCIFOLIA DE CHAMELA, JALISCO: UN ENFOQUE EXPERIMENTAL

TESIS

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A mis padres, hermanos
y a los pequeñines de la casa,
mis sobrinos, con gran cariño

CONTENIDO

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Resumen

El tema central de los experimentos que forman esta tesis es plasticidad en plantas. Este tópico es abordado desde el punto de vista de las respuestas de diferentes especies a diferentes disponibilidades de los recursos luz y nutrimentos, evaluadas principalmente por medio de su influencia en el crecimiento. Se inicia con diseños experimentales con un gran número de especies (34) que evalúan y describen patrones generales de crecimiento ante disponibilidades contrastantes de algún recurso, para lo cual se comparan, las respuestas en el crecimiento y su relación con los diferentes parámetros que pueden influenciarlo. Después, en un menor número de especies (10), se evalúan el efecto de cambios en la disponibilidad de algún recurso (luz) en el crecimiento, fotosíntesis y condutancia estomática. Para continuar con mayor detalle, se incluyen diseños donde se pretende integrar las respuestas a variaciones en recursos capturados por la parte aérea de la planta (luz) y los capturados en el suelo (nutrimentos). Los cambios en luz aplicados pretenden simular las variaciones abruptas de este recurso causadas por eventos como: perturbaciones o los cambios dados por el caracter estacional de la selva baja caducifolia. Los cambios en la disponibilidad de nutrimentos en el suelo pretenden simular la característica distribución en parches de la disponibilidad de estos recursos en sistemas naturales. Finalmente, considerando que variaciones en la disponibilidad de recursos pueden generarse por la actividad de individuos vecinos, ya que éstos al consumir los mismos recursos reducen su disponibilidad, se analiza la relación entre las respuestas a variaciones en luz, nutrimentos distribuidos en parches y la influencia de vecinos en individuos de dos especies.

Se apoya que las especies de rápido, en comparación con las de lento crecimiento, tienden a producir mayor cantidad de biomasa y área foliar (AF), sus hojas son más delgadas con menor contenido de carbono, su producción de biomasa y tasa de crecimiento (RGR) es más afectada en condiciones de deficiencia de nutrimentos y luz, cuando crecen en baja disponibilidad de nutrimentos asignan mayor cantidad de biomasa a la raíz (mayor proporción raíz/vástago: R/S y biomasa de la raíz respecto a la biomasa de toda la planta: RWR). Al analizar en gran número de especies la relación entre la RGR y los diferentes parámetros que pueden influir en ella se obtuvo que las variaciones interespecíficas del cociente de área foliar (LAR) y el área foliar específica (SLA) son los principales determinantes de la RGR y no variaciones interespecíficas en parámetros de asignación de biomasa como R/S o RWR. Existe también una relación directa y significativa entre la respuesta en la tasa de crecimiento (ΔRGR) y la tasa de crecimiento alcanzada en condiciones de alta disponibilidad de nutrimentos y luz, considerando la ΔRGR como una medida de la magnitud de la plasticidad por estos recursos, las especies de rápido RGR son más plásticas que las de crecimiento lento.

Ante cambios en la intensidad de luz las especies de rápido RGR mostraron mayor capacidad para aclimatarse y su patrón de aclimatación fue diferente al de las especies de lento crecimiento. Esto es, la RGR en las especies de rápido RGR fue mayor en los individuos transferidos de luz baja a alta, incluso que la de los individuos en luz permanentemente alta (LH > HH) y, fue menor en los transferidos de luz alta a baja (HH > HL > LL) incluso menor que en los de luz permanentemente baja (LL). En las especies con RGR intermedias la aclimatación de RGR fue como sigue HH = LH > LL = HL. La especie de lento crecimiento mostró un patrón de aclimatación opuesto HH = HL > LL = LH. Estas tendencias de aclimatación están asociadas con cambios en la tasa de asimilación neta (NAR) y en SLA, esto sugiere la importancia de las hojas y sus características en determinar la RGR.

Cuando los nutrimentos en el suelo están distribuidos en parches, la tendencia indica que a mayor RGR mayor capacidad de Forrajeo por dichos parches. La especie de lento RGR fue incapaz de localizar sus raíces en parches ricos, sólo responde a variaciones en luz. Las especies de rápido RGR tienden a producir raíces en parches ricos y obtener beneficio produciendo mayor área foliar, biomasa y RGR, esta tendencia se reduce significativamente cuando la intensidad de luz es menor. Cuando la luz cambia los individuos que muestran mayor aclimatación por luz (LH y HH) muestran mayor capacidad de forrajeo por parches ricos. La presencia de un individuo de otra especie puede modificar la relación que existe entre la capacidad de aclimatación a cambios en luz y la capacidad de forrajeo por nutrimentos, provocando una reducción en la biomasa de raíces producida en el parche rico y la biomasa total de la planta. Esta reducción ocurre en los individuos que crecen en las condiciones de luz donde se logra mayor respuesta (HH y LH) y es mayor en la especie con mayor RGR, aunque provoca en ambas la modificación de los patrones de aclimatación y forrajeo en algunos parámetros.

Abstract

The central topic of this thesis is plasticity in tropical deciuous woody species, this mechanism is studied considering the plant growth responses to different light and nutrients availabilities. The thesis begins with a comparative experiment designed to estimate the growth responses of 34 woody-seedling species to contrasting nutrient availabilities. Following, I evaluate the responses of 10 woody species to reciprocal transfers of light conditions, in this experiment I included, additional to the growth analysis, the photosynthesis and stomatal conductance responses. A third experiment was designed to estimate the root and above-ground responses of the plants when confronted contrasting and discrete nutrient and light availabilities. In particular the changes in light conditions simulate the kind of light environments that are induced with natural disturbances and/or with the influence of the markadely seasonal drought. Finally, considering that the activity of other species generate variations in the availability of resources, I analized the responses of different species to variations in light, patchy distribution of soil nutrients and the influence of neighbours.

With these experiments it is supported that species with fast growth rate, that seems to predominate in sites with high abundance of resources tend to produce higher biomass and leaf area and their leaves are thinner with lower carbon content than slow-growing species. Their production of biomass and growth rate is more affected when grown under nutrient and light deficiency. When the fast-growing species are under low nutrient availability they allocate more biomass to the root (higher root/shoot ratio and root weight ratio: RWR). Analyzing in a high number of species, the relationship between the relative growth rate (RGR) and the different parameters that can influence their expression it was obtained that interspecific variations of leaf area ratio (LAR) and specific leaf area (SLA) are the main determinants of the RGR. Interspecific variations in parameters related with the biomass allocation as R/S ratio or RWR were non-significantly associated with the RGR. There is also a positive and significant relationship between the response in the RGR (ΔRGR) and the growth rate under high availability of nutrients and light. Considering the ΔRGR as a measure of the magnitude of plasticity for these resources the fast-growing species were more plastic than the slow-growing species.

When the light intensity has variations the fast-growing species show a higher capacity to acclimate and their pattern of acclimation is different to that of the slow-growing species. That is, the RGR and the total biomass produced by the fast-growing species is higher in the plants transferred form low to high (LH) light intensity and even higher than those plants under high light conditions (LH>HH). This response is lower in the plants transferred from high to low (HL) light intensity and even lower than those plants that grow under low light conditions (HH>LL>LH). In the species with intermediate growth rate the pattern of acclimation of RGR was as folows: HH=LH>LL=HL. A contrasting pattern of acclimation was showed in the RGR of the slow-growing: HH=HL>LL=LH. These tendencies of acclimation in RGR are associated with changes in the net assimilation rate (NAR) and in the SLA, this suggest the importance of the leaves and its characteristics to determine the RGR.

When the soil nutrients are distributed in patches, the tendency showed by the species appears to indicate that at higher RGR higher capacity to forage for nutrient rich patches. The slow-growing species was unable to localize their roots into the rich patches. The fast-growing species tend to produce roots in rich patches and tend to obtain a benefit producing higher leaf area, biomass and growth rate; this tendency is significantly reduced when the light intensity is lower. When the light intensity has changes the plants that show a higher acclimation for light (LH and HH) exhibit a higher capacity to forage for rich nutrient patches. The presence of one plant of different species can modify the existing relationship between the capacity to acclimate to light changes and the foraging capacity for rich patches, causing a reduction in the root biomass into the rich patch and in the total plant biomass. This reduction occurs in the plants that were growing under a higher response to light is obtained (LH and HH), and is higher in the species with higher growth rate. However, a modification of the patterns of acclimation and foraging in some of the growth parameters occurr in both species under competition.

Capítulo I

Introducción General

El proceso de crecimiento de una planta es el resultado de una compleja interacción entre su genotipo y la influencia del ambiente. El potencial de crecimiento de un individuo está determinado genéticamente, pero el grado en que se alcanza dicho potencial está regulado por la influencia del ambiente (Kozlowski et al. 1991). En particular, los recursos esenciales para las plantas, como parte de su ambiente, influyen en su crecimiento y asignación de biomasa a través de cambios en el balance entre su suministro (disponibilidad) y demanda (Marshall y Poorter 1991). Esto está relacionado con cambios en las tasas y balances entre procesos como: fotosíntesis, respiración, absorción de agua y minerales, síntesis hormonal, entre otros.

Las plantas experimentan continuas variaciones ambientales en su hábitat natural. La disponibilidad de uno o varios de los recursos esenciales para su crecimiento, como luz, nutrimentos y agua, frecuentemente se encuentran en niveles menores a los óptimos (Chapin 1991). Las variaciones en la disponibilidad de estos recursos pueden deberse a diferentes causas. La intensidad y calidad espectral de la luz pueden ser modificadas tanto por variaciones diurnas, estacionales y en las condiciones del tiempo, como por la influencia de las plantas vecinas (Björkman 1981, Smith 1981, Vázquez-Yanes et al. 1990). La cantidad de agua disponible para las plantas depende principalmente del patrón de precipitación, la temperatura, las características del suelo y la actividad de las raíces (Nobel 1991). Por otra parte, las variaciones en la disponibilidad de nutrimentos obedecen a variaciones en las características de la roca madre, la topografía, la disponibilidad de agua, las características del suelo, la dinámica de descomposición de materia orgánica y la actividad de las plantas vecinas (Chapin 1980). Esta heterogeneidad se ha asociado, en sistemas tropicales perennifolios, a la dinámica de perturbación natural como la formación y cierre de claros (Chazdon y Fetcher 1984a, b, Denslow 1987, Chazdon et. al 1988, Martínez-Ramos et. al 1988).

Debido a que las plantas están expuestas continuamente a variaciones ambientales, parecería lógico suponer que evolutivamente hayan generado mecanismos para adaptarse a éstas (Smith 1990). Uno de los mecanismos con que cuentan las especies para afrontar las variaciones ambientales es la plasticidad, la cual es la habilidad de un genotipo para modificar su morfología y/o fisiología como respuesta a cambios en su ambiente (Bradshaw 1965, Schlichting 1986, Sultan 1987, West-Eberhard 1989). Así, la plasticidad es una manifestación flexible de un genotipo que está íntimamente relacionada con las variaciones ambientales (ya que a partir de un genotipo, el ambiente puede influenciar la expresión de diferentes fenotipos). La plasticidad le da cierto valor adaptativo a un individuo, ya que le confiere mayor capacidad para aclimatarse a las condiciones ambientales (Smith 1990). Las especies pueden diferir en su capacidad de respuesta a variaciones ambientales, lo que podría implicar que bajo un rango de diferentes ambientes la selección natural favorezca distintos fenotipos más que uno solo (Oyama 1994).

En investigaciones realizadas principalmente con plantas herbáceas de zonas templadas se han descrito las características que presentan las especies adaptadas a sitios donde prevalecen condiciones de alta vs. baja disponibilidad de recursos (Grime y Hunt 1975, Grime 1979, Chapin 1980, 1988, Grime et al. 1986, Grime et al. 1988, Chapin et al. 1993). Estos grupos de características representan los dos extremos de un gradiente continuo de respuestas que pueden existir en la naturaleza. De acuerdo con estos estudios las especies que habitan en sitios con disponibilidades de recursos prevalecientemente altas, tienen tasas de crecimiento rápidas, que son mantenidas por tasas fotosintéticas y de absorción de nutrimentos también rápidas. Estas especies producen hojas poco longevas que se recambian continuamente e invierten pocos recursos en la defensa contra herbívoros. En contraste con las anteriores, las especies que habitan sitios donde prevalece la baja disponibilidad de recursos presentan tasas de crecimiento, de absorción de nutrimentos y fotosintéticas lentas, producen hojas que permanecen activas durante largos periodos de tiempo, invierten en la producción de metabolitos de defensa contra herbívoros y son beneficiadas al asociarse con otros organismos como las micorrizas (Allen 1991). Estas características les confieren tolerancia a la escasez de recursos.

De acuerdo con la teoría de optimización de recursos, los grupos de características antes mencionados surgen evolutivamente por la acción de la selección natural y tienden a lograr la optimización de la captura de recursos que lleva a la expresión de la máxima sobrevivencia, crecimiento y reproducción posibles bajo las características ambientales de alta y baja disponibilidad de recursos, respectivamente.

Se ha propuesto que cuando las condiciones ambientales cambian, por ejemplo de prevalecientemente altas a bajas y vice versa, ya sea temporal (manifestándose como pulsos) o espacialmente (manifestándose como parches), (Grime et al. 1986, Crick y Grime 1987, Campbell y Grime 1989, Grime 1994), en las especies de lento crecimiento, que habitan sitios donde prevalece una baja disponibilidad de recursos, la productividad, crecimiento y asignación de biomasa se ven poco afectados por cambios en la disponibilidad de recursos. Adicionalmente se ha propuesto que estas especies presentan gran capacidad para responder a pulsos de alta disponibilidad de recursos, debido a su capacidad para mantener activas sus estructuras de captura de recursos durante todo el tiempo. Esto se ha interpretado como la manera en que estas especies manifiestan su plasticidad ante un ambiente cambiante. En cambio, en las especies de sitios donde prevalece una gran disponibilidad de recursos, su productividad, tasas de crecimiento y fotosíntesis así como su asignación interna de biomasa son fuertemente afectadas por la disminución de los recursos disponibles. Cuando un recurso disminuye, estas especies son capaces de asignar mayor cantidad de energía a la producción y desarrollo de las estructuras necesarias para capturar el recurso que está limitando su crecimiento, presentando gran capacidad de aclimatación (capacidad plástica para responder a cambios en el ambiente, comparada con la respuesta a condiciones prevalecientemente altas o bajas en cuanto a disponibilidad de recursos) (Strauss-deBennedetti y Bazzaz 1991). Adicionalmente, las especies de tasa de crecimiento rápida que habitan sitios ricos, tienen la capacidad plástica para continuamente buscar, localizar y explotar parches ricos en recursos, los cuales son rápidamente consumidos por la gran actividad del propio organismo y de sus vecinos (Grime et al. 1986). A esta manifestación de la plasticidad se le ha denominado forrajeo (Grime et al. 1986, Slade y Hutchings 1987). La existencia en el suelo de parches ricos en nutrimentos y el hecho de que las raíces de algunas especies al encontrarlos, incrementen su actividad, biomasa y ramificación para explotarlos se ha documentado ampliamente (Drew et al 1973, Drew 1975, Drew y Saker 1975 , Grime 1979, Grime et al. 1986, Crick and Grime 1987, Slade y Hutchings 1987, Eissenstat y Caldwell 1988a, Jackson y Caldwell 1989, Campbell et al. 1991 a, b, Caldwell 1994, Hutchings y de Kroon 1994). Aunque los parches ricos en recursos que las raíces de una planta pueden ocupar generalmente son una porción muy pequeña del volumen total de suelo, son suficientes para provocar un beneficio en el crecimiento (Grime et al. 1986, Chapin 1980). Sin embargo, diferentes especies pueden manifestar diferente capacidad de forrajeo (Caldwell 1994).

En la presente tesis se plantean una serie de objetivos e hipótesis para evaluar la plasticidad de diferentes especies de la selva baja caducifolia a variaciones en la disponibilidad de luz y nutrimentos. Con este propósito general se diseñaron 4 experimentos:

1) Para probar las predicciones generadas a partir de plantas herbáceas de zonas templadas respecto a las respuestas de diferentes especies a disponibilidades contrastantes de recursos, se diseñó un experimento con 34 especies leñosas (principalmente árboles), donde se evalúa el efecto de disponibilidades contrastantes

de nutrimentos en el crecimiento y asignación de biomasa (capítulo 2). Se incluyó un gran número de especies para establecer tendencias en cuanto a las características de crecimiento y los diferentes parámetros que influyen en él.

2) Para evaluar las respuestas de diferentes especies a cambios en la disponibilidad de recursos (aclimatación), se diseñó un experimento con 10 especies con diferentes tasas de crecimiento, para evaluar su respuesta en condiciones contrastantes de intensidad de luz (prevalencientemente alta vs. baja) y compararla con aquella mostrada ante cambios de dicho recurso (plantas transferidas de alta a baja y vice versa) (capítulo 3).

3) Con la finalidad de integrar las respuestas plásticas que pueden mostrar diferentes especies para la captura de recursos en la parte aérea vs la parte subterránea, se siguió el mismo diseño planteado en el inciso anterior y se le adicionó el efecto de la capacidad de las especies para explorar y explotar un parche rico en nutrimentos en el suelo (capítulo 4). Esto está relacionado directamente con el compromiso entre el costo y el beneficio de la captura de un recurso respecto a su disponibilidad y a la disponibilidad de algún otro recurso esencial para el crecimiento.

4) Para evaluar la relación entre la respuesta a cambios en la intensidad de luz, la capacidad de forrajeo y su efecto en la interacción competitiva entre las especies, se realizó un experimento con 2 especies usando el diseño mencionado en el inciso 3, pero adicionando el efecto de la competencia interespecífica (capítulo 4).

Las hipótesis a falsificar son las siguientes:

La plasticidad de las especies en cuanto su capacidad de respuesta en el crecimiento y asignación de biomasa ante diferentes disponibilidades de luz y nutrimentos será diferente.

Ante cambios en la intensidad de luz, la expresión de plasticidad será diferente, en el grado (i. e. magnitud) y la dirección (i.e. patrón, Schlichting y Levin

1984, Schlichting 1986, Kuiper y Kuiper 1988) de la respuesta plástica, entre las especies de rápido y lento crecimiento. En comparación con las de lento crecimiento, la manifestación de plasticidad en las especies de rápido crecimiento será a través de una mayor respuesta en el crecimiento, asignación de biomasa y fotosíntesis a la nueva condición lumínica.

Las especies mostrarán diferente magnitud en la respuesta a variaciones en luz y en la capacidad para explorar y explotar parches de abundancia de nutrimentos en el suelo. La mayor respuesta la mostrarán las especies de rápido crecimiento. A su vez, la capacidad de forrajeo de estas especies será más afectado por la disminución de luz que en las especies de lento crecimiento.

Se espera un mayor éxito competitivo (evaluado en cuanto a producción de biomasa y tasa de crecimiento) en las especies con mayor plasticidad por luz y mayor capacidad de forrajeo por nutrimentos.

Como ya se mencionó, los estudios con gran número de especies, donde se analiza qué determina la tasa de crecimiento y cómo ésta puede ser modificada por diferentes disponibilidades de nutrimentos se han realizado con plantas herbáceas de zonas templadas. Sin embargo, no existen estudios similares sobre las respuestas de plantas de especies tropicales con crecimiento secundario.

La mayoría de las investigaciones que se han reportado sobre la respuesta de las plantas a cambios en la intensidad de luz, se han realizado con una o pocas especies, lo que reduce la posibilidad de establecer tendencias en las respuestas. Además, se han incluido principalmente especies de plantas de selvas tropicales perennifolias (Rice y Bazzaz 1989a, b, Ramos y Grace 1990, Pompa y Bongers 1991, Sims y Pearcy 1991, Strauss-Debenedetti y Bazzaz 1991, Ackerly 1993, Turnbull et al. 1993) en las cuales no existe una restricción en disponibilidad de recursos regulada principalmente por el patrón de precipitación como en las selvas tropicales caducifolias.

En sistemas naturales, como en la selva baja caducifolia, existe variación en la intensidad de la luz y en la distribución espacial de los nutrimentos en el suelo (ver descripción del sitio de estudio), de tal forma que la captura de un recurso depende de la disponibilidad del otro. Como se mencionó anteriormente las especies difieren en su capacidad para responder a cambios en luz y para obtener beneficio de parches en el suelo ricos en nutrimentos. Sin embargo, no existe información sobre la interacción entre variaciones en los dos recursos, es decir, cómo cambios en la disponibilidad de luz pueden influir en la capacidad de forrajeo por nutrimentos, o si el tener acceso a un parche rico en nutrimentos modifica la capacidad de aclimatación a cambios en luz. Tampoco se sabe si la interacción entre los dos recursos antes mencionados difiere entre especies con tasas de crecimiento diferentes.

Algunos estudios han documentado que diferencias en la capacidad de forrajeo entre las especies pueden influir en la interacción competitiva entre éstas (Caldwell 1988, Eissenstat y Caldwell 1988b, Caldwell et al. 1991 a, b, Caldwell 1994), debido a que el tener acceso a mayor cantidad de recursos, por tener la capacidad de explotar parches ricos, favorece la producción de individuos con mayor talla y tasa de crecimiento, y a su vez provoca la reducción de los recursos disponibles para individuos vecinos. Sin embargo, esta ventaja podría disminuir si algún otro recurso esencial como la luz disminuye, debido tanto a la interdependencia entre la captura de recursos en la parte aérea y subterránea (Grime 1994) como a diferencias en la capacidad de respuesta a cambios entre las plantas de especies vecinas.

Recientemente ha cobrado mayor interés el efecto de modificaciones en el ambiente, y por lo tanto en los recursos disponibles, causados por las actividades humanas (el 44% del área tropical latinoamericana para 1980 se deforestó para convertir en pastizales, Houghton et al. 1991) y el posible efecto del cambio global sobre la vegetación del planeta. Esto acentúa la necesidad de conocer la forma en que las posibles modificaciones causadas al ambiente pueden tener efecto sobre la sobrevivencia y crecimiento de las especies, y por lo tanto, sobre la diversidad. Sin embargo, la mayoría de los estudios realizados sobre el efecto de variaciones en la disponibilidad de recursos en el crecimiento y asignación de recursos se han realizado con plantas herbáceas de zonas templadas, pocas investigaciones se han realizado con plantas tropicales, como es el caso de variaciones en luz; no obstante, estos estudios incluyen casi exclusivamente especies de la selva alta perenifolia. Esto es sorprendente ya que hasta 1986 se había reportado que aproximadamente el 42% de las selvas tropicales son selvas bajas caducifolias (Murphy y Lugo 1986). Entre las selvas bajas caducifolias, la de Chamela, Jalisco alberga la mayor diversidad de especies vegetales (Lott et. al 1987). Aunado a esto se conoce que las selvas bajas caducifolias son de los sistemas sometidos a las tasas más altas de deforestación para su conversión a pastizales ($1.35X10^6$ ha/año), se estima que aproximadamente el 78% de su área original ya ha sido modificada (Houghton et al. 1991).

Sitio de estudio

Los estudios presentados en esta tesis fueron realizados con plántulas de especies leñosas de la Selva Baja Caducifolia de Chamela, en la costa de Jalisco, México (19° 30'N, 105° 03'W). Esta región tiene un clima clasificado como cálido subhúmedo (AwO(x')), el más seco de los subhúmedos, tiene una temperatura promedio de 24.9 °C (1977 -1984). Presenta un régimen de lluvias claramente estacional con una precipitación total anual de 748 mm, concentrados principalmente entre los meses de julio y octubre (80% de la precipitación total) (Bullock 1986).

Este patrón está fuertemente influenciado por la incidencia de ciclones tropicales, los cuales ocurren principalmente entre agosto y octubre. Debido en parte a la presencia de ciclones en esta zona, tanto la cantidad de lluvia como la frecuencia de días lluviosos son impredecibles (García-Oliva et al. 1991), pudiendo existir anualmente al menos un periodo mayor a 20 días y otro de al menos 13 días sin precipitación dentro de la época de lluvias (Bullock 1986). Este régimen de lluvias provoca variaciones en la caída de la hojarasca, en el proceso de descomposición de la materia orgánica, en la disponibilidad de agua en el suelo y por lo tanto, en la disponibilidad de nutrimentos. Dichas variaciones ocurren tanto estacionalmente (sequía vs. lluvia) como dentro de la época de lluvias (Martínez-Yrizar, 1980, Martínez-Yrizar y Sarukhán 1990, Solís 1993). Adicionalmente, existen variaciones espaciales en la disponibilidad de nutrimentos en el suelo causados por la heterogeneidad en las características del suelo, por diferencias en las propiedades de la materia orgánica que provocan diferencias en la cantidad, tipo de nutrimentos y tasas de descomposición (Martínez-Yrizar, 1980).

Las variaciones de luz en la selva baja caducifolia sin duda están relacionadas con el carácter caducifolio de esta selva, donde durante el periodo de sequía se registran valores de radiación fotosintéticamente activa (PAR) de 58 mol m^{-2} $día^{-1}$ arriba del dosel y aproximadamente 45 y 30 mol m^{-2} $día^{-1}$ a los 5 y 0.2m de altura, respectivamente. Estos valores se reducen considerablemente durante el periodo lluvioso siendo aproximadamente 35, 10 y 3 mol m^{-2} $día^{-1}$ arriba del dosel y a los 5 y 0.2 m de altura, respectivamente (1978-1988) (Barradas 1991). Cuando inicia el periodo de lluvias y los árboles producen hojas, las plantas del sotobosque experimentan grandes cambios en la cantidad y calidad de la luz provocados por la sombra que producen las numerosas capas de hojas de los árboles que las rodean, existiendo solamente el 19% de transmitancia de PAR a 0.2 m de altura comparada con 95% a 10m (Barradas 1991). Cambios repentinos en la luz pueden también ocurrir como resultado de la apertura de pequeños claros creados por la caída de ramas o árboles muertos que permanecen en pie y son derribados por los fuertes vientos durante los ciclones o tormentas tropicales, así como por los rayos de sol que penetran el dosel e incrementan, por cortos periodos de tiempo, la intensidad de luz que reciben las plantas del sotobosque (Chazdon 1988).

Otra característica sobresaliente de esta selva es la gran diversidad de especies que alberga. El número total de especies en un área de 350 Km^2 es de 1120 (Lott 1993) y el número de especies por cada 1000 m^2 es de 83 a 92, con una densidad promedio de individuos de 4500 por hectárea (diámetro a la altura del pecho $\leq$ 2.5 cm) y un índice de diversidad de Shannon-Weiner de 4.76 a 6-06, el cual es superior al de otras selvas caducifolias que reciben mayor cantidad de precipitación (Lott et al. 1987).

Capítulo II

Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico

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Nutrient availability and growth rate of 34 woody species from a tropical deciduous forest in Mexico

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Summary

1. To test the predicted relationship between growth rate and biomass allocation in relation to nutrient availability, seedlings of 34 woody species from the tropical deciduous forest in Mexico were grown under two contrasting nutrient conditions.

2. Dry biomass, relative growth rate (RGR), root/shoot ratio (R/S), specific leaf area (SLA), leaf area ratio (LAR), leaf weight ratio (LWR), root weight ratio (RWR), net assimilation rate (NAR) and the nitrogen and carbon leaf percentage were determined following an initial and final harvest. In all the parameters evaluated, the trend followed by the species under low nutrient conditions was similar to the trend attained in high nutrient conditions but with different magnitude.

3. The species with the largest seed biomass was *Thevetia ovata* (3808·6 mg). *Lagrezia monosperma* had the smallest seeds (0·13 mg) and the highest RGR in the high nutrient treatment. However, the relationship between RGR and seed biomass among the 34 species studied was weak ($r = -0{\cdot}50$ in low and $-0{\cdot}62$ in high nutrients).

4. Higher biomass allocation to roots was shown under low nutrient condition but the relationship between RGR and root/shoot ratio was non-significant.

5. Species variation in RGR to both the nutrient treatments employed is followed by species variations in LAR ($r = 0{\cdot}50$) more than changes in NAR ($r = 0{\cdot}20$). Changes in LAR are explained by LWR ($r = 0{\cdot}62$) and SLA ($r = 0{\cdot}70$). Under low and high nutrients, the RGR was highly correlated with SLA ($r = 0{\cdot}67$ and $0{\cdot}60$), suggesting the importance of both the total leaf area produced and the leaf morphological characteristics in determining the RGR.

6. A general characteristic of the distribution of the species' responses in RGR to both nutrient treatments was the existence of a continuum, for all of the parameters studied. This suggests differences in the species' resource utilization and tolerance, which are reflected in different plastic capacities.

Key-words: Biomass allocation, growth analysis, nutrient availability, plasticity

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Introduction

Much of our current ecological knowledge about the influence of nutrient stress on relative growth rate and biomass allocation originated from studies conducted with herbaceous temperate species (Chapin 1980; Hunt & Lloyd 1987; Körner & Renhardt 1987; Grime, Hodgson & Hunt 1988; Shipley & Keddy 1988; Shipley & Peters 1990; Robinson 1991; Lambers & Poorter 1992). Based on these studies, it has been suggested that species from infertile soils have lower maximum relative growth rates, larger investment in chemical defences and higher biomass allocation to roots than plants from fertile habitats (Grime & Hunt 1975; Grime 1979; Chapin 1980, 1988). Species with low maximum relative growth rates have less allocation to roots when grown under fertile conditions (Hunt & Lloyd 1987; Shipley & Peters 1990; Garnier 1991). In this sense, it has been suggested that plants with high potential maximum RGR do not tend to predominate in infertile environments because they are more sensitive to low nutrient supply. When grown under nutrient stress, species associated with fertile environments show a higher specific leaf area (SLA leaf area per unit leaf weight) than species related to infertile environments. Studies on resource capture specialization in fertile and infertile environments (Grime, Crick & Rincón 1986; Crick & Grime 1987; Campbell & Grime 1989), in addition to the economic interpretation of resource limitation in plants, have contended that the responses of plants to variations in nutrient supply should involve compensatory changes in root/shoot allocation in order to increase the acquisition of the soil resources which are limiting growth (Bloom, Chapin & Mooney 1985; Chapin 1991). The studies mentioned above have also contributed to establishing that plants adapted to infertile environments show nutrient accumulation in plant tissue and low tissue turnover rates coupled with a long-lived root system and low morphological plasticity (Grime *et al.* 1986; Crick & Grime 1987). In addition, it has been predicted that in response to nutrient enrichment, species adapted to poor soils usually show smaller changes in their characteristic low growth and absorption rates (Chapin 1980; Shipley & Keddy 1988). These plants maximize nutrient intake more through a constant high root/shoot ratio and possibly mycorrhizal associations than through high root absorption capacity (Chapin 1980, 1988). In contrast, species adapted to nutrient-rich soils sustain fast growth and high yield maintained by a high rate of nutrient absorption under abundant resources but the growth rate and biomass production and allocation of such species are highly affected by resource limitation. When nutrients are scarce, these species reduce their yield and growth rate and increase the biomass allocation to roots as a mechanism to acquire resources through plastic morphological adjustments (Grime *et al.* 1986).

More recently, the impact of human activities and the possible influence of climatic global change on vegetation processes and biodiversity of tropical ecosystems, has prompted the need to apply a more integrative comparative approach, which would increase our understanding about how plants respond to changes in the availability of soil resources. The pioneering comparative experimental studies of Grime and co-workers (Grime *et al.* 1988) and the C-S-R model of plant strategies (Grime 1977) have proved to be useful methodologies and conceptual frameworks to identify groups of species showing similar responses to variations in resources in temperate ecosystems (Grime & Hillier 1992; Chapin 1993; Chapin, Rincón & Huante 1993). A similar approach has not been used in tropical deciduous forests, where human activities are increasingly affecting natural vegetation, causing destruction and dereliction and inducing changes in soil resources. This is surprising in view of the urgent need to predict species responses to variations in resources and species recovery from disturbance in highly diverse seasonal tropical environments. In this sense, comparative studies related to the growth responses of the species to different levels of soil resources are needed to gain more insight into species responses to changes in the environment and the mechanisms controlling species regeneration and maintenance of diversity. The tropical deciduous forest in the Pacific Coast of Mexico provides a good opportunity to conduct comparative nutrient related growth experiments owing to the high diversity of plant species (83–92 species per 1000 m^2) (Lott, Bullock & Solís-Magallanes 1987; Lott 993), co-occurring in an environment in which the availability of soil resources is restricted by, among other things, seasonal drought (8 months).

The experiment described here tests the predicted relationship between the relative growth rate, the biomass allocation and the external nutrient supply in 34 tropical deciduous forest seedling species and the relevance of growth parameters such as net assimilation rate, leaf area ratio, specific leaf area and leaf weight ratio to explain interspecific variation in relative growth rate in tropical woody plants.

Materials and methods

The woody species studied in this research are listed in Table 1. Mature seeds of each species were collected from at least 10 different individuals, in the Biology Station at Chamela in the Pacific Coast of Mexico (19°30′N, 105°03′W). Average seed dry biomass was determined from 50 randomly selected seeds (including seed coats). Preliminary germination tests were conducted in all species to determine germination requirements and time of emergence. Scarification was conducted in some species. Seedlings at 5 days old were transplanted in free drainage PVC pots (35 × 12 cm) containing 4000 cm^3 of pure silica sand. A rich and poor nutrient environment was provided by adding 24 g and 1/10 of 14-14-14 NPK continuous 120 days feeding fertilizer (Osmocote®) at the beginning of the experiment. One seedling per pot was allocated randomly for each nutrient treatment. The complete design consisted of 340 plants, two nutrient treatments (2·4 and 24 g per pot), 34 native species, initial harvest at the beginning of the experiment and a final harvest with five replicates per treatment, species and harvest. The plants grew in a glasshouse for 60 days in the Biology Station at Chamela during the rainy months of August and September. All seedlings were watered twice daily.

After 60 days plants were harvested, leaf area was measured (Delta T, England), plants were dried in an oven (80 °C) for 48 h and the dry weights of leaves, stems and roots were obtained separately. These data were analysed following the classical growth analysis methods described by Evans (1972) and Hun (1982). The average relative growth rate (RGR, dry biomass increment per unit total plant biomass per unit time) of each species was determined according to: $RGR = (\ln W_{t_2} - \ln W_{t_1})/(t_2 - t_1)$ where W is the average total plant dry biomass in g and t is time in days. Calculations were made for the net assimilation rate (NAR, the rate of dry matter production per unit of leaf area), the specific leaf area (SLA, the ratio of foliage leaf area to foliage dry biomass), the leaf area ratio (LAR, the ratio between total leaf area and total plant dry biomass) as well as the leaf, stem and root weight ratios (LWR, SWR and RWR, the ratio of foliage, stem and root weight to total dry weight,

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Table 1. List of species studied, nomenclature in accordance with Lott (1985, 1993). In addition, average seed biomass ($n = 50$), growth form (Sh = shrub and ST = shrub or small tree) and wood density (WD) are presented

	Species	Seed biomass		WD	
		Family	(mg)	Growth form	(g cm^{-3})
1	*Acacia farnesiana*	Leguminosae	48·8	Sh or ST	—
2	*Albizia occidentalis*	Leguminosae	109·7	Sh or ST	0·81*
3	*Amphipterygium adstringens*	Julianaceae	38·5	Tree	0·41†
4	*Bernardia spongiosa*	Euphorbiaceae	247·4	Sh or ST	—
5	*Caesalpinia coriaria*	Leguminosae	68·4	Tree	1·14†
6	*Caesalpinia eriostachys*	Leguminosae	230·6	Tree	0·74‡
7	*Caesalpinia platyloba*	Leguminosae	305·9	Sh or ST	0·92*
8	*Caesalpinia sclerocarpa*	Leguminosae	70·9	Tree	1·39†
9	*Ceiba pentandra*	Bombacaceae	116·0	Tree	0·36*
10	*Celaenodendron mexicanum*	Euphorbiaceae	99·7	Tree	0·94‡
11	*Chloroleucon mangense*	Leguminosae	39·8	Tree	0·99†
12	*Cochlospermum vitifolium*	Cochlospermaceae	39·3	Tree	0·27‡
13	*Cordia alliodora*	Borraginaceae	14·0	Tree	0·73†
14	*Cordia elaeagnoides*	Borraginaceae	27·3	Tree	0·88*
15	*Coccoloba barbadensis*	Polygonaceae	120·8	Tree	0·71†
16	*Crescentia alata*	Bignoniaceae	34·1	Tree	0·71‡
17	*Enterolobium cyclocarpum*	Leguminosae	703·2	Tree	0·49‡
18	*Guazuma ulmifolia*	Sterculiaceae	4·9	Sh or ST	0·67†
19	*Heliocarpus pallidus*	Tiliaceae	0·66	Tree	0·69‡
20	*Hintonia latiflora*	Rubiaceae	1·4	Sh or ST	0·74*
21	*Ipomoea wolcottiana*	Convolvulaceae	66·8	Tree	0·57†
22	*Lagrezia monosperma*	Amaranthaceae	0·14	Shrub	0·87‡
23	*Lysiloma microphyllum*	Leguminosae	30·5	Sh or ST	0·92†
24	*Mimosa tenuiflora*	Leguminosae	8·6	Shrub	—
25	*Pithecellobium dulce*	Leguminosae	177·4	Tree	1·0*
26	*Plumeria rubra*	Apocynaceae	49·1	Tree	—
27	*Recchia mexicana*	Simaroubaceae	425·5	Tree	1·02‡
28	*Ruprechtia fusca*	Polygonaceae	20·5	Tree	0·70*
29	*Spondias purpurea*	Anacardiaceae	1621·5	Tree	0·31†
30	*Tabebuia donnell-smithii*	Bignoniaceae	4·7	Tree	0·53†
31	*Tabebuia chrysantha*	Bignoniaceae	73·8	Tree	0·72†
32	*Thevetia ovata*	Apocynaceae	3808·6	Shrub	0·72*
33	*Thouinia paucidentata*	Sapindaceae	15·7	Sh or ST	0·94‡
34	*Trichilia trifolia*	Meliaceae	32·3	Sh or ST	0·80*

† From Barajas-Morales (1985) and Barajas-Morales & Gómez (1989).
* From Kitajima (1994).
‡ From Borchert (1994).

respectively) (Causton & Venus 1981; Hunt 1982) and the root to shoot dry biomass ratio (R/S).

In addition, the plastic response in RGR to both nutrient treatments was estimated by considering the difference between the average RGR achieved by the species, in high minus low nutrient treatment. The leaf nitrogen and carbon percentage was determined by complete and instantaneous oxidation of samples by 'flash combustion' and separation by gas chromatography in a carbon/nitrogen analyser (Carlo Erba instrument, NA 1500, Italy). Differences between nutrient treatments were tested by a Student's t-test using log-transformed data in order to meet the assumptions of the test.

Using data from low and high nutrients the relationships between relative growth rate and parameters such as NAR, LAR, SLA, LWR, RWR, SWR, R/S ratio were calculated, as well as the association with seed dry biomass, wood density and the response in RGR to both treatments. The relationships between the several parameters determined were tested with linear regressions using log-transformed to meet the assumptions of the analysis (Zar 1974).

Results

The list of the woody species studied including their family, seed biomass, growth form and wood density (WD) values are shown in Table 1. The studied species belong to 17 families. Leguminosae was the largest family studied, comprising 11 species. The Bignoniaceae family was represented by three species and the Apocynaceae, Boraginaceae, Euphorbiaceae and Polygonaceae by two species each. Twenty-one of the species included are trees, 10 are shrubs or small trees and three are shrubs (Lott 1985, 1993). Seed biomass varied from 3808·6 mg in *Thevetia ovata* (Apocynaceae) to 0·013 mg in *Lagrezia monosperma* (Amaranthaceae). Considering wood density, *Caesalpinia sclerocarpa* and *Caesalpinia* *coriaria* had the hardest wood (1·39 and 1·14 WD, respectively) and the species with softest wood were *Cochlospermum vitifolium*, *Spondias purpurea* and *Amphypterigium adstringens* (0·27, 0·31 and 0·39, respectively).

The range of biomass produced by the 34 species under low nutrients was from 0·028 to 7·29 g (260×) and from 0·14 to 29·02 g (207×) in high nutrients. All species, except *Trichilia trifolia*, produced more biomass under higher nutrients supply. The total dry biomass attained under low and high nutrients availability is shown in Table 2. The largest difference was shown by *S. purpurea* with 4·86 g in low and 29·02 g in high nutrients. Non-significant differences between treatments were shown only by *T. trifolia*, which apparently was not affected by the low nutrient treatment.

The dry biomass allocation to roots is listed, as the root weight ratio (RWR) and the R/S ratio, in Table 2. All species had a clear tendency to allocate more biomass to roots in the nutrient-poor treatment. Non-significant differences were detected in RWR and R/S ratio between high and low nutrients for *Plumeria rubra*, *T. ovata* and *T. trifolia*. These last two species had a high R/S ratio in high nutrients. When nutrients were abundant (+N treatment) all species allocated more biomass to the shoot but under conditions of nutrient limitation (–N treatment) the allocation to roots was higher than biomass allocation to shoot (R/S ratio > 1) in *A. adstringens*, *Ceiba pentandra*, *C. vitifolium*, *Chloroleucon mangense*, *S. purpurea* and *Tabebuia chrysantha*. These species showed the largest difference in R/S ratio between treatments but not the highest RGR. The stem weight ratio (SWR, Table 2) was higher under high nutrients in most species; *A. adstringens* and *C. pentandra* showed the largest difference between treatments. *Thevetia ovata* and *P. rubra* showed greater SWR under low nutrients but this was not related to biomass allocation to roots or wood density.

Differences in total leaf area (Table 3) were larger in high than in low nutrients. Only *T. trifolia* showed non-significant differences. The fast growing species *Albizia occidentalis*, *C. pentandra*, *Heliocarpus pallidus*, *Ipomoea wolcottiana*, *L. monosperma* and *S. purpurea* showed a large increase in leaf area when grown under high-nutrient availability. The leaf area ratio (LAR, Table 3) was larger under high nutrients but was non-significant for 19/34 species. *Tabebuia donnell-smithii* was the most responsive species. The SLA was non-significnatly different among nutrient treatments in 25/34 species, and significantly higher (*t*-test, $P < 0·05$) in the rich treatment for six species, where *T. donnell-smithii*, *Pithecellobium dulce* and *C. sclerocarpa* achieved the largest difference between nutrient treatments (Table 3). The LWR ranged from 0·193 (*P. rubra*) in low nutrient to 0·649 (*Ruprechtia fusca*) in high-nutrient level. The largest differences between treatments in LWR were achieved by *C. coriaria* and *T. chrysantha*. Only 18/34 species showed significant differences between both treatments (Table 3).

The relative growth rates attained by the species in both nutrient treatments are presented in Fig. 1. Excepting *T. trifolia*, all species achieved higher RGR when grown under high nutrients. The range of values in the nutrient-rich treatment from *Celaenodendron mexicanum* and *T. trifolia* to *L. monosperma* represents a five-fold difference in values of RGR (0·031 to 0·157 g g^{-1} day^{-1}, respectively). A similar difference among species (4·9-fold) was maintained under low nutrients (from *Recchia mexicana*, 0·021, to *H. pallidus*, 0·103 g g^{-1} day^{-1}). The RGR for *C. mexicanum*, *R. mexicana* and *T. trifolia* under both nutrient conditions was lower than the RGR attained for most of the species, even under low nutrients.

In most of the species (30/34) the net assimilation rate (NAR) was greater under high nutrients but was significantly different between high and low nutrients (*t*-test, $P \leq 0·05$) only in 17/34 species. *Mimosa tenuiflora* and *Enterolobium cyclocarpum* showed the highest difference between high and low nutrients. In the rest of the species the NAR under low nutrients was close to the NAR under high nutrients even when the differences were significant (Table 3).

As an indicator of plasticity, the species response to nutrients, based on RGR values *vs* the RGR attained under high nutrients, is presented in Fig. 2 for each of the species studied. *Mimosa tenuiflora*, *L. monosperma* and *T. donnell-smithii* were the species with higher growth response values and *T. trifolia* had the lowest.

The percentage of leaf nitrogen (Table 2) was greater in high nutrients for all species, except for *Hintonia latiflora*, *R. fusca* and *Thouinia paucidentata*. The largest difference between leaf nitrogen attained in high *vs* low nutrients was shown by *C. mangense*, *T. trifolia*, *H. latiflora* and *Bernardia spongiosa*. All species showed a higher percentage of leaf carbon under high nutrients but the difference between both nutrient treatments was greater for *Guazuma ulmifolia* and non-significant for 10/34 of the species studied (Table 2).

Discussion

In the early 60 days of seedling growth investigated, a consistent continuous gradient was observed in the distribution of the growth responses of the species studied under both nutrient treatments (Fig. 2). In addition, the trend shown by the species under high nutrients was similar to the trend under low nutrients, for all the growth parameters (Table 4) but with different magnitude and slightly different order of species. Considering this we must recognize that both nutrient treatments employed represent two distant availabilities in a continuum between low and high nutrient availability and the 34 species investigated represent approximately 7% of the total woody species present in the tropical deciduous forest. It must also be indicated that nutrient requirements of the species may change during their life cycle and are influenced by

Table 2. Total dry biomass (g), root/shoot ratio (R/S), root weight ratio (RWR), stem weight ratio (SWR), leaf nitrogen (%) and leaf carbon (%) attained by the 34 species studied under low (–N) and high (+N) whole nutrient level

	Total dry biomass		R/S ratio		RWR		SWR		Leaf nitrogen		Leaf carbon	
Species	–N	+N	–N	+N	–N	+N	–N	+N	–N	+N	–N	+N
Acacia farnesiana	1·24	10·36**	0·557	0·327*	0·357	0·242*	0·332	0·375	3·91	5·29*	44·69	43·51***
Albizia occidentalis	1·5	14·07***	0·893	0·530***	0·471	0·345***	0·217	0·267*	3·15	3·42	43·48	42·18*
Amphipterygium adstringens	2·49	13·19**	1·363	0·709*	0·557	0·413*	0·154	0·284*	3·36	3·87*	43·90	43·81**
Bernardia spongiosa	2·17	10·57***	0·354	0·218**	0·260	0·179**	0·301	0·362*	2·25	3·70**	40·23	42·26**
Caesalpinia coriaria	1·45	2·5***	0·661	0·411*	0·396	0·285*	0·397	0·345	4·22	4·55	43·75	45·22**
Caesalpinia eriostachys	2·48	8·56***	0·973	0·419***	0·491	0·293***	0·235	0·327***	3·05	3·96**	46·71	45·90**
Caesalpinia platyloba	2·8	8·1**	0·851	0·452***	0·459	0·309**	0·202	0·284	2·80	3·76*	45·58	42·58*
Caesalpinia sclerocarpa	0·45	2·0***	0·964	0·457**	0·487	0·312***	0·221	0·288***	3·90	4·88	44·51	43·04*
Ceiba pentandra	2·85	24·05***	1·455	0·635**	0·585	0·384**	0·177	0·322**	2·84	2·86	41·01	43·22**
Celaenodendron mexicanum	0·29	3·7*	0·602	0·364*	0·373	0·266*	0·163	0·152	2·77	3·75***	44·26	43·01***
Chloroleucon mangense	0·23	2·6***	1·039	0·466**	0·504	0·315***	0·233	0·362***	4·15	6·10***	44·19	41·29***
Cochlospermum vitifolium	0·14	1·71***	1·530	0·526*	0·585	0·344**	0·191	0·292*	3·32	4·17**	44·47	45·38*
Cordia alliodora	0·34	5·27***	0·820	0·510*	0·449	0·337**	0·125	0·101*	4·07	4·48*	40·04	45·4**
Cordia elaeagnoides	0·7	2·02**	0·562	0·403*	0·359	0·284*	0·137	0·223**	4·05	3·99	40·98	43·46*
Coccoloba barbadensis	0·48	7·13**	0·517	0·316**	0·340	0·238*	0·155	0·139	3·79	3·64	42·44	42·13*
Crescentia alata	2·6	7·26**	0·830	0·514**	0·451	0·337**	0·173	0·232*	2·84	3·66*	42·82	46·26
Enterolobium cyclocarpum	2·96	13·8**	0·769	0·611*	0·434	0·378*	0·310	0·357**	3·06	4·35*	45·05	41·82
Guazuma ulmifolia	0·28	5·32**	0·494	0·387	0·326	0·278	0·180	0·255*	3·38	4·51	39·67	42·92*
Heliocarpus pallidus	0·49	11·96**	0·629	0·389**	0·386	0·279**	0·164	0·238**	2·89	3·38	41·58	42·67**
Hintonia latiflora	0·035	0·18**	0·523	0·246**	0·342	0·197**	0·176	0·211	5·49	3·94***	41·99	43·48***
Ipomoea wolcottiana	6·5	24·75**	0·832	0·453*	0·450	0·310**	0·320	0·347	2·76	4·07*	43·39	41·03
Lagrezia monosperma	0·24	6·95**	0·528	0·297**	0·345	0·227**	0·160	0·263*	4·04	4·81*	41·49	41·81
Lysiloma microphyllum	0·84	3·58***	0·699	0·290**	0·408	0·224***	0·247	0·356**	3·65	4·06	45·78	45·25**
Mimosa tenuiflora	0·17	5·99**	0·623	0·227**	0·379	0·184**	0·278	0·401**	4·56	4·65	44·23	46·16***
Pithecellobium dulce	0·93	5·57***	0·633	0·375***	0·387	0·271***	0·330	0·392**	4·42	5·66**	44·71	43·17
Plumeria rubra	0·43	1·44***	0·326	0·352	0·243	0·257	0·567	0·498	3·36	4·26*	42·75	44·2
Recchia mexicana	0·99	2·4**	0·649	0·330***	0·391	0·246***	0·306	0·388	2·80	3·80**	45·31	41·4*
Ruprechtia fusca	0·32	2·95**	0·565	0·257***	0·359	0·203***	0·104	0·151	4·18	3·57**	42·78	44·78
Spondias purpurea	4·9	30·22***	1·569	0·873**	0·604	0·465**	0·125	0·238***	3·02	3·39*	40·83	46·42**
Tabebuia donnell-smithii	0·05	1·3**	0·534	0·264***	0·347	0·207**	0·166	0·180	3·82	4·79**	42·77	47·54*
Tabebuia chrysantha	1·12	4·1***	1·059	0·429**	0·510	0·299***	0·141	0·181***	3·34	4·22**	44·88	44·87
Thevetia ovata	7·31	15·65**	0·475	0·430	0·321	0·299	0·367	0·316*	2·14	3·15***	44·41	45·16
Thouinia paucidentata	0·15	2·32***	0·468	0·250***	0·318	0·199***	0·135	0·184	3·81	3·16*	43·64	45·55
Trichilia trifolia	0·13	0·14	0·593	0·608	0·371	0·377	0·173	0·192	2·42	4·39***	42·33	44·60*

Asterisks denote significant differences between nutrient treatments (*t*-test) at * $P < 0·05$, ** $P < 0·01$ and *** $P < 0·001$.

Table 3. Leaf area (cm^2), leaf area ratio (LAR, cm^2 g^{-1}), specific leaf area (SLA, cm^2 g^{-1}), leaf weight ratio (LWR, g g^{-1}) and net assimilation rate (NAR, g cm^{-2} day^{-1}) attained by the 34 species studied under low (–N) and high (+N) whole nutrient level

	Leaf area		LAR		SLA		LWR		NAR	
Species	–N	+N	–N	+N	–N	+N	–N	+N	–N	+N
Acacia farnesiana	201·97	1117·4***	120·57	141·51	384·47	374·49	0·314	0·384	0·0008	0·0009
Albizia occidentalis	171·22	1863·8***	119·42	133·63	376·52	346·15	0·316	0·386*	0·0005	0·0007*
Amphipterygium adstringens	226·05	1274·2***	101·41	118·88	368·54	360·38	0·276	0·327	0·00092	0·0012
Bernardia spongiosa	198·59	1037·5***	101·01	107·7	228·64	233·68	0·441	0·460	0·0013	0·0015
Caesalpinia coriaria	38·31	499·73**	59·30	154·03**	285·18	407·39**	0·204	0·375**	0·0010	0·0012
Caesalpinia eriostachys	172·35	759·19***	70·78	90·77**	257·79	239·35*	0·274	0·783***	0·00069	0·00082*
Caesalpinia platyloba	142·26	626·18**	54·41	77·62*	161·15	194·68	0·337	0·402	0·00112	0·00111
Caesalpinia sclerocarpa	34·24	372·88***	76·03	167·31***	259·65	416·25***	0·290	0·402**	0·0005	0·00047
Ceiba pentandra	210·23	2090·4***	74·07	88·57	310·93	299·87	0·236	0·295*	0·0008	0·0011**
Celaenodendron mexicanum	28·59	64·11**	93·59	123·28**	203·79	213·25	0·462	0·578**	0·00024	0·00031
Chloroleucon mangense	12·83	288·74***	54·95	120·43**	206·38	356·00***	0·266	0·334*	0·00049	0·00071*
Cochlospermum vitifolium	50·68	916·44***	79·57	129·91*	336·79	355·08	0·233	0·366*	0·00064	0·00078
Cordia alliodora	11·95	304·60***	85·13	180·76***	199·69	322·37**	0·424	0·559***	0·00035	0·00047*
Cordia elaeagnoides	109·58	1048·4**	199·16	204·14	397·96	411·63	0·500	0·495	0·00035	0·00055**
Coccoloba barbadensis	75·41	210·64**	110·54	128·53	220·58	205·54	0·500	0·621**	0·0007	0·00077
Crescentia alata	213·16	603·58**	85·07	87·14	225·41	199·87	0·375	0·434*	0·001	0·0012
Enterolobium cyclocarpum	145·82	743·79***	59·45	66·64	223·17	257·86	0·265	0·259	0·00073	0·00137*
Guazuma ulmifolia	109·40	829·94**	178·94	169·40	375·17	366·03	0·478	0·464	0·00044	0·0007**
Heliocarpus pallidus	114·20	1548·6***	138·16	156·44	294·37	328·64	0·466	0·480	0·00073	0·00093
Hintonia latiflora	3·83	29·20***	131·43	178·03	273·51	294·84	0·481	0·600**	0·00028	0·00043*
Ipomoea wolcottiana	508·04	2771·3***	85·15	124·90*	351·76	353·48	0·241	0·350*	0·00089	0·00087
Lagrezia monosperma	53·27	1190·0**	234·89	194·37	470·91	368·85*	0·500	0·526	0·00045	0·00083**
Lysiloma microphyllum	75·43	314·02***	90·00	92·53	262·98	213·04	0·344	0·426*	0·00062	0·00097
Mimosa tenuiflora	9·88	248·74**	32·28	39·88	88·89	95·57	0·363	0·419	0·00145	0·00271*
Pithecellobium dulce	64·39	443·59***	73·22	80·40	256·60	237·77	0·285	0·336*	0·00063	0·00102**
Plumeria rubra	25·80	74·96*	57·65	49·68	297·89	201·17**	0·193	0·243	0·00068	0·00118*
Recchia mexicana	49·37	158·97***	52·30	67·89*	142·99	138·22*	0·366	0·495**	0·00031	0·00019
Ruprechtia fusca	52·06	449·60**	164·51	164·46	309·25	252·16	0·530	0·649**	0·00038	0·00065*
Spondias purpurea	414·96	2677·5***	88·87	91·61	332·40	307·32	0·266	0·298	0·00144	0·00171*
Tabebuia donnell-smithii	8·20	400·3**	160·11	293·03*	331·72	473·42*	0·479	0·608*	0·00021	0·00038*
Tabebuia chrysantha	123·18	629·03***	117·15	162·93**	331·39	312·03	0·351	0·520***	0·00057	0·00061
Thevetia ovata	411·54	1108·2***	56·64	70·41**	181·04	184·13	0·313	0·382**	0·00121	0·00125
Thouinia paucidentata	26·84	385·86***	146·96	171·04	281·11	275·43	0·525	0·624	0·00045	0·00061**
Trichilia trifolia	17·79	18·45	136·40	137·90	301·44	325·05	0·454	0·424	0·00042	0·00044

Asterisks denote significant differences between nutrient treatments (*t*-test) at * $P < 0·05$, ** $P < 0·01$ and *** $P < 0·001$.

other factors including mycorrhizae (Huante, Rincón & Allen 1993) or nitrogen-fixing associations.

Predictions about plant responses to different nutrient availability, already established with temperate plants (Grime & Hunt 1975; Grime 1979; Chapin 1980; Hunt & Lloyd 1987; Körner & Renhardt 1987; Grime, Hodgson & Hunt 1988; Shipley & Keddy 1988; Lambers & Poorter 1992) are supported here. There was a clear tendency to allocate more biomass to roots when nutrients were limited. Under low nutrient conditions most of the species reduced their SLA. This decrease in SLA has been attributed to accumulation of non-structural carbohydrates (Lambers *et al.* 1981) or secondary compounds (Waring *et al.* 1985). Considering interspecific differences of RGR in the contrasting nutrient treatments tested, the species with higher RGR under high nutrient conditions had also a higher RGR under low nutrient conditions (*G. ulmifolia*, *H. pallidus*, *L. monosperma*, *M. tenuiflora* and *S. purpurea*). The net assimilation rate was greater in the high nutrient level for the species with high RGR and non-significantly different between treatments in most of the species with low RGR. Species with a high growth rate (Fig. 1) showed a higher growth plasticity (Fig. 2). For example, a low plasticity in RGR and a larger tolerance to nutrient limitation was exhibited by *T. trifolia*, while a high growth plasticity and low tolerance to nutrient deficit was shown by species such as *M. tenuiflora*, *L. monosperma* and *T. donnell-smithii* (Figs 1 and 2).

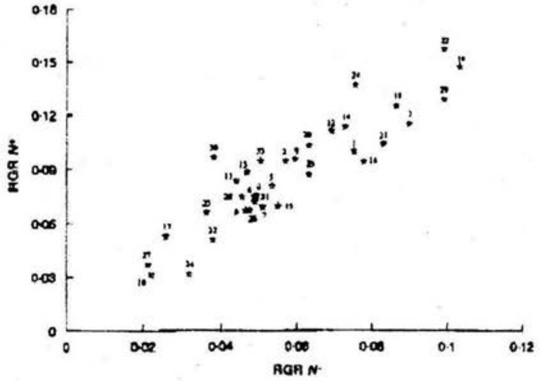

Fig. 1. Relationship between the relative growth rate ($g\,g^{-1}\,day^{-1}$) attained for the 34 studied species under low (N−) and high (N+) nutrient levels. Numbers correspond to species as listed in Table 1.

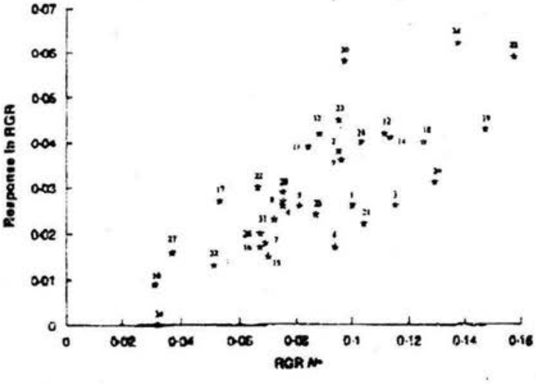

Fig. 2. Relationship between the response in RGR (difference between the RGR attained under high minus RGR in low nutrient treatment) and the relative growth rate attained under the high nutrient treatment (N+) for the 34 species studied. Numbers correspond to species as listed in Table 1.

Table 4. Linear regression coefficients and the probability of the coefficient being different from zero for the values of each parameter attained in low vs high nutrient treatments

	r	*P*
Total dry biomass	0·84	0·000001
Leaf area	0·78	0·000001
Relative growth rate	0·86	0·000001
Leaf area ratio	0·71	0·000002
Net assimilation rate	0·86	0·000001
Specific leaf area	0·70	0·00015
Leaf weight ratio	0·92	0·000001
Stem weight ratio	0·86	0·000001
Root weight ratio	0·73	0·00001
Root:shoot ratio	0·72	0·00001

The differences in growth parameters of the species studied were not associated to growth form or to wood density (Table 5). Studies with tropical semideciduous species have suggested a relationship between wood density and the species tolerance to shade (Augspurger 1984) and tree water status (Borchert 1994). Our results show a weak relationship between seed biomass and RGR ($r = -0{\cdot}62$, $P < 0{\cdot}01$ in high and $r = -0{\cdot}54$, $P < 0{\cdot}01$ in low nutrients), as well as between seed biomass and total dry biomass in both nutrient treatments, ($r = 0{\cdot}4$, $P < 0{\cdot}05$ in high and $r = 0{\cdot}55$, $P < 0{\cdot}01$ in low nutrients). Seed biomass has been reported to have a positive correlation with the total bimoass produced and a negative correlation with plant relative growth rate (Fenner 1983) as well as with the resource availability where the species tend to establish. In this sense, it has been suggested that species with big seeds tend to produce plants with large biomass, in order to achieve a low RGR and to establish under conditions with low availability of resources, like the low light environment under the canopy. In contrast, species with small seeds have plants with low biomass accumulation and high RGR (Table 5) and are able to establish in resources-rich sites such as canopy gaps (Foster 1986; Mazer 1990; Marañon & Grubb 1993; Rincón & Huante 1993). However, often a weak negative correlation between growth rate and seed biomass has been found, suggesting the importance of other factors (biomass allocation, generational time,

Table 5. Linear regression coefficients between pairs of parameters at * $P<0·05$. TDB, total dry biomass; RGR, relative growth rate; NAR, net assimilation rate; LAR, leaf area ratio; SLA, specific leaf area; LWR, leaf weight ratio; R/S, root/shoot ratio; WD, wood density; RWR, root weight ratio; SWR, stem weight ratio. –N, low nutrient treatment; +N, high nutrient treatment

	Low (–N) *r*	High (+N) *r*
TDB *vs* Seed biomass	0·40*	0·55*
TDB *vs* Leaf area	0·88*	0·92*
RGR *vs* Seed biomass	–0·54*	–0·62*
RGR *vs* WD	–0·29	–0·28
RGR *vs* Leaf area	0·41*	0·63*
RGR *vs* NAR	0·29	0·23
RGR *vs* LAR	0·50*	0·50*
RGR *vs* SLA	0·68*	0·60*
RGR *vs* LWR	0·24	0·02
RGR *vs* R/S	0·24	0·11
RGR *vs* RWR	0·20	0·06
RGR *vs* SWR	–0·27	–0·04
LAR *vs* SLA	0·70*	0·71*
LAR *vs* LWR	0·62*	0·62*
LWR *vs* RWR	–0·57*	–0·61*
LWR *vs* SWR	–0·55*	–0·79*
SWR *vs* RWR	–0·36*	0·05
NAR *vs* RWR	0·23	0·28
WD *vs* LWR	0·21	0·30
WD *vs* RWR	–0·45*	–0·52*
WD *vs* SWR	0·24	0·04
NAR *vs* Nitrogen	–0·51*	–0·20
RGR *vs* Nitrogen	0·11	–0·04
LAR *vs* Carbon	–0·55*	–0·36*
SWR *vs* Carbon	0·32	0·40*
RGR *vs* Carbon	–0·41*	–0·35*

stress and disturbance) in the RGR variation (Shipley & Peters 1990), as well as the taxonomic relatedness of the species, as proposed by Kelly & Purvis (1993).

Different attempts have been made to explain interspecific differences in RGR through analysis of NAR and LAR (Hunt 1982; Lambers & Poorter 1992). In several comparative growth studies with a large number of species, LAR and its components SLA and LWR, more than NAR, were the most important parameters influencing RGR (Lambers & Poorter 1992). In this investigation, the total leaf area produced ($r=0·4$, $P<0·05$ in low and $r=0·63$, $P<0·01$ in high nutrients) and the LAR ($r=0·5$, $P<0·01$) are significant and positively correlated with RGR in both nutrient conditions (the high and low) but not with LWR (Table 5). Those differences shown in LAR are explained by its two components, LWR ($r=0·62$, $P<0·01$) and SLA ($r=0·7$, $P<0·001$). Under both low and high nutrients, the RGR was highly correlated to SLA ($r=0·68$ and 0·6, $P<0·01$). This could indicate the importance of the total amount of leaf area produced as well as other leaf characteristics, such as anatomy, morphology and leaf chemical composition (Lambers & Poorter 1992; Van Arendonk & Poorter 1994) to determine the RGR.

Biomass allocation among leaves, stem and roots in our 34 species is closely associated (Table 5). Under the high nutrient levels the biomass allocation to leaves (LWR) is highly negatively correlated to allocation to stem ($r=-0·79$, $P<0·001$) and roots ($r=-0·61$, $P<0·01$). Under the low nutrient level there is a greater biomass allocation to roots and consequently a lower allocation to leaves. This is confirmed by the correlation between root to shoot ratio with LWR and RWR ($r=-0·55$, $P<0·01$, and $r=0·9$, $P<0·001$, respectively). The negative correlations between LWR, SWR and RWR are logically necessary, given that $\mathrm{LWR}+\mathrm{RWR}+\mathrm{SWR}=1$.

Considering the relationship of RGR and biomass allocation to roots and shoot, Garnier (1991) showed that under productive conditions, the difference in growth rate among the species is linked to differences in the specific activities of their leaves and roots, and much less to differences in biomass allocation, measured as R/S ratio. In this sense, he proposed that fast-growing species are those for which the ratio of the specific activities of roots and leaves is high, while slow-growing species are those for which this ratio is low. In this study the correlation between RGR and R/S ratio was very low ($r=0·24$ and 0·11, $P>0·05$). Biomass allocation to roots (RWR) was higher in low nutrients but this change in allocation was not proportional to the changes in RGR shown by the species; i.e. the interspecific variations in allocation to roots are not associated to interspecific variations in RGR.

In a comparative investigation of 24 herbaceous plants with different growth rate, Poorter, Remkes & Lambers (1990) found a positive relationship between plant nitrogen concentration and $\mathrm{RGR}_{\mathrm{max}}$ for grasses and a non-significant relation for dicots, which they attributed to differences between taxonomic groups. Nitrogen concentration of the species studied here was not correlated to the RGR attained under high nutrients (presumably $\mathrm{RGR}_{\mathrm{max}}$), not even among the 11 species of the Leguminosae family studied. The difference between the leaf nitrogen concentration at high *vs* low nutrients was similar in species with high (*T. donnell-smithii*) and low (*T. trifolia*) RGR response. The greater nutrient concentration under resource abundance appears to be caused by a higher nitrogen allocation to leaves likely to produce a higher photosynthetic rate (Chapin *et al.* 1987) and to maintain a faster growth rate.

Lower leaf carbon concentrations were shown by the six species with the highest RGR (fast-growing species). This pattern has been partially explained by Lambers & Poorter (1992) but as they indicated, and our correlation coefficients suggest ($r=-0·41$, $P<0·05$ in low and $r=-0·35$ in high nutrients), this is only of minor importance to explain the variations in RGR.

A wide variety of response values in RGR and biomass allocation among species is documented in this investigation. The great differences between the RGR in high and low suggest greater plastic adjustments of the species in growth rate. The distribution of the plastic growth responses attained by the woody seedlings followed a continuum rather than discrete easily identifiable groups. This response pattern provides an indication of the ecological potential of the species to compensate for nutrient deficiencies and, indirectly, the sort of habitats in which they can establish and successfully compete for soil resources. In spite of this continuum of the growth parameters, it is possible to distinguish, at the extremes of the gradient, two contrasting groups of species using the biomass allocation patterns and relative growth rate shown by the species in both the nutrient treatments tested (Fig. 2). The first corresponds to *M. tenuiflora*, *L. monosperma* and *T. donnell-smithii*, which are fast-growing species that achieved more biomass and greater RGR under high nutrients, which had a larger biomass allocation to the root system when grown under low nutrients and showed a greater growth plasticity to nutrients. Fast-growing species of this tropical deciduous forest have been found to be highly demanding of other resources such as light (Rincón & Huante 1993) and phosphorus (Huante, Rincón & Chapin 1995) as well as being low or non-mycorrhizal dependent (Huante *et al.* 1993). These species present a dichotomous root branching pattern (Huante, Rincón & Gavito 1988), which has been associated with a more effective exploration and exploitation of zones with high nutrient availability (Fitter 1985). Based on the characteristics described above, it could be expected that fast-growing species would tend to occupy sites with abundant resources, such as disturbed sites or gaps. This trend suggests that research related to the role of natural disturbance in maintaining plant diversity in this seasonal ecosystem might be relevant. The second contrasting group of species in the gradient of growth response (Fig. 2) includes *T. trifolia*, *C. mexicanum* and *T. ovata*, which had a low relative growth rate under both nutrient treatments, even lower than the RGR for most species under low nutrients. These species also had a consistent high biomass allocation to roots under both nutrient treatments and exhibit low growth plasticity. *Celaenodendron mexicanum* has been documented to have a poorly branching root pattern (Huante *et al.* 1988) and to be shade tolerant (Rincón & Huante 1993). These slow-growing and tolerant species could be expected to occur in sites with low resource availability. Considering these two extreme growth responses, it is reasonable to suggest that different stresses and disturbances create a wide range of habitats where species with contrasting nutrient resource requirements will be able to establish and sustain growth.

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Capítulo III

Acclimation to changes in light intensity in tropical deciduous woody-seedlings with contrasting growth rates

Abstract

We evaluated the plasticity and acclimation responses in growth, biomass allocation, photosynthesis and stomatal conductance, to changes in light intensity (transfers) in woody species from the tropical deciduous forest. We studied the fast-growing species *Apoplanesia paniculata*, *Cochlospermum vitifolium*, *Cordia alliodora*, *Heliocarpus pallidus* and *Ipomoea wolcottiana*, the slow growing species *Celaenodendron mexicanum* and the species with intermediate growth rates *Caesalpinia eriostachys*, *Caesalpinia platyloba*, *Plumeria rubra*. and *Trichilia trifolia* Treatments consisted in two contrasting light intensities (high, H, 1200 μmol m^{-2} s^{-1} and low, L, 400 μmol m^{-2} s^{-1}) during 52 days and two transfers: from high to low (HL) and from low to high (LH) light intensity, maintaining plant controls in high (HH) and low (LL) light. We conducted a growth analysis based on plant harvests at the beginning of the experiment (five days old seedlings), at the time of transfer (57 days old) and at the end of the experiment (109 days old). The photosynthetic capacity (Amax) and stomatal conductance were measured at day of the transfer of light condition and at the end of the experiment. We hypothesized that the expression of plasticity and acclimation (in magnitude) is related with the growth rate of the species. It is expected different responses among species, the fast-growing are expected to show the highest plastic and acclimation response and the slow-growing species the lowest response, in terms of growth rate, biomass allocation and photosynthetic capacity.

After 52 days of growth under high light intensity, the fast-growing species had high biomass production, leaf area, RGR, net assimilation rate (NAR), Amax and stomatal conductance. Under low light intensity these parameters were highly reduced. The proportion of total biomass allocated to leaves was higher under L and the leaves produced were thinner (higher specific leaf area) than under H. Compared with the fast-growing, the slow growing species had lower leaf area, RGR, NAR, Amax and stomatal conductance. These parameters were slightly higher under H than under L, but the total leaf area produced and leaf weight ratio was not significantly different between L and H, they produced thinner leaves under L. The species with intermediate growth rate had an intermediate response to light, their trend in biomass, leaf area, RGR, NAR, Amax and stomatal conductance is similar to the fast-growing species but with lower magnitude, however the pattern of biomass allocation to leaves is similar to that of the slow-growing species.

After 104 days of growth, the fast-growing species acclimated its RGR and NAR of the phenotype LH with respect to the phenotype HH, showing the highest values under LH. In the species with intermediate growth rate the acclimation was in the same direction (LH with HH), but with non-significant differences between these phenotypes. The slow-growing species Celaenodendron mexicanum had the lowest acclimation. In addition, the pattern of the acclimation of RGR, NAR, Amax and stomatal conductance in this species was opposite to the rest of the studied species, that is, the phenotype LH acclimated with respect to LL, and HL acclimated with HH. In conclusion, the results support that the fast-growing species exhibit a higher and the slow-growing species a lower plasticity and acclimation capacity, respectively, but with different pattern of acclimation to increments and decrements of light intensity. This was associated to leaf characteristics as the specific leaf area and the net assimilation rate rather than the biomass allocation to leaves (leaf weight ratio) or the root:shoot ratio.

Key words: tropical deciduous forest, growth analysis, biomass allocation, photosynthesis, light transfers, acclimation, plasticity.

Introduction

The light environment that plants experience in their natural habitat is highly heterogeneous in time and space therefore, a sun or shade adapted species could experience sudden changes in light availability caused by sunflecks, clouds, tree or branch fall, canopy closure, phenological processes in seasonal systems, etc (Chazdon and Fetcher 1984a, b, Vázquez-Yanes et al. 1990). Considering the light heterogeneity, it is reasonable to infer that the successful growth of sun and shade adapted plants will depend, to some extent, on their ability to respond to a range of light conditions (plasticity) (Bradshaw 1965), and their capacity to adjust its morphology and physiology when those light conditions change (acclimation) (Strauss-Debenedetti and Bazzaz 1991).

Considerable attention has been given to investigate the characteristics of species adapted to sun and shaded environments (Boardman 1977, Grime 1979, Bazzaz and Pickett 1980, Björkman 1981, Smith 1981, Mooney et al. 1978, 1983, Augspurger 1984, Oberbauer and Strain 1985, Walters and Field 1987, Sims and Pearcy 1989, Denslow et al. 1990, Sánchez-Coronado et al. 1990, Lambers and Poorter 1992, Rincón and Huante 1993, Kitajima 1994). These studies have provided information about the plastic capacity of different species adapted to habitats in which high or low light conditions prevail. In general, species adapted to high light intensity show higher biomass production and relative growth rate, lower specific leaf area and have higher rates of photosynthesis per unit of leaf area than species adapted to low light intensity. Species adapted to shade have lower biomass production, relative growth and photosynthetic rates, have a high investment to leaves with high specific leaf area and less non-structural carbohydrates than sun adapted species.

Most studies of the response of tropical plants to changes in light environment have been conducted with plants from the tropical rain forest. In this forest the variations in light conditions are associated, among other factors, with the dynamics of natural gaps (Bazzaz 1979, Denslow 1980, 1987, Martinez-Ramos 1985). However, some characteristics of the highly diverse tropical deciduous forests (Gentry 1982, Lott 1993) suggest other sources of light variations, and that gap dynamics could be different than in tropical rain forests. The tropical deciduous forest has a characteristic seasonal pattern of rain (Bullock 1986), this pattern cause variations in plant phenology (periods of leaf production and shedding), which in turn modified the light available at soil level. During the rainy season there is a characteristic dry period termed "canicula" (some years one month long) which contribute to the lost of part of the tree leaves (Bullock 1986), resulting in changes in light availability. Seed dispersal generally occurs during the dry season (Bullock and Solís-Magallanes 1990) and it appears that seeds remain in the seed bank until the arrival of the rainy period which provides favorable conditions for germination and growth. However, at least the firsts stages of seedling growth occur during the tree leaf production and, hence during changes in the light conditions. Another factor that produces light variations in tropical deciduous forests is the occurrence of standing dead-trees and branches creating small gaps with higher light intensity. These dead-trees can also fall and create gaps during the windy periods of tropical storms. However, tree fall appears to create bigger gaps in the tropical deciduous forest, but with smaller size than those produced in tropical rain forests, because the tropical deciduous forest is less dense, less stratified (Lott et al. 1987) and with lower maximum tree height (about 15 m) (Lott 1985).

In spite of the importance of light changes in plant growth, most studies have been focused on plant responses to different constant light conditions and few investigations have evaluated the effect of changes in light intensity on the growth (Fetcher et al. 1983, Rice and Bazzaz 1989a, b, Pompa and Bongers 1991) and photosynthesis (Ramos and Grace 1990, Strauss-Debenedetti and Bazzazz 1991, Sims and Pearcy 1991, Turnbull et al. 1993). In addition, these studies have been conducted with one or few plant species, reducing the possibility of a comparative analysis. In this study, we evaluated the capacity of ten woody-species from the tropical deciduous forest, to show plastic and acclimation responses to contrasting changes in light intensity (transfers). The selection of the species studied was based on previous results, which indicated contrasting growth response of the species to light intensity (Rincón and Huante 1993) and nutrient availability (Huante et al. 1995). Thus, the ten species selected cover a wide range of growth rates for woody-seedlings in this forest. We hypothesized that, the expression of plasticity and acclimation (in magnitude and direction) in the different parameters of growth and photosynthesis is related with the growth rate of the species. It is expected different plasticity to contrasting light intensity and acclimation to changes in light intensity among the different species. It is expected that the fast-growing species showed the highest plastic and acclimation response and the slow-growing species the lowest response, in terms of growth rate, biomass allocation and rate of photosynthesis. Considering that fast-growing species has been associated to changing environments as canopy gaps where there is a sudden increment of light intensity , it is expected that these species showed a higher response to light transfer from low to high light intensity than slow-growing species.

Materials and Methods

Plant material

The fast-growing woody species Apoplanesia paniculata Presl (Leguminosae), Cochlospermum vitifolium (Willd) Spreng. (Cochlospermaceae) Cordia alliodora (Ruiz & Pav.) Oken (Boraginaceae), Heliocarpus pallidus Rose (Tiliaceae) and Ipomoea wolcottiana Rose (Convolvulaceae), the slow growing species Celaenodendron mexicanum, Standl. (Euphorbiaceae) and the species with intermediate growth rates Caesalpinia eriostachys Benth. (Leguminosae), Caesalpinia platyloba S. Wats. (Leguminosae), Plumeria rubra L. (Apocynaceae) and Trichilia trifolia L. (Meliaceae) were used in this study (Rincón and Huante 1988, 1993, 1994, Huante et al. 1995). Nomenclature of the species is in accordance to Lott (1993).

Experimental procedure

Mature seeds of the studied species were collected from at least ten individuals at the Station of Biology Chamela, at the Pacific coast of Mexico (19^{o} 30' N, 105^{o} 03' W). Seeds were germinated on humid pure silica sand. Five days after germination, seedlings were transplanted to 5 kg black plastic bags (one seedling per bag) filled with a mixture of soil from the forest and silica sand (2:1 v/v). This mix was fertilized with 10 g of 14-14-14 NPK continuous 120 days feeding fertilizer (Osmocote ®) at the beginning of the experiment, in order to prevent nutrient limitation and were watered every day. Seedlings were grown inside a greenhouse built in a solarium at the tropical deciduous forest. Two light sections were created in this greenhouse: a high light section (H) with an average maximum daily intensity of 1200 µmol m^{-2} s^{-1} (80% full-sun) and low (L) with 400 µmol m^{-2} s^{-1} (25% full-sun), registered with quantum sensors (LI-COR, Nebraska). These light conditions were designed to simulate the light intensities experience by seedlings growing in a small gap and under a not very dense canopy (E. Sanchez-Coronado unpublished data). These conditions were created covering the greenhouse walls with white and black plastic screen, respectively. The red:far red ratio was always higher than 1 (measured with a spectroradiometer LI-COR, Nebraska). No artificial light was provided. The day length during the time of the experiment was of 13 hours.

Thirty six plants of each species were growing one per plastic bag. These plants were randomly divided and assigned to the two contrasting intensities described above during 52 days. After this time six individuals under H and six under L were harvested as described later, in addition six plants growing under high light were transferred to low light (HL) and six of the individuals growing under low light were transferred to high light (LH), the rest of the plants were maintained growing under high (HH) and low (LL) light intensity. The plants were under these last conditions during another 52 days. Thus, the total growth period was 104 days.

Growth and allocation measurements

At the time of transplanting (five days old seedlings) the seedlings leaf area and the plant dry biomass of six individuals was registered. At 52 and 104 days of growth under the different light conditions (57 and 109 days old plants, respectively), six plants per treatment and per species were harvested, leaf area was measured (Delta T, England), roots were carefully washed and leaves, stems and roots were obtained separately. Plants were oven dried (80 °C) for 48 hours and dry biomass of each plant part was obtained. Data were analyzed following the classical growth analysis methods described by Evans (1972) and Hunt (1982). The average relative growth rate (RGR, dry biomass increment per unit total plant biomass per unit time) of each species was determined for two time periods (initial harvest to 52 days and 52 to 104 days) according to: $RGR = (\ln Wt_2 - \ln Wt_1)/(t_2 - t_1)$ where W is the average total plant dry biomass in g and t is time in days. The net assimilation rate (NAR, the rate of dry matter production per unit of leaf area), the specific leaf area (SLA, the ratio of foliage leaf area to foliage dry biomass), the leaf area ratio (LAR, the ratio between total leaf area and total plant dry biomass) as well as the leaf weight ratio (LWR, the ratio of foliage weight to total dry weight) (Causton and Venus 1981, Hunt 1982) and the root to shoot dry biomass ratio (R/S) were also calculated. Differences between light treatments (H and L) at 52 days were tested by student "t" test ($p \leq 0.05$). At the end of the experiment (104 days) the differences (between HH, HL, LH and LL) were tested by one-way analysis of variance ($p \leq 0.05$), using log-transformed data when needed, in order to meet assumptions of the analysis. After ANOVA differences among means were tested by Tukey multiple comparisons test (Zar 1974). As a measure of the magnitude of plasticity or acclimation we calculated the difference in RGR between the treatments where the highest and the lowest RGR value was attained (ΔRGR). Spearman rank correlations were calculated to identify the relationship between the highest relative growth rate and the different parameters studied at 52 and 104 days of plant growth (Zar 1974).

Gas exchange measurements

Measurements of the maximum rate of photosynthesis (Amax) and stomatal conductance were made on the slow-growing species *Celaenodendron mexicanum*, the fast-growing species *Heliocarpus pallidus*, and the species with intermediate growth rate *Caesalpinia eriostachys* and *Caesalpinia platyloba*. Photosynthesis measurements were taken after ten minutes of exposure to 400-500 and 1300-1400 mol m^{-2} s^{-1} for plants growing under low and high light intensity, respectively. Based on light curves reported for tropical plants, the maximum photosynthetic capacity is reached in general between 1000-1500 and 300-800 for sun and shade plants respectively (Walter and Field 1987, Pearcy 1987, Ramos and Grace 1990, Strauss de-Benedetti and Bazzaz 1991, Tinoco-Ojanguren and Pearcy 1992, Ackerly and Bazzaz 1995). Thus, our photosynthesis measurements can be considered as maximum photosynthetic capacity (Amax). Plants transferred from high to low were measured at low light and the plants from low to high were measured at high light intensity. These light intensities were maintained using a halogen lamp (100 watts) during the gas exchange measurements when needed. In order to prevent an increment of temperature, the artificial light was passed throughout a transparent acrylic box filled with water, the box was located between the lamp and the leaf. Ambient temperature was $32 \pm 1.5\ ^{o}C$. Measurements were made in the third youngest leaf per plant (three replicates) just prior the light transfer and 52 days after the transfer (the end of the experiment). We used a portable, closed gas exchange system (LI-COR, Model 6200, Nebraska), equipped with a quarter litre chamber.

Results

Growth responses to contrasting light intensities before transfers

After 52 days of plant growth under high and low light intensities, and just before the light transfers, the total dry biomass (Fig. 1a) and the relative growth rate (Fig. 1b) attained by the species was higher in H than in L, excepting for the species with the slowest growth rate (Celaenodendron mexicanum and Trichilia trifolia) which had non-significant differences between treatments ($p > 0.05$). The total leaf area produced was larger in H for all species excepting Caesalpinia platyloba, Celaenodendron mexicanum and Trichilia trifolia which in both light treatments achieved similar leaf area (Table 1). The leaf area ratio (LAR) and its components: the specific leaf area and the leaf weight ratio also showed large differences among species. All species (except Celaenodendron mexicanum) showed lower LAR and SLA under H. The proportion of the total plant biomass allocated to leaves (LWR) was higher under L for the fast growing species Apoplanesia paniculata, Cordia alliodora, Heliocarpus pallidus and Ipomoea wolcottiana (Table 1).

Growth responses to light transfers

The responses showed by all species under contrasting light intensities at 52 days (H vs L) were maintained after 104 days of growth in HH and LL, however, at this time, the species Celaenodendron mexicanum and Trichilia trifolia showed a significant higher total dry biomass (Fig. 2a) and leaf area under HH than under LL (Table 2).

All species showed the highest biomass production under HH and the lowest under LL (Fig. 2a). For Celaenodendron mexicanum there were significant differences in biomass between HL and LH, but there were not significant differences between HL and LH for any other species (Fig. 2a).

All species (excepting Celaenodendron mexicanum) showed the highest RGR (Fig. 2b) and NAR (52-104 days) under LH (Table 2). RGR was significantly greater under LH than under HH for the fast-growing species, but there were non-significant differences between HH and LH in the species with intermediate RGR (Fig. 2b). Contrasting with these trends, Celaenodendron mexicanum (the species with the slowest RGR) showed a higher RGR under HH and HL than under LH and LL (Fig. 2b).

After 104 days of growth, the leaf area produced by all species (Table 2) was the highest under HH and the lowest under LL. The leaf area produced under HH was non-significantly different to that under LH for Caesalpinia platyloba, Ipomoea wolcottiana and Trichilia trifolia and that under HL for Celaenodendron mexicanum. In the light transfers the leaf area produced under HL was similar to LH for

Caesalpinia eriostachys, Cochlospermum vitifolium, Heliocarpus pallidus and Plumeria rubra. LL was non-significant different to LH for Celaenodendron mexicanum. The leaves with higher LAR and SLA were those under LL, in Celaenodendron mexicanum LL was not different to LH. In all species the LAR was the lowest under HH. In the fast-growing species and in Plumeria rubra and Trichilia trifolia the LAR under HL was higher than that under LH. The SLA under both transfers (HL and LH) were not different for Caesalpinia eriostachys, Caesalpinia platyloba and Plumeria rubra. The LWR (Table 2) was unchanged under all treatments by Caesalpinia eriostachys, Caesalpinia platyloba, Celaenodendron mexicanum, Plumeria rubra and Trichilia trifolia. LWR was higher under LL in the fast-growing species Heliocarpus pallidus, Ipomoea wolcottiana, Apoplanesia paniculata, Cochlospermum vitifolium and Cordia alliodora.

The R/S ratio (Table 2) was unchanged among all treatments for Apoplanesia paniculata, and Caesalpinia platyloba. In Caesalpinia eriostachys, Cordia alliodora, Heliocarpus pallidus, Ipomoea wolcottiana, Plumeria rubra and Trichilia trifolia, there was a higher allocation to the shoot (lower R/S ratio) under LL than under HH. These R/S values under LL were similar to that under HL for Caesalpinia eriostachys, Cordia alliodora and Ipomoea wolcottiana.

Gas exchange

Before light transfers, at 52 days of growth under H and L (Table 3) the photosynthetic capacity (Amax) and the stomatal conductance for Celaenodendron mexicanum in H and L was similar, while Heliocarpus pallidus, Caesalpinia eriostachys and Caesalpinia platyloba had the highest Amax and stomatal conductance under H. Heliocarpus pallidus had the highest difference in Amax between H and L treatments. After 52 days of light transfer, the pattern of acclimation (direction of the response, Kupier and Kupier 1988) was different among species. The highest Amax and stomatal conductance for the slow-growing species Celaenodendron mexicanum was showed under HL, LH and HH and the lowest under LL. In the rest of the species the highest values of both parameters were exhibited under LH and HH and the lowest under HL and LL, but in Heliocarpus pallidus stomatal conductance in LL was lower than in HL.

Fig 1. shows the relationship among the highest values of RGR, NAR and Amax for the species studied. The species with high RGR (Heliocarpus pallidus) have also a high Amax and NAR. The species with the lowest RGR (Celaenodendron mexicanum) has also a lowest Amax and NAR.

The relationship between the highest RGR and the difference between the highest and the lowest RGR (ΔRGR) attained by each species is showed in figure 2. The ΔRGR is considered as a measure of the response in RGR to the light treatments, in this sense, ΔRGR is considered as a measure of the magnitude of acclimation. There was a positive relationship between the highest RGR and the response in RGR among the species studied. where at higher RGR greater response in RGR (ΔRGR) to light changes. The fast-growing species Cochlospermum vitifolium, Cordia aliiodora and Ipomoea wolc among species. The highest Amax and stomatal conductance for the slow-growing species Celaenodendron mexicanum was showed under HL, LH and HH and the lowest under LL. In the rest of the species the highest values of both parameters were exhibited under LH and HH and the lowest under HL and LL, but in Heliocarpus pallidus stomatal conductance in LL was lower than in HL.

Fig 3. shows the relationship among the highest values of RGR, NAR and Amax for the species studied. The species with high RGR (Heliocarpus pallidus) have also a high Amax and NAR. The species with the lowest RGR (Celaenodendron mexicanum) has also a lowest Amax and NAR.

The relationship between the highest RGR and the difference between the highest and the lowest RGR (ΔRGR) attained by each species is showed in Fig. 4. The ΔRGR is considered as a measure of the response in RGR to the light treatments, in this sense, ΔRGR is considered as a measure of the magnitude of acclimation. There was a positive relationship between the highest RGR and the response in RGR among the species studied. where at higher RGR greater response in RGR (ΔRGR) to light changes. The fast-growing species Cochlospermum vitifolium, Cordia alliodora and Ipomoea wolcottiana showed the highest acclimation and the slow-growing species Celaenodendron mexicanum showed the lowest. Among treatments the highest RGR occurred in the phenotype LH for the fast-growing species, in the LH and HH for the species with intermediate RGR and, in the phenotypes HL and HH for the species with the slowest RGR (Celaenodendron mexicanum).

Discussion

The growth characteristics showed by the species studied reflect different amount (i.e. magnitude of response) and pattern (direction of the response) of plasticity (Schlichting 1986, Kupier and Kupier 1988). Fast-growing species showed to be more plastic, followed by the intermediate growth rate species, and the slow-growing species with the less plasticity. Some plant characteristics exhibited greater plasticity (RGR in this study) than others (LWR), likely because the plasticity of some traits may allow the homeostasis of others (Bradshaw 1965). The overall effect of the plasticity of some plant characteristics and stability of others should allow to have a growth advantage under heterogeneous conditions (Rice and Bazzaz 1989b).

The attributes showed by fast-growing species when grown under high light intensity (high leaf area production, RGR, NAR, Amax and stomatal conductance) have been associated with adaptation to establish and grow in sites where abundance in resources prevails (e.g. high light) as canopy gaps (Bazzaz 1979, Denslow 1980, Augspurger 1984). In addition, it has been suggested that a slow rate of growth indirectly confers stress resistance by reducing carbon demands for growth (Chapin et al. 1990, 1993). In general, Amax and stomatal conductance follow a similar pattern, this has been attributable to an internal regulation of carbon dioxide concentration by matching stomatal conductance to photosynthetic potential (Farquhar and Sharkey 1983), plants with low photosynthetic rate have low stomatal conductance and, therefore, low transpiration rate (Chapin et al. 1993). It has also suggested that the reduction of carbon demand for growth allows greater allocation to other processes that directly contribute to stress resistance such as storage (Chapin et al. 1990, 1993) and chemical defenses against pathogens and herbivores (Mooney and Gulmon 1982). These characteristics enable the species with slow growth rate to grow in sites where low availability of resources prevails (e.g. shade conditions) as the forest understory (Bazzaz 1979, Denslow 1980, Augspurger 1984). In the tropical deciduous forest of Chamela, Jalisco trees and saplings of Celaenodendron mexicanum dominate the canopy and the understory forming small and relatively dense monospecific-forests surrounded by the contrasting highly diverse tropical deciduous forests (Lott 1985, Martijena and Bullock 1994), suggesting shade tolerance of saplings and seedlings of this species. Celaenodendron mexicanum has been documented to be a drought- (Martijena and Bullock 1994) and low-nutrient-resistant species, which has a slow growth (Rincón and Huante 1988, Huante et al 1995a, Chapter II), forms associations with arbuscular micorrhyzae fungi (E. Rincón, unpublished data), has thick leaves (low SLA), more coriaceous (96.5 g m-2) than leaves of other species from the tropical deciduous forest (22-87 g m-2, n=15 species) (Castellanos et al. 1989) and with high content of secondary metabolites as terpenes and flavonoids (Castañeda et al. 1992), which suggest a plant investment in defenses against herbivory. Previous studies of herbivory (Filip et al. 1995) realized with several of the species included in this study show a higher percentage of leaf area loss by folivory (long-term measurements) in the fast-growing species Ipomoea wolcottiana (29.65%) and Heliocarpus pallidus (17.88%) than in the species with intermediate growth rate Plumeria rubra (8.67%) and Trichilia trifolia (1.95%), this last species had the lowest RGR among the species with intermediate RGR. Ipomoea wolcottiana and Heliocarpus pallidus are species that grow in disturbed sites (Lott 1993), which presumably have a high resource availability. This suggest a positive relationship between growth rate and the percentage of herbivory, where at low RGR low herbivory and vice versa.

Previous investigations related with responses of tropical seedlings to transfers of light intensity (Rice and Bazzaz 1989a, b, Sims and Pearcy 1989, Denslow et al. 1990, Pompa and Bongers 1991, Ackerly 1993, Turnbull et al. 1993) revealed that shade plants transferred to the sun have a higher RGR than plants growing in the sun. In the reciprocal transfer, sun plants transferred to the shade do have lower RGR than the shade plants. In this study the plants under LH had the highest RGR only in the fast-growing species, in the species with intermediate growth rate there is a benefit in RGR in the transfer LH because the RGR was similar to that achieved under HH, but an opposite pattern of response that suggest the lack of any effect of the transfer of light intensity was showed by the slow-growing species. It has been suggested that shade leaves have a higher benefit (in terms of return of carbon invested) than sun leaves, owing to their lower C investment per unit leaf area (Sims and Pearcy 1991), which results in a higher LAR (Rice and Bazzaz 1989a) and hence, a higher capacity for light capture, which allows a faster growth. Our fast-growing species had higher LAR and RGR under LH than under HH. These studies do not support the predictions of Rice and Bazzaz (1989b) who proposed that in light transfers it could be expected that growth rates observed in a particular environment should be highest in plants that have developed in that environment, while plants transferred from a different set of conditions should exhibit lower growth rates. In this sense, sun plants are predicted to grow more rapidly in a sun environment than shade plants transferred to sun environment, and the converse in the shade environment. A plastic response to changes from low to high light intensities could be expected in species that naturally experience increases in light as those produced by gap formation. As mentioned above Cordia alliodora, Heliocarpus pallidus and Ipomoea wolcottiana can be found growing in natural or man-disturbed areas (Lott 1993) where changes form low to high light intensities can be expected.

A plant transferred from L to H will face the new light environment with leaves acclimated to shade. Thus the potential of acclimation to the new environment will depend in some extent by the plant ability to modificate the leaves developed under the previous environment or by the rate of new leaves production with characteristics favourables to the exploitation of the new conditions. In the shade species Alocasia macrorrhyza has been documented that leaf anatomic characteristics such as: number of cell layers and differentiation are determined early in the leaf ontogeny (Sims and Pearcy 1992), thus, the acclimation of plants transferred to other light condition will depend, among other things, of their ability to produce new leaves. However, certain degree of acclimation in leaves produced before the light transfer has been reported in other species (Chow and Anderson 1987, Sebaa et al. 1986). It has been documented that the rate of plant leaf production is higher in sun leaves and lower (higher longevity) in shade leaves (Chabot and Hicks 1982). In addition fast-growing pioneer tree species have a high rate of leaf production with low leaf longevity (Ackerly 1993) and slow-growing species produce leaves at slower rates. For example, in a 50 days period growing under high light intensity Ipomoea wolcottiana was able to produce 19 leaves and Celaenodendron mexicanum five leaves (Huante 1992). It is probably that this low rate of leaf production cause, in some extent, the lack of responsiveness to light transfers in Celaenodendron mexicanum.

The correlations between the different parameters evaluated and the highest RGR attained for all the species (Table 4), show that interspecfic variations in NAR and SLA are highly associated with interspecific variations in the RGR, at both times 52 and 104 days of plant growth. Species with high SLA, NAR and Amax have high RGR and species with low SLA, NAR and Amax have low RGR (Fig. 3). Most of the studies conducted with a high number of species (Lambers and Poorter 1992 and references there in) have shown that the main parameter correlated with RGR is the LAR (as well as its components SLA and LWR), and interspecific differences in the rate of biomass gain per unit leaf area (NAR) are of secondary importance. This was also found in a comparative study conducted with 34 woody species grown under contrasting nutrient availability, where the species studied here were included (Huante et al. 1995). A low NAR rather than low LAR has been suggested to cause the low RGR of shade adapted species, when grown under high light intensity (Poorter 1989). Variations in LAR, are caused by variations in SLA or LWR. Variations in the leaf mass area (LMA, proportion of leaf mass per unit of leaf area, the inverse of SLA) has been correlated with variations in leaf toughness, leaf chemical defenses and life span (Koike 1988, Lei and Lechowicz 1990, Reich et al. 1991). In this study the low correlation between RGR and LAR could be a consequence of the low correlation between RGR and LWR. This last correlation could be due to the low responsiveness of the allocation to leaves (LWR). Previous studies have also showed that leaf allocation varies little or not at intensities about 50% of full sun (Ackerly 1993).

It has been suggested that plants growing under low light intensity shift its biomass allocation to leaves in detrimental of the allocation of roots and stem (Pons 1977, Werner et al. 1982, Lambers and Poorter 1992) which led to a higher LWR and lower R/S ratio (Kitajima 1994) than plants growing under high light intensity. However, the LWR was the least plastic trait and the interspecific variations showed in the R/S ratio, reported here and in previous studies (Corré 1983) even when nutrient availability is the resource tested (Garnier 1991, Huante et al. 1995), appear to indicate that they are not associated with interspecific variations in RGR in any simple way. Thus, in a changing light environment a high light harvesting and growth rate appears to be reached by changes in SLA more than modifications in LWR.

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Table 1. Net assimilation rate (NAR, g cm^{-2} s^{-1}), total leaf area (LA, cm^{2}), leaf area ratio (LAR, cm^{2} g^{-1}), specific leaf area (SLA, cm^{2} g^{-1}), leaf weight ratio (LWR, g g^{-1}) and root/shoot ratio (R/S) showed by the ten species at 52 days of growth under high (H) and low (L) light intensity. Ap = *Apoplanesia paniculata*, Cc = *Caesalpinia eriostachys*, Cp = *Caesalpinia platyloba*, Cm = *Celaenodendron mexicanum*, Cv = *Cochlospermum vitifolium*, Ca = *Cordia allidodra*, Hp = *Heliocarpus pallidus*, Iw = *Ipomoea wolcottiana*, Pr = *Plumeria rubra* and Tt = *Trichilia trifolia*. Small letters show significant differences (Student "t", $p < 0.05$).

	Species									
	Slow RGR	Intermediate RGR				Fast RGR				
NAR										
H	0.00008^{a}	0.00065^{a}	0.00070^{a}	0.00079^{a}	0.00049^{a}	0.00092^{a}	0.00070^{a}	0.00073^{a}	0.00093^{a}	0.00111^{a}
L	0.00004^{a}	0.00061^{a}	0.00038^{b}	0.00028^{b}	0.00028^{b}	0.00035^{b}	0.00074^{a}	0.00030^{b}	0.00050^{b}	0.00038^{b}
LA										
H	30.7^{a}	576.6^{a}	367.4^{a}	404.7^{a}	52.8^{a}	748.1^{a}	1175.8^{a}	612.4^{a}	1204.7^{a}	4313.6^{a}
L	27.9^{a}	349.5^{b}	351.0^{a}	155.1^{b}	56.3^{a}	213.4^{b}	327.4^{b}	216.7^{b}	523.6^{b}	928.6^{b}
LAR										
H	168.2^{a}	125.7^{a}	116.1^{b}	123.7^{b}	183.4^{b}	164.5^{b}	191.6^{b}	156.6^{b}	173.3^{b}	121.8^{b}
L	184.3^{a}	114.2^{a}	198.7^{a}	339.9^{a}	314.9^{a}	371.1^{a}	286.5^{a}	330.5^{a}	287.9^{a}	278.2^{a}
SLA										
H	271.2^{b}	285.0^{b}	248.4^{b}	278.0^{b}	337.5^{b}	354.8^{b}	444.9^{b}	313.7^{b}	384.4^{b}	367.9^{b}
L	311.0^{a}	238.4^{a}	406.4^{a}	686.2^{a}	484.1^{a}	729.6^{a}	752.2^{a}	512.4^{a}	572.0^{a}	475.4^{a}
LWR										
H	0.62^{a}	0.44^{a}	0.47^{a}	0.44^{a}	0.54^{a}	0.46^{b}	0.43^{a}	0.50^{b}	0.45^{b}	0.33^{b}
L	0.59^{a}	0.48^{a}	0.49^{a}	0.48^{a}	0.65^{a}	0.51^{a}	0.39^{a}	0.64^{a}	0.50^{a}	0.58^{a}
R/S										
H	0.43^{a}	0.45^{a}	0.37^{a}	0.15^{a}	0.39^{a}	0.31^{a}	0.28^{a}	0.54^{a}	0.31^{a}	0.37^{a}
L	0.30^{b}	0.35^{b}	0.27^{b}	0.14^{a}	0.21^{b}	0.29^{a}	0.25^{a}	0.31^{b}	0.21^{b}	0.18^{b}

Table 2. Net assimilation rate (NAR, g cm^{-2} s^{-1}), total leaf area (LA, cm^2), leaf area ratio (LAR, cm^2 g^{-1}), specific leaf area (SLA, cm^2 g^{-1}), leaf weight ratio (LWR, g^2 g^{-1}) and root/shoot ratio (R/S) showed by the ten species at 104 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity. Species names as in Table 1. Small letters show significant differences at $p < 0.05$ after ANOVA and Tukey multiple rank test.

	Species									
	Slow RGR	Intermediate RGR				Fast RGR				
NAR										
HH	0.00019^{a}	0.00027^{a}	0.00033^{a}	0.00049^{a}	0.00037^{a}	0.00021^{b}	0.00062^{a}	0.00029^{a}	0.00027^{a}	0.00034^{a}
HL	0.00017^{a}	0.00015^{b}	0.00011^{b}	0.00016^{b}	0.00017^{b}	0.00002^{c}	0.00017^{b}	0.00005^{b}	0.00011^{c}	0.00012^{b}
LH	0.00006^{b}	0.00027^{a}	0.00025^{a}	0.00045^{a}	0.00027^{b}	0.00032^{a}	0.00059^{a}	0.00034^{a}	0.00033^{a}	0.00060^{a}
LL	0.00008^{b}	0.00006^{b}	0.00009^{b}	0.00017^{b}	0.00013^{b}	0.00015^{c}	0.00013^{b}	0.00016^{c}	0.00007^{b}	0.00013^{b}
LA										
HH	87.5^{a}	1337.3^{a}	1029.8^{a}	938.1^{a}	274.9^{a}	799.5^{a}	4773.2^{a}	1377.9^{a}	3311.2^{a}	4264.5^{a}
HL	85.2^{a}	919.1^{b}	520.6^{b}	646.1^{b}	182.0^{b}	215.7^{c}	2866.8^{b}	652.3^{c}	2599.3^{b}	2567.4^{b}
LH	42.1^{b}	966.2^{b}	929.7^{a}	609.5^{b}	$241.2^{a b}$	478.7^{b}	2513.4^{b}	1009.6^{b}	2062.8^{b}	4074.4^{a}
LL	50.3^{b}	642.2^{c}	417.6^{b}	266.4^{c}	132.9^{b}	237.7^{c}	524.6^{c}	440.8^{c}	1046.7^{c}	1617.6^{b}
LAR										
HH	102.1^{b}	76.7^{c}	71.6^{c}	50.6^{b}	109.2^{c}	$36..7^{b}$	63.2^{c}	78.1^{c}	93.6^{c}	38.0^{c}
HL	129.7^{a}	88.4^{b}	91.8^{b}	92.7^{a}	$168.1^{a b}$	63.0^{b}	139.0^{b}	117.0^{b}	155.6^{b}	66.7^{b}
LH	148.9^{a}	83.5^{b}	104.1^{b}	68.4^{b}	134.8^{b}	76.6^{b}	94.6^{b}	108.1^{b}	98.5^{c}	54.8^{b}
LL	146.0^{a}	128.1^{a}	122.2^{a}	115.6^{a}	188.2^{a}	101.1^{a}	201.0^{a}	143.1^{a}	224.8^{a}	120.1^{a}
SLA										
HH	214.4^{b}	216.7^{b}	173.3^{c}	242.9^{c}	206.6^{b}	231.7^{b}	385.1^{c}	229.5^{c}	358.3^{b}	298.8^{b}
HL	224.1^{b}	239.1^{b}	238.0^{b}	347.1^{b}	334.9^{a}	312.3^{a}	$567.0^{a b}$	$269.3^{a b}$	520.6^{a}	384.8^{a}
LH	284.3^{a}	238.6^{b}	234.3^{b}	302.8^{bc}	254.3^{b}	257.5^{b}	$459.5^{b c}$	$267.3^{a b}$	386.2^{b}	307.4^{b}
LL	262.3^{a}	375.9^{a}	299.9^{a}	438.7^{a}	336.0^{a}	319.9^{a}	658.5^{a}	300.8^{a}	510.6^{a}	397.3^{a}
LWR										
HH	0.48^{a}	0.35^{a}	0.41^{a}	0.21^{a}	0.53^{a}	0.27^{b}	0.17^{b}	0.34^{b}	0.26^{b}	0.13^{b}
HL	0.58^{a}	0.38^{a}	0.39^{a}	0.27^{a}	0.50^{a}	0.13^{a}	$0.25^{a b}$	$0.43^{a b}$	0.30^{b}	0.17^{b}
LH	0.52^{a}	0.35^{a}	0.44^{a}	0.24^{a}	0.53^{a}	0.30^{b}	$0.20^{a b}$	0.40^{a}	0.26^{b}	0.18^{b}
LL	0.56^{a}	0.35^{a}	0.41^{a}	0.26^{a}	0.56^{a}	0.32^{b}	0.33^{a}	0.47^{a}	0.44^{a}	0.31^{a}
R/S										
HH	0.38^{a}	0.53^{a}	0.37^{a}	0.29^{a}	0.40^{a}	0.46^{a}	0.54^{b}	0.92^{a}	0.35^{a}	0.77^{a}
HL	0.25^{b}	0.37^{b}	0.38^{a}	$0.24^{a b}$	0.49^{a}	0.54^{a}	0.39^{c}	0.56^{c}	0.32^{a}	0.55^{b}
LH	0.38^{a}	$0.46^{a b}$	0.36^{a}	$0.24^{a b}$	0.39^{a}	0.49^{a}	0.67^{a}	0.79^{b}	0.31^{a}	0.75^{a}
LL	0.33^{a}	0.41^{b}	0.30^{a}	0.19^{b}	0.25^{b}	0.49^{a}	0.51^{b}	0.48^{c}	0.25^{b}	0.41^{b}

Table 3. Photosynthetic rate (µmol CO_2 m^{-2} s^{-1}) and stomatal conductance (mol m^{-2} s^{-1}) measured in A) 52 days old plants under high (H) and low (L) light intensity and B) for 104 days old plants under prevailing high (HH), low (LL) and tranfered from high to low (HL) and low to high (LH). Species names as in table 1. The average of one leaf of three different planst. Small letters show significant differences $p < 0.05$ (ANOVA and Tukey multiple comparisons).

A)

	Cm	Cp	Ce	Hp
Photosythesis				
H	2^{a}	10.47^{a}	11.99^{a}	12.43^{a}
L	2.6^{a}	5.2^{b}	3.72^{b}	3.19^{b}
Stomatal Cond				
H	0.0407^{a}	0.13^{a}	0.116^{a}	0.373^{a}
L	0.044^{a}	0.018^{b}	0.048^{b}	0.0476^{b}

B)

Photosythesis				
HH	5.876^{a}	8.456^{a}	7.30^{a}	15.58^{a}
HL	4.58^{a}	5.486^{b}	4.87^{b}	10.13^{b}
LH	4.73^{a}	8.026^{a}	8.47^{a}	15.66^{a}
LL	3.706^{b}	5.29^{b}	5.49^{b}	7.63^{b}
Stomatal Cond				
HH	0.123^{a}	0.15^{a}	0.102^{a}	0.36^{a}
HL	0.08^{ab}	0.076^{b}	0.084^{b}	0.215^{b}
LH	0.091^{a}	0.115^{a}	0.126^{a}	0.476^{a}
LL	0.059^{b}	0.0769^{b}	0.086^{b}	0.169^{c}

Table 4 Spearman rank correlation between the highest relative growth rate (RGR) and different growth parameters considering the ten species studied at 52 and 104 days of plant growth. TDB = Total dry biomass, SLA = Specific leaf area, LAR = Leaf area ratio, LWR = Leaf weight ratio, NAR = Net assimilation rate and R/S = Root/shoot ratio.

	52 days		104 days	
	r	p	r	p
RGR vs TDB	0.76	0.01	0.52	0.12
SLA	0.73	0.02	0.62	0.05
LAR	0.05	0.09	-0.13	0.71
LWR	-0.55	0.1	-0.57	0.08
NAR	0.89	0.0004	0.88	0.0008
R/S	-0.42	0.22	0.46	0.17

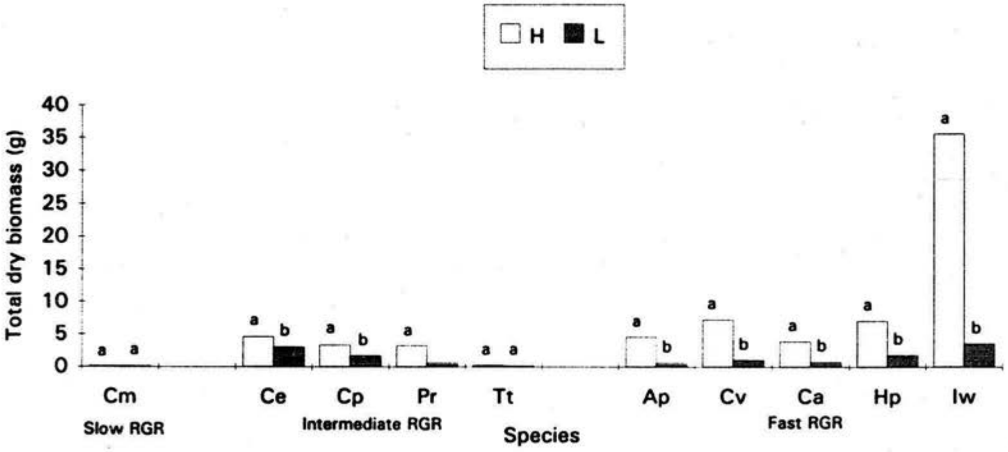

Figure 1a. Total biomass production (g) by the ten species at 52 days of growth under high (H) and low (L) light intensity. Ap = *Apoplanesia paniculata*, Ce = *Caesalpinia eriostachys*, Cp = *Caesalpinia platyloba*, Cm = *Celaenodendron mexicanum*, Cv = *Cochlospermum vitifolium*, Ca = *Cordia allidodra*, Hp = *Heliocarpus pallidus*, Iw = *Ipomoea wolcottiana*, Pr = *Plumeria rubra* and Tt = *Trichilia trifolia*. Small letters show significant differences (Student "t", $p < 0.05$).

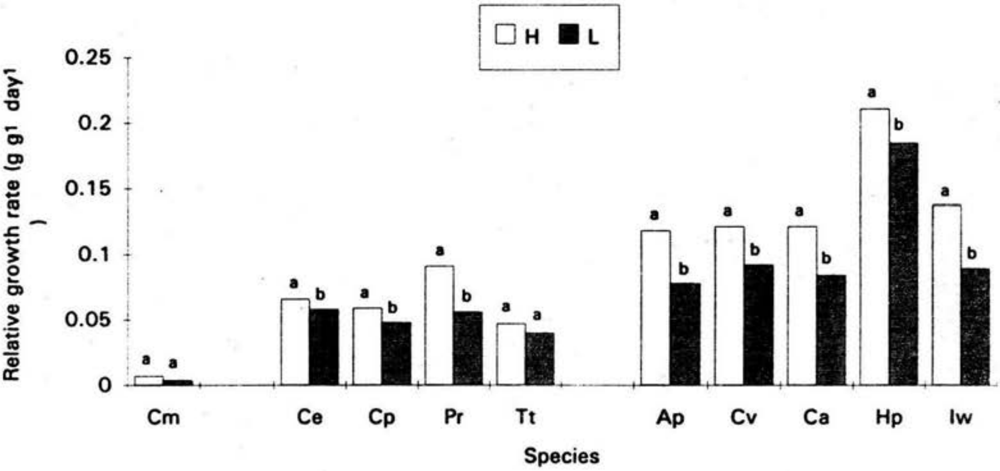

Figure 1b. Relative growth rate (RGR, g g^{-1} d^{-1}) showed by the ten species at 52 days of growth under high (H) and low (L) light intensity. Species names as in figure 1a. Small letters show significant differences (Student "t", $p < 0.05$).

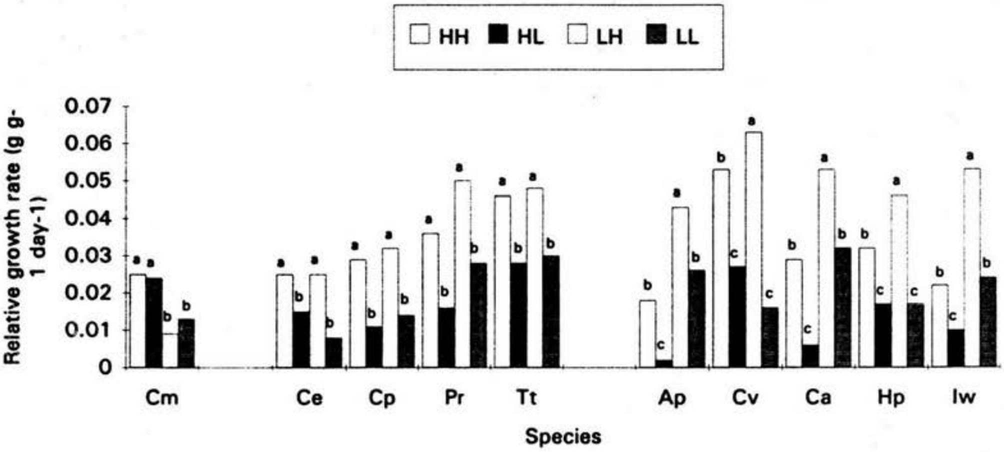

Figure 2a. Total biomass production (Biomass, g) showed by the ten species at 104 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity. Species names as in Table 1. Small letters show significant differences at $p < 0.05$ after ANOVA and Tukey multiple rank test.

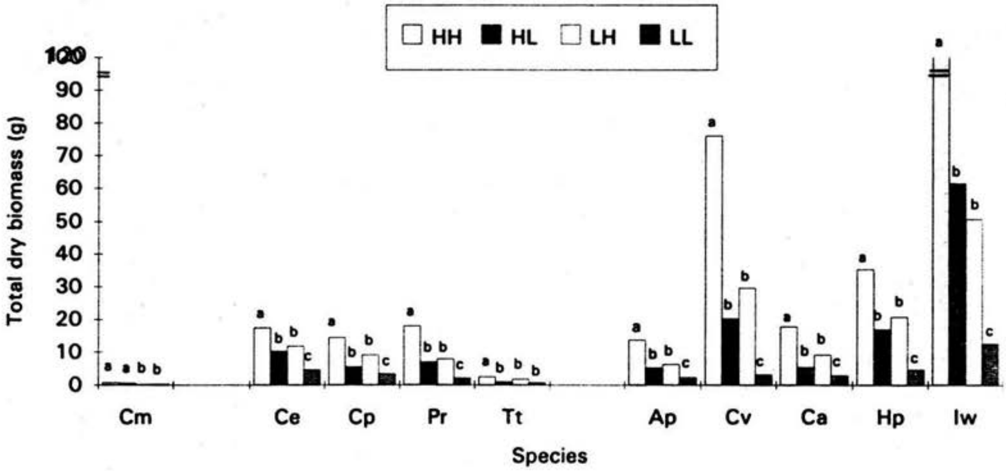

Figure 2b. Relative growth rate (RGR, g g^{-1} d^{-1}) showed by the ten species at 104 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity. Species names as in Table 1. Small letters show significant differences at $p < 0.05$ after ANOVA and Tukey multiple rank test.

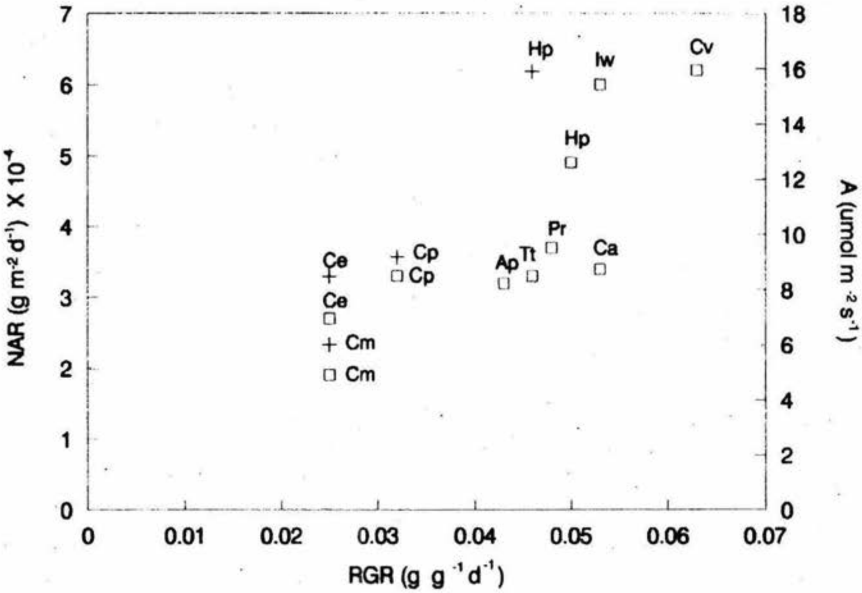

Figure 3. The relationship among the highest relative growth rate (RGR), net assimilation rate (NAR, □)and the rate of photosynthesis (A, +) showed by the species. Species names as in Table 1.

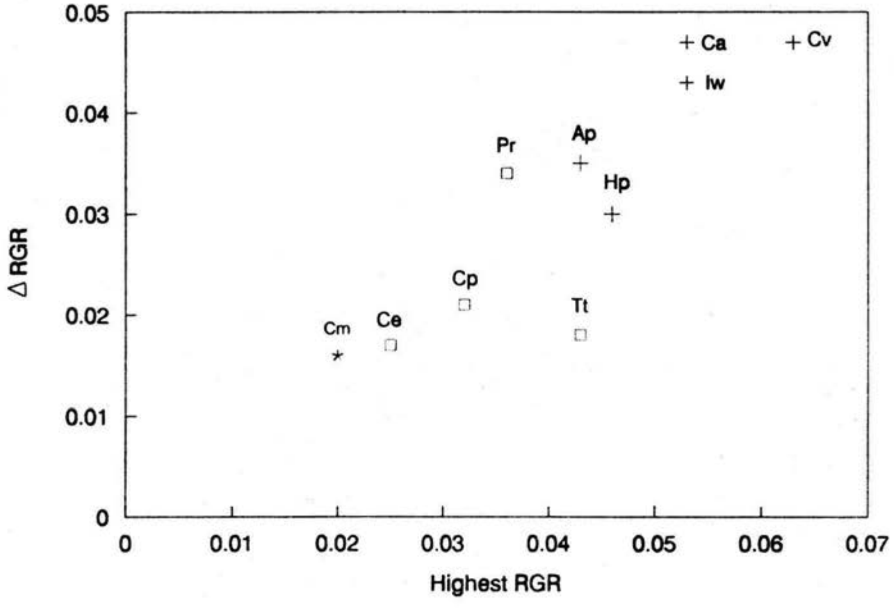

Figure 4. The relationship between the difference of the highest minus the lowest RGR (ΔRGR) and the highest relative growth rate (RGR g g^{-1} day^{-1}) showed by the species. Symbols represent the treatments where the highest RGR was attained (+ for LH, □ for HH and LH and ∗ for HH and HL). Species names are as in Table 1.

Capítulo IV

Foraging for nutrients, responses to light and competition in tropical deciduous tree-seedlings

Abstract

In this study we compare the capacity of five species to respond to changes in light intensity and the ability to search and exploit soil patches with abundance of nutrients (foraging). In addition, it is evaluated if the responses to changes in light intensity and the ability to forage for nutrients have an effect on the competitive ability of the species. Two experimental designs were used: in the first, plants were exposed to high (H) and low (L) light intensity during 42 days. At this time half of the plants from H were transferred to L (HL treatment), and half of the plants from L were transferred to H (LH). In a factorial combination with these light conditions, two soil nutrient patch treatments: fertilized (+Fp) and unfertilized (-Fp) were included. The patch consisted in a plastic net cylinder (5% of the soil volume) introduced to the soil avoiding the center of the bag. The +Fp treatment was created adding to the center of the patch 10g of fertilizer and the surrounding area was filled with soil from the forest and sand as the rest of the soil volume. Plants were growing under these conditions during another 42 days. The second design included the same light and patch treatments described above but the effect of interespecific competition between two species was included, plants were growing individually or with the presence of one plant of different species.

The studied species showed different abilities to respond to changes in light intensity and to forage for a soil nutrient patch. Three different tendencies were distinguished: 1) the slow-growing species Celaenodendron mexicanum was unable to localize and produce roots into the patch area. The responses exhibited by this species were those related with the different light conditions as: slightly higher plant dry mass and growth rate under HH and HL than under LH and LL, with thinner leaves (higher SLA) under LL and LH. 2) In the second trend are the species with intermediate growth rate, which were able to produce more root mass into the fertilized patch but only under HH and LH. The RGR and total dry mass in both species was HH > LL and the light transfer LH = HH and HL = LL. However, the total dry mass produced was: LH-Fp = HL+Fp. There was in LH a strong reduction owing to the lack of fertilized patch (LH-Fp) which eliminate the benefit of the light condition, this response suggest a change in the pattern of acclimation to light changes. 3) The third trend is exhibited by the species with the highest RGR, which showed the highest plasticity. Under LL and HL these species did not show an effect of the fertilized patch. The highest patch exploitation, productivity and RGR occurred under LH and HH (LH was even higher than HH in H. pallidus). Under LH and HH there was a strong reduction of productivity and RGR due to the absence of a fertilized patch, thus the productivity under HH-Fp and LH-Fp was similar to that under HL+Fp. Again the results suggest a modification of the acclimation pattern expected by light changes evaluated separately of nutrient resources.

When Caesalpinia eriostachys and Heliocarpus pallidus were growing in competition showed a reduction in the total mass and leaf area produced as well as the RGR attained, but even that the magnitude of the reduction was higher in H. pallidus, their biomass achieved was always higher than C. eriostachys. Both species had a benefit of the fertilized patch, in terms of dry mass and RGR, when growing alone and under HH and LH, but not in the RGR under low light conditions. The nutrient patch did not cause big changes in the characteristics of the leaves (LAR, SLA) and the proportion of dry mass allocated to them (LWR), the changes observed in theses parameters followed the expected changes caused by light levels. When growing in competition there was a general reduction of the expected benefit of the fertilized patch for the total dry mass under HH for C. eriostachys. In H. pallidus this reduction was also in the leaf area produced and the RGR. In the leaf area for H. pallidus, the pattern of acclimation to light changes growing individually corresponds to: HH+Fp and LH+Fp > LL+Fp and HL+Fp, this pattern was modified when was growing in competition: HH, HL and LH (all under +Fp) > LL+Fp.

The trends showed in this study suggest a different magnitude and pattern of plasticity among the species in response to light changes and foraging for soil nutrients, as well as the magnitude and the pattern of plasticity can be modified by the influence of a neighbour plant of another species.

Key words: growth analysis, resource allocation, acclimation, plasticity, soil nutrient patch, root foraging, tropical deciduous forest, interspecific competition

Introduction

In their natural habitat plants are exposed to continuous changes in the availability of their essential resources (light, nutrients and water). In this sense, the survival, growth and reproduction of the plants will be determined, in some extent, by their capacity to exhibit modifications in their physiology and/or morphology as response to the influence of the environment (plasticity sensu Bradshaw 1965). Numerous studies have reported how different resource availability, influence the plant growth, these studies have been conducted mainly under prevailing high vs low availability of the essential resources (Grime 1979, Chapin 1980, Denslow 1980, Björkman 1981, Augspurger 1984, Robinson and Rorison 1988, Rincón and Grime 1989, Huante et al. 1995). The responses obtained from these investigations provided information about the plastic ability of the species. In accordance, plants adapted to grow in areas with low resource availability, have low relative growth rates, low nutrient uptake rates, low biomass production, low photosynthetic rates and a constant allocation of biomass to acquire the limiting resource. In contrast, high growth and photosynthetic rate maintained by high rate of nutrient uptake, has been predicted to be the response of plants adapted to sites with abundance of resources (Grime 1979, Chapin 1980, 1988, 1991, Lambers and Poorter 1992). Recently the interest in understanding the plastic responses that exhibit the plants when are subject to changes in resources has increased. In this respect, experiments have been conducted where plants are transferred between environments with contrasting resource availabilities, and the phenotype that was subject to changes is compared in relation to the phenotype developed under prevailing high or low conditions (Grime et al. 1986, Crick and Grime 1987, Pompa and Bongers 1991, Sims and Pearcy 1991, Strauss-Debenedetti and Bazzaz 1991, Ackerly 1993). From these studies, it has been predicted that plants exposed to environments with continuous changes show a higher plastic capacity than individuals that confront occasionally changes in their environment (Pearsons 1991). A high plastic response in heterogeneous environments allows plants to allocate limiting resources in ways that maximize the absorption of the essential resources (Gersani and Sachs 1992). Grime and co-workers suggested that the expression of plasticity in changing environments is different among different species and is related with the characteristics of resource availability of the habitat where the species have been living (Grime 1979, Grime et al. 1986, Crick and Grime 1987). In accordance, when the resource availability increase, plants from habitats with low resource availability maintain its characteristic low biomass accumulation, low relative growth rate and do not modify their internal pattern of resources allocation. The plastic expression in these plants consist in maintaining active and with continuously high allocation of biomass to structures that capture the resource that is limiting their growth (e.g. large root biomass in plants from nutrient poor soils) (Grime 1979, Chapin 1980, Grime et al. 1986). Large responses to changes in resources availabilities are expected in plants from rich sites, in these plants a decrease in resources cause a reduction in productivity and growth rates. Plasticity in these species is manifested by the capacity to change continuously the allocation of biomass to structures that favor the exploration and exploitation of the highly changing environment created by the self plant activity and their neighbours (Grime et al. 1986, Crick and Grime 1987).

A particular case of changes in the availability of resources is the spatial heterogeneity of the soil nutrients that experience the root systems of wild plants, existing sites with higher abundance of nutrients (nutrient patches) than the surrounding soil volume (Chapin 1980, Grime et al. 1986, Grace 1991, Hutchings and deKroon 1994). Several plants respond to this heterogeneity showing a foraging behaviour (Drew et al. 1973, Drew 1975, Grime et al. 1986, Crick and Grime 1987, Slade and Hutchings 1987, Eissenstat and Caldwell 1988, Hutchings and Slade 1988, Jackson and Caldwell 1989, Hutchings and deKroon 1994 and references there in). In accordance to Grime et al. (1986) plasticity in plants from habitats with low stress and low disturbance is manifested throughout foraging behaviour. This behaviour consist in a continuous placement of resource-acquiring structures (fine-roots in the case of soil nutrients) into patches with higher resource abundance, which enhance the acquisition of resources (Grime et al. 1986). In this sense, the foraging response in a plant involve the search and/or ramification of structures to exploit the high resource habitats (Grime et al. 1986, Slade and Hutchings 1987).

The ability to explore, to place acquiring structures and to exploit a patch with abundance of resources is different among species (Caldwell 1994) and it can influence the competitive interactions between them (Hutchings and de Kroon 1994). In an experiment with temperate herbaceous plants, Campbell et al. (1991a, b) showed that a rapid proliferation of roots and develop of leaves in rich patches appears to confer success to fast-growing species. Eissenstat and Caldwell (1988) and Jackson and Caldwell (1989) showed in a field experiments a different magnitude and speed of root growth in response to local injection of enriched nutrient solution. The most responsive species (Agropyron desertorum) was tested to be a stronger competitor for water (Eissenstat and Caldwell 1988b).

The capacity of the species to show plastic responses is determined by the genotype and the phenotypic expression is subject to trade-off relationships between the cost to produce a structure to exploit the limiting resource and the benefit derived from this exploitation. The magnitude of the plastic response depends on the final balance between this trade-off relationship and the developmental pattern of the species. It is expected that this balance change when more than one resource is changing, in these situations relationships related with priorities of resources capture are involved. For example, in nutrient poor soils plants will invest more energy to root growth by the reduction of the allocation to the shoot and under low light intensity the growth of photosynthetic tissue will increase at expenses of root growth. These changes in the allocation of plant biomass tend to maximize the plant growth rate under the particular environmental conditions (Bloom et al. 1985). However, few studies have analyzed if a reduction in light have an effect on the ability of the roots to search and exploit soil nutrient patches (Caldwell 1994).

Most of the ecological investigations about plant responses to changes in resource availability have been conducted with temperate and mainly herbaceous plants. Temperate ecosystems have several different characteristics in relation to resource availability compared with tropical systems, these differences could be of ecological relevance. Temperate environments have large annual fluctuations of temperature and photoperiod which cause growth reduction, these ecosystems are dominated by a few number of plant species. In contrast, tropical systems have a characteristic high diversity of plant species and due to its geographical position (near the Ecuator) the temperature is less variable. In particular, the tropical deciduous forest has a characteristic seasonal pattern of precipitation which cause high restrictions in water and nutrient availability during about eight months (Murphy and Lugo 1986, Bullock 1986), this constrains plant growth and has an important effect on the deciduous character of this forest. Furthermore, the large heterogeneity in the spatial distribution of the soil nutrient availability is due, to the rain pattern, the dynamics of the organic matter decomposition and the spatially variable soil characteristics (Martínez-Yrizar 1984, Solís 1993).

The objectives of this study were to evaluate, in seedlings from the tropical deciduous forest 1) the relationship between the capacity of five species to respond to changes in light intensity and the ability to search and exploit soil patches with abundance of nutrients (foraging for nutrients), and 2) if the responses to changes in light intensity and foraging for soil nutrients have an effect on the competitive interaction of the species. Because nutrient absorption by roots is an energy requiring process and species differ in their ability to adjust desbalances in resource availabilities which could modify the competitive interactions of the species. We expect different ability to search and exploit a fertilized soil patch where higher ability is expected in the fast-growing species and a lower in the slow-growing species. Under light limitation we expect a lower ability to forage for soil nutrients, this response is predicted to be higher in the species with the highest growth. When light intensity change we predict a higher foraging response in plants that experience changes from low to high light intensities (LH) for the fast-growing species and under LH as well as continuous high light conditions (HH) for the species with intermediate growth rate; because it has been tested that under these light conditions the highest growth rate is reached (see Chapter III). In competition we expect a higher competitive success in the species with higher light plasticity and foraging response in terms of dry mass production and relative growth rate.

Materials and Methods

The experiments were conducted in the tropical deciduous forest reserve of Chamela, located at the Pacific coast of Mexico (19° 30′ N 105° 03′ W). The climate in this region is the driest end of the hot-humids (AwO(x′)), with 24.9°C mean temperature and with a characteristic seasonal pattern of precipitation (total annual average of 748 mm, 1977-1984). The rain falls between July and October, but the amount and the periodicity of rain is highly variable (annual precipitation range from 453.6 to 937.1 mm) (Bullock 1986), this variation causes changes in the availability of nutrients in the soil (Solís 1993). Spatial distribution of soil mineral nutrient content is highly variable where phosphorus is the element with higher variation (Huante et al. 1995). Plant diversity is estimated as 1120 species in 350 km^2 (Lott 1993) and 28-31 tree species ($\leq$ 10 cm DBH) per 1000 m^2 (Lott et al 1987), even higher than other deciduous forest with higher precipitation (Lott 1985).

The species studied were Caesalpinia eriostachys, Caesalpinia platyloba (Leguminosae), Celaenodendron mexicanum (Euphorbiaceae), Cordia alliodora (Borraginaceae) and Heliocarpus pallidus (Tiliaceae). These species were selected based on habitat preferences, the characteristics of their root system (Huante et al. 1992) and the relative growth rates (RGR) exhibited in previous experiments where they were grown during 60 days under contrasting nutrient availabilities; the RGR under the highest nutrient treatment are the values considered here (Rincón and Huante 1994, Huante and Rincón 1995b). Caesalpinia eriostachys is the most common species in Chamela, this species contributes to the standing-crop biomass with 37% (Matínez-Yrizar et al. 1992) and has an intermediate RGR (average 0.067 $g\ g^{-1}\ day^{-1}$). Caesalpinia platyloba is a mature forest species that has showed an intermediate RGR (0.069 $g\ g^{-1}\ day^{-1}$) and low variation in RGR at different phosphorus availabilities (Huante et al. 1995a). Celaenodendron mexicanum tends to dominate in small areas inside the forest (Martijena and Bullock 1994), seedlings of this species show a high tolerance to shade and low nutrient conditions, its RGR (0.031 g g^{-1} day^{-1}) is the lowest among the species included in this study. Cordia alliodora tends to grow in small disturbed sites (Lott 1993), its RGR is 0.088 g g^{-1} day^{-1}. Heliocarpus pallidus contributes with 1.83 % to the standing crop biomass (Martínez-Yrizar et al. 1992), has a high growth rate (0.147 g g^{-1} day^{-1}) and tends to grow in disturbed sites (Lott 1993).

The experiments were conducted in a greenhouse built in a solarium. The greenhouse was divided in two light sections: a high light treatment with an average maximum daily intensity of 1200 µmol m^{-2} s^{-1} and a low light treatment with 400 µmol m^{-2} s^{-1} (quantum sensor LI-COR, Nebraska). The light treatments were created covering the greenhouse walls with a black and white plastic screen for low and high light intensities respectively, the red:far red ratio was always higher than 1. Seeds used were collected from at least 10 trees and germinated on humid pure silica sand.

Experiment 1.

Four species with contrasting growth rates were included: Caesalpinia platyloba, Celaenodendron mexicanum, Cordia alliodora and Heliocarpus pallidus. Seedlings with three-days of germinated were transplanted to 7 kg black plastic bags filled with a mixture of soil from the forest and silica sand (1:2, v:v), these bags where designed to contain a soil patch area as showed in Figure 1a. The soil patch (Fig. 1) was constructed with plastic net forming a cylinder (5 cm of diameter and 8 cm of length, corresponding to 5% of the total soil volume). Two treatments in this patch were tested (with and without fertilization), in both treatments the cylinders were filled with the same mix of soil:sand as in the rest of the bag, but in one treatment, the cylinder included 10 g of gradual liberation fertilizer (Osmocote 14-14-14) located in the center of the patch and avoiding 1 cm in both top and bottom, in order to compensate for nutrient diffusion, this corresponded to the fertilized patch treatment (+Fp). The unfertilized patch treatment (-Fp) corresponded to those bags that contained a cylinder without fertilizer addition as showed in the Fig. 1. The position of the patch into the plastic bag was avoiding the center of the bag, place that was reserved to the seedling (Fig. 1), in that way the exploration of the patch is not expected to occur by the main root by gravity, but throughout ramification of lateral root growth. Tap water was supplied to the plants every day.

The patch treatments were run in a factorial combination with low (L) and high (H) light conditions. After 42 days of growth, half of the plants under H were transferred to L (HL treatment) and the half under L were transferred to H (LH treatment), maintaining the respective controls under high (HH) and low (LL) light intensity. The time of light transfer was selected considering that from the maximum to the minimum photosynthetically active radiation (PAR) registered in the forest from leafless to leafed takes between 35 and 75 days (1984-1988, Barradas 1991). The plants were growing under these last conditions during another 42 days. Thus, the total growth period of the experiment was 84 days. Five plant replicates per all of the possible combinations between the two patch treatments and the four light conditions were included.

Experiment 2

The design involved the same light (HH, HL, LH and LL) and patch (-Fp and +Fp) treatments mentioned in the experiment 1 but, in addition, interspecific competition was included in factorial combination with light and soil patch treatments. The species studied were Caesalpinia eriostachys and Heliocarpus pallidus. Treatments consisted in seedlings growing alone and in competition with the other species. In this experiment, the position of the patch was located in the center of the plastic bag and the seedlings were transplanted to an opposite position one each other avoiding the center of the bag as showed by the Fig. 1b, this arrangement give, to both species, the same probability of reach the soil patch. The duration of the experiment was a little longer than the experiment 1, three days old seedling were transplanted to the bags at three days, the light transfer treatments were realized after 50 days of growth and the total growth period was of 100 days. Five pots per treatment were included.

In both experiments three harvests were conducted, an initial realized after 3 days of seed germination (at time of transplanting), an intermediate conducted after 42 or 50 days of growth (experiment 1 and 2 respectively) and a final harvest after 84 and 100 days of growth (experiment 1 and 2 respectively). In each harvest the whole root system was carefully obtained using water and sieves to facilitate the separation of the soil particles and the roots inside the soil patch were separated. The separation of roots by species was facilitated by the dark brown and white root colour of Caesalpinia eriostachys and Heliocarpus pallidus, respectively. Plant shoot was separated in stems and leaves and the leaf area per plant was measured (Delta-T, England). All plant parts were dried in at 80ºC oven during 48 hours and weighted.

The following parameters were calculated according with Evans (1972) and Hunt (1982): the dry mass accumulation, the root dry mass inside the soil patch, the relative growth rate (the dry mass production per unit of time, RGR), the leaf area ratio (the ratio of total leaf area to whole plant dry mass, LAR), specific leaf area (the proportion of leaf area by leaf dry mass, SLA), leaf weight ratio (the proportion of leaf dry mass by the total plant dry mass, LWR) and the root/shoot ratio (dry mass accumulated in the root compared with the mass in the shoot, R/S).

For experiment 1, treatment effects in all parameters were tested by two way analysis of variance, at 42 and 84 days separately, with soil patch and light condition as factors. In the experiment 2 a three-way analysis of variance was used with soil patch, light condition and competition status as factors, for data at 50 and 100 days of growth separately. In both experiments log-transformed data were used when needed to meet the assumptions of the analysis, means were tested by Tukey multiple comparisons (Zar 1974).

Results

Experiment 1

The species studied showed a contrasting capacity to localize root biomass into the soil patch (explore) and to obtain a benefit from the fertilized patch (exploit). The responses exhibited to changes in light intensity were also different among species, showing in some of them an interaction between both light condition and foraging capacity.

Celaenodendron mexicanum

This species was the only one that, at any time and light condition, did not produce root mass inside the soil nutrient patch (Fig. 2a). At 42 days, the total dry mass produced and the RGR were higher under H than under L (Figs. 2a,b). The total leaf area produced (LA), the LAR and SLA were higher under L independently of the nutrient patch treatments. At 84 days of growth the total dry mass and the RGR were higher under HH and HL and lower under LH and LL but were unresponsive to the nutrient patch (Fig. 3). The LAR was higher under LL and HL (-FP and +FP). At both 42 and 84 days the LWR and R/S ratio were unresponsive to all treatments (Table 1 and 2).

Rest of the species at 42 days

The patch dry mass, total dry mass and RGR were the highest under H+Fp and the lowest under L but without patch effect (Fig. 2). The LA was the highest under H+Fp and not different of L+Fp in Caesalpinia platyloba and Cordia alliodora (Table

1). The LAR and SLA were unresponsive to the fertilized patch and higher under L than H. The LWR was the lowest under H-Fp and non different in the rest conditions. The R/S ratio was the highest under H-Fp and non-different in the rest conditions except in Cordia alliodora where H-Fp=H+Fp, no patch effect was showed under L (Table 1)

Rest of the species at 84 days

For the three species, the biomass into the patch was +Fp > -Fp only in the light conditions HH and LH. The highest value was under HH+Fp = LH+Fp for Caesalpinia platyloba and Cordia alliodora and under LH+Fp for Heliocarpus pallidus. The total dry biomass produced and the RGR of Caesalpinia platyloba were unresponsive to the fertilized patch. In the resting two species the dry biomass was the highest under HH+Fp and the RGR had a patch effect only in HH and LH. In Heliocarpus pallidus LH+Fp was the treatment with the highest RGR (Fig. 3).

The plant leaf area was higher in all light conditions +Fp than -Fp excepting the LL and the LH for Caesalpinia platyloba. The highest leaf area was under HH+Fp. In general, the LAR and SLA were unresponsive to patch treatments (except the LAR under LL for H. pallidus and the SLA under HL in C. platyloba) and their variations were associated to light changes as follows: LL = HL >LH = HH. Slightly changes were showed by Caesalpinia platyloba (HL-Fp > HL+Fp), Cordia alliodora (LH-Fp > LH+Fp) and Heliocarpus pallidus (LL-Fp > LL+Fp), in the rest of the treatments were non-different. The highest R/S ratios were under HH and the lowest under LL (without patch effect) in Caesalpinia platyloba and Cordia alliodora. (Table 2).

Experiment 2

Both species Caesalpinia eriostachys and Heliocarpus pallidus responded to light changes and foraging behaviour and were affected by the interspecific competition. Although the magnitude of the response and the growth parameters affected differed between these species.

Caesalpinia eriostachys

At 50 days of growth (just before the light transfers), the root mass into the soil patch of plants growing individually and in competition, was the highest under H+Fp and non different among the rest of the treatments (Table 3). The total dry mass, RGR and leaf area were H+Fp > H-Fp at both growing alone or in competition, however under L in these parameters were L+Fp > L-Fp growing alone and L+Fp = L-Fp growing in competition (Table 3). Growing individually and in competition there was a patch effect for the LAR under L (L+Fp > L-Fp) but not under H (Table 3). The SLA was higher under L than H, but did not show significant patch and competition effects in both light treatments. The LWR was unresponsive to the light conditions, but was +Fp > -Fp. The R/S ratio was -Fp > +Fp under both H and L and in competition (Table 3).

At 100 days of growth, HL was the only light treatment that did not show a significant effect of the patch with respect to the root mass into the patch, for the other light treatments this root mass was +Fp > -Fp, the highest values were showed under HH+Fp and LH+Fp and the lowest under LL-Fp. In competition the values under LH (in both + and - Fp) were reduced (Table 4). The total dry mass produced was always higher under +Fp (Table 4). The highest production of dry mass was under HH+FP > LH+Fp. In competition the dry mass was HH+FP = HL+Fp = LH+Fp. The RGR was the highest under HH+Fp = LH (in both + and -Fp), in competition RGR under LH+Fp and HL+Fp has an increment (Table 4). The RGR under LL and did not show a patch and competition effect.

The total leaf area produced had a patch effect (+Fp > -Fp) in all light treatments growing alone, but LL-Fp = LL+Fp when in competition. The highest value was showed under HH+Fp and the lowest in all light conditions with -Fp. Competition caused a reduction in leaf area under HH+Fp and LH+Fp, owing to this reduction the leaf area was under HH+Fp = HL+Fp and LH+Fp < HL+Fp. The highest LAR and SLA was showed under LL (+Fp and -Fp) than for the other light conditions. Competition only caused a reduction in LAR under HH-Fp. The R/S ratio was higher in -Fp, showing the largest patch response under HH and the lowest under HL and LL. In competition the R/S ratio under LH+Fp and HH-Fp was higher than growing individually (Table 4).

Heliocarpus pallidus

At 50 days of growth, when was growing alone the root mass into the patch was the highest under H and the lowest only at L-Fp, but in competition L-Fp = L+Fp. The root biomass into the patch under H+Fp was higher in competition (Table 3). The total dry mass did not show modifications by competition and was the highest under H+Fp and the lowest under L-Fp. The RGR and the leaf area produced showed a light and patch effect: H+Fp > H-Fp > L+Fp = L-Fp, but for L-Fp the leaf area in competition was higher than growing alone (Table 3). In the LAR and SLA there was a non-significant effect of the nutrient patch, the differences showed among treatments were due to light treatments when was growing alone but in competition H-Fp > H-Fp. The LWR was the lowest in H-Fp, but in competition H-Fp = H+Fp. The R/S ratio was the lowest under L+Fp in competition and the highest under H-Fp (Table 3).

At 84 days, the root dry mass into the patch was the highest under HH+Fp and LH+Fp growing alone but only under HH+Fp (LH+Fp was reduced) when in competition (Table 4). The total dry mass and leaf area at both alone and in competition were +Fp > -Fp in all light conditions, HH+Fp = LH+Fp and were the highest values. Competition caused a reduction in all of the treatments (except HL+Fp). There was a patch effect on RGR only under LH and HL, the highest RGR was under LH+Fp growing alone and the lowest under HL-Fp, competition only caused a reduction in RGR under HL+Fp (Table 4). In the LAR there was not effect of the patch in all light treatments growing alone and in competition. The highest LAR was under LL and HL and the lowest under LH and HH (Table 4). In competition the LAR was HL+Fp < HL-Fp. The SLA showed a similar light trend, but LL-Fp > LL+Fp and in competition LH-Fp > LH+Fp (Table 4). The LWR was the highest in HL+Fp and no patch effect was showed in the rest of the treatments. This significant difference between HL-Fp and HL+Fp and the light effect were lost in competition (Table 4). The R/S ratio was under -Fp > -Fp for HH and LH. In competition the R/S ratios increased under HH+Fp and HL+Fp (Table 4).

Discussion

This study shows evidence about the different ability of the species studied to respond to changes in light intensity and to forage for soil nutrients with a patchy distribution. Several studies have separately documented plant responses to changes in light intensity and the ability of plants to show a foraging behaviour. With respect to changes in light intensity it has been documented that shade (low light intensity) plants have a lower RGR than sun (high light intensity) plants. When plants from high light are transferred to low light (HL) its RGR, productivity and photosynthetic capacity is lower than plants under high light. In contrast when plants developed under low light conditions are transferred to high light (LH) they reach a similar or even higher RGR and productivity than those plants under high light (Rice and Bazzaz 1989, Sims and Pearcy 1989, Denslow et al. 1990, Pompa and Bongers 1991, Turnbull et al. 1993). In addition it has been suggested that shade plants are able to acclimate rapidly to sun conditions, but high light plants acclimate slowly to shade (Pompa and Bongers 1991). Several studies have documented a proliferation of roots with an increase of root branching, biomass and the uptake of nutrients in soil patches with high resource abundance (Drew 1975, Drew and Saker 1975, Grime et al. 1986, Crick and Grime 1987, Hutchings 1988, Eissenstat and Caldwell 1988a, b, Jackson and Caldwell 1989, Caldwell et al. 1991, Caldwell 1994, Grime 1994, Fitter 1994, Hutchings and de Kroon 1994 and references there in). A general increase of root functions cause a benefit in plant growth, even that often the soil volume of the rich patch is only a small proportion of the total soil volume available for the plant (Chapin 1980, Grime et al. 1986, Caldwell et al. 1991).

The exploitation of below-ground resources (as the ability to forage for soil-patches with high resource availability) depends on the resources captured above-ground, because the different root functions involves energy-demanding processes. The relationship between light availability and root foraging behaviour has been studied by Jackson and Caldwell (1992) and in this study. Jackson and Caldwell (1992) showed a higher uptake of phosphate in plants growing in enriched soil patches than those under non-enriched patches when growing under high light intensity, but this response in phosphate uptake was not evident when plants were shaded. In the study reported here, the root foraging for a fertile patch was influenced by changes in light intensity. A differential capacity to respond to both light changes and patchy distributed soil nutrients was found among species. These differences were exhibited in the amount (i. e. magnitude of the response) as well as the pattern of plasticity (direction of the response) (Kuiper and Kuiper 1988).

Grime et al. (1986) proposed that plasticity in slow-growing species is manifested throughout the ability to obtain benefit from short-time pulses with high abundance of resources more than to exploit high-resource patches. In these species the exploitation of rich pulses is possible due to their capacity to maintain active its long-lived structures of resources capture, the duration of the rich pulses often is insufficient to achieve morphological changes as those needed to exploit a rich soil patch (Grime et al. 1986, Crick and Grime 1987, Campbell and Grime 1989, Grime 1994). In this study the species with the slowest RGR (Celaenodendron mexicanum) was the only species unable to encounter the fertilized patch (looking at the lack of root mass into the soil patch) at any light condition. This could be due, in some extent to its low RGR and the characteristics of their root system, as described earlier by Huante et al. (1992) has a low rooting density. The responses showed by this species were those related with light conditions and exhibited a lower plasticity in RGR and an opposite pattern of light acclimation (HH = HL and LH = LL) compared with the rest of the studied species. In addition, Celaenodendron mexicanum produces thinner leaves (higher SLA) under LL and LH, which suggest certain tolerance to shade.

In response to changes in light intensity it has been documented a higher acclimation in growth and photosynthesis of plants transferred from low to high (LH) than from high to low (HL), as well as the growth and photosynthesis of LH plants is similar or even higher to those plants under HH (Rice and Bazzaz 1989, Simas and Pearcy 1989, Denslow et al. 1990, Pompa and Bongers 1991, Turnbull et al. 1993, Ackerly 1993). Those responses could be due to a higher return in carbon investment of the shade leaves than sun leaves, owing to their lower C investment per unit of leaf area (Sims and Pearcy 1991) and to the rate of leaves production (Ackerly 1993). As predicted in this study, under the light conditions (LH and HH) with a higher response to light, there was a strong reduction of plant mass and RGR due to the absence of a fertilized patch, in a way that the plant dry mass of Caesalpinia eriostachys under LH-Fp = HL+Fp due to a strong reduction under LH-Fp, in Heliocarpus pallidus the RGR and dry mas under HH-Fp and LH-Fp was similar to HL+Fp again due to a strong reduction caused by the absence of a fertilized patch. This suggest a modification of the expected pattern of acclimation to light changes. It has been documented that when light is reduced the plant reduce first the root growth than the rate of respiration (Crapo and Ketellapper 1981) which leads to a reduction in nutrient demand, an increase in the shoot/root ratio and a general reduction of the root function (Lambers et al. 1990). So, plant shading can reduce the growth rate of both shoot and root and consequently the demand for nutrients is reduced. In this study the root biomass allocated to the patch was reduced when light intensity decreased (HL treatment). In the species with high RGR and high plasticity there were indications of an increase in LAR and SLA and a higher allocation of biomass to the shoot (lower R/S ratio) under LL and HL, characteristic that favour a higher light harvesting (Lambers and Poorter 1992).

In soils with high abundance of nutrients distributed in patches, as those experienced by wild plants, where there are sites (Chapin 1980, Grime et al. 1986, Eissenstat and Caldwell 1988, Hutchings and de Kroon 1994), it can be expected a strong competition among individuals to place their roots and exploit the high-resources patches. High nutrient patches can rapidly be occupied by species with morphologically responsive root systems as those of the species with high growth rate. However, these fast-growing species are highly affected by the reduction of any of their essential resources, and it could be expected that different species showed different sensitivity to resource reductions and thus a different capacity to acquire above and below-ground resources (Lambers and Poorter 1992, Caldwell 1994). In this sense, the presence of a neighbour exploiting a soil patch with high resource abundance could modify in different magnitude the exploitation of their competing plant through the reduction of the resources availables (Grime et al. 1986). It has been documented that fast-growing species have a higher productivity than slow-growing species, this difference is maintained even at low resource availabilities (Lambers and Poorter 1992). Both Caesalpinia eriostachys and Heliocarpus pallidus growing in competition showed a reduction in the total mass and leaf area produced as well as the RGR attained, but even that the magnitude of the reduction was higher in H. pallidus, the biomass achieved was always higher than C. eriostachys. H. pallidus has been tested to show a higher plasticity in growth rate and biomass production under different light intensities (Rincón and Huante 1993), whole nutrients (Rincón and Huante 1994, Huante et al. 1995b) and phosphorus (Huante et al. 1995a).

Both species benefited of the fertilized patch in terms of dry mass and RGR, when growing alone and under HH and LH, but not in the RGR under low light conditions. The nutrient patch did not cause big changes in the characteristics of the leaves (LAR, SLA) nor in the proportion of dry mass allocated to them (LWR); the changes observed in these parameters followed the expected changes caused by light levels. The main effect of competition for C. eriostachys was the reduction of the exploitation of the fertilized patch on the total dry mass produced under HH. The influence in the amount of root proliferation in fertile soil patches by the presence of roots of other species has been previously documented (Caldwell et al. 1991 a, b). In H. pallidus the competition caused a reduction in dry mass (even under -Fp), leaf area and in lower extent in RGR, it appears that the mass production and leaf area of H. pallidus is more affected by competition than C. eriostachys. The pattern of acclimation to light changes showed in the leaf area produced when H. pallidus was growing individually corresponds to: HH+Fp = LH+Fp > LL+Fp = HL+Fp; this pattern was modified when was growing in competition as follows: HH = HL = LH (all under +Fp) > LL+Fp; thus, competition caused a reduction of leaf area in the more productive conditions (HH+Fp and LH+Fp). As growing individually, in this species, there were no big effects on the LAR, SLA and LWR, suggesting the existence of bellow ground competition more than a strong shading between species. It has been documented in previous studies that even in conditions where there is a clear competition for light, root competition can be more pronounced (Martin and Field 1984, Cook and Ratcliff 1985). Experiments about root competition for high nutrient patches conducted by Caldwell and co-workers have suggested interference in the root systems of the competing species by different root densities and speed of growth of the species (Caldwell et al. 1991a, Eissenstat and Caldwell 1988); however, those densities were not proportional to the exploitation of P by the species (Caldwell et al 1991b). Other studies (Drew et al. 1973, Hutchings & de Kroon 1994, Caldwell et al. 1991, De Jager & Posno 1979, Drew & Saker 1975, Birch & Hutchings 1994) showed that whole plant growth in a patchy environment can be similar to, or even higher than in an environment in which the same supply of resources is uniformely distributed.

This study in address how can be affected the root foraging capacity of different species by changes in light intensity and by the activity of neighbours. At the same time how the acclimation responses to light changes can be influenced by the capacity to exploit a soil rich patch. The study suggest a different magnitude and direction (i.e. pattern of response) of the plastic abilities among the species with respect to light changes and foraging for soil nutrients. Also, the magnitude and the direction of plasticity can be modified by the influence of a neighbour plant of another species. In systems such as the tropical deciduous forest where there is heterogeneity of soil (Solís 1993) and light (Barradas 1991) resources, the plant success could be determined, in some extent, by its growth responses to confront the heterogeneity in resources and the influence of neighbours.

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Table 1. Total leaf area (LA, cm^2), leaf area ratio (LAR, cm^2/g), specific leaf area (SLA, cm^2/g), leaf weight ratio (LWR, $g\ g^{-1}$) and root/shoot ratio (R/S) showed by the four species at 42 days of growth under high (H) and low (L) light intensity combined in a factorial design with a unfertilized (-Fp) an fertilized (+Fp) nutrient patch. Species names as follows: Cp = *Caesalpinia platyloba*, Cm= *Celaenodendron mexicanum*, Ca= *Cordia alliodora* and Hp = *Heliocarpus pallidus*. Small letters show significant differences ($p<0.05$) between treatments by species as indicated by the underlines.

	Cp		**Cm**		**Ca**		**Hp**	
	-Fp	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**
LA								
H	167.6^{b}	282.40^{a}	15.28^{b}	23.72^{b}	35.05^{b}	57.11^{a}	157.94^{b}	439.29^{a}
L	222.2^{b}	303.61^{a}	29.82^{a}	29.53^{a}	33.68^{b}	60.11^{a}	114.08^{b}	147.40^{b}
LAR								
H	104.27^{b}	140.89^{b}	96.70^{b}	111.03^{b}	115.4^{b}	157.05^{b}	214.95^{b}	237.61^{b}
L	142.05^{b}	192.94^{a}	238.60^{a}	258.10^{a}	223.5^{a}	268.74^{a}	401.64^{a}	438.84^{a}
SLA								
H	195.1^{c}	263.10^{b}	199.28^{b}	195.53^{b}	240.72^{b}	298.92^{b}	431.61^{b}	411.22^{b}
L	375^{a}	396.06^{a}	431.55^{a}	479.23^{a}	403.72^{a}	467.56^{a}	658.24^{a}	718.17^{a}
LWR								
H	0.37^{b}	0.53^{a}	0.48^{a}	0.573^{a}	0.486^{b}	0.524^{a}	0.495^{b}	0.578^{a}
L	0.53^{a}	0.49^{a}	0.55^{a}	0.544^{a}	0.555^{a}	0.574^{a}	0.610^{a}	0.616^{a}
R/S								
H	0.53^{a}	0.355^{b}	0.44^{a}	0.312^{a}	0.69^{a}	0.63^{a}	0.56^{a}	0.26^{b}
L	0.33^{b}	0.34^{b}	0.40^{a}	0.396^{a}	0.51^{b}	0.44^{b}	0.24^{b}	0.23^{b}

Table 2. Total leaf area (LA, cm^2), leaf area ratio (LAR, $cm^2\ g^{-1}$), specific leaf area (SLA, $cm^2\ g^{-1}$), leaf weight ratio (LWR, $g\ g^{-1}$) and root/shoot ratio (R/S) showed by the four species at 84 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity combined in a factorial design with a unfertilized (-Fp) and fertilized (+Fp) soil nutrient patch. Species names as in Table 1. Small letters show significan differnces ($p<0.05$) among treatments by species as indicated by the underlines.

	Cp		**Cm**		**Ca**		**Hp**	
	-Fp	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**	**- Fp**	**+Fp**
LA								
HH	328.8^{b}	459.3^{a}	47.93^{b}	82.92^{a}	172.51^{e}	438.5^{a}	789.2^{d}	1704^{a}
HL	289.3^{b}	533.6^{a}	38.88^{b}	104.8^{a}	173.24^{e}	233.98^{c}	448.9^{c}	1083^{c}
LH	352.5^{b}	366.5^{b}	32.20^{b}	53.90^{b}	254.54^{c}	324.6^{b}	856.8^{d}	1455^{b}
LL	323.8^{b}	284.1^{b}	34.07^{b}	38.55^{b}	194.20^{e}	210.9^{ce}	474.1^{e}	289.4^{e}
LAR								
HH	49.5^{b}	58.38^{b}	98.16^{b}	130.5^{b}	71.88^{b}	56.61^{b}	80.74^{c}	70.94^{c}
HL	84.2^{a}	101.86^{a}	171.92^{a}	178.3^{a}	125.6^{a}	115.89^{a}	101.5^{b}	125.9^{ab}
LH	64.8^{b}	58.58^{b}	124.53^{b}	135.3^{b}	93.11^{ab}	70.43^{b}	92.23^{b}	97.14^{b}
LL	100.5^{a}	96.94^{a}	186.28^{a}	164.4^{a}	124.6^{a}	102.69^{a}	138^{a}	105.3^{b}
SLA								
HH	156.4^{c}	167.2^{bc}	205.77 b	228.6^{b}	202.5^{c}	189.3^{c}	251.53^{b}	245^{b}
HL	202.1^{b}	281.1^{a}	225.7^{b}	226.6^{b}	301.1^{a}	272.48^{a}	365.73^{a}	371.6^{a}
LH	195.7^{b}	188.3^{b}	263.4^{a}	297.4^{a}	241.2^{bc}	205.96^{c}	263.32^{b}	294.5^{b}
LL	258.9^{a}	255.67^{a}	283.3^{a}	285.8^{a}	327.7^{a}	269^{ab}	455.55^{a}	376.4^{a}
LWR								
HH	0.32^{b}	0.35^{b}	0.48^{a}	0.57^{a}	0.348^{b}	0.30^{b}	0.28^{b}	0.289^{b}
HL	0.42^{a}	0.26^{c}	0.52^{a}	0.60^{a}	0.407^{a}	0.42^{a}	0.32^{a}	0.340^{a}
LH	0.33^{b}	0.31^{b}	0.48^{a}	0.60^{a}	0.382^{a}	0.34^{b}	0.35^{a}	0.331^{a}
LL	0.39^{a}	0.38^{a}	0.46^{a}	0.58^{a}	0.378^{a}	0.38^{a}	0.32^{a}	0.279^{b}
R/S								
HH	0.54^{a}	0.56^{a}	0.52^{a}	0.43^{a}	1.48^{a}	1.68^{a}	0.74^{b}	0.56^{c}
HL	0.53^{a}	0.38^{b}	0.46^{a}	0.41^{a}	1.12^{bc}	1.05^{c}	0.91^{a}	0.44^{c}
LH	0.59^{a}	0.50^{a}	0.61^{a}	0.48^{a}	1.26^{b}	1.41^{ab}	0.48^{c}	0.47^{c}
LL	0.44^{b}	0.42^{b}	0.43^{a}	0.35^{a}	1.70^{a}	1.05^{c}	0.84^{a}	0.98^{a}

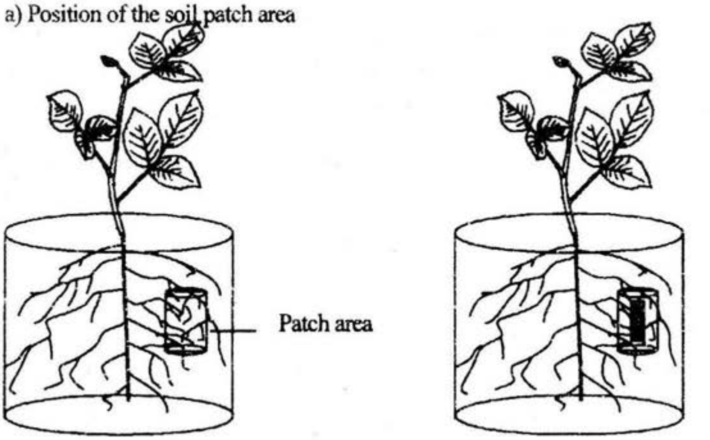
Table 3. Total dry mass into the soil nutrient patch (g), total dry mass production (g), total leaf area (LA, cm^{2}), leaf area ratio (LAR, cm^{2} g^{-1}), specific leaf area (SLA, cm^{2} g^{-1}), leaf weight ratio (LWR, g g^{-1}) and root/shoot ratio (R/S) showed by the four species at 50 days of growth under high (H) and low (L) light intensity combined in a factorial design with a unfertilised (-Fp) an fertilised (+Fp) nutrient patch. Species names as follows: Ce = *Caesalpinia eriostachys* growing individually Ce-Hp = Ce growing in competition with Hp, Hp = *Heliocarpus pallidus* growing individually and Hp-Ce= Hp growing in competition with Ce. Small letters show significant diferences among treatments ($p<0.05$) as indicated by the underlines.

	Ce		**Ce-Hp**		**Hp**		**Hp-Ce**	
	-Fp	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**
Patch dry mass								
H	0.014^{b}	0.05^{a}	0.010^{bc}	0.058^{a}	0.0096^{b}	0.009^{b}	0.007^{bc}	0.026^{a}
L	0.011^{b}	0.024^{ab}	0.009^{bc}	0.0076^{c}	0.0034^{c}	0.0076^{b}	0.004^{c}	0.003^{c}
Dry mass								
H	2.54^{bc}	5.7^{a}	2.36^{bc}	5.50^{a}	1.27^{b}	4.60^{a}	0.93^{bc}	5.03^{a}
L	1.5^{c}	2.91^{b}	1.53^{c}	1.84^{c}	0.58^{c}	1.79^{b}	0.66^{c}	1.44^{b}
RGR								
H	0.061^{b}	0.077^{a}	0.06^{b}	0.077^{a}	0.18^{b}	0.21^{a}	0173^{bc}	0.207^{a}
L	0.051^{c}	0.064^{b}	0.051^{c}	0.054^{bc}	0.16^{c}	0.18^{b}	0.167^{c}	0.178^{b}
LA								
H	215^{c}	558.37^{a}	195.80^{c}	559.1^{a}	256^{c}	1027.4^{a}	213.8^{c}	924.2^{a}
L	218.8^{c}	553.9^{a}	229.9^{bc}	326.7^{b}	235.2^{c}	664.48^{b}	270.1^{b}	604.4^{b}
LAR								
H	86.44^{c}	96.04^{c}	85.34^{c}	101.63^{c}	203.3^{bc}	229.13^{b}	234.3^{b}	184.1^{c}
L	149.5^{b}	190.46^{a}	147.8^{b}	176.7^{a}	407.77^{a}	397.56^{a}	410.66^{a}	455.8^{a}
SLA								
H	267.6^{cd}	242.5^{bc}	275.9^{c}	237.8^{bc}	440.2^{c}	418.9^{c}	512^{b}	400.8^{c}
L	391.7^{a}	403.22^{a}	402.42^{a}	395.3^{a}	740.7^{a}	709.34^{a}	802.77^{a}	780.5^{a}
LWR								
H	0.32^{cd}	0.40^{bc}	0.31^{d}	0.43^{ab}	0.46^{c}	0.55^{ab}	0.458^{c}	0.459^{c}
L	0.38^{c}	0.47^{ab}	0.37^{c}	0.45^{ab}	0.55^{ab}	0.56^{a}	0.511^{ab}	0.582^{a}
R/S								
H	0.74^{a}	0.44^{bc}	0.79^{a}	0.35^{c}	0.51^{a}	0.25^{b}	0.51^{a}	0.31^{b}
L	0.46^{b}	0.27^{d}	0.39^{bc}	0.28^{d}	0.27^{b}	0.19^{c}	0.20^{c}	0.12^{d}

Table 4. Total dry mass into the soil nutrient patch (g), total dry mass production (g), the relative growht rate (RGR, g g^{-1} day^{-1}), total leaf area (LA, cm^2), leaf area ratio (LAR, cm^2 g^{-1}), specific leaf area (SLA, cm^2 g^{-1}), leaf weight ratio (LWR, g g^{-1}) and root/shoot ratio (R/S) showed by the four species at 100 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity combined in a factorial design with a unfertilized (-Fp) and fertilized (+Fp) soil nutrient patch. Species names as in Table 3. Small letters show significant differences among treatments ($p<0.05$) as indicated by underlines.

	Ce		**Ce-Hp**		**Hp**		**Hp-Ce**	
	-Fp	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**	**-Fp**	**+Fp**
Patch dry mass								
HH	0.031^{d}	0.15^{a}	0.049^{c}	0.11^{a}	0.034^{cd}	0.53^{a}	0.021^{d}	0.478^{a}
HL	0.033^{cd}	0.046^{c}	0.063^{b}	0.077^{b}	0.057^{c}	0.037^{c}	0.177^{c}	0.056^{c}
LH	0.036^{d}	0.10^{a}	0.017^{e}	0.032^{d}	0.040^{c}	0.48^{a}	0.0196^{de}	0.281^{b}
LL	0.017^{e}	0.048^{c}	0.065^{b}	0.03^{d}	0.034^{cd}	0.075^{c}	0.0168^{de}	0.029^{d}
Dry mass								
HH	3.91^{e}	20.99^{a}	5.99^{d}	14.22^{b}	8.74^{d}	37.40^{a}	6.06^{e}	25.28^{b}
HL	3.41^{e}	7.80^{cd}	3.42^{e}	11.72^{b}	6.87^{e}	15.67^{c}	3.91^{f}	14.34^{c}
LH	5.57^{d}	11.41^{b}	5.97^{d}	10.2^{b}	8.73^{d}	35.68^{a}	6.20^{e}	28.23^{b}
LL	4.01^{e}	6.98^{c}	3.37^{e}	4.56^{d}	6.64^{b}	14.05^{c}	4.34^{f}	10.50^{d}
RGR								
HH	0.0068^{d}	0.026^{b}	0.018^{c}	0.018^{c}	0.039^{c}	0.042^{c}	0.035^{cd}	0.032^{c}
HL	0.0064^{d}	0.007^{d}	0.007^{d}	0.014^{cd}	0.034^{d}	0.024^{e}	0.029^{d}	0.019^{f}
LH	0.027^{b}	0.028^{b}	0.026^{b}	0.034^{a}	0.055^{b}	0.065^{a}	0.044^{b}	0.063^{a}
LL	0.018^{c}	0.017^{c}	0.016^{c}	0.017^{c}	0.049^{bc}	0.046^{c}	0.037^{cd}	0.042^{c}
LA								
HH	221.2^{e}	1178.1^{a}	204.1^{e}	755.5^{b}	766.9^{e}	3053.5^{a}	417.1^{f}	1897^{b}
HL	254^{d}	587.93^{c}	202.5^{e}	757.2^{b}	1051^{d}	2440^{b}	597.9^{ef}	1506^{bc}
LH	285.9^{d}	740.00^{b}	301.9^{d}	571.3^{c}	845.6^{e}	3041.8^{a}	517^{f}	1792^{b}
LL	328.5^{d}	543.5^{c}	301^{d}	441.1^{cd}	928.8^{d}	1979^{b}	576.5^{ef}	1384^{c}
LAR								
HH	60.77^{bc}	55.59^{c}	34.80^{d}	56.17^{c}	87.63^{cd}	81.47^{cd}	80.49^{cd}	77.44^{cd}
HL	74.94^{b}	75.71^{b}	60.26^{bc}	69.56^{bc}	154.3^{a}	168.52^{a}	157.20^{a}	117.3^{b}
LH	51.46^{c}	64.23^{bc}	52.87^{c}	53.66^{c}	98.6^{bc}	85.41^{cd}	84.47^{cd}	71.98^{d}
LL	82.71^{ab}	78.69^{ab}	90.73^{a}	93.49^{a}	138.9^{a}	140.2^{a}	136.2^{ab}	134.6^{ab}
SLA								
HH	218.9^{b}	184.26^{c}	206.22^{c}	188.3^{c}	379.5^{cd}	315.39^{d}	354.4^{d}	299.4^{de}
HL	253.7^{b}	218.7^{bc}	253.11^{b}	221.7^{bc}	559.1^{ab}	513.54^{b}	558.6^{ab}	430.8^{bc}
LH	233.6^{b}	237.4^{b}	255.29^{b}	230.2^{b}	397.3^{cd}	328.3^{d}	347.96	260.1^{e}
LL	309^{a}	296.72^{a}	342.79^{a}	322.1^{a}	605^{a}	511.9^{b}	560.5^{ab}	495.2^{bc}
LWR								
HH	0.28^{bc}	0.30^{ab}	0.168^{d}	0.298^{ab}	0.23^{c}	0.26^{bc}	0.226^{c}	0.257^{bc}
HL	0.29^{ab}	0.35^{ab}	0.237^{c}	0.312^{ab}	0.28^{b}	0.32^{a}	0.277^{b}	0.271^{bc}
LH	0.22^{cd}	0.27^{bc}	0.208^{cd}	0.235^{c}	0.25^{bc}	0.26^{bc}	0.244^{bc}	0.271^{bc}
LL	0.27^{bc}	0.27^{bc}	0.264^{bc}	0.294^{ab}	0.228^{c}	0.27^{bc}	0.242^{bc}	0.269^{bc}
R/S								
HH	0.76^{c}	0.52^{d}	1.27^{a}	0.57^{c}	0.83^{b}	0.48^{cd}	1.35^{a}	0.37^{d}
HL	0.77^{bc}	0.51^{d}	0.99^{ab}	0.44^{d}	0.55^{cd}	0.35^{d}	0.83^{b}	0.44^{d}
LH	0.83^{bc}	0.62^{c}	0.98^{ab}	0.91^{b}	0.68^{bc}	0.40^{d}	0.64^{bc}	0.37^{d}
LL	0.81^{bc}	0.59^{d}	0.75^{bc}	0.48^{d}	0.70^{bc}	0.47^{cd}	0.58^{cd}	0.37^{d}

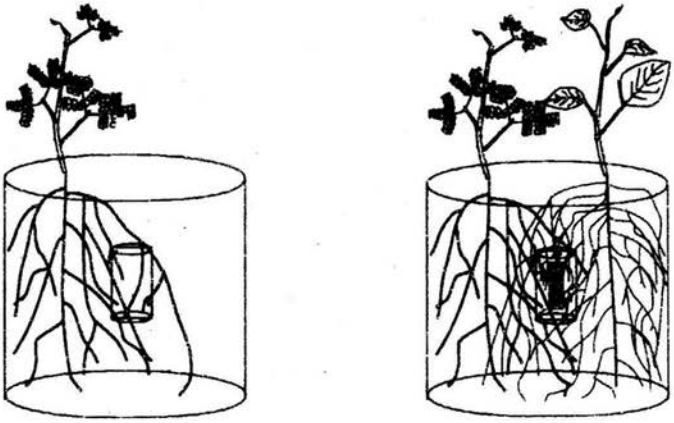
a) Position of the soil patch area



Unfertilized patch treatment (-Fp)

Fertilized patch treatment (+Fp)

B) Position of the patch in the experiment of competition



Unfertilized patch treatment (-Fp)

Fertilized patch treatment (+Fp)

Figure 1. Diagram of the design of the soil patch treatments for A) the experiment 1 and B) the experiment 2.

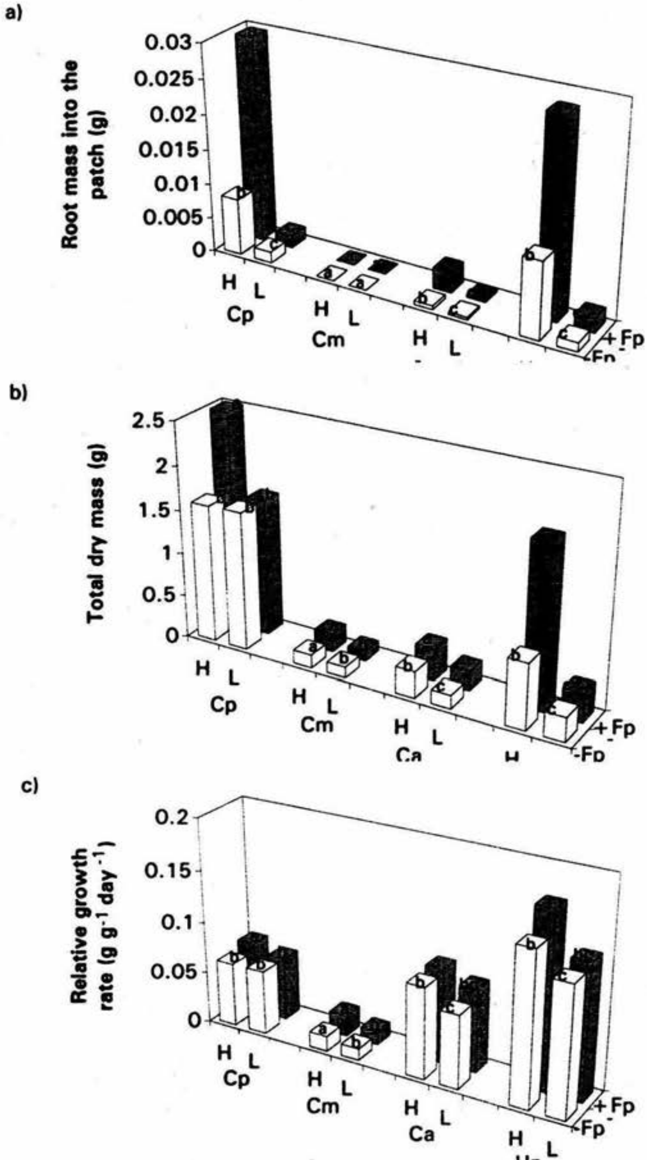


Figure 2. a) Root mass into the patch (g), b) total dry mass production (g) and c) relative growth rate (RGR, g g^{-1} day^{-1}) showed by the four species at 42 days of growth under high (H) and low (L) light intensity combined in a factorial design with a unfertilized (-Fp) an fertilized (+Fp) nutrient patch. Species names as follows: Cp = *Caesalpinia platyloba*, Cm= *Celaenodendron mexicanum*, Ca= *Cordia alliodora* and Hp = *Heliocarpus pallidus*. Small letters show significant differences ($p<0.05$) between treatments by species.

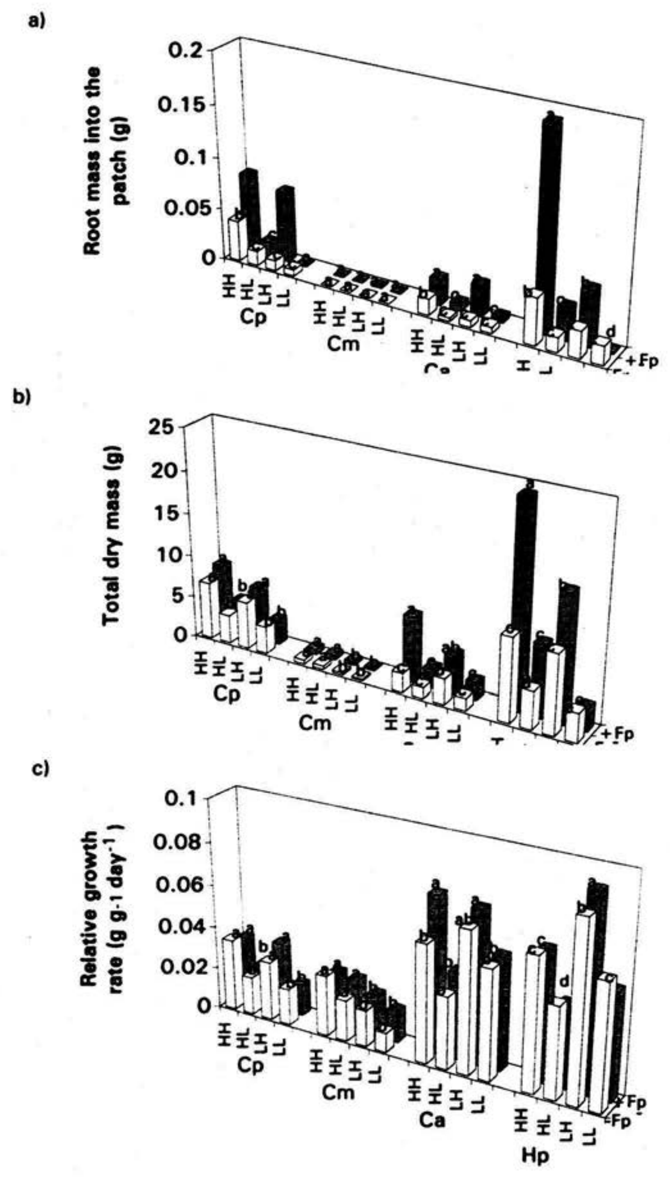


Figure 3. a) Root mass into the patch (g), b) total dry mass production (g) and c) relative growth rate (RGR, g g^{-1} day^{-1}) showed by the four species at 84 days of growth under high (HH), high-low (HL), low-high (LH) and low (LL) light intensity combined in a factorial design with a unfertilized (-Fp) and fertilized (+Fp) soil nutrient patch. Species names as in Fig. 2. Small letters show significan differnces ($p<0.05$) among treatments by species.

Appendix A. F values and the significance level (*, $p<0.05$, ** $p<0.01$ and *** $p<0.001$, numbers without asterisk are non-significant) of a two-way ANOVA for the factors light and soil patch nutrients at 42 days of growth.

Caesalpinia platyloba

	Dry mass	RGR	LA	LAR	SLA	LWR
light	4.0*	4.05*	12.9**	3.95*	19.2**	16.9***
patch	4.1*	4.08*	2.1	3.9*	1.5	5.7*
light x patch	3.7	3.71	0.5	0.98	0.43	6.7*

Celaenodendron mexicanum

	Dry mass	RGR	LA	LAR	SLA	LWR
light	11.4*	29.4***	7.5*	41.4***	37.3***	0.67
patch	1.94	3.4	1.2	0.6	0.27	2.93
light x patch	3.5	2.12	1.4	0.013	0.37	4.1

Cordia alliodora

	Dry mass	RGR	LA	LAR	SLA	LWR
light	13.2**	10.6**	0.01	62.7***	45***	4.1*
patch	4.4*	4.98*	11.7**	3.7	3.1	4*
light x patch	3.9*	4.4*	0.21	0.017	0.013	3.5

Heliocarpus pallidus

	Dry mass	RGR	LA	LAR	SLA	LWR
light	124***	92.5***	35.1***	165***	110***	18.8***
patch	23.2***	15.9***	32.1***	3.9	0.2	6.4*
light x patch	9.8**	5.3*	10.2**	0.23	1.96	4.7*

Appendix B. F values and the significance level (*, p<0.05, ** p<0.01 and *** p<0.001, numbers without asterisk are non-significant) of a two-way ANOVA for the factors light and soil patch nutrients at 84 days of growth.

Caesalpinia platyloba

	Root patch	Dry mass	RGR	LA	LAR	SLA	LWR
light	3.5*	22.4***	5.7**	3.5*	68.9***	54.1***	10.9***
patch	3.6*	4.21*	0.01	7.4**	2.36	25.2***	23.2***
light x patch	0.55	1.59	0.24	3.9*	4.06*	23.5***	25.5***

Celaenodendron mexicanum

	Root patch	Dry mass	RGR	LA	LAR	SLA	LWR
light	----	31.2***	4.33*	14.7***	16.4***	10.19***	4.58**
patch	----	3.01	3.4	50.6***	2.9	1.7	124***
light x patch	----	1.22	1.1	8.46***	3.0	1.05	1.09

Cordia alliodora

	Root patch	Dry mass	RGR	LA	LAR	SLA	LWR
light	11.7***	11.1***	8.14***	4.2*	11.3***	35.8***	3.35*
patch	34.3***	21.9***	4.6*	8.7**	4.8*	1.31	0.75
light x patch	7.3**	3.5	3.4	4.1*	0.15	2.1	0.55

Heliocarpus pallidus

	Root patch	Dry mass	RGR	LA	LAR	SLA	LWR
light	126***	177***	71***	114***	25.9***	61.8***	3.7*
patch	7.4**	69.6***	7.6**	69***	2.86	0.52	1.4
light x patch	6.7**	17.6***	2.03	39.1***	7.18**	4.32*	5.5**

Capítulo V

Discusión General

El tema central de los experimentos que forman esta tesis es plasticidad en plantas. Este tópico es abordado desde el punto de vista de las respuestas de diferentes especies a diferentes disponibilidades de los recursos luz y nutrimentos, evaluadas principalmente por medio de su influencia en el crecimiento. Se inicia con diseños experimentales tendientes a evaluar y describir patrones generales de crecimiento ante disponibilidades contrastantes de algún recurso, para lo cual se analiza comparativamente, entre gran número de especies (34), la respuesta en el crecimiento y su relación con los diferentes parámetros que pueden influenciarlo. Se continua con la evaluación de preguntas más detalladas, usando un menor número de especies (10), sobre el papel de cambios en la disponibilidad de algún recurso (luz) en el crecimiento y algunos parámetros fisiológicos como fotosíntesis y conductancia estomática. Para continuar con mayor detalle, se incluyen diseños donde se pretende integrar las respuestas a variaciones en recursos capturados por la parte aérea de la planta (luz) y los capturados en el suelo (nutrimentos). Los cambios en luz aplicados pretenden simular variaciones abruptas en la disponibilidad de este recurso causadas por eventos como: perturbaciones o los abruptos cambios dados por el carácter estacional de la selva baja caducifolia. Los cambios en la disponibilidad de nutrimentos en el suelo pretenden simular la característica distribución en parches de la disponibilidad de estos recursos en sistemas naturales. Finalmente, considerando que variaciones en la disponibilidad de recursos pueden generarse por la actividad de individuos vecinos, ya que éstos al consumir los mismos recursos reducen su disponibilidad, se analiza conjuntamente la relación entre las respuestas a variaciones en luz, nutrimentos distribuidos en parches y la influencia de vecinos en individuos de dos especies. A continuación se discutirá la contribución de este trabajo, mediante el análisis de las principales tendencias encontradas y la relación que guardan con las hipótesis generadas y con estudios reportados en la literatura.

El análisis de crecimiento realizado con 34 especies leñosas aporta evidencia sobre la existencia de una relación directa entre la biomasa total y el área total producida, así como entre la tasa de crecimiento (RGR) y parámetros como el área foliar total producida, el cociente de área foliar (LAR) y el área foliar específica (SLA), y una relación inversa entre la RGR y el contenido de carbono de las hojas, tanto en condiciones de alta como de baja disponibilidad de nutrimentos. No obstante, en condiciones contrastantes de luz, existe también una relación directa entre la RGR y la tasa de asimilación neta (NAR) (capítulo 3). Aunque, el resultado final en cuanto a la tasa de crecimiento comparativamente entre especies es el mismo, es decir, las especies que expresan un rápido crecimiento en un determinado recurso, muestran también un crecimiento rápido en abundancia de los otros recursos. Esto se puede observar en la Fig. 1 donde se relacionan las tasas de crecimiento expresadas por diferentes especies en condiciones de alta disponibilidad de nutrimentos (capítulo 2), de luz (capítulo 3) y de fósforo (Huante et. al 1995). Las tendencias señaladas anteriormente entre la RGR y los diferentes parámetros que pueden influenciarla documentan que las especies de rápido crecimiento producen mayor cantidad de biomasa y área foliar y el general sus hojas son más delgadas, con menor contenido de carbono que las especies de lento crecimiento. Estas tendencias apoyan lo reportado previamente sobre las respuestas a disponibilidades contrastantes de luz y nutrimentos (Boardman 1977, Mooney et al. 1978, Grime 1979, Chapin 1980, Björkman 1981, Smith 1981, Augspurger 1984, Oberbauer y Strain 1985, Hunt y Lloyd 1987, Körner y Renhardt 1987, Grime et al. 1988, Shipley y Keddy 1988, Denslow et al. 1990, Lambers y Poorter 1992). Adicionalmente se documenta la existencia de una relación directa entre la respuesta en la tasa de crecimiento (evaluada como la diferencia entre la máxima menos la mínima RGR obtenida, ΔRGR) y la tasa de crecimiento alcanzada en condiciones de alta disponibilidad de nutrimentos y luz, es decir que las especies con mayor respuesta en

RGR son aquellas con crecimiento rápido mientras que las de menor respuesta en RGR son las de crecimiento lento. Si se considera la ΔRGR como una medida de la magnitud de la plasticidad por estos recursos, esto parece indicar y apoyar la hipótesis propuesta en esta tesis respecto a que las especies de rápido crecimiento son más plásticas que las de lento crecimiento. Adicionalmente, se ha sugerido que las especies de lento crecimiento producen hojas más longevas, con baja tasa de crecimiento, con metabolitos secundarios que les brindan protección contra herbívoros y su crecimiento y producción de biomasa se benefician más de asociaciones con otros organismos como las micorrizas que las especies de rápido crecimiento (Grime 1979, Chapin 1980, Coley et. al 1985). Los estudios realizados por Huante et al. (1993) parecen apoyar lo antes mencionado para el efecto de micorrizas, aunque el número de especies incluidas es muy pequeño. En relación con la herbivoría, usando los datos reportados por Filip et al. (1995) sobre el porcentaje de pérdida de área foliar por herbivoría, para algunas especies estudiadas en esta tesis, se puede observar (Fig. 2) su relación con la tasa de crecimiento máxima obtenida. Esta relación parece apoyar lo antes sugerido, excepto en la especie Cordia alliodora, la cual con base en su RGR se podría esperar mayor porcentaje de pérdida de área foliar, sin embargo, la baja folivoría que presenta podría deberse a que esta especie presenta mirmecofilia, lo que probablemente la protege de la influencia de herbívoros.

Otra variable que se ha sugerido que es importante en determinar la RGR es la biomasa de las semillas, donde se ha propuesto una relación negativa entre ambos parámetros. Sin embargo, en la evidencia reportada en la literatura existe controversia, ya que también se ha documentado la existencia de una relación directa (Thompson 1987, Shipley y Keddy 1988) y, aunque la mayoría de los estudios han documentado una relación inversa significativa, ésta generalmente es débil (i.e. bajo coeficiente de correlación) (Grime 1979, Fenner 1983, Gross 1984, Shipley et al.

1989, Shipley y Peters 1990). Si bien en los estudios reportados en esta tesis la especie con semillas más pequeñas tuvo la mayor tasa de crecimiento, la relación entre la RGR y la biomasa de las semillas es débil pero significativa, lo que podría sugerir la importancia de otros factores como la asignación de biomasa y las relaciones filogenéticas (Kelly y Purvis 1993, Grime 1994) en determinar las variaciones en RGR. En cuanto a la asignación de biomasa, se ha propuesto que las especies tienden a asignar su biomasa interna de tal manera que se favorezca la explotación del recurso que limita el crecimiento y se espera que esta respuesta sea de mayor magnitud en las especies de rápido crecimiento (Chapin 1980). Los resultados de esta tesis muestran que cuando las especies crecen en baja disponibilidad de nutrimentos aumenta su asignación de biomasa a la raíz (aumenta RWR y R/S), sin embargo, no existe una relación interespecífica significativa entre R/S y RGR.

En los últimos años se ha avanzado en el conocimiento de los determinantes de las variaciones interespecíficas en RGR (Grime y Hunt 1975, Körner y Renhardt 1987, Shipley y Keddy 1988, Poorter et al. 1990, Shipley y Peters 1990, Garnier 1991, Lambers y Poorter 1992). Sin embargo, no existe información de este tipo sobre especies con crecimiento secundario pertenecientes a zonas con ambientes tropicales.

Las tendencias anteriormente expuestas provienen de estudios donde prevalecen condiciones de baja o alta disponibilidad de recursos. Cuando un mismo individuo experimenta cambios en algún recurso (como la luz), existe una tendencia en las especies de rápido crecimiento a mostrar una mayor capacidad de aclimatación en cuanto a la biomasa total producida y a la RGR, los individuos transferidos de L a H (LH) mostraron valores similares a los presentados por los individuos que crecieron en HH (LH tiende a aclimatarse con respecto a HH). Los individuos transferidos de H a L (HL) tuvieron valores similares a aquéllos en LL

(HL tiende a aclimatarse con respecto a LL), alcanzando en LH valores incluso mayores que los de HH y los de HL menores que aquéllos alcanzados en LL. Las especies con tasas de crecimiento intermedia tienden a presentar una magnitud de aclimatación también intermedia y el patrón de aclimatación es similar al mostrado por las especies de rápido crecimiento (LH se aclimata con respecto a HH y HL con LL), pero sin existir diferencias significativas entre ambos pares de fenotipos. Las especies con la menor tasa de crecimiento, (en esta tesis evaluado sólo con Celaenodendron mexicanum) tienden a mostrar la menor magnitud de cambio en todos los parámetros de crecimiento, es decir, el menor grado de aclimatación. Su patrón de aclimatación tiende a ser muy diferente comparado con las especies de rápido crecimiento, ya que el fenotipo HL se aclimata con respecto a HH y el LH con respecto al fenotipo LL, sin existir diferencias significativas entre ambos pares de fenotipos. Estas tendencias sugieren la existencia de una tendencia general entre la tasa de crecimiento y la magnitud y dirección de la aclimatación, donde a mayor tasa de crecimiento mayor aclimatación hacia el fenotipo LH respecto al HH y a menor tasa de crecimiento menor aclimatación pero en dirección del fenotipo HL respecto al HH. Esta misma tendencia la muestran las especies en cuanto a características fisiológicas como tasa fotosintética y conductancia estomática. Una rápida aclimatación se ha asociado con especies que habitan sitios con gran competencia, ya que una rápida respuesta favorece la rápida captura de recursos (Grime et al. 1986), la producción de plantas con mayor biomasa y por lo tanto mayor probabilidad de superioridad competitiva, si se compara con algún otro individuo de la misma edad pero con menor capacidad de aclimatación. Estas tendencias apoyan las hipótesis planteadas sobre mayor capacidad de aclimatación en especies de rápido crecimiento comparativamente respecto a las de crecimiento lento, también apoyan las tendencias encontradas en estudios realizados con plantas de selvas altas perennifolias, respecto a la superioridad del fenotipo LH respecto al

HH (Rice y Bazzaz 1989a, Pompa y Bongers 1991, Strauss-Debenedetti y Bazzaz 1991, Sims y Pearcy 1991, Turnbull et. al 1993). Sin embargo, no se había documentado una tendencia en aclimatación diferente para especies de lento crecimiento, no obstante, cabe señalar que la tendencia reportada en esta tesis obedece al patrón mostrado por sólo una especie, lo que sugiere la necesidad de contar con más evidencias que permitan establecer con precisión el patrón de la aclimatación en especies con crecimiento lento.

Las tendencias de aclimatación en RGR a cambios en la intensidad de luz están asociadas con cambios en NAR y las características de las hojas como SLA. Esto parece indicar la importancia de las hojas y sus características en determinar la tasa de crecimiento. Las hojas producidas bajo alta y baja intensidad de luz difieren en sus características anatómicas y fisiológicas. Cuando una planta que crece en luz alta es transferida a luz baja o vice versa, las hojas presentan características asociadas al ambiente previo al cambio, de tal forma que su aclimatación al nuevo ambiente depende, en parte, de la capacidad de sus hojas para superar la posible fotoinhibición, la capacidad para modificar los componentes que determinan su capacidad fotosintética (capacidad de carboxilación, capacidad de transporte de electrones, conductancia estomática y la relación peso:área foliar, LMA) (Pearcy y Sims 1994), así como de la velocidad con la que puedan producir nuevas hojas adaptadas a las nuevas condiciones lumínicas, debido a que las hojas producidas en luz alta son menos longevas y por lo tanto se recambian más rápidamente que aquéllas producidas en luz baja (Chabot y Hicks 1982). Una mayor longevidad de hojas se ha reportado como una de las características de las especies de lento crecimiento y mayor recambio foliar en las especies de crecimiento rápido, probablemente a esto se deba la menor velocidad de respuesta y el patrón de aclimatación (HL con respecto a HH) de las especies de lento crecimiento. Se ha sugerido que las hojas producidas en luz baja son más eficientes, en términos del retorno de carbono invertido, debido a su menor inversión de carbono por unidad de área (Sims y Pearcy 1991). De acuerdo con lo reportado por Sims y Pearcy (1992) para la especie Alocasia macrorrhyza, las características de las hojas se determinan durante las etapas tempranas de su desarrollo, entonces inicialmente la adaptación a un nuevo ambiente será enfrentada con hojas desarrolladas en el ambiente previo al cambio, entonces las plantas que son transferidas de baja a alta intensidad de luz enfrentan el nuevo ambiente con hojas más eficientes que aquéllas plantas transferidas de alta a baja intensidad de luz. Sin embargo, datos producidos con otras especies han documentado cierto grado de aclimatación en las hojas desarrolladas previamente al cambio de luz (Chow y Anderson 1987, Sebaa et al. 1986).

En ambientes donde la distribución de nutrimentos en el suelo es heterogénea, la tendencia parece indicar que a mayor tasa de crecimiento mayor capacidad de forrajeo en parches ricos en nutrimentos. Las especies de lento crecimiento son incapaces de localizar y explotar parches ricos en nutrimentos. Las especies de rápido crecimiento tienden a producir más raíces para la explotación de dichos parches y obtienen beneficio tanto en la cantidad de biomasa y área foliar que pueden producir, como en su tasa de crecimiento. Sin embargo, en estas especies la explotación de parches ricos en nutrimentos puede reducirse considerablemente en condiciones de sombra, resultando en la reducción de la productividad y tasa de crecimiento. Ante cambios en luz, el fenotipo que muestra mayor aclimatación tiende a ser el que muestra mayor capacidad para explotar el parche, esto es, el fenotipo LH para las especies de rápido crecimiento y el LH y HH para las de crecimiento intermedio. Sin embargo, la reducción en la producción de biomasa por no existir un parche rico en el fenotipo LH (i. e. LH-Fp) provoca que no exista diferencia con el fenotipo HL+Fp, es decir, debido tanto al beneficio de HL por tener parche rico como a la reducción en LH por no tener un parche rico en nutrimentos. Esto enfatiza la importancia de analizar conjuntamente el efecto de cambios en recursos cuya captura esta inter-relacionada, ya que la disminución de uno provoca cambios en la captura del otro. La pérdida o reducción de la habilidad para explotar un parche rico en nutrimentos cuando la intensidad de luz es limitante se ha documentado muy poco (Jackson y Caldwell 1992). Este es el primer estudio donde se muestra cómo la capacidad de forrajeo ante cambios en la intensidad de luz puede afectar diferencialmente a las especies y cómo, a su vez, la tendencia en aclimatación que se puede esperar como respuesta a cambios en el ambiente lumínico puede ser alterada por tener acceso o no a un parche rico en nutrimentos. Adicionalmente esta tesis aporta evidencia que sugiere que la interrelación entre la capacidad para aclimatarse a cambios en luz y la capacidad de forrajeo por nutrimentos puede reducirse (considerando la biomasa de raíces producida en el parche y la biomasa total) por la presencia de individuos de otra especie, esta reducción es más pronunciada en la especie que tiene la mayor tasa de crecimiento y ocurre en aquellos fenotipos que muestran los valores más altos (HH y LH). En parches ricos en nutrimentos se puede esperar gran competencia para su explotación, de tal forma que la especie que podría obtener mayor beneficio sería aquélla con mayor capacidad para encontrarlos y explotarlos rápidamente. En estudios previos (Grime et. al 1986, Crick y Grime 1987, Hutchings y de Kroon 1994 y referencias ahí citadas) y en esta tesis se ha documentado que esta capacidad de forrajeo es mayor en especies de rápido crecimiento, las cuales tienden a habitar sitios con abundancia en recursos, donde existe mayor competencia, entonces se ha propuesto que la capacidad de forrajeo es un mecanismo que favorece la captura de recursos en dichas especies (Grime et. al 1986). Sin embargo, los sitios más productivos, que se espera soporten mayor número de individuos, la luz llega a ser limitante, por lo que relaciones de compromiso entre respuestas a cambios en luz y forrajeo por nutrimentos deberían considerarse.

En conclusión, existe un conjunto diverso de respuestas en crecimiento, en los extremos de ese conjunto se encuentran especies con características plásticas contrastantes. Las especies de rápido crecimiento, que presumiblemente habitan sitios con abundancia de recursos, son más plásticas en condiciones contrastantes de disponibilidad de recursos, cuando los recursos varían muestran mayor capacidad para aclimatarse y su patrón de aclimatación es diferente al de las especies de lento crecimiento. Las especies de rápido crecimiento tienden también a mostrar la capacidad plástica para localizar y aumentar la producción de raíces finas en parches en el suelo ricos en nutrimentos, mientras que las especies de lento crecimiento no son plásticas en este sentido. El efecto de la disminución de recursos por una planta vecina de otra especie es mayor en la especies de crecimiento más rápido, aunque provoca en ambas la modificación de los patrones de aclimatación y forrajeo en algunos parámetros.

El análisis basado en las relaciones de costo-beneficio de la captura de recursos (Bloom et al. 1985) provee una posible explicación a las tendencias aquí mostradas. De acuerdo con Bloom et al. (1985) en ambientes con abundancia de recursos, el costo asociado a la captura de cada recurso es relativamente bajo, mientras que en ambientes con baja disponibilidad de recursos, el costo de producción de una nueva unidad de biomasa es alto, en consecuencia, el alto costo del crecimiento se ve reflejado en una tasa de crecimiento máxima lenta en plantas adaptadas a ambientes pobres. Las plantas características de ambientes ricos son generalmente más plásticas en su asignación en respuesta a estres ambiental. Esta es la respuesta esperada desde un punto de vista económico ante una situación donde los costos varían mucho. En ambientes variables, las disponibilidad de recursos es heterogénea tanto espacial como temporalmente, entonces, un patrón de asignación muy plástico favorece que las plantas dominen la captura de los recursos limitantes (Bloom et al. 1985). Por ejemplo, un gran incremento en la asignación al crecimiento de la parte aérea en respuesta a la sombra permite que una planta pueda crecer por encima de individuos vecinos. Las plantas de ambientes pobres son menos plásticas en su patrón de asignación, presumiblemente porque experimentan con frecuencia condiciones crónicas de disponibilidad de recursos (Bloom et al. 1985).

Si consideramos que en ambientes heterogéneos la sobrevivencia, el crecimiento y la reproducción de las plantas podrían estar determinados, en cierta medida, por su habilidad para responder a dicha heterogeneidad, entonces el conocer las características de respuesta de diferentes especies a la heterogeneidad ambiental podría ayudarnos a incursionar en el entendimiento sobre el mantenimiento de una alta diversidad vegetal, como la de la selva baja caducifolia. La disponibilidad de recursos parece estar asociada con la diversidad de especies, ya que en los sitios más productivos como los tropicales albergan la mayor diversidad de especies (Gentry 1988, Faber-Langendoen y Gentry 1991). En sistemas tropicales las perturbaciones y su consecuente generación de heterogeneidad ambiental se han asociado con la alta diversidad. Connell (1978) propone que la frecuencia de los eventos de perturbación son importantes en la regulación de la diversidad, donde perturbaciones frecuentes favorecerían una rápida colonización y dominancia de especies de rápido crecimiento (colonizadoras) ya que serían las únicas que tendrían el tiempo necesario para establecerse antes de que otra perturbación ocurriera y, probablemente debido a que rápidamente la luz llegaría a ser limitante, entonces las especies dominantes serían las mejor competidoras por luz (Schulze y Chapin 1987). A frecuencias de perturbación muy altas, la diversidad se reduciría por exclusión competitiva. A frecuencias intermedias de eventos de perturbación, un mayor número de especies podría migrar a la comunidad y así aumentaría la diversidad. Probablemente la migración de nuevas especies se favorezca a estas frecuencias debido a que, con el tiempo, podrían haber modificaciones en la disponibilidad de recursos (generados por el tiempo mismo y por la actividad de las plantas colonizadoras) que favorezcan la supresión, en cierta medida, de las especies dominantes, por medio de respuestas como las mostradas por las especies de rápido crecimiento, en las que la capacidad de obtener beneficio de parches ricos en nutrimentos se reduce al disminuir la luz y a su vez el patrón de aclimatación se modifica al no tener acceso a nutrimentos, provocando una disminución (en la biomasa total producida) en aquéllas condiciones donde se podría esperar mayor respuesta. Por otro lado, la interacción competitiva entre las especies y cómo ésta es afectada por cambios en la disponibilidad de recursos podrían también influir en la supresión de las especies dominantes y la aparición de nuevas especies con potencialidades de producción de biomasa y crecimiento diferentes.

Sin duda, eventos de perturbación generados por actividades humanas ejercen una fuerte presión en las selvas bajas caducifolias. Estos eventos han aumentado su frecuencia con el paso del tiempo, amenazando cada vez con mayor intensidad la diversidad de estos sistemas, tanto por el área que es convertida a tierras de cultivo (milpas, huertos, pastizales, etc.) que reduce las áreas de selva (para 1980 el 44% del área tropical latinoamericana, Houghton et al. 1991) y provoca una fuerte erosión (alrededor de 0.2 y 130 ton/ha año para áreas con selva y con cultivo de maíz y/o pasto, respectivamente, Maass et. al 1988), como por la modificación de su dinámica natural en actividades como la extracción selectiva de especies. Una medida para poder establecer posibles planes de recuperación y conservación de estas selvas es el conocer cómo diferentes grupos de especies responden a cambios en la disponibilidad de recursos, para así poder contar con mayores elementos para la construcción de modelos predictivos sobre el efecto de cambios en estos sistemas. Esto se basa en la premisa de que eventos como la perturbación ya sea natural o inducida por el hombre, así como eventos a nivel global como el cambio climático, generan cambios en la disponibilidad de los recursos esenciales para las plantas.

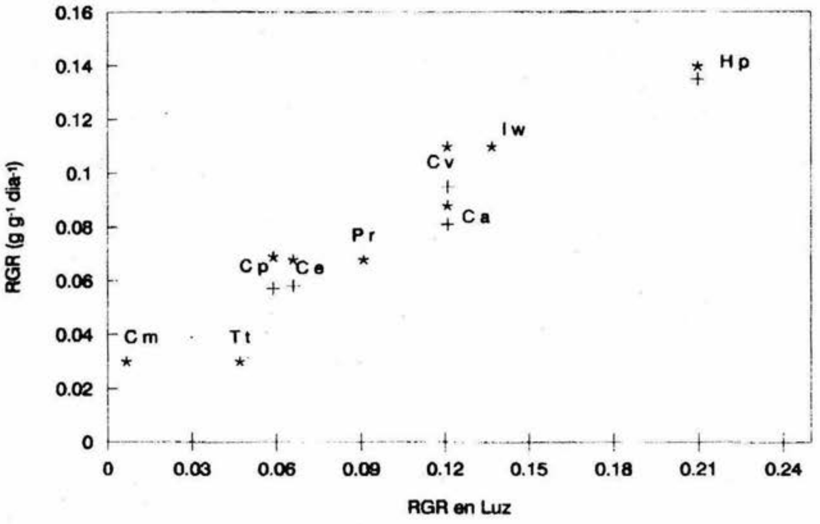


Figura 1. Tasa relativa de crecimiento máxima (RGR) mostrada ante abundancia de nutrimentos (+), fósforo (*) (Huante et. al 1995) y alta intensidad de luz. Ce = *Caesalpinia eriostachys*, Cp = *Caesalpinia platyloba*, Cm = *Celaenodendron mexicanum*, Cv = *Cochlospermum vitifolium*. Ca = *Cordia alliodora*, Hp = *Heliocarpus pallidus*, Iw = *Ipomoea wolcottiana*, Pr = *Plumeria rubra* and Tt = *Trichilia trifolia*. $r^2 = 0.95$, $p < 0.0001$.

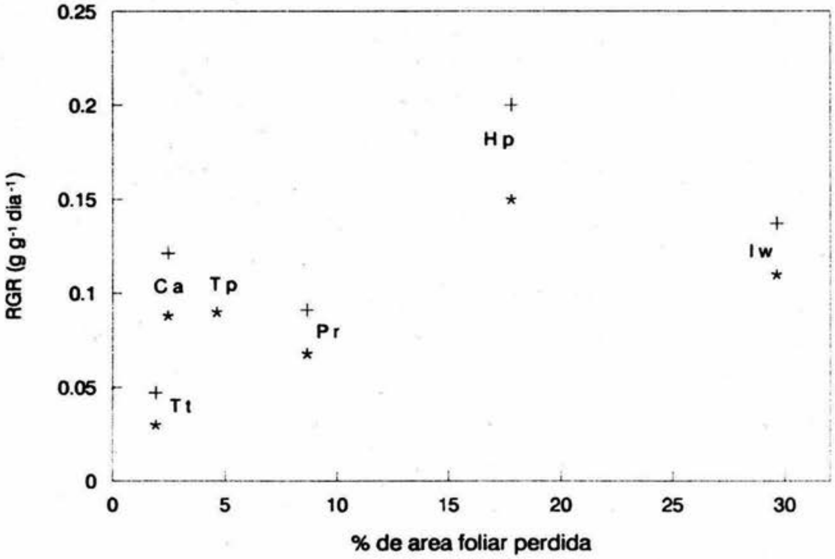


Figura 2. Relación entre el porcentage de área foliar perdida por herbivoría (tomado de Filip et al. 1995) y la tasa relativa de crecimiento (RGR) máxima obtenida en condiciones de gran disponibilidad de nutrimentos (*) e intensidad de luz alta (+). r2 = 0.63, p = 0.055.

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