

Influence of mineral nutrient availability on growth of tree seedlings from the tropical deciduous forest

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Abstract. The effects of different nutrient availabilities on growth and biomass partitioning in seedlings from the tropical deciduous forest in Mexico were compared. The tree species studied were *Heliocarpus pallidus*, a species associated with disturbed parts of the forest, and *Caesalpinia eriostachys*, *Jacquinia pungens* and *Recchia mexicana*, species from mature, undisturbed habitats. The tropical deciduous tree seedlings were grown in pure silica sand for 50 days inside growth chambers under four nutrient regimes; 5, 20, 100 and 200% Long Ashton nutrient solutions. Data showed contrasting responses among species to different nutrient availabilities. Except *Jacquinia pungens*, all species had increased growth and productivity as nutrient level increased from 5 to 100%; however, no significant differences in these parameters were detected between 100 and 200% in all species. Compared with mature forest species, pioneer species showed higher variations in biomass production, relative growth rate and net assimilation rate. In contrast to mature forest species, root/shoot ratios in *Heliocarpus pallidus* were greater and thus showed higher biomass allocation to roots when nutrient supply was limited. This response suggests higher phenotypic plasticity in pioneer species. Species from mature parts of the forest (*Caesalpinia eriostachys*, *Recchia mexicana*) showed less dependency on nutrient supply than pioneer species. These responses appear to support observations from studies with temperate plants investigating growth responses to soil fertility.

Key words: Nutrition – Growth analysis – Biomass allocation – Tropical deciduous forest – Plasticity

Introduction

Nutrient availability in natural soils varies both spatially and temporally (Chapin 1980; Chapin et al. 1987). This

variability is more evident in seasonal environments; in temperate regions low temperatures during the winter limit water and nutrient availability; in dry tropical regions low moisture also limits both water and nutrient availability. In the North American tropical deciduous forest, the dry season can be 8 months long. In this forest, nutrient supply varies with changes in water availability, litter quality and decomposition rates. In addition, natural disturbances, such as tree-fall, may influence soil nutrient availability at a more local scale.

Plant nutrient ecological theory, developed primarily from comparisons of temperate habitats of contrasting nutrient availability, predicts that species from infertile soils will have low relative growth rates, high allocation of biomass to roots, and large investment in chemical defences, compared to species from fertile habitats (Grime and Hunt 1975; Grime 1977, 1979; Chapin 1980, 1988). Responses of plants to variations in nutrient supply should involve compensatory changes in root/shoot allocation in order to increase the acquisition of limiting soil resources (Bloom et al. 1985; Chapin 1991). In this respect it has been proposed that plants with high relative growth rates tend not to predominate in infertile environments because they are more sensitive to insufficient or low nutrient supply. Studies analyzing resource capture and using micro-economic theory to describe the behavior of plants in fertile and infertile environments (Bloom et al. 1985; Grime et al. 1986; Crick and Grime 1987; Campbell and Grime 1989), have established that plants adapted to infertile environments have a high 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 and Grime 1987). In addition, these studies predict that species adapted to nutrient rich soils are able to respond to nutrient enrichment by having a high rate of nutrient absorption and thus fast growth and a high yield. In contrast, plants adapted to poor soils usually exhibit little to no response to nutrient enrichment. In these plants, nutrient intake is accomplished through a constantly high root/shoot ratio and possibly mycorrhizal associations

Table 1. Mineral nutrient content of soil samples from the tropical dry forest of Chamela, Jalisco. These data were obtained from 34 soil samples (20 cm deep) collected along a transect every 10 m. Analysis of soil nutrient content was conducted as follows: Na, K, Ca and Mg were extracted with pH 7 solution in ammonium acetate and analyzed using atomic absorption spectrophotometer (Black 1980); extractable phosphorus (PO₄) with Mulich II solution; total nitrogen and phosphorus was measured in an autoanalyzer after acid digestion (Technicon Industrial Systems 1977)

Soil mineral nutrient content (ppm)		
	Average	Range
Sodium	15.794	10–25
Calcium	1854.11	480–3520
Magnesium	149.88	78–234
Phosphate	38.0	16–59
Total phosphorus	520.38	279–953
Total nitrogen	3217.67	1701–4802
Potassium	76.6	42–117

rather than through a high root absorption capacity (Chapin 1980, 1988).

The experiment described here examines aspects of the response of tropical species to nutrient supply. Specifically, the relationship between the relative growth rate and biomass allocation and the external nutrient supply in tree seedlings of contrasted ecology from the Mexican tropical deciduous forest are detailed.

Materials and methods

The tropical dry forest in the Pacific coast of Mexico presents a highly seasonal climate (Lott et al. 1987). The rainy season, which determines for most of the species the growth period, occurs between July and October. The average annual precipitation is 748 mm (1977–1984) with a standard deviation of 119 mm and a range from 585 to 961 mm; the average annual temperature is 24.9°C (Bullock 1986). During the 4 month growth season, coinciding with the summer, 80% of the rain occurs. It appears that during this period soil resources are not drastically limiting for plant establishment and growth. Previous observations about the soil characteristics including the nutrient availability have shown a high variation (Table 1). The soil at the tropical deciduous forest in the Pacific Coast of Mexico has been characterized as a sandy loam (64% sand, 13% loam and 23% clay) with pH between 6.5 and 7.3 and organic matter content between 1 and 6% (Huante et al. 1992).

The species investigated were *Caesalpinia eriostachys* Benth. (Leguminosae) and *Recchia mexicana* Moc & Sesse (Simaroubaceae), both species tend to occupy mature non-disturbed parts of the forest. *C. eriostachys* is the most abundant species in the forest and contributes 33.4% to the total above-ground phytomass (Martinez-Yrizar et al. 1992). *Jacquinia pungens* A. Gray (Theophrastaceae), one of the few species which retains its leaves during the dry season, and

Heliocarpus pallidus Rose (Tiliaceae) a fast growing pioneer species associated with natural gaps and human disturbed areas, were also studied (Table 2).

Mature seeds were collected from at least 10 different trees from each of the species at the Tropical Station of Biology of Chamela at the State of Jalisco in the Pacific coast of México (19° 30' N, 105° 03' W). Seed biomass was determined in 50 randomly selected seeds of each species (Table 2). Seeds were germinated in humid pure silica sand inside germination chambers set to 35/25°C day/night with 13 h photoperiod. Five days following germination, seedlings were transplanted to 12×30 cm PVC pots with drainage holes. The pots were filled with pure silica sand previously washed with abundant distilled water. The pots were randomly arranged inside growth chambers (Conviron E-15 Winnipeg, Canada) with a temperature of 30/25°C day/night, a relative humidity of 60%, photoperiod of 13 h, and a light intensity of 400 μmol m⁻² s⁻¹ (provided by fluorescent and tungsten lamps).

Four nutrient treatments were provided using Long Ashton nutrient solution (Hewitt 1966) at four concentrations: 5, 20, 100 and 200%. Seedlings were watered every second day with 200 ml nutrient solutions and on intermediate days with distilled water in order to prevent nutrient accumulation. The experimental design involved 4 nutrient treatments, 6 replicates, 4 species and 2 harvests (initial harvest at 5 days and final harvest at 50 days). At harvest all the individual plants were divided into root and shoot components; leaf area was measured in an area measurement system (Delta T, England). All plants were dried at 80°C for 48 h and dry weights were determined. From these data we calculated relative growth rates (RGR, dry weight increment per unit total plant weight per unit time, mg mg⁻¹ day⁻¹), net assimilation rate (the increase of plant dry weight per unit leaf area and unit time), the leaf weight and root weight ratios (LWR and RWR, the ratio of foliage and root weight to total dry weight, respectively), the relation between root and shoot dry matter (R/S; Evans 1972; Hunt 1982) and the nutrient dependency (the difference between the average total dry biomass achieved by the species in the highest minus total dry biomass at the lowest nutrient availability and expressed as a percentage of the average dry biomass attained in the highest nutrient treatment). Data were subjected to analysis of variance, after log-transformation in order to meet assumptions of normality (Zar 1974).

Results

Figure 1 shows the biomass production achieved by the four species in each nutrient treatment; the data indicate an increase in biomass production with an increment in nutrient supply, except for *Jacquinia pungens*. This tendency, however, was not significant between the 100 and 200% nutrient treatments in any species. *J. pungens* showed no significant differences ($P < 0.05$, $F = 14.71$) in biomass production among 20, 100 and 200% nutrient levels applied, but the biomass achieved under the 5% nutrient treatment was significantly lower. In relation to biomass production the most responsive species to variations in nutrient supply was *Heliocarpus pallidus*.

Table 2. Average seed biomass ($n = 50$), habitat preference and nutrient dependency (%) and the response in relative growth rate (the difference between relative growth rates achieved in the highest minus the lowest nutrient supply) of the four species studied

Species	Seed biomass (mg)	Habitat preference	Nutrient dependency (%)	Response in RGR (mg mg ⁻¹ day ⁻¹)
<i>Caesalpinia eriostachys</i>	219.4	Wide distribution	62.3	0.026
<i>Heliocarpus pallidus</i>	0.7	Open sites	97.1	0.071
<i>Jacquinia pungens</i>	74.8	Mature forest	51.9	0.015
<i>Recchia mexicana</i>	573.7	Mature forest	81.0	0.031

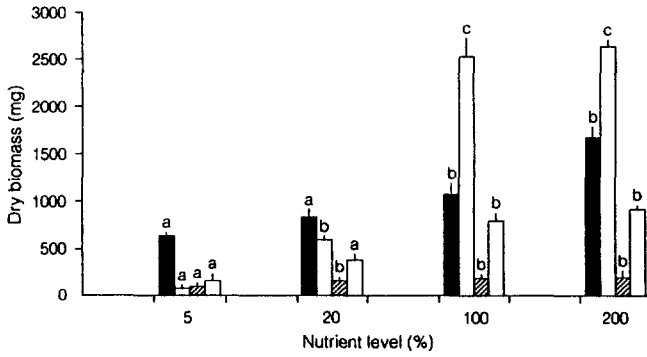


Fig. 1. Dry biomass (mg) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

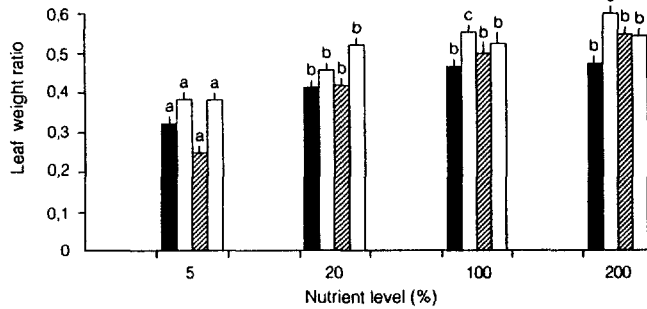


Fig. 2. Leaf weight ratio (mg mg^{-1}) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

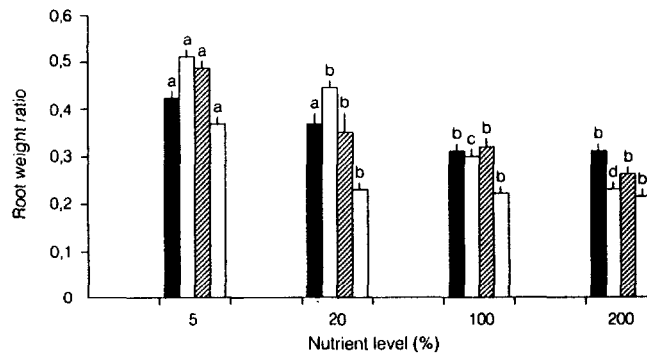


Fig. 3. Root weight ratio (mg mg^{-1}) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

An indication of the response of the species in terms of the biomass allocation to nutrient treatments is expressed by LWR, RWR (Figs. 2, 3) and the relation between the root and shoot biomass (R/S; Fig. 4). With the exception of *H. pallidus* growing under the poorest nutrient conditions, all

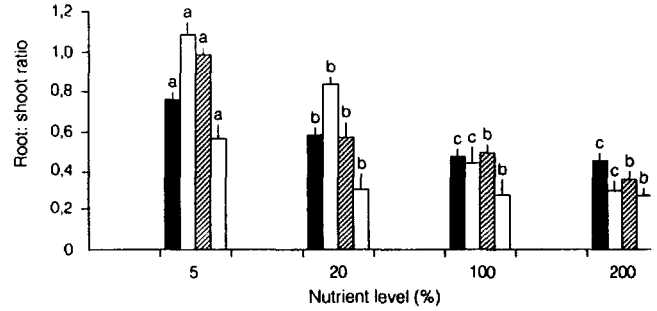


Fig. 4. Root to shoot ratio (R/S) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

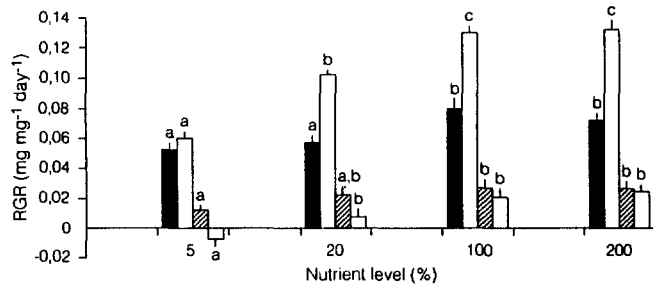


Fig. 5. Relative growth rate ($\text{mg mg}^{-1} \text{day}^{-1}$) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

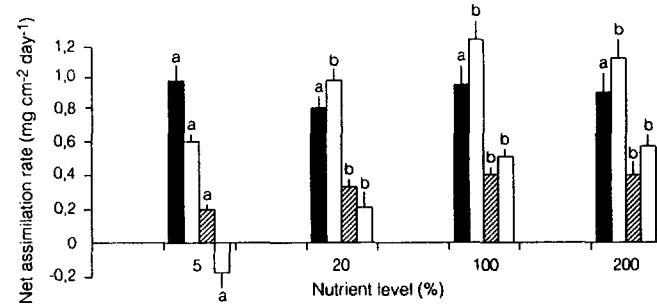


Fig. 6. Net assimilation rate ($\text{mg cm}^{-2} \text{day}^{-1}$) of the four study species after 50 days growing under different nutrient percentages. Vertical lines show standard error. Small letters indicate significant differences ($P < 0.05$) among treatments. ■ C. eri; □ H. pall; ▨ J. pung; □ R. mex

species in all treatments had R/S ratios lower than 1. There was a clear tendency to increase RWR, to reduce leaf biomass allocation (LWR) and to increase the R/S ratio (root biomass production) as nutrient supply decreased.

The relative growth rate exhibited by all of the species was low, as expected for tree species (Grime and Hunt 1975). In terms of the average relative growth rate, all species achieved the lowest values under the poorest nutrient treatment applied (Fig. 5); *Recchia mexicana* had a negative growth rate under the 5% nutrient treatment. The

species associated with undisturbed or mature parts of the forest, *Caesalpinia eriostachys*, *J. pungens* and *R. mexicana* demonstrated a moderate increase of growth as nutrient availability increased. The highest RGR, in all treatments, was observed in the pioneer species *H. pallidus* and it also showed the largest increment in growth rate as nutrient levels increased. In all species no significant ($P < 0.05$) difference was found between the relative growth rate attained between the 100 and 200% nutrient treatments.

The net assimilation rate (Fig. 6) was low in *J. pungens* and *R. mexicana*; it did not significantly change in *C. eriostachys* for all treatments and it varied considerably in *H. pallidus* (from 0.59 to 1.19). With the exception of *C. eriostachys* there was a tendency to increase the net assimilation rate as the nutrient availability increased.

Different nutrient dependencies were shown by the species (Table 2). The mature forest species, *J. pungens* and *R. mexicana*, achieved lower nutrient dependency than *C. eriostachys*. *H. pallidus*, a gap requiring species, had the highest nutrient dependency.

Discussion

The results reported here support the theory developed mainly with temperate plants in relation to plant responses to soil fertility (Grime 1979; Chapin 1980, 1988; Lambers and Poorter 1992). *H. pallidus*, a species associated with open sites, exhibited higher nutrient dependency and greater response in growth to nutrient increase as well as greater biomass allocation to roots when nutrients were less available, compared with mature forest species. For this tropical dry forest, species growth responses to different light levels were similarly associated with species habitat preferences where mature forest species showed the greatest shade tolerance (Rincón and Huante 1993).

Studies with species from the tropical rain forest at Guanacaste Costa Rica, emphasize that nutrient limitations to plant growth vary depending on species selected (Denslow et al. 1987). These observations were probably related to the specific nutrient requirements of individual species and the habitat characteristics where this species typically grew. In the present study we found a clear tendency with respect to habitat preference and nutrient demands, which suggest different levels of tolerance to nutrient deficiency by the study species.

The mature forest species *J. pungens* showed the least response to changes in nutrient availability in terms of growth rate, biomass allocation and a low nutrient dependency; this suggests the highest tolerance of this species to poor nutrient conditions. This species retains its leaves during the dry season; the stress tolerance of this species has been also documented in other studies (Janzen 1970). Janzen (1970) hypothesized that *J. pungens* originated from more stressful environments, so the water and nutrient conditions experienced during the dry season in their present habitat likely corresponds to the moister conditions of their habitat of origin.

C. eriostachys showed an intermediate tolerance to low nutritional conditions. This species is the most abundant

and widely dispersed species in the forest (Lott et al. 1987; Martinez-Yrizar et al. 1992). This wide range is due, in part, to an intermediate degree of tolerance to nutritional stress.

Studies about gap dynamics conducted in tropical rain forests have documented that natural open sites have high resource availability (Denslow 1980; Martinez-Ramos et al. 1988). In this sense, the low growth rate and high biomass allocation to roots, when grown in low nutrient concentrations, and high nutrient dependency as exhibited by *H. pallidus*, suggest a low tolerance in this species to poor nutrient conditions. This response is in accordance with the habitat preference of this species which tends to occupy disturbed parts of the forest.

The response in biomass allocation exhibited by *H. pallidus* suggests higher phenotypic plasticity in species associated with open sites; this plasticity could be considered as a plant mechanism to acquire nutrients and to maintain high growth (Grime et al. 1986). If we consider the response in RGR (Table 2) as a quantitative expression of plasticity, different degrees of plasticity in growth rate can be used to rank the species as follows: *H. pallidus* > *R. mexicana* > *C. eriostachys* > *J. pungens*. No relation was found between this pattern of plasticity and seed biomass. However, we must consider that this study comprised the seedling growth period and that nutrient requirements may change during the life span of the species as suggested by Schilchting (1986) and Parrish and Bazzaz (1985).

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