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REGULAR ARTICLE

The effects of water availability on root growth and morphology in an Amazon rainforest

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Abstract This study examined how root growth and morphology were affected by variation in soil moisture at four Amazon rainforest sites with contrasting vegetation and soil types. Mean annual site root mass, length and surface area growth ranged between 3–7 t ha^{-1}, 2–4 km m^{-2} and 8–12 m^2 m^{-2} respectively. Mean site specific root length and surface area varied between 8–10 km kg^{-1} and 24–34 m^2 kg^{-1}. Growth of root mass, length and surface area was lower when soil water was depleted ($P<0.001$) while specific root length and surface area showed the opposite pattern ($P<0.001$). These results indicate that changes in root length and surface area per unit mass, and pulses in root growth to exploit transient periods of high soil water availability may be important means for trees in this ecosystem to increase nutrient and water uptake under seasonal and longer-term drought conditions.

Keywords Amazon rainforest · Soil water availability · Root mass growth · Root length · Root surface area · Specific root length

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Introduction

Roots play a key role in terrestrial biogeochemical cycling (Nadelhoffer and Raich 1992; Hendrick and Pregitzer 1993; Jackson et al. 1997; Roderstein et al. 2005) but are relatively understudied compared to components of above-ground plant growth (see reviews by Jackson et al. 1997; Norby and Jackson 2000; Trumbore and Gaudinski 2003). To address this deficiency an increasing number of studies have focused upon the role of roots in ecosystem carbon (C) allocation and cycling (See reviews by Atkin et al. 2000; Fitter et al. 2000; Pregitzer et al. 2000; Zak et al. 2000 and references therein). However, the majority of these studies have focused upon the effects of increasing carbon dioxide (CO_2) and temperature, in temperate or boreal regions. Information about the effects of changes in soil moisture in tropical regions is scarcer, but potentially has important implications for the terrestrial C balance (Houghton et al. 2001; IPCC 2001).

There are several different, though not mutually exclusive, mechanisms whereby soil water availability may affect root growth. The functional balance theory suggests that plants actively adjust growth of different organs to maximise uptake of the most limiting resource (Thornley 1972; Cannell and Dewar 1994). When water is limiting, plants should shift allocation of C towards roots where photosynthate can be used to increase water uptake. This shift in allocation should increase root mass growth as soil moisture declines.

Plants may also respond to drought stress by closing their stomata (Farquhar and Von Caemmerer 1982). Decreased stomatal conductance reduces not only water transpiration from the plant, but also CO_2 diffusion into the plant. Thus plants faced with soil moisture deficit may assimilate less CO_2 compared to their counterparts growing in wetter soils (Williams et al. 1998; Schwarz et al. 2004). The product of this change in the total amount of labile C available to the plant would likely be a decline in root mass production as soil moisture falls.

The processes outlined above have focused upon plant level C fixation or allocation, but local soil conditions may also provide a mechanism for altering root production. As the soil dries, root turgor pressure can fall and the soil may become denser. Together these factors decrease the ability of root systems to penetrate soil (Whalley et al. 1998; Bingham and Bengough 2003; Bengough et al. 2006). Thus, a decline in soil moisture could impede root production mainly through changes in soil physical properties, without altering plant C capture or growth strategy.

Additionally, an alternative plant strategy may be to stimulate water uptake not by increasing the total mass of root material, but by producing finer roots with relatively greater length and surface area per unit mass. This would lead to an increase in root specific length (SRL; km kg^{-1}) and root specific area (SRA; m^2 kg^{-1}) under drier conditions. However, information on root length and surface area is even scarcer than for root mass. A global review by Jackson et al. (1997) estimated root standing crop length and surface area in ten major terrestrial biomes based upon 11 studies that presented root length, and just seven studies that reported values for root surface area. No data existed for half of the biomes surveyed. This lack of data hinders attempts to accurately model the behaviour of terrestrial ecosystems, and their potential responses to climate change. The overall objective of this study, therefore, was to improve understanding of how plants may alter root characteristics to adapt to changes in water availability. Our specific aims were to:

1) Quantify the growth rate of tree root mass, length, and surface area, and SRL and SRA at three rain forest sites with contrasting soil and vegetation types in the eastern Amazon.
2) Test the following hypothetical responses of trees at the sites to seasonal, and longer-term, soil moisture deficit: (H_1) increase in growth rate of root mass, length and surface area, and (H_2) increase in SRL and SRA.

Data are presented from an Amazon rainforest because the region plays a key role in global biogeochemical cycling and climate (IPCC 2001; Houghton et al. 2001), but may experience increasing drought stress over this century (Shukla et al. 1990; Trenberth and Hoar 1997; Costa and Foley 2000; Silva Dias et al. 2002; Andreae et al. 2004; Schoengart et al. 2004). Seasonal drought effects were assessed by comparing root growth and morphology between the wet and dry seasons on all sites. Effects of longer term drought were inferred from measurements on an additional site from which approximately 50% of incident rainfall had been excluded for 5 years.

Table 1 Key vegetation and soil features for each site surveyed

	Sand	Dry	Clay	Fertile
Vegetation type				
Tree number (stems per hectare)[a]	434	421	419	544
Stem basal area (m^2 ha^{-1})[a]	24	24	25	37
Leaf area index (m^2 m^{-2})[b]	5	5	6	–
Soil type[c]				
Clay content (%)	18	13	42	20
Silt content (%)	5	4	14	22
Sand content (%)	77	83	44	57
pH	4	4	5	5
Carbon content (g kg^{-1})	9	12	22	46
Nitrogen content (g kg^{-1})	0.4	0.3	2	3
C/N ratio	23	35	9	15
P (mg kg^{-1})	3	3	4	36
Ca^{2+} (mg kg^{-1})	63	13	65	2,213
Mg^{2+} (mg kg^{-1})	43	4	39	313

[a] For all stems over 10 cm diameter at breast height, measured in January 2005

[b] Mean of 25 replicates recorded each month in 2005 (25×12=300 replicates)

[c] Soil type values are collated from data in Ruivo and Cunha (2003) and Sotta (2006).

– Data not available

Materials and methods

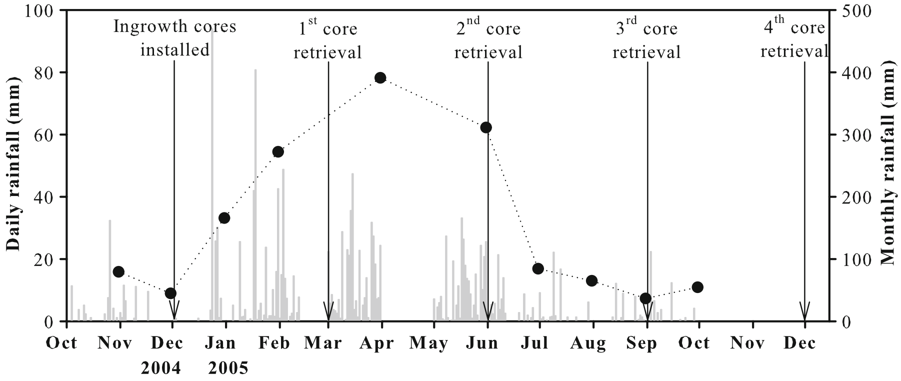
Site and experimental design

The experimental site is located in the Caxiuanã National Forest, Pará State, north-eastern Brazil (1°43′ 3.5″ S, 51°27′36″ W). The forest is a lowland *terra firme* rainforest with a high annual rainfall (~2,500 mm) and a pronounced dry season (Fisher et al. 2006). Across the entire year, mean soil surface temperature is ~25°C (±5°C), whilst diurnal variation is typically 1–2°C. The most widespread soil type is a highly weathered yellow Oxisol (US Department of Agriculture soil taxonomy) though there is substantial spatial variation in the relative proportion of sand and clay. There are also patches of relatively fertile soil, called anthropogenic dark earths (ADE) or *Terra Preta do Indio*, which mark areas that were intensively managed by indigenous populations of pre-Columban inhabitants (Ruivo and Cunha 2003; Lehmann et al. 2003). To represent existing soil type variation in the region, one-hectare measurement sites (see Table 1 for additional site details) were established on a well drained sandy Oxisol (Sand site), a clay-rich Oxisol (Clay site), and an ADE (Fertile site). In January 2002, a fourth one-hectare site (Dry site), on a sandy Oxisol soil, was modified by the installation of plastic panels placed at 2 m above the ground in order to exclude approximately 50% of incident rainfall (Fisher et al. 2006; Metcalfe et al. 2007a). Data from the Dry site were combined with data from the other, unmodified, sites to examine root responses over a wider range of soil moisture than currently exists naturally. A detailed site inter-comparison, before the imposition of the drought treatment on the Dry site, indicated that there was close environmental, structural and functional similarity between the Sand and Dry sites (P. Meir, unpublished data). The boundaries of the Dry site were trenched to a depth of 1 m and lined with plastic to minimize lateral flow of water into the site, and to channel water away from the plot interior.

Measurements

Within each site, 16 plots (area=10 m^2) were established at least 10 m from the perimeter of each site to minimize edge effects from surrounding soil

Fig. 1 Daily and monthly rainfall over the study period. Rainfall data are missing for the following periods: April 15–May 1, October 13–December 30



and vegetation types. If a plot measurement was obstructed by a tree, a new location was chosen 1 m away in a random direction. All plots within each site were located 10 m from each other. Root growth was estimated using the ingrowth core method (Vogt et al. 1998; Steingrobe et al. 2000; Hendricks et al. 2006). At the beginning of November 2004, soil cores (diameter=14 cm, area=154 cm^2) were extracted from all plots on each site using semi-circular opposable cutting blades, the roots were carefully removed by hand in a laboratory and the remaining soil was reinserted into the same holes surrounded by plastic mesh bags (mesh aperture diameter=1 cm). This was repeated four times (every 3 months) between November 2004 and November 2005 (Fig. 1). The amount of root material which grew

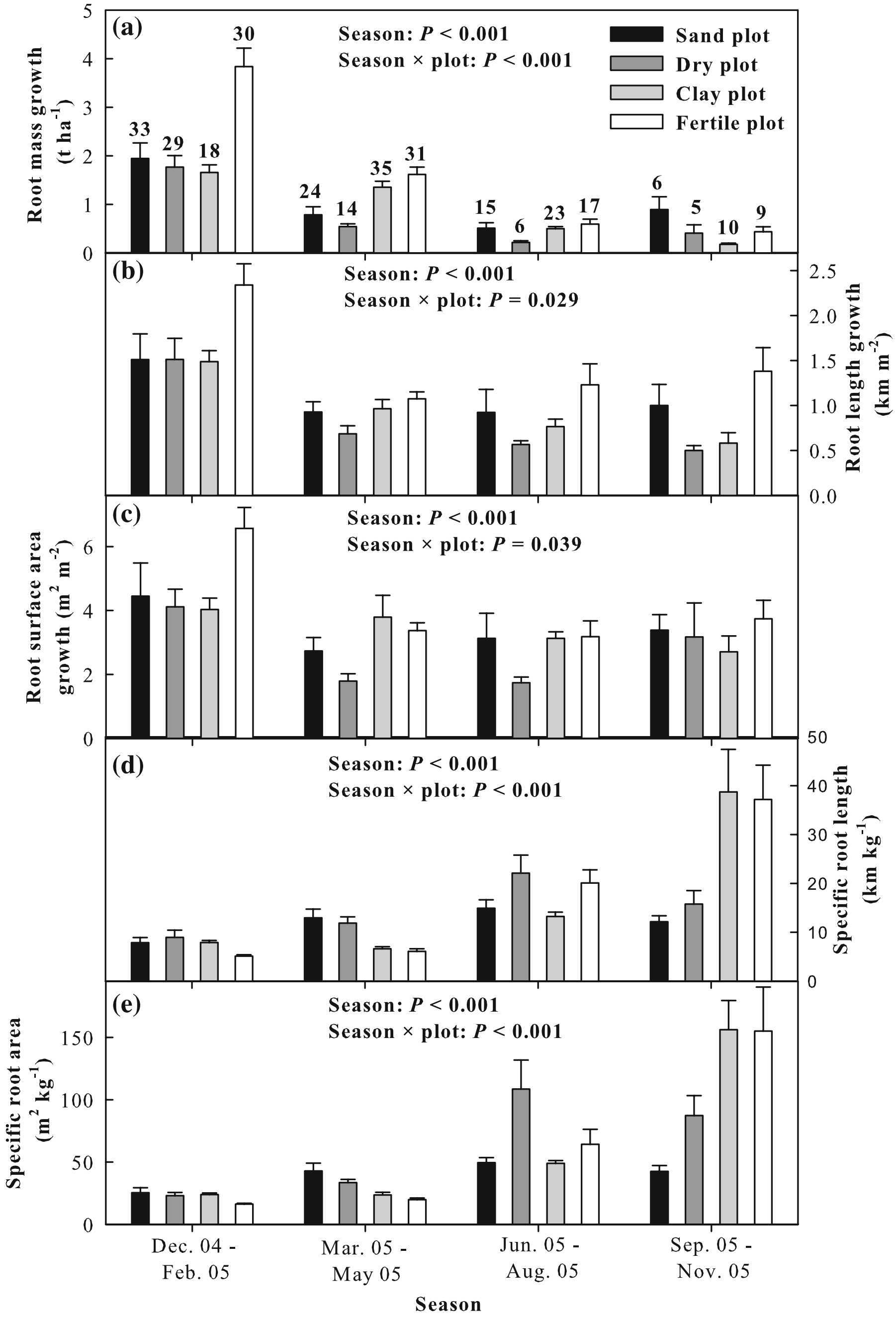


Fig. 2 Seasonal pattern of root mass growth, root length growth, root surface area growth, SRL and SRA in the surface 30 cm soil layer. **a**, **b**, **c**, **d** and **e** Data on root mass growth, root length growth, root surface area growth, SRL and SRA respectively. *Error bars* indicate SE of the mean, *n* is 16. *Numbers above columns* in **a** denote mean volumetric soil moisture (%) on each site and measurement session

into the mesh bags was used to calculate new root growth for each three-month interval. The sampling frequency of 3 months was chosen to capture seasonal trends in root growth whilst minimizing sample disturbance associated with repeated core extraction and root cutting. Evidence from root observation chambers at the same site suggest that it took much longer than 3 months for root density in initially root-free soil to approach ambient levels, and over 3 months the rate of growth was approximately linear while the amount of root mortality was negligible (Metcalfe et al. 2007b). Roots were retrieved from the soil in the laboratory by hand following the method described by Metcalfe et al. (2007c) which corrects for underestimates in, particularly fine, root mass, and placed into plastic bags to minimize desiccation. Soil samples could not be washed or sieved because this would have substantially altered the structure and texture of the soil samples. Root vitality could not be reliably assessed visually, and so samples were not divided into live and dead classes. Root samples were then cleaned of residual soil and detritus with a soft brush and scanned at high resolution (600 dpi) within 48 h of removal from the soil. From the scans, root length (divided into 0. 1 mm diameter categories) and surface area was calculated using image analysis

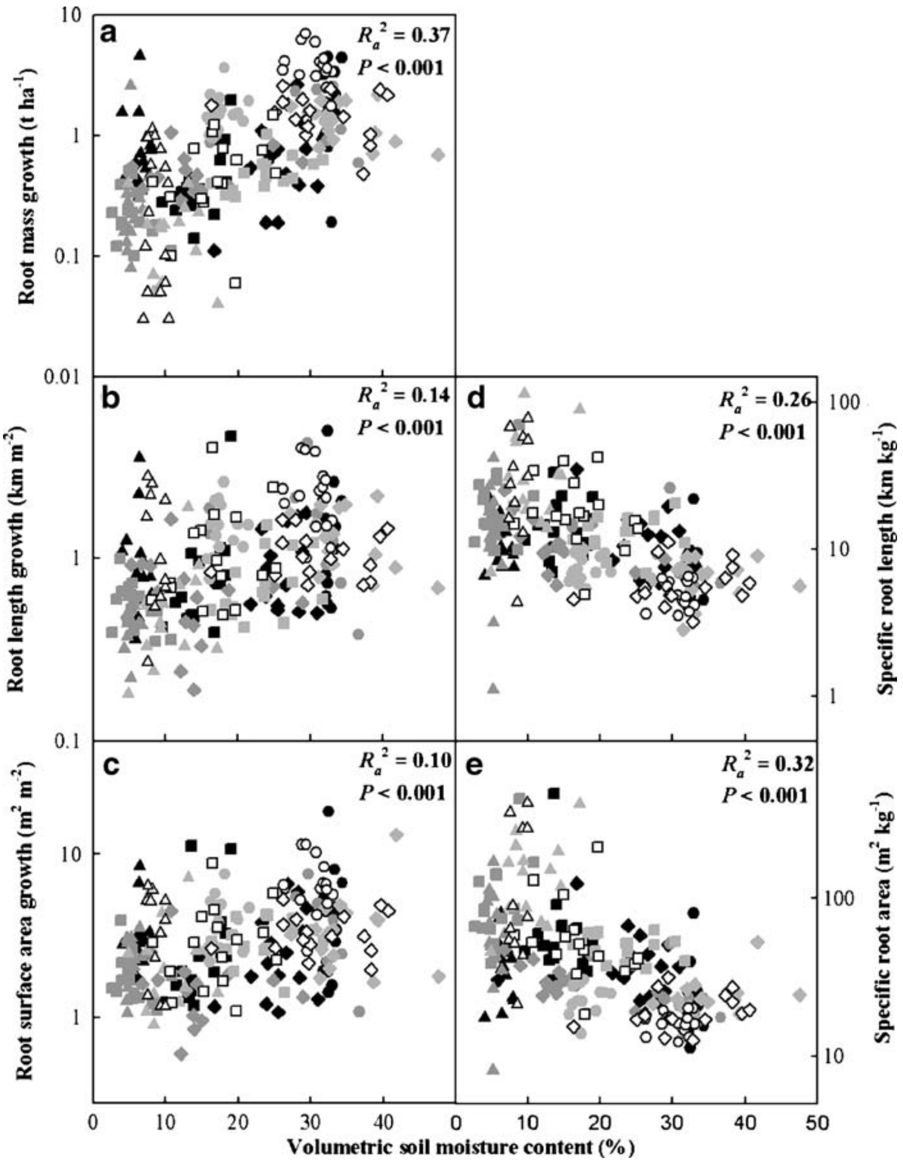


Fig. 3 The relationship between volumetric soil moisture and root growth of mass, length, surface area growth, SRL and SRA in the surface 30 cm soil layer. **a**, **b**, **c**, **d** and **e** Data on root mass growth, root length growth, root surface area growth, SRL and SRA respectively. Sites: *circles* sand; *squares* dry; *diamonds* clay; *triangles* fertile. Measurement sessions: *black* December 2004–February 2005; *dark grey* March 2005–May 2005; *light grey* June 2005–August 2005; *white* September 2005–November 2005

software (WinRHIZO Pro version 2003b, Regent Instruments, Canada). Roots greater than 5 mm diameter constituted a very small proportion of total length (average across all sites of 0.7%), and so were grouped together into a single category.

Root samples from the ingrowth cores were dried at 70°C to constant mass and weighed. From the ingrowth core data, SRL and SRA were estimated by dividing root length and surface area respectively, by root dry mass. Before ingrowth core extraction, *in situ* soil moisture and soil temperature were recorded at a depth of 30 cm, and ground surface organic litter above each core was removed, dried at 70°C to constant mass and weighed. Soil moisture was recorded with a time domain reflectometer (CS616 probe, Campbell Scientific, Loughborough, UK) which relates the oscillation frequency of electricity passing through two probe rods inserted into soil to the average water content of the soil medium around the rods. Soil temperature was recorded with an electronic thermometer attached to a metal measurement rod inserted into the soil (Testo 926 probe, Testo Ltd., Hampshire, UK).

Statistical analysis

Statistical analysis was carried out using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA). Variance among plots in each site was comparable to variance between sites, and therefore plot measurements within each site were treated as independent values. Data that were not normally distributed were log transformed to conform to the assumptions of parametric analysis. The effect of soil moisture, soil temperature and litter mass upon the root variables was assessed using a linear regression. A repeated measures analysis of variance (ANOVA) was used to evaluate differences between wet and dry season plot measurements on all sites. Overall differences in annual root growth and morphology between the sites were assessed with a univariate ANOVA.

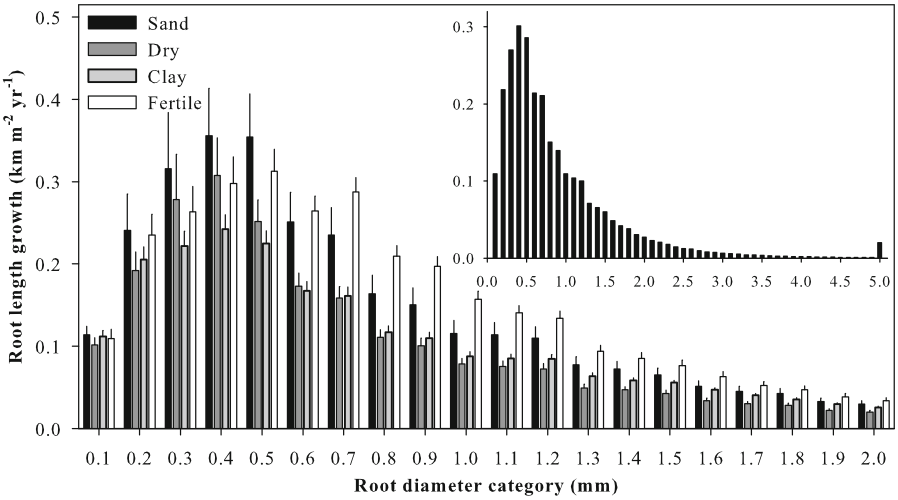
Results

Growth of root mass, length and surface area

On all sites, growth of root mass, length and surface area in the surface 30 cm soil layer declined during the transition from the wet to dry season, though there was substantial within- and between-site variation around this general trend (Fig. 2a–c). Soil temperature and ground surface organic litter mass together did not explain the observed variation in plot root growth. Instead, there was a significant positive relationship between ingrowth core soil moisture and root growth recorded every 3 months (Fig. 3a–c).

Across the sites surveyed, fine roots (<2 mm in diameter) accounted for 92–93% and 70–75% of total root length and surface area respectively (Fig. 4). Very fine roots (<1 mm in diameter) constituted a considerable proportion of total root length and surface area (69–75% and 35–42% respectively, Fig. 4) and also displayed the greatest seasonal shifts in growth (Fig. 5). While coarse roots (>5 mm in diameter)

Fig. 4 Total root length growth, divided into 0.1 mm diameter categories, in the surface 30 cm soil layer on the different sites. The *figure inset* shows mean root length growth across all sites, including all diameter categories measured. *Error bars* indicate SE of the mean, *n* is 16



accounted for less than 1% of total root length grown within the ingrowth cores (Fig. 4), they contributed up to 10% of total root surface area grown annually.

Specific root length and surface area

On all sites, SRL and SRA measured in the surface 30 cm soil layer increased during the transition from the wet to dry season (Fig. 2d,e). In contrast to root growth, SRL and SRA were significantly higher where soil moisture was depleted (Fig. 3d,e). This was because the rate of increase of root growth with soil moisture was greater for mass than it was for length and surface area (Fig. 3a–c). Thus, more root length and surface area per unit mass was produced under drier conditions.

Discussion

Root characteristics

Estimates of total root mass growth from this study range between 3–7 t ha^{-1} year^{-1} in the surface 30 cm

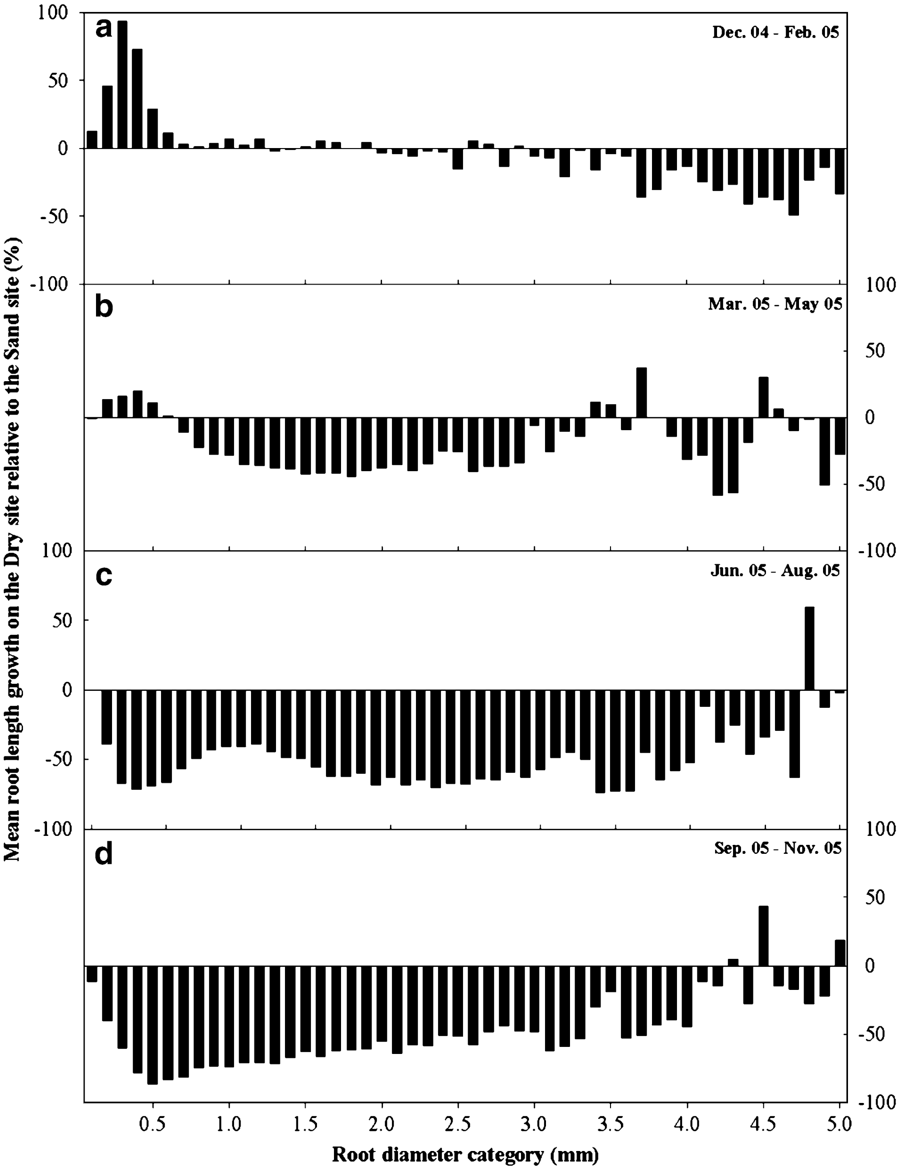


Fig. 5 Seasonal root length growth, divided into 0.1 mm diameter categories, on the sand site relative to the dry site. **a**, **b**, **c** and **d** Data from ingrowth core growth between December 2004–February 2005, March 2005–May 2005, June 2005–August 2005 and September–November 2005 respectively. *Columns* indicate the difference between site mean root length in different diameter categories (*n* is 1), so there are no error bars

soil layer (Table 2), which is consistent with most other results from the region (Jordan and Escalante 1980; Cuevas and Medina 1988; Sanford 1990; Cavelier et al. 1999; Silver et al. 2005; Metcalfe et al. 2007b; Sierra et al. 2007). Relatively high values of root mass growth have been reported: 5.1–20.8 t ha^{-1} year^{-1} (Roderstein et al. 2005) and over 9.9 t ha^{-1} year^{-1} (Priess et al. 1999) but both studies were at more dynamic high altitude rainforests in the western Amazon. Application of a standardized methodology to record root activity across the region could reveal the extent to which the differences between this and other studies, in terms of root growth, reflect real biological patterns rather than variation in equipment and methodology.

Much less information is available regarding root length and surface area. While rhizotrons also provide data on root length (e.g.: Field studies: Itoh 1985; Sword et al. 1996; West et al. 2003; Davis et al. 2004. Reviews: Vogt et al. 1998; Hendricks et al. 2006), the unit of measurement (root length per unit area of observation screen) is not easily integrated into models of plant water and nutrient uptake. A global review of values in the literature estimated mean standing crop root length in tropical evergreen forests of 4.1 km m^{-2}, and mean forest SRL of 12.2 km kg^{-1} (Jackson et al. 1997). Research at a disturbed tropical forest site in Costa Rica estimated standing crop root surface area of 4.1 m^2 m^{-2} (Berish 1982), while another study, at a temperate deciduous forest, reported root standing crop surface area of 14.8 m^2 m^{-2} (Farrish 1991). To our knowledge, this study presents the first data on growth, instead of standing crop, of root length and surface area per unit ground area. Clearly, additional root length and surface area growth data are required to determine how these root characteristics vary between ecosystems, and respond to environmental change.

Root responses to soil moisture

At this study site, we found no evidence that either seasonal or longer-term (on the Dry site) soil moisture deficit led to an increase in root growth (Figs. 2 and 3, see H_1 in the introduction). However, root growth displays considerable spatial heterogeneity and consequently more intensive sampling may be required to fully resolve the effects of soil moisture deficit on root growth. In a review of five stand-level irrigation studies (ranging in duration from 2–10 years), Joslin et al. (2000) found only one study which reported a significant increase in root mass growth under drier conditions. The other studies reviewed found either insignificant increases or no change. In this study, growth of root mass, length and surface area (Fig. 3a–c) are consistently lower when soil conditions are drier. This suggests that, at least at this site, root growth in the surface 30 cm soil layer is not strongly affected by the changes in plant allocation predicted by the functional balance theory (Thornley 1972; Cannell and Dewar 1994). Instead our results are consistent with the theory of control of root growth by local soil conditions (Whalley et al. 1998; Bingham and Bengough 2003; Bengough et al. 2006), and/or the amount of CO_2 assimilated through photosynthesis (Farquhar and Von Caemmerer 1982; Williams et al. 1998; Schwarz et al. 2004). These hypotheses are corroborated by existing studies in Amazon forest that have demonstrated the

Table 2 Root standing crop, growth and morphology, measured in the surface 30 cm soil layer at the study sites

	Sand plot	Dry plot	Clay plot	Fertile plot
Standing crop				
Total mass (t ha^{-1})	35 (9, 70)	25 (4, 85)	31 (12, 60)	23 (8, 53)
Fine mass (t ha^{-1})	14 (5, 29)	10 (4, 18)	15 (8, 26)	11 (5, 23)
Growth				
Mass (t ha^{-1} year^{-1})	4 (2, 7)	3 (1, 4)	4 (3, 5)	7 (4, 9)
Length (km m^{-2} year^{-1})	3 (2, 7)	3 (1, 4)	2 (2, 3)	4 (2, 5)
Surface area (m^2 m^{-2} year^{-1})	11 (5, 23)	8 (5, 13)	9 (6, 12)	12 (8, 15)
Morphology				
SRL (km kg^{-1})	10 (7)	10 (6)	9 (7)	8 (5)
SRA (m^2 kg^{-1})	33 (21)	34 (21)	33 (26)	24 (18)

Values represent means (5th percentile, 95th percentile).

potential importance of soil penetrability for root activity (Carvalheiro and Nepstad 1996; Moutinho et al. 2003), and the suppression of photosynthetic uptake by extended drought conditions (Fisher et al. 2007). Whatever the underlying causal mechanisms, the observed changes in surface root growth could significantly alter the pattern of C and nutrient cycling within the forest.

Comparison of root length growth between the Dry and Sand sites indicates that long-term exposure to drier conditions does increase root growth responses to seasonal rises in water availability (Fig. 5). While root length growth is relatively higher on the plots on the Sand site compared to the Dry site plots during the dry season, this pattern is reversed during the wet season even though the Dry site plots remain drier than the other plots throughout the year (Fig. 5). This implies that plants on the Dry site may be compensating for lower annual growth rates by increasing growth during seasonal periods of relatively high soil moisture. While this interpretation is based upon only 1 year of measurement, it is corroborated by a range of studies which find that prior exposure to water stress leads to higher growth either in other portions of the root system where conditions are more favourable (for example, in deeper soil layers), or for the root system as a whole when the soil is rewetted (Fernandez and Caldwell 1975; Meisner and Karnok 1992; Dickman et al. 1996; Hendrick and Pregitzer 1996, 1997; Torreano and Morris 1998; Comas et al. 2005).

Measurements of root morphology from this study support the hypothesis that plants respond to soil moisture deficit by increasing SRL and SRA (Figs. 2 and 3, see H_2 in introduction). The advantage to the plant of modifying root morphology instead of growth is that it potentially increases water and nutrient uptake, without requiring extra photosynthate to construct and sustain more root material. In addition, fine roots tend to be more dynamic than coarse roots with higher growth rates and turnover (Eissenstat et al. 2000), which is beneficial for searching out and exploiting transient patches of high soil moisture.

Conclusion

This study tests several key hypotheses regarding how plants alter root characteristics in response to soil moisture deficit. Root growth is consistently lower in drier soils, while SRL and SRA display the opposite response. The pattern of root growth observed is consistent with a decline in C assimilation and/or changes in soil properties which impede the ability of roots to penetrate the soil (either directly through altered soil impedance, or indirectly through changes in root turgor), under drier conditions. Observed changes in SRL and SRA suggest that altering root morphology may provide an important additional strategy for plants to increase water uptake. There is substantial spatial heterogeneity in root growth and morphology, but these variables respond to changes in soil moisture in a similar way across different vegetation and soil types. Whilst there is a significant relationship between some root characteristics and soil moisture at this study site, none of the environmental variables measured (soil moisture and temperature, ground surface organic litter mass) can explain the majority of within-site spatial variation. Therefore, a more comprehensive measurement program may be required to further elucidate the effects of other potentially important drivers (e.g.: above-ground growth, soil fertility) of root patterns and processes.

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