Root system analysis of seedlings of seven tree species from a tropical dry forest in Mexico

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Summary. Root attributes of tree seedlings of seven species from the tropical deciduous forest along the Pacific Coast of Mexico are described using morphometirc root system analysis. Mean relative growth rate, root/shoot ratios, specific root length, root density, mean number of roots tips and root length/leaf area ratio were determined in seedlings grown for 35 days inside growth chambers. All the species had low relative growth rates, low root/shoot ratios and low root densities (<0.5 cm/cm^3). The species associated with disturbed habitats, in contrast to the species characteristic of undisturbed areas, presented small seeds, a dichotomous root branching pattern and large specific root length. No relationship was found between seed size and mean relative growth rate among the species studied.

Key words: Tropical deciduous forest – Tree seedlings – Root morphology – Growth analysis – Legumes

Introduction

Two of the most striking characteristics of the tropical dry forest of the Pacific Coast of Mexico are its diversity of plant species and its highly seasonal climate, which periodically changes the vegetation physiognomy (Lott 1985). The species richness has been estimated at 758 species (93 tree species per 1000 m^2) and is higher than other Neotropical dry forests, which have higher mean annual precipitation (Lott et al. 1987). Climate is remarkably seasonal with a mean annual temperature of 24.9°C and mean annual precipitation of 748 mm (1977–1984; standard deviation of 119 mm, range of 585–961 mm); 80% of the rain occurs between July and October (Bullock 1986).

For most of the species (Bullock and Solis-Magallanes 1990) the rainy season determines the most favourable growth conditions. Although the arrival of the rain is highly predictable, interannual variation in mean precipitation is high. Distribution of rainy days within the rainy season is very patchy (Bullock 1986; Bullock and Solis-Magallanes 1990). Under these conditions, in which water supply restricts growth periodically, we can assume that allocation of dry matter to roots will increase capture of soil resources in a pulsed environment.

Research in species establishment and regeneration in tropical dry forest is very scarce. However, under this regime, it can be expected that species establishment must occur during the wet season, when water and nutrients are not drastically limited. In this sense, it is reasonable to suppose that seed size, emergence time, seedling growth form and relative growth rate may affect establishment success. In particular, root characteristics appear to be important to exploit soil resources during the wet season, in a system where temporal growth differentiation appears to be irrelevant.

To study some of the mechanisms of seedling resource capture and establishment it is helpful to investigate their root morphology as a first approach towards a more functional understanding. Comparative quantitative information on root seedling morphology and dry matter partitioning may also help to explain species co-existence, because distribution and abundance of adults in a plant community are affected by events during seedling establishment. The work reported here was designed to describe the root systems of tree seedlings of seven co-occurring species from the tropical dry forest in México. Our approach is to describe root seedling morphology by using the attributes of the complete root system.

Materials and methods

The species chosen for study were *Apoplanesia paniculata* Presl. (Leguminosae) and *Cordia elaeagnoides* DC. (Boraginaceae), both from disturbed habitats; *Caesalpinia eriostachys* Benth. (Leguminosae),
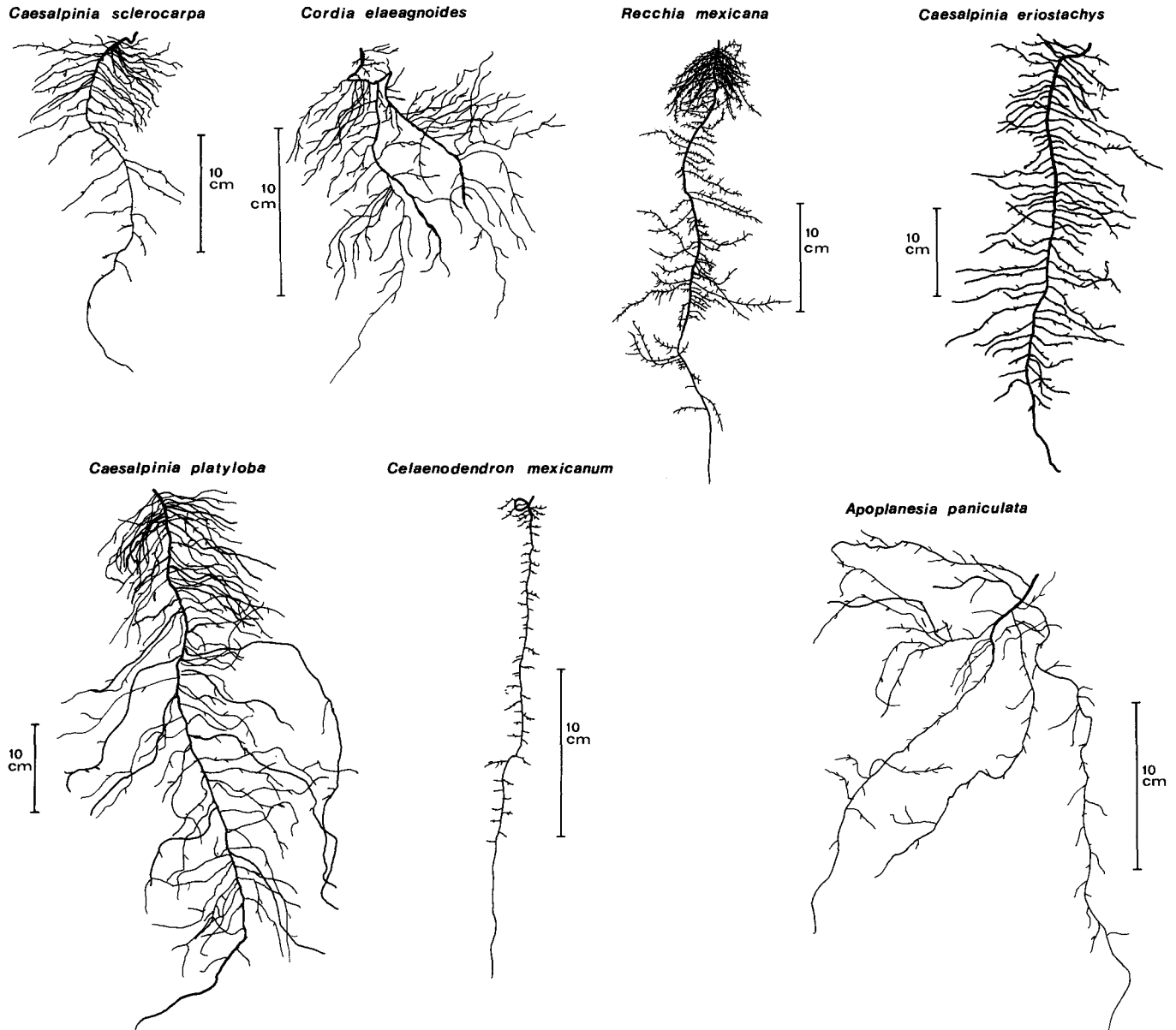
Fig. 1. Root diagrams of the seven tree species chosen for this investigation. *Apoplanesia paniculata* and *Cordia elaeagnoides*, both species from disturbed habitats, have dichotomously branching system. The rest of the species present a herringbone pattern

Caesalpinia platyloba S. Watt. (Leguminosae), *Caesalpinia sclerocarpa* Standl. (Leguminosae), *Celaenodendron mexicanum* Standl. (Euphorbiaceae) and *Recchia mexicana* Moc. & Sesse. (Simarubaceae), all of which occur in undisturbed parts of the forest.

Mature seeds of all seven species used in this investigation were collected from at least five different individuals per species at the Tropical Dry Forest Biological Station at Chamela (19°30′N, 105°03′W). Mean seed weight was determined from 25 randomly selected seeds. The seeds were germinated on 1% agar in distilled water inside germination chambers at 30/25° C. Three days after germination seedlings were transplanted to black plastic bags (20 × 60 cm) filled with recently collected soil from the deciduous forest. The soil was collected from the top 10 cm of the profile, sieved to pass 4 mm and the dead root particles were carefully removed. The soil collected was characterized as a sandy loam (64% sand, 13% loam and 23% clay), with pH between 6.5 and 7.1 and organic matter content between 3% and 5%.

The 3-day-old seedlings were placed randomly inside growth chambers (Conviron E-15, Winnipeg, Canada). Growth conditions were set to 30/25°C day/night with 60% relative humidity and 13 h photoperiod. Light intensity (380 µmol m^{-2} s^{-1}) was provided by fluorescent and tungsten lamps. The seedlings were watered daily with a 5% Long Ashton nutrient solution (Hewitt 1966). The design of the experiment comprised one final harvest including four replicates for each species. After 35 days the seedlings were harvested. For each replicate shoot and root were carefully separated, and leaf area was determined in a Delta-T leaf area measurement system. The root system was carefully removed from the soil and all the segments were counted and measured following the morphometric root analysis described in detail by Fitter (1982).

The morphometric root analysis suggested by Fitter (1982, 1985, 1987) is based on the analysis of branching systems without loops. This approach has been also applied to the study of rivers (Strahler 1957), lungs (Horsfield and Cumming 1976) and plant shoots (Barker et al. 1973). The morphometric analysis establishes a series of orders based on the growing tips of the root; terminal, recently formed segments will correspond to order 1, older segments will be assigned higher orders. In this way the identity of the root elements will constantly change as the
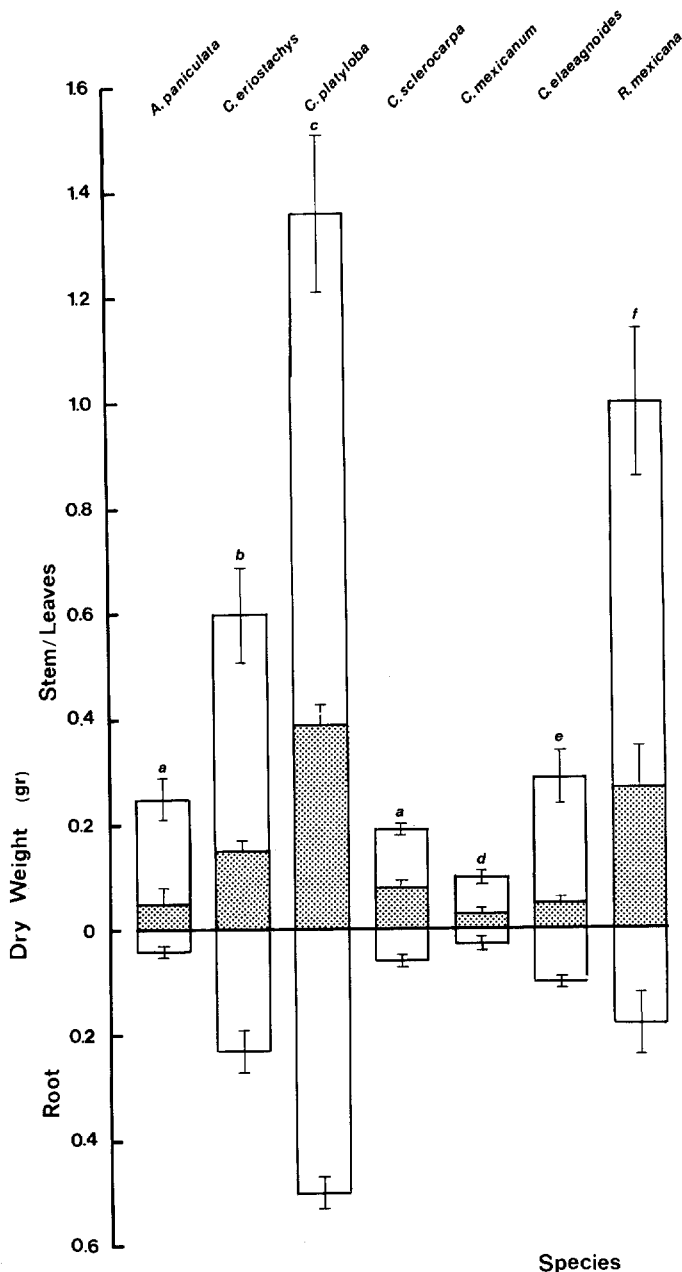
Fig. 2. Dry biomass allocation for roots, stem (*shaded area*) and leaves for the seven species studied. *Apoplanesia paniculata, Caesalpinia eriostachys, C. platyloba, C. sclerocarpa, Celaenodendron mexicanum, Cordia elaeagnoides* and *Recchia mexicana*. 95% confidence limits are indicated as *vertical bars. Small letters* show significant differences (*P* <0.05) among the species

system develops. This branching process follows the Horton's Law of branching, e. g. the number of branches in each order is a constant proportion of that in the next order. This relationship allows us to generate a branching ratio (R_b), using the number of elements per order and a length ratio (R_1) using the total length of the segments in each order (Horsfield et al. 1976). In addition, diagrams of the roots were obtained by making silhoutte drawings from photographs taken of the root systems during the final harvest.

After performing all measurements roots and shoots were dried at 80°C for 48 h to obtain dry weights. The dry weight data were analysed following the classical growth analysis methods described in detail by Evans (1972) and Hunt (1982). The mean relative growth rate (RGR, dry

weight increment per unit total plant weight per unit time, mg/mg day⁻¹) of each species was determined according to Hunt (1982):

$$RGR = (\ln W_{t2} - \ln W_{t1})/(t_2 - t_1)$$

where *W* is the mean total plant dry weight in milligrams and *t* is time in days. Four ratios were obtained: the ratio of total root length to total weight (specific root length, SRL) together with the specific leaf area (SLA, the ratio of foliage leaf area to foliage dry weight; Causton and Venus 1981; Hunt 1982), the root length/leaf area ratio (Körner and Renhardt 1987) and the root/shoot dry weight ratio. The relation between total root length and soil volume, rooting density was also determined (Caldwell and Richards 1986). Significant differences among the species for each measured parameter were tested by analysis of variance, using log-transformed data where necessary to meet assumptions of normality (Zar 1974).

Results

Despite the fact that the species were grown in soil from their habitat, nodules were not observed in the four legumes studied. No attempt was made to determine mycorrhiza infection. The seven species had sharply contrasting root forms (Fig. 1). Both species from disturbed habitats, *A. paniculata* and *C. elaeagnoides*, have dichotomously branching systems. The other five species present a herringbone pattern. The information in Table 1 summarizes the data obtained with the morphometric analysis, including the mean total root length and the R_b and R_1. Except for *Caesalpinia sclerocarpa* all the species achieved similar length ratios; by contrast, differences emerged in the branching ratios. *Caesalpinia eriostachys, Celaenodendron mexicanum* and *Recchia mexicana* achieved similar values between 12 and 15; the rest of the species ranged between 5 and 8. Total root length also varied among the species, being the longest in *Caesalpinia platyloba* (1611.3 cm) and the shortest in *Celaenodendron mexicanum* (220.2 cm).

Table 1 and Fig. 2 show the allocation of dry matter to roots and shoots (stem/leaves) for each species and the total mean RGR attained for the seven plant species after the 35 days of the experiment. Little difference in RGR emerged among the species; however legumes appear to show slightly greater rates. *Apoplanesia paniculata* and *Recchia mexicana* achieved the lowest root/shoot ratios (0.16 and 0.18); the rest of the species reached ratios between 0.29 and 0.38. The SRL and SLA are shown comparatively in Fig. 3. The SRL values in combination with the root diagrams (Fig. 1) show different root patterns. Clearly *Apoplanesia paniculata* and *Cordia elaeagnoides*, both species from disturbed areas and with the smallest seeds, showed the bigger SRL, which suggest that they have a thin root system. In contrast, *Caesalpinia eriostachys* and *Caesalpinia platyloba*, species with the largest seeds, present a deeper and thicker root system. Species with thicker leaves with a small are a were *Caesalpinia platyloba* and *Recchia mexicana*, as indicated by the SLA.

The rooting density indicates the size of the root and the volume of soil that is explored by the root; these values (Fig. 4) appear to be small in all the species (<0.5 cm/cm³) (see Caldwell 1988). The mean number of root tips (Fig. 5) corresponded to order 1 of the morphometric root analysis and indicates the number of finest roots, which tend to be the most active in absorption and exudation. *Recchia mex-*
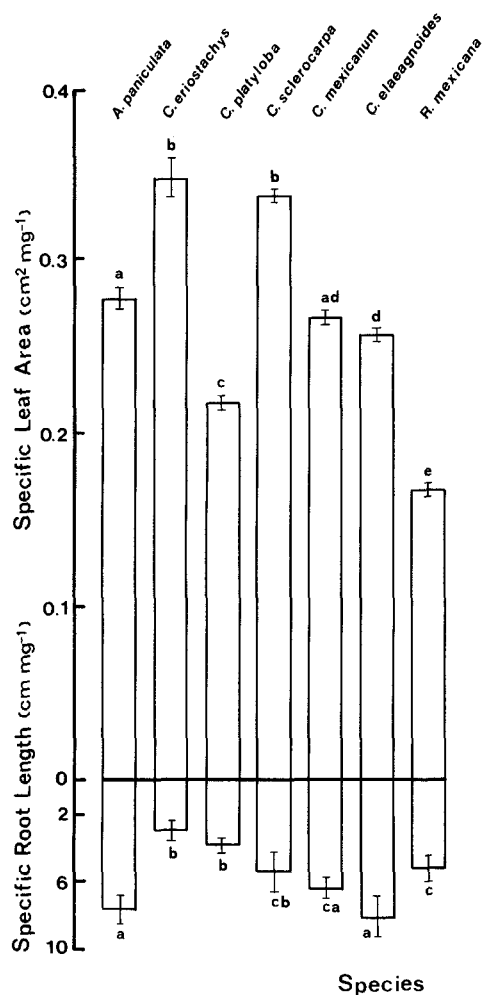
Fig. 3. Specific root length and specific leaf area for *Apoplanesia paniculata, Caesalpinia eriostanchys, C. platyloba, C. sclerocarpa, Celaenodendron mexicanum, Cordia elaeagnoides* and *Recchia mexicana.* 95% confidence limits are shown as *vertial bars*; *small letters* indicate significant differences (*P* <0.05)
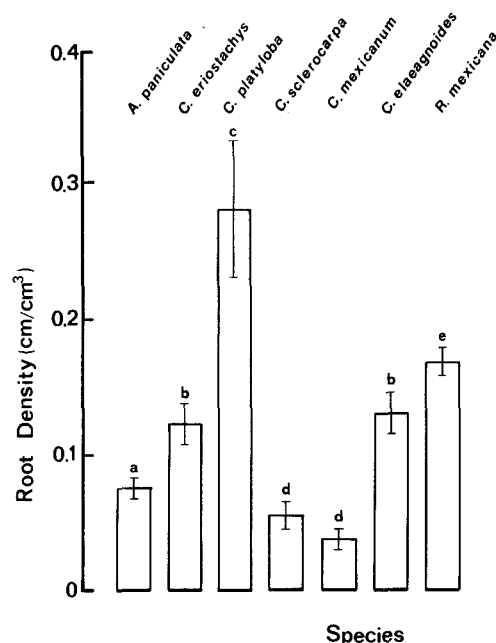

Fig. 4. Rooting density (mean total root length per soil volume) of *Apoplanesia paniculata, Caesalpinia eriostachys, C. platyloba, C. sclerocarpa, Celaenodendron mexicanum, Cordia elaeagnoides* and *Recchia mexicana.* 95% confidence limits are indicated as *vertical bars*. *Small letters* show significant differences (*P* <0.05)

icana had the highest number of root tips and largest seed size. The root length/leaf area ratios are described in Fig. 6. It appears that there is a tendency for all the species to develop more root length per unit leaf area.

Discussion

The mean RGR attained for the tree seedling species was very similar and consistently low. Comparative growth studies carried out by Jarvis and Jarvis (1964) and Grime and Hunt (1975) in temperate species, and Rincon and Huante (1988) in tropical dry forest species have shown slow growth in tree seedlings. This has been attributed to expenditure in woody tissue. To establish the relative importance of leafyness and leaf efficiency in determining the

Table 1. Summary of the branching and length ratios attained for the species together with the average total root length, average seed weight, mean total relative growth rate (mg/day⁻¹) and root/shoot ratio (mg/mg) for the seven species studied. Significant differences (*P* <0.05) among the species are indicated with letters

| Species	Branching ratio	Length ratio	Mean total root length (cm)	Seed weight (mg)	Root/shoot ratio (mg/mg)	Relative growth rate (mg/mg day⁻¹)
Apoplanesia paniculata	7.29 a	4.20 a	414.2 a	2.1	0.16 a	0.15 a
Caesalpinia eriostachys	15.07 d	3.64 b	729.0 b	239.8	0.38 b	0.12 b
C. platyloba	8.14 a	3.67 b	1611.3 c	233.2	0.36 b	0.17 c
C. scleroacarpa	5.87 b	22.68 c	311.6 d	74.4	0.29 b	0.13 b
Celanodendron mexicanum	12.05 c	3.02 d	220.2 e	63.8	0.34 b	0.09 d
Cordia elaeagnoides	6.57 ab	3.30 b	768.4 b	17.7	0.33 b	0.13 b
Recchia mexicana	12.02 c	2.56 d	947.5 f	573.7	0.18 a	0.10 d
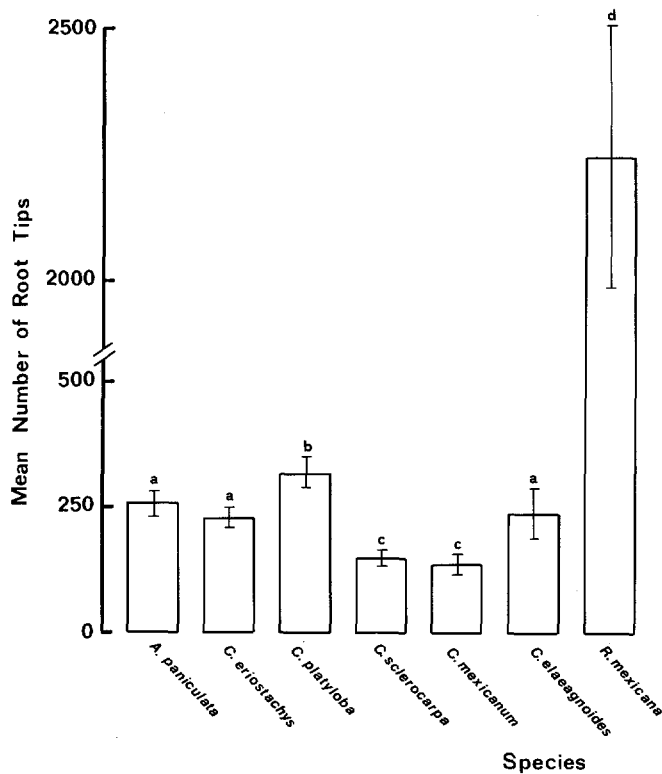
Fig. 5. Mean number of root tips for *Apoplanesia paniculata*, *Caesalpinia eriostachys*, *C. platyloba*, *C. sclerocarpa*, *Celaenodendron mexicanum*, *Cordia elaeagnoides* and *Recchia mexicana*. Small letters indicate significant differences ($P < 0.05$) among the species. *Vertical bars* show 95% confidence limits

Fig. 6. Root length/leaf area ratios for *Apoplanesia paniculata*, *Caesalpinia eriostachys*, *C. platyloba*, *C. sclerocarpa*, *Celaenodendron mexicanum*, *Cordia elaeagnoides* and *Recchia mexicana*. Small letters indicate significant differences ($P < 0.05$) among the species. *Vertical lines* on the bars show 95% confidence limits

RGR in each species, it is necessary to perform a more detailed functional growth analysis (Hunt 1982). However, some observations can be made with regard to the RGR, the morphology and dry matter partitioning attained by the species. While seed dry weight was not related to growth rate, it is clear that high seed weight was associated with high yields (Fig. 2, Table 1).

The two species from disturbed habitats showed the lowest seed dry weight coupled with relatively high growth rates (Table 1). The lack of comparative information about RGR in tropical dry forest tree species make it difficult to evaluate the possible advantage of slow growth in tropical seasonal systems, in which the growth season is short.

All the species allocated more biomass to the shoot, particularly more dry weight to leaves than to stems (Fig. 2), and showed consequently low root/shoot ratios (Table 1). These appear to suggest that the species are adapted to non-nutrient limited environments (Chapin 1980, 1988). However, this hypothesis must be tested experimentally.

The gross morphology of the seven species studied has been expressed by the SRL and SLA. The low SLA values suggest species with thick leaves of small area, a characteristic that is more pronounced in *Caesalpinia platyloba* and *Recchia mexicana*, both of which have large seeds (Table 1). In contrast, relatively high SRL values represent long thin roots and were found in the two species from
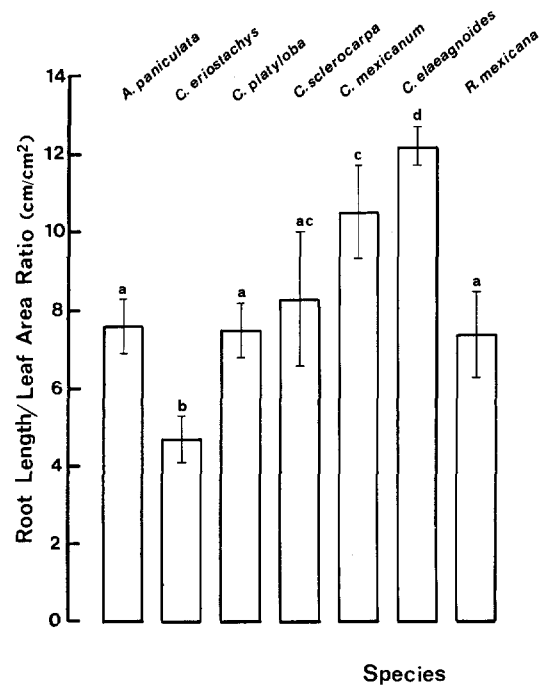
disturbed habitats (A. *paniculata* and C. *elaeagnoides*). These species have small seeds and are the only two which show a dichotomous branching in the root system.

The root length/leaf area ratios indicate very broadly the structural cost invested in resource-capture surfaces. A bigger ratio reflects a higher expenditure in roots associated with the water and nutrient cost of sustaining the photosynthetic capacity. There was a tendency in all the species to develop more root length per unit leaf area. In this sense, it seems that *C. eriostachys* is the species more efficient in terms of the expenditure in roots versus leaf area. However, it is necessary to conduct more investigations in relation to water use efficieny and photosynthesis to assess how tropical deciduous trees adjust physiologically to changes in resource availability and to the different demands for defence, storage and reproduction, in an environment in which the growth season is short (Bloom et al. 1985).

The four species of legumes included in the study, even those belonging to the same genera, did not show similar characteristics. Explanations for co-existence in this diverse dry forest, in which temporal differentiation of root/shoot activity is difficult to evoke, are more likely to come from different spatial exploitation of the resources (Fitter 1986; Bullock and Solis-Magallanes 1990; Kummerow et al. 1990). This hypothesis appears to be supported by the contrasting morphologies of the root systems of the seven species studied, which seem to indicate different mechanisms for exploiting the soil environment. In particular, the two species characteristic of disturbed habitats showed a dichotomous root branching pattern. It has

been suggested (Fitter 1985) that this type of root system provides more effective exploration and exploitation of zones of high nutrient availability.

The low values of root density shown by all the species also appear to suggest that competition between individual roots for the same soil resources is unlikely (Caldwell 1987), at least during early establishment. However, it is evident that more experimental evidence is needed to increase our understanding of the mechanisms which control the tree seedling establishment process of species-rich tropical deciduous forest. The results of this investigation provide research opportunities to study physiological attributes of tropical deciduous tree seedlings, in particular water and nutrient use efficiency. It also opens a field for investigations in dry matter partitioning in seedlings from the north American tropical deciduous forest.

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