

ROOT AND SHOOT GROWTH IN RESPONSE TO SOIL DRYING IN FOUR AMAZONIAN WEEDY SPECIES¹

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ABSTRACT- Maximum rooting depth, root distribution profile and biomass allocation patterns were measured for seedlings of the Amazonian weedy species *Ipomoea asarifolia*, *Stachytarpheta cayennensis*, *Solanum crinitum* and *Vismia guianensis* grown in both watered and unwatered soil columns in a glasshouse. The objective was to determine whether seedlings of these species show below and above ground responses to soil drying that could be characterized as enhanced ability to acclimate to water deficits. All seedlings were initially grown in well-watered conditions for 21 days. After that period, two watering treatments were imposed for an additional 21-day period. One group of seedlings was watered daily another group was not watered. Rooting depth was not significantly affected by treatments for none of the species. However, soil drying significantly increased root/shoot ratio in *Ipomoea* and *Stachytarpheta*, and caused changes in the root distribution profile of all species. Well-watered plants generally maximized root development in the shallowest soil layers, while the opposite was observed for water-limited plants. These results are discussed in relation to their ecological significance to Brazilian Amazonia.

Additional index terms: allocation, drought, root growth, root length density, root/shoot ratio, tropical.

CRESCIMENTO DA RAIZ E PARTE AÉREA EM RESPOSTA AO SECAMENTO DO SOLO EM QUATRO PLANTAS INVASORAS DA AMAZÔNIA

RESUMO- A profundidade máxima e perfil de distribuição vertical das raízes e os padrões de alocação de biomassa foram medidos nas espécies invasoras *Ipomoea asarifolia*, *Stachytarpheta cayennensis*, *Solanum crinitum* e *Vismia guianensis*, cultivadas em colunas de solo com e sem irrigação, em casa de vegetação. O objetivo foi determinar se estas espécies apresentam respostas ao secamento do solo que podem ser caracterizadas como uma forma de

aclimação ao déficit hídrico. Inicialmente, todas as plantas foram cultivadas sem déficit hídrico por 21 dias. Após esse período, dois regimes de irrigação foram estabelecidos por um período adicional de 21 dias. Um grupo de plantas era irrigado diariamente; outro grupo não recebia irrigação. A profundidade das raízes não foi significativamente afetada pelos tratamentos em nenhuma das espécies. No entanto, o estresse hídrico aumentou significativamente a relação raiz/parte aérea em *Ipomoea* e *Stachytarpheta* e alterou o perfil da distribuição radicular em todas as espécies. De um modo geral, as plantas irrigadas maximizaram o desenvolvimento radicular nas camadas mais rasas do solo, enquanto que o oposto foi observado nas plantas não irrigadas. Estes resultados são discutidos com relação ao, seu significado ecológico para a Amazônia Brasileira.

Termos adicionais para indexação: crescimento radicular, erva daninha, estresse hídrico, relação raiz/parte aérea, tropical.

INTRODUCTION

Seedling survival in drought prone environments may depend upon the species' ability to compensate for the negative effect of low water potentials in the soil and atmosphere by adjusting root and shoot morphological and physiological patterns (Kramer, 1983; Morgan, 1984). In this context an improved plasticity in promoting a shift in the allocation of assimilates from shoot to root and in adjusting the growth and distribution of the root system in response to soil drying are generally considered important acclimation mechanisms to drought (Molyneux & Davies, 1983; Sharp & Davies, 1979; Morgan, 1984).

While it could be argued that for some crop plants (mainly the ones in which only the above ground biomass is harvested) a relatively high investment in the root systems may not be very advantageous due to the growth and maintenance costs in root development, for wild plant species such investment could be advantageous. Hence, seedlings of invasive plants species that exhibit a great plasticity in root

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growth and distribution in response to soil drying could be considered well adapted to environments where limited soil water availability is a major constraint to plant growth.

In the experiment described in this paper I have compared root penetration and growth, and biomass allocation patterns, in response to soil drying in seedlings of *Ipomoea asarifolia* (Desr.) Roem. & Schultze (*Convolvulaceae*), *Stachytarpheta cayennensis* (Rich) Vahl. (*Verbenaceae*), *Solanum crinitum* Lam. (*Solanaceae*) and *Vismia guianensis* (Aubl.) Choisy (*Guttiferae*). These species are considered important weedy species of anthropogenic and (or) naturally disturbed habitats in eastern Brazilian Amazonia (Albuquerque, 1980; Dantas, 1989 and Dias Filho, 1990), a region characterized by significant diurnal and seasonal drought stress. Despite the ecological and economic importance of these species to the Amazon region, little is known about their response to drought and their ability to acclimate to water deficits. The objective was to determine whether seedlings of these species show below and above ground responses to soil drying that could be characterized as enhanced ability to acclimate to water deficits.

MATERIAL AND METHODS

Plant material and growing conditions- Seeds from *Ipomoea asarifolia*, *Stachytarpheta cayennensis*, *Solanum crinitum* and *Vismia guianensis* were collected from plants invading pasture areas of Paragominas, PA (3° 05' S - 47° 21' W) in eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and when radicles reached 5 to 10 mm in length, seedlings were transferred to soil columns (one seedling per column) to allow relatively unrestricted root development. The soil column was a polythene tube 1 m long and 76 mm in diameter, filled with 2.3 kg of fritted clay (OilDri Corporation of America, Chicago, IL). This rooting medium was used because it was relatively easy to separate from roots and had high water-holding capacity, allowing gradual soil drying similar to what may occur under natural conditions. Tubes were closed at the bottom with a plastic mesh to hold the growth medium and allow free drainage. Before seedling transplant, each soil column was saturated with 2.1 L of a nutrient solution (150 g L⁻¹ N, 300 g L⁻¹ P₂O₅, 150 g L⁻¹ K₂O, 0.2 g L⁻¹ B, 0.7 g L⁻¹ Cu, 1.5 g L⁻¹ Fe, 0.5 g L⁻¹ Mn, 0.005 g L⁻¹ Mo and 0.6 g L⁻¹ Zn; 3.5 g L⁻¹).

Tubes were placed in a greenhouse for the duration of the experiment. Minimum and maximum temperatures (mean s.e.) in the greenhouse were 25 ± 2.2 °C (night) and 33 ± 2.1 °C (day). A maximum photosynthetic photon flux density (PPFD) of approximately 1000 μmol m⁻² s⁻¹ was supplemented and photoperiod extended to 12 hours

by 400 W high-pressure sodium vapor lamps. Relative humidity of the air was maintained at around 80 %.

Treatments and measurements- All seedlings received a 21-day pretreatment in which the soil columns were irrigated daily with either 100 ml of deionized water or, on alternating days, with 100 ml of nutrient solution (the same solution applied before planting). A transparent plastic cover, with a central opening to allow seedling development, was placed on the surface of each column to reduce moisture loss from the growth medium. Following the pretreatment two treatments were applied for an additional 21 days to compare root development under well-watered and water-limited conditions. Seedlings in one treatment received 100 ml d⁻¹ of deionized water; seedlings in the second treatment were not watered. Each treatment was applied to seven seedlings of *Ipomoea*, *Stachytarpheta* and *Solanum* and to three seedlings of *Vismia*.

To determine the vertical distribution of roots within the columns, at the end of the 42-day experiment, plants were clipped at the soil surface and each column was cut into sections of either 50 mm (*Solanum* and *Vismia*) or 100 mm (*Ipomoea* and *Stachytarpheta*) in depth. Roots in each column section were extracted and washed. For each seedling, maximum rooting depth (to the maximum 50 or 100 mm), shoot mass, total leaf area, and root mass (vertical distribution of root dry mass in the column) were calculated for all species. Roots and shoots of each seedling were dried at 70 °C for 48 h. Leaf area was measured using a leaf area meter (Model LI-3000 with conveyor belt assembly LI-3050. Li-Cor, Inc. Lincoln, NE). Attributes measured for each plant were used to estimate biomass allocation patterns: leaf area ratio (leaf area per unit dry mass of whole plant, LAR), specific leaf area (leaf area per unit of leaf dry mass, SLA) and leaf, stem and root mass ratios (respectively, leaf, stem or root dry mass per unit of dry mass of whole plant, LMR, SMR and RMR). All of the above biomass allocation variables were calculated according to Hunt (1990).

Experimental design and statistical analysis- Soil columns were arranged in the greenhouse in a completely randomized design with seven (*Ipomoea*, *Stachytarpheta* and *Solanum*) or three (*Vismia*) replicates. Each replicate was an individual column planted with a single plant and placed at a particular location inside the greenhouse. For each species, differences between treatments in maximum rooting depth, root/shoot ratio, root dry mass accumulation and biomass allocation patterns were determined by paired *t*-tests; homogeneity of variances was assessed by Levene's test (Milliken & Johnson, 1992). When necessary the data were log or square root transformed for the test. Transformed data were back transformed for presentation.

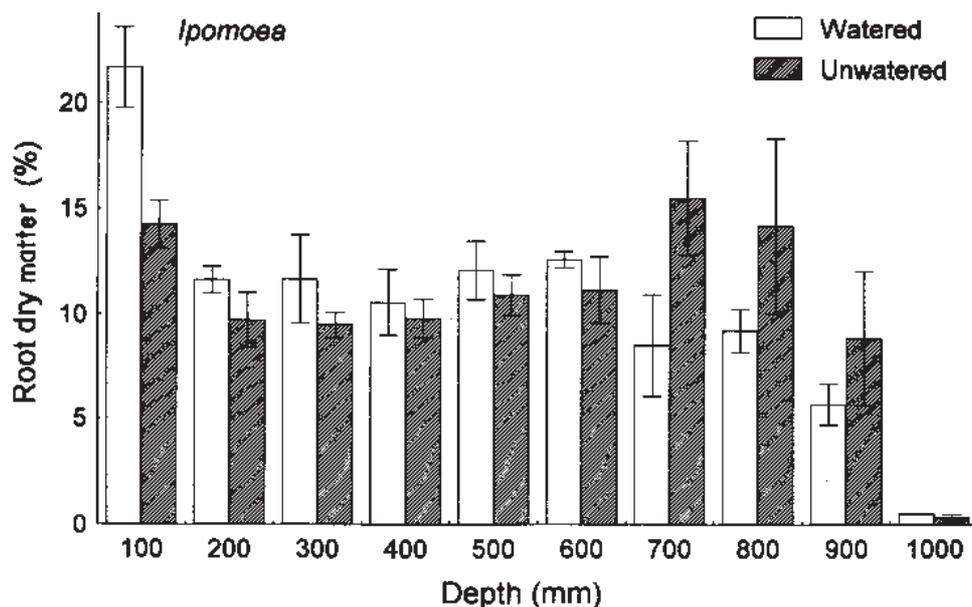


FIGURE 1- Percentage of total root dry mass in consecutive 100 mm soil layers in watered and unwatered columns for *Ipomoea*. Values are means of seven seedlings standard error.

RESULTS

Root/shoot ratio- Soil drying increased root/shoot ratio by 45 % ($t=4.1$, $P<0.001$) in *Ipomoea* and by 38 % ($t=6.0$, $P<0.001$) in *Stachytarpheta* (data not shown). For *Solanum*, no significant difference ($t=0.8$, $P=0.41$) in root/shoot ratio could be detected between treatments; however, plants in unwatered soil displayed a mean root/shoot ratio 15 % higher than in watered soil. Contrary to these species, root/shoot ratio in *Vismia* had a tendency to be higher in watered soil; however, the difference between watering regimes was not statistically significant for this species ($t=1.5$, $P=0.37$).

Rooting depth- No significant difference in maximum rooting depth could be detected between treatments for any of the species ($t<1.15$, $P>0.27$) (data not shown). However, a tendency for greater rooting depth in unwatered soil was suggested by the data from *Stachytarpheta*, while an opposite tendency was observed in *Vismia*. Among species, rooting depth was maximum for *Ipomoea*, followed by *Solanum*, *Stachytarpheta* and *Vismia*.

Root growth- Root dry matter distribution in the profile was influenced by watering regimes in all studied species. In watered conditions, root development in *Ipomoea* was maximum at the 0-100 mm layer (Fig. 1) while in unwatered conditions, maximum root development had a tendency to be greater between the 600-700 and 700-800 mm layers.

For *Stachytarpheta*, root dry mass in watered soil was maximum at the 0-100 mm layer, and significantly greater than for unwatered plants ($t=9.22$, $P<0.001$) (Fig. 2). In unwatered soil relative root mass was equivalent at the 0-100 and the 100-200 mm soil layers and was significantly greater at 100-200 mm than for watered plants ($t=9.37$,

$P<0.001$). Also; no statistical difference between treatments could be detected at 200-300 mm and no roots grew beyond 300 mm.

In *Solanum*, root dry matter in unwatered conditions had a tendency to be greater at 150-200 mm (Fig. 3), while in watered soil, root dry mass was similar at depths up to 300 mm, showing a tendency to decrease thereafter. Otherwise the rooting depth distributions of *Solanum* appeared similar between the two treatments.

Root dry mass distribution in *Vismia* followed the same pattern observed in the other species (Fig. 4). In watered soil, *Vismia* maximized root development in the surface layer (0-50 mm) and showed a tendency to decrease root development in the subsequent layers. In unwatered soil, root development had a tendency to be maximum at the

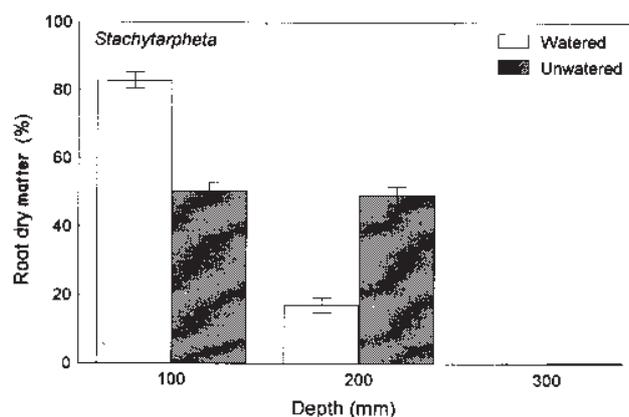


FIGURE 2- Percentage of total root dry mass in consecutive 100 mm layers in watered and unwatered columns for *Stachytarpheta*. Values are means of seven seedlings standard error.

TABLE 1- Biomass (g) of the four species under two watering regimes after 42 days. Values are means (s.d.); n= 3 for *Vismia* and 7 for the other species. The P-value denotes statistical differences between treatments according to the paired t-test.

	Watered		Unwatered		P
<i>Ipomoea</i>					
Leaf dry mass	1.77	0.07	0.87	0.04	0.008
Stem dry mass	2.71	0.09	0.86	0.03	<0.001
Shoot dry mass	4.48	0.16	1.74	0.06	0.02
Root dry mass	2.16	0.45	1.54	0.43	0.001
Total biomass	6.64	0.16	3.27	0.06	0.001
Number of leaves	12	4.2	9.8	3.1	0.2
Leaf area (cm ²)	680.8	34	296.7	12	0.005
<i>Stachytarpheta</i>					
Leaf dry mass	0.20	0.05	0.16	0.03	0.11
Stem dry mass	0.05	0.02	0.04	0.01	0.10
Shoot dry mass	0.25	0.07	0.19	0.03	0.10
Root dry mass	0.12	0.04	0.16	0.02	0.08
Total biomass	0.37	0.11	0.36	0.05	0.7
Number of leaves	19.4	3.1	8.0	1.1	<0.001
Leaf area (cm ²)	54.5	12.6	37.9	5.5	0.008
<i>Solanum</i>					
Leaf dry mass	2.08	0.25	0.41	0.01	0.002
Stem dry mass	0.45	0.06	0.09	0.004	0.003
Shoot dry mass	2.54	0.3	0.49	0.02	0.002
Root dry mass	1.49	0.16	0.35	0.03	0.003
Total biomass	2.01	0.69	0.92	0.21	0.002
Number of leaves	8.7	1.0	5.6	0.9	<0.001
Leaf area (cm ²)	689.0	76.7	82.6	3.4	<0.001
<i>Vismia</i>					
Leaf dry mass	0.05	0.03	0.03	0.02	0.5
Stem dry mass	0.007	0.005	0.006	0.002	0.6
Shoot dry mass	0.06	0.04	0.04	0.02	0.5
Root dry mass	0.03	0.02	0.02	0.005	0.3
Total biomass	0.086	0.059	0.055	0.024	0.5
Number of leaves	18.0	7.2	15.3	3.1	0.6
Leaf area (cm ²)	20.6	14.6	10.2	4.5	0.3

50-100 mm layer (Fig. 4). *Vismia* developed no roots below 200 mm in either treatment.

Biomass production and allocation pattern- Total dry matter was reduced by soil drying in *Ipomoea*, *Solanum* and *Vismia*, though not significantly ($P > 0.05$) in *Vismia* (Table 1). In *Stachytarpheta*, total biomass was unaffected by soil drying (Table 1). For *Ipomoea* and *Solanum*, the decline in total above-ground biomass was apparently the major cause for the significant reduction in total plant biomass in response to soil drying (Table 1). In contrast to the other species that had their below ground biomass reduced by soil drying, root dry mass in water-limited *Stachytarpheta* increased; however, this increase was not statistically

TABLE 2- Leaf area ratio (LAR= leaf area per total plant dry mass, m² kg⁻¹) and specific leaf area (SLA = leaf area per leaf dry mass, m² kg⁻¹) of well-watered and water-limited plants. Values are means (s.d.), n=7 for *Ipomoea*, *Stachytarpheta* and *Solanum*, and n=3 for *Vismia*. For each species, means within columns are significantly different at the $P < 0.05$ level (*), at the $P < 0.01$ level (**), or at the $P < 0.001$ level (***), in the paired t-test.

Watering regime	LAR		SLA	
<i>Ipomoea</i>				
Watered	10.2	1.8	38.4	4.3 *
Unwatered	8.9	1.2	34.2	1.0 *
<i>Stachytarpheta</i>				
Watered	14.8	1.7 ***	27.5	2.7 **
Unwatered	10.6	0.4 ***	23.4	1.0 **
<i>Solanum</i>				
Watered	17.2	0.3 ***	33.3	2.0 ***
Unwatered	9.9	1.8 ***	20.2	1.9 ***
<i>Vismia</i>				
Watered	23.1	1.9 **	44.8	4.7 *
Unwatered	18.5	0.2 **	33.1	4.0 *

significant (Table 1). A common response to soil drying in all species was a tendency to reduce both the total number and area of leaves. This may have ultimately contributed to the observed reduction in the total dry matter production in most water-limited plants.

All species varied in their biomass allocation patterns in response to the watering regimes. *Ipomoea* and *Stachytarpheta* significantly increased their relative investment in root tissue (root mass ratio, RMR) in response to low water availability ($t=4.1$, $P<0.001$). However, in *Solanum* and *Vismia*, no significant difference in RMR could be detected between watering regimes ($t=0.6$, $P>0.37$) data not shown.

In *Stachytarpheta*, the amount of biomass allocated to leaves (LMR) was significantly higher ($t=5.1$, $P<0.001$) in watered soil. For the remaining species, no significant difference in LMR could be detected between treatments. Low water availability decreased allocation of biomass to support tissues (SMR) in *Ipomoea* and *Stachytarpheta* ($t=3.6$, $P<0.004$), whereas no treatment effect ($t=0.8$, $P>0.48$) could be detected in *Solanum* and *Vismia*.

Water limitation significantly decreased plant leafiness, i.e., leaf area per unit mass of whole plant (LAR) in *Stachytarpheta*, *Solanum* and *Vismia* (Table 2). However, no significant difference in LAR could be detected for *Ipomoea* (Table 2). In all the four species studied, specific leaf area (SLA) was significantly lower in unwatered soil (Table 2).

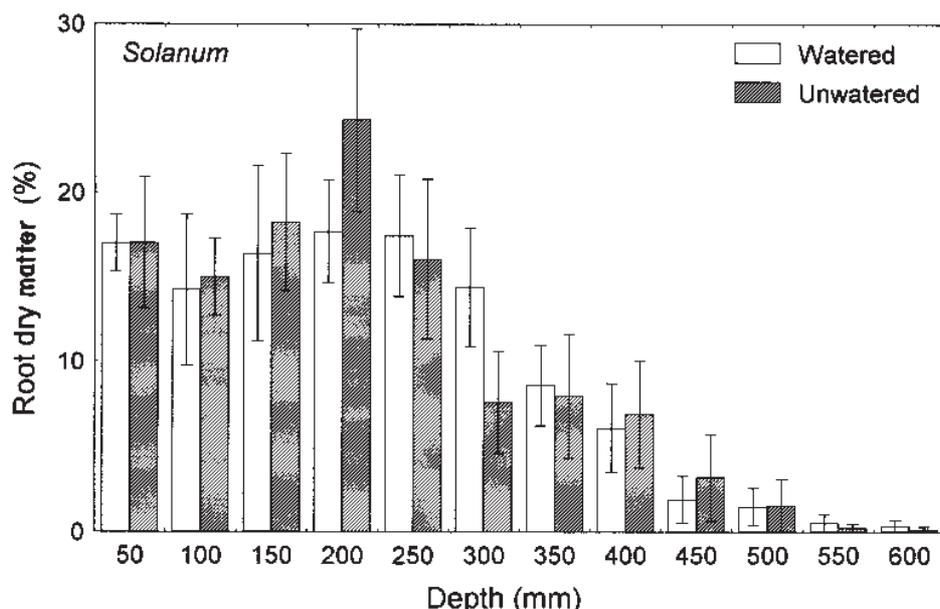


FIGURE 3- Percentage of total root dry mass in consecutive 50 mm layers in watered and unwatered columns for *Solanum*. Values are means of seven seedlings standard error.

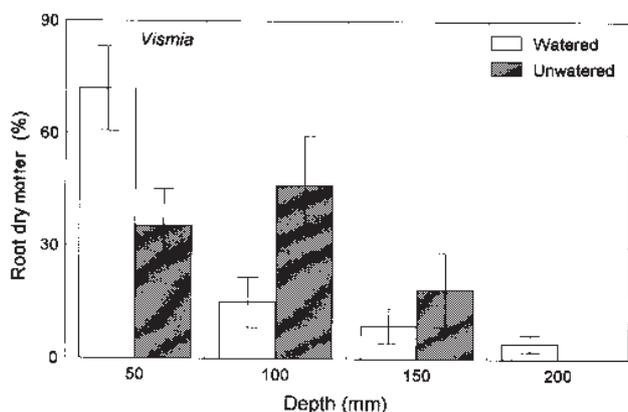


FIGURE 4- Percentage of total root dry mass in consecutive 50 mm layers in watered and unwatered columns for *Vismia*. Values are means of seven seedlings standard error.

DISCUSSION

A reduction in shoot growth relative to root growth is a common response to soil drying (Kramer, 1983). Plants exposed to drought stress usually show an enhanced allocation to roots (e.g., Dale & Causton, 1992) and, as a consequence, an increase in their root to shoot ratios (e.g., Hoogenboom et al, 1986; Khalil & Grace, 1992, Motzo et al., 1993; Nash & Graves, 1993; Wan et al., 1993, Weerathworn et al., 1992). Of the four species studied, only *Vismia* did not show a tendency to increase its root/shoot ratio and RMR in response to soil drying. It is possible that the relatively low growth rate of this species at the early stages of seedling development (data not shown), may have in part limited its capability to efficiently adjust to soil drying by promoting a rapid shift in biomass allocation to roots. In the present

investigation, the ability of the studied species to increase RMR in response to soil drying was positively related to their known growth rate at early stages of seedling development and also to their seed mass (*Ipomoea* > *Solanum* > *Stachytarpheta* > *Vismia*). This finding is consistent with the view that fast-growing species and (or) species with comparatively larger seeds generally have a higher degree of plasticity in root morphology (e.g., Baker, 1972; Evans & Etherington, 1991; Lambers & Poorter, 1992) and as such have the capacity to respond relatively faster to drought.

The significantly higher specific leaf area (SLA) in the well-watered plants of all species (Table 2) is consistent with the results of Jones et al. (1980), Khalil & Grace (1992), Retuerto & Woodward (1993) and Van Loo (1992) who found that water deficit reduces SLA. Also, the reduction in the leaf area ratio (LAR) in response to soil drying observed in the present study (Table 2) is a common response reported in the literature for water stressed plants (Khalil & Grace, 1992; Retuerto & Woodward, 1993).

By significantly increasing RMR and (or) decreasing SLA and LAR in response to reduced water supply, all four species revealed the ability to optimize water use in situations when low soil water potential would be concurrent with high evaporative demand. However, among the species studied, *Stachytarpheta* was apparently more efficient in significantly adjusting all of the above traits in response to drought (Table 2).

Results from other studies on the effect of soil drying on rooting depth are variable. Some report an increase (Box et al., 1989 for wheat; Hoogenboom et al., 1986 for soybean; Leidi & Gutierrez, 1993 for cotton seedlings; and Sharp & Davies, 1985 for corn) or, depending on the species, either an increase, a

decrease, or no significant effect of soil drying on root depth (Evans & Etherington, 1991, Reader et al., 1993). In the present study, no significant increase in rooting depth in response to soil drying could be detected for any of the species studied. However, although not statistically significant ($P=0.08$), the mean maximum rooting depth of water-limited *Stachytarpheta* was 12 % higher than that of well-watered plants. Also, depth of root penetration was not significantly reduced in any of the species in unwatered soil. Because of the vulnerability of the surface soil to drying, the ability to sustain root growth in drying soil that was observed in all the studied species would be of great importance for promoting seedling establishment of these species in natural conditions.

Although water content of the growth medium was not monitored in this experiment, it could be observed during root sampling at the end of the experiment that moisture content in the unwatered soil was, as expected, less at the top layers and increased with depth, while in watered soil, moisture was distributed more uniformly. All of the four species studied were capable of altering their root distribution profile to take advantage of this soil moisture availability pattern. In general, root dry matter accumulation, was maximized at the upper layers in the watered soil and at deeper layers in the unwatered soil (Figs. 1 to 4). Similar patterns of redistribution of root growth in response to drying soil have also been observed in corn (Sharp & Davies, 1985), sycamore seedlings (Khalil & Grace, 1992) and peanut (Meisner & Kamok, 1992). Interestingly, in unwatered *Stachytarpheta* the relative root dry mass density was similar between the 0-100 and the 100-200 mm layers (Fig. 2). However, during root sampling, in unwatered columns unlike in watered conditions roots in the 0-100 mm soil layer had a much higher proportion of suberized biomass than in the subsequent layers (data not shown). This increase in root suberization at the shallowest (driest) soil layer, as suggested elsewhere (Nobel & Sanderson, 1984), could probably reflect a mechanism to prevent water movement from the roots to the dry soil.

All four species studied showed to some extent morphological acclimation to soil drying. They were able to maintain root growth and also to alter the root distribution profile in response to drying soil. Only *Vismia* did not show a significant shift in biomass allocation (greater partitioning into root tissue) in response to soil drying. However, despite its comparatively low plasticity, very small seedling size and shallow rooting depth, all water-limited *Vismia* seedlings were able to survive throughout the experimental period. Such behavior suggests the presence of very efficient traits that may improve this species' ability to adjust and to partially offset the

damaging effects of soil drying. The finding that in *Ipomoea* and *Solanum* seedlings, root growth, expressed as the relative dry matter distribution in the soil profile, and maximum rooting depth were comparatively higher than for the other two species studied, was compatible with the previous knowledge that these species are relatively not very conservative in their use of water (Dias Filho & Dawson, in press; Dias Filho et al., in press). A fast and vigorous root growth, as suggested by the present data, could help seedlings of these species to compensate for that water use characteristic by being relatively better equipped to exploit and (or) compete for soil water.

Stachytarpheta was particularly efficient in modifying its below and above ground biomass patterns (*i.e.*, showing a great plasticity) in response to soil drying. Under natural conditions such ability could help reduce its transpirational demand relative to water absorption and thus improve this species establishment capability in drying soil. This correlates with the observation that, in Brazilian Amazonia, *Stachytarpheta* is known to exploit seasonally dry, open habitats (Dias Filho, 1990). Because *Stachytarpheta* is the only species studied that reproduces exclusively from seeds (no vegetative reproduction), this species might be under greater selective pressures for traits that promote seedling survival in drought-prone environments (*e.g.*, plasticity in root development) and as such would show a comparatively superior acclimation to soil drying. In other studies (Reader et al., 1993; Sydes & Grime, 1984) a positive correlation between plasticity in root development and dependence on regeneration by seed has also been demonstrated.

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