Journal of Tropical Forest Science 1 (3): 268 - 279

ROOT SYSTEMS OF THREE ADJACENT, OLD GROWTH AMAZON FORESTS AND ASSOCIATED TRANSITION ZONES

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Received January 1989.

SANFORD, Jr. R.L. 1989. Root systems of three adjacent, old growth Amazon forests and associated transition zones. In the north central Amazon three distinct forest types frequently grow in association with only narrow transition zones between them. These forest types (tierra firme, caatinga and bana) grow on different soils and although these forests are readily distinguished aboveground, belowground differences in root biomass and distribution are less pronounced. Biomass and vertical distribution of roots, with particular emphasis on fine roots are reported. Allometric equations are calculated on the basis of aboveground stem basal area and stand volume. From 23 to 56% of the fine roots are concentrated above the mineral soil in a dense surface root mat. Fine root biomass ranges from 5.5 $kg\ m^{-2}\ ha^{-1}$ in bana forest to 10.7 $kg\ m^{-2}\ ha^{-1}$ in tierra firme/caatinga.

Key words: Root biomass- root distribution - forest-root allometry - Amazon - transition forest.

Introduction

The root systems of tropical trees are perhaps the least studied and least understood component of rain forests. In contrast to the more visible aboveground segments of trees, rain forest tree roots are rarely observed or measured, and comparative studies have not previously been attempted for distinct but adjacent forest types and their associated transition areas. Previous studies of root systems in Amazonian forests estimated total root biomass and depth distribution within a single stand on a homogeneous soil type (Stark & Spratt 1977, Klinge & Herrera 1978, Bongers *et al.* 1983,) but did not distinguish roots finer than 6 *mm* in diameter. Although this definition of fine roots is appropriate for estimating total biomass, it is not useful for quantifying fine root biomass and distribution. As a proportion of total root biomass, fine roots (<2 *mm* or <1 *mm* diameter) usually account for no more than 15 to 20%, and usually less than 5% of total forest biomass.

The importance of fine roots in nutrient cycling and as a component of forest productivity is not proportional to their contribution to total biomass. Small diameter roots (<2 *mm*) are often assumed to be the most important size fraction for mineral uptake in woody plants (Bohm 1979). Although this assumption is not yet fully validated for tropical trees, it was assumed in this study that small diameter roots are functionally distinct from larger roots. Accordingly, root diameter size classes in this study are biased toward fine roots (three size classes less than 5 *mm*). This is done to more closely examine the distribution of fine roots according to depth distribution and within each forest type and associated transition areas.

The purposes of this study were to: (1) measure root biomass, its horizontal distribution along a transect that traverses the three major forest types and associated forest transition areas, (2) determine root vertical distribution to a depth of 50 *cm*, and measure root distribution among size classes, and (3) correlate the measurements with easily measured aboveground vegetation characteristics.

The study area

San Carlos de Rio Negro is situated on the Rio Negro in the Amazon Territory of Venezuela (1°56'N, 67°03'W, 119 *m* elevation). Rainfall varies considerably from month to month and year to year with all months receiving >200 *mm*, and average annual rainfall > 3500 *mm*. Average monthly temperature varies 2°*C* throughout the year with a mean annual temperature of 26°*C* (Hueveldop 1980).

The topography near San Carlos consists of hills that rise as much as 50 *m* above mean river level. On the tops of the hills Oxisols have formed that support a diverse (88 species/*ha*) mixed species evergreen "tierra firme forest" (Uhl & Murphy 1982). In the swales between ridges, alluvial quartzitic sands have formed deep Spodosols that support Amazon "caatinga forest" (sometimes called white-sand). The caatinga forests are less productive than the mixed species evergreen forests (Klinge *et al.* 1977). In addition a perched water table causes flooding during the wettest months. Occasionally sandy domes occur in swales within the caatinga forests. These sandy domes consist of excessively well drained Spodosols with a heath-like vegetation termed "bana forest". Productivity, species diversity, and canopy height are lowest for bana compared to the other forest types. Sclerophylly is characteristic in bana forest and the canopy is open, permitting direct sunlight to reach the forest floor of bleached white sand (Klinge & Medina 1978). This topographic and pedologic diversity supports three distinct forest types and several transition zones that occur between the distinct forest type (Figure 1). These forest types are relatively nutrient poor when compared to other tropical forests worldwide (Jordan & Herrera 1981, Vitousek & Sanford 1986). They are distinct with regard to aboveground biomass, leaf litter production and nutrient concentration (Table 1).

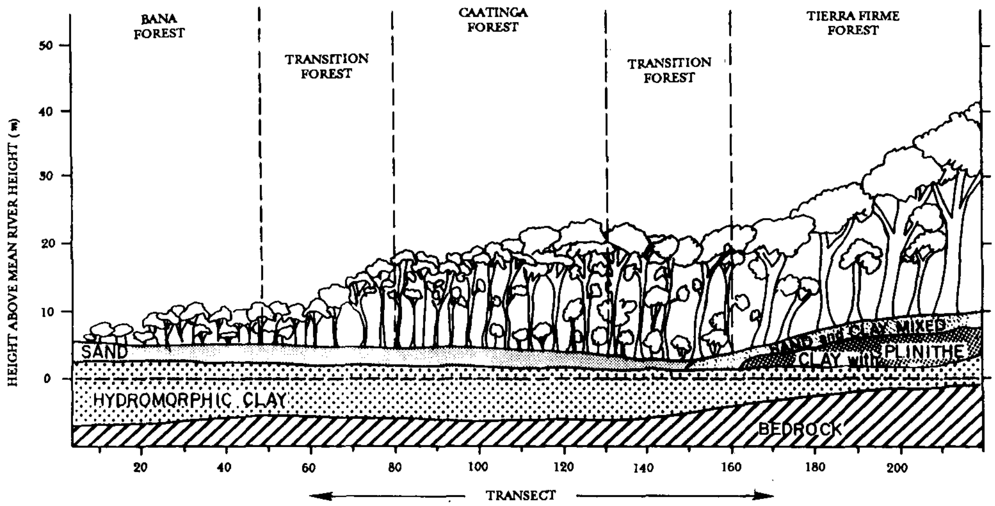

Figure 1. Schematic diagram of Amazon forests along the 210 *m* transect near San Carlos de Rio Negro, Venezuela

Table 1. Aboveground biomass, leaf litter production, and nutrient concentration for three Amazon forests near San Carlos de Rio Negro, Venezuela

		Aboveground Biomass Nutrient *kg ha⁻¹*					
	$T\ ha^{-1}$	N	P	K	Ca	Mg	Ref
Bana	37	212	28	155	276	43	Herrera 1979b
Caatinga	185	336	32	321	239	53	Herrera 1979b
Tierra firme	335	1084	40	302	260	69	Jordan *et al.* 1982, Jordan & Uhl 1978

	Leaf Litter Production	Leaf Litter Nutrient Concentration $mg\ g^{-1}$ Dry Weight					
	$T\ ha^{-1}\ y^{-1}$	N	P	K	Ca	Mg	Ref
Bana	2.1	5.8	0.2	4.7	7.4	2.5	Cuevas & Medina 1986
Caatinga	4.0	7.0	0.5	2.1	7.7	3.1	Cuevas & Medina 1986
Tierra firme	7.6	16.3	0.3	2.4	1.7	0.7	Cuevas & Medina 1986

Methods

A 210 *m* N-S transect was measured out in the intensive study forest area that Brunig *et al.* (1979) and Herrera (1979a) used to delineate forest types and forest-soil correlations. The transect begins in tierra firme forest, passes through caatinga forest and terminates in bana forest. It also traverses tierra firme-caatinga transition forest and caatinga-bana transition forest (Figure 1).

At 10 *m* intervals along the transect 25 x 25 *cm* pits were excavated to 50 *cm* depth. The root mat (consisting of roots that grow above the mineral soil) was cut out with a knife and sorted separately. Roots in these forests tend to be concentrated near or above the surface of the mineral soil; hence the uppermost 5 *cm* of mineral soil was excavated by hand with machete and shovel. A second 5 *cm* layer was excavated similarly. Thereafter, the soil was excavated in 10 *cm* depth increments to a maximum depth of 50 *cm*. The roots from each depth were sorted from the soil with a 2 x2 *mm* screen mesh. A 10% (by volume) soil subsample from each depth was passed through a 0.5 *mm* screen mesh for retrieval of very fine roots. All root material was washed and subsequently sorted into nine diameter size classes: <1, 1<2, 2<5, 5<10, 10<20, 20<30, 30<40, 40<50 and >50 *mm*. Diameter was determined at the midpoint of each root segment. Roots were dried for 72 *h* at 80° *C* and weighed to the nearest 0.01 *g*.

The stems of all trees >5 *cm* dbh were measured for height and diameter in a 100 m^2 plot centered on each pit. Basal area for each plot was calculated with the formula:

$$\text{Basal area} = \sum_{i=1}^{n} \pi D_i^2/4$$

where D = Diameter of each stem. Volume of the stems on each plot was calculated with the formula:

$$\text{Volume} = \sum_{i=1}^{n} D_i^2 H_i$$

where D = Diameter and H= Height of each stem.

The depth of the root mat above the mineral soil surface was measured at 1 *m* intervals across a 5 *m* wide band down the entire length of the transect. These data were used to determine the average depth of the mat of roots growing above the mineral soil in each plot. Elevation along the transect was surveyed at 5 *m* intervals (Figure 2).

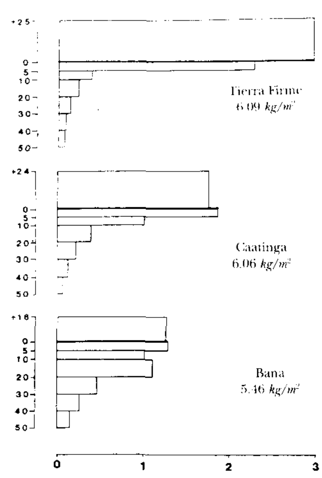

Figure 2. Vertical root biomass at standard depths and in surface root mat for three forest types at San Carlos (Average values based on five pits in each forest type)

Results and discussion

Total root biomass

Total root biomass and root biomass distribution at each depth interval for the forest types are given in Table 2. The three forest types have roughly similar values for total root biomass (tierra firme 6.09 $kg\ m^{-2}$, caatinga 6.06 $kg\ m^{-2}$, bana 5.46 $kg\ m^{-2}$). The tierra firme root biomass estimated here agrees well with the estimate (based on a much larger sample size) of 5.56 $kg\ m^{-2}$ made by Stark and Spratt (1977). The caatinga and bana forest type root biomass estimates of Klinge and Herrera (1978) are two to three times larger than estimated by this study (9.65 $kg\ m^{-2}$) and 18.16 $kg\ m^{-2}$, respectively) and the surface mat root estimate of the earlier study is approximately two times larger than estimated by this study for caatinga and bana forests.

Table 2. Total root biomass ($kg\ m^{-2}\ ha^{-1}$, dry weight) at various depths for three forest types and associated transition forests (Values are means ± 1 standard error)

	Standard Soil Depths (*cm*)							
Forest type	Surface mat	0-5	5-10	10-20	20-30	30-40	40-50	Total
Tierra firme n=5	2.94±2.65	2.28±1.21	0.37±0.19	0.20±0.07	0.13±0.08	0.09±0.03	0.08±0.06	6.09
Tierra firme/ Caatinga n=4	5.75±4.68	3.04±2.49	1.47±0.28	0.32±0.09	0.09±0.02	0.03±0.04	0.01±0.01	10.70
Caatinga n=5	2.34±1.63	1.92±1.26	1.00±0.56	0.43±0.20	0.21±0.15	0.08±0.09	0.04±0.07	6.06
Caatinga/Bana n=3	4.93±3.57	1.71±1.39	1.17±0.75	0.51±0.35	0.26±0.22	0.18±0.14	0.11±0.14	8.87
Bana n=5	1.25±0.43	1.27±1.09	1.01±0.15	1.11±0.36	0.47±0.29	0.24±0.22	0.13±0.10	5.46

For the caatinga forest this discrepancy might be explained by the caatinga/ tierra firme transition forest. My estimate for root biomass in this zone (10.70 $kg\ m^{-2}$) is similar to the previous estimate (9.66 $kg\ m^{-2}$) for caatinga forest. Presumably there was no attempt to identify samples from this transition forest in the earlier study.

The discrepancy for bana forest is more difficult to explain. One probable explanation is that bana forests are highly variable from site to site with regard to total root biomass. This may be due to the depth of the hardpan, proximity to more nutrient rich tierra firme forest, or to the species mix within the bana forest. Another reason may be the time of year that the samples were taken. The perched water table that occurs during the wet season may cause high root mortality resulting in lesser root biomass.

The large root biomass estimate for the caatinga/tierra firme transition forest is probably due to the influence of topography (Figure 1). This forest occurs on a Spodosol at the foot of an Oxisol ridge. More than half of the root biomass in this transition zone is found above the mineral soil in a deep surface root mat. This extensive root mat and resulting large total root biomass may be in response to the surface runoff from the comparatively nutrient rich adjacent Oxisol.

Distribution of total root biomass

Tropical forests have been described as shallow rooted ecosystems (Richards 1952, Ahn 1960, Burgess 1961, Whitmore 1975). The forest types that I examined exhibit this tendency in varying degrees (Figure 2). Although there is no generally agreed upon definition for "shallow rooted", 20 *cm* has been proposed (Jenik 1978) and 20 *cm* depth is used in this study to compare root biomass distribution between forest types. Tierra firme, caatinga, and bana forest types have 95, 95 and 85%, respectively, of total root biomass in the upper 20 *cm* of mineral soil and above the mineral soil in a root mat (Table 2). Even more striking, tierra firme, caatinga and bana forests have 48, 39 and 23%, respectively, of total root biomass in the surface mat alone. The percent of total roots growing in shallow soil and above the mineral soil is revealing when examined in the context of nutrient scarcity: in comparatively nitrogen rich Oxisols supporting tierra firme forests, more roots are concentrated near the surface. In Spodosols supporting comparatively phosphorus rich caatinga and bana forests, roots are not concentrated as near to the surface as are roots in tierra firme forests.

The most shallow rooted forest types were expected to occur in situations where most nutrient cycling would be via litter decomposition, and earlier studies indicated that this would be the case for bana and caatinga forests growing on Spodosol. Surprisingly, roots were more concentrated near the surface in tierra firme forest growing on Oxisols. There are several possible explanations for this phenomenon: (1) Shallow rooted systems may be a result of canopy litter production and decomposition rates, that is, the greater the amount of nutrient turnover due to litterfall, the greater the surface root concentration. This would be important only in systems where nutrient input from litter exceeds that of nutrient release by soil weathering. (2) Decomposition of litter may be slower in the caatinga and bana forests. These forests are known to exhibit sclerophylly (Sobrado & Medina 1980) and slower biogeochemical cycling due to low quality litter allows for a buildup of resistant soil organic matter. The Spodosols in these forests have a deep "O" horizon which is indicative of slow decomposition rates. (3) Drainage may be important in developing superficial root systems. During the wet season the bana and caatinga forests are temporarily flooded due to a cemented B_{ir} Horizon at 150 *cm* depth. In the dry season these forests experience drought stress due to the low water holding capacity of these soils. A less shallow root distribution may be the result of dry season drought stress causing deeper root growth. (4) Physical soil characteristics may cause superficial root growth. The Oxisols on this transect have abundant plinthite concretions beginning at 15 to 30 *cm* depth and extending to the granite saprolite. Plinthite, though not concreted into a single impeding layer in these forest soils, may deter root growth into deeper areas of the soil profile. In contrast, the Spodosols are porous allowing comparatively easy root penetration as far as the hardpan. (5) Most of the root biomass is in the form of large roots. Although large roots are important structurally for support, and physiologically as storage compartments, fine roots are better indicators of nutrient absorption capacity than large roots. A correlation between nutrient availability and root distribution could be best understood by examining fine root distribution in these forest types.

Small diameter root biomass

The distribution and amounts of fine root biomass follow a trend similar to that for total root biomass (Table 3). The caatinga/bana transition is similar to the adjacent major forest types but the caatinga/tierra firme ecotone has a much higher total fine root biomass than any other forest type. The large root biomass is due to the very large biomass of <1 *mm* sizes roots, particularly in the surface mat (Figure 3). The high value is due primarily to the pit excavated at 130 *m* on the transect. This is the lowest point in the transect, and also where a high, dense surface mat of roots occurs (Table 4). The large fine root biomass may be in response to surface runoff from the tierra firme Oxisol. Nutrients carried to the toe of the slope during periods of very high runoff are absorbed by the well developed surface root mat.

Table 3. Amazon forest root diameter biomass (Values are $g\ m^{-2}$ dry mass ± 1 standard deviation; (Sample sizes (n) for each forest type and transition zone follow Table 2)

	Forest Type																			
	Tierra firme n=5				Tierra firme/Caatinga Transition n=4				Caatinga n=5				Caatinga/Bana Transition n=3				Bana n=5			
	Root Diameter Classes (mm)																			
Standard Soil Depths	< 1	1 < 2	2 < 5	Total	< 1	1 < 2	2 < 5	Total	< 1	1 < 2	2 < 5	Total	< 1	1 < 2	2 < 5	Total	< 1	1 < 2	2 < 5	Total
Surface	612.4 ± 435.4	182.6 ± 71.2	434.2 ± 308.2	1229.2	2809.9 ± 4040.6	184.4 ± 44.7	208.1 ± 111.7	3202.4	687.4 ± 323.6	208.4 ± 79.2	351.8 ± 185.7	1247.6	498.5 ± 167.5	225.8 ± 152.7	512.1 ± 163.4	1236.4	601.1 ± 254.2	115.6 ± 48.1	232.9 ± 84.4	949.6
0-5 cm	144.8 ± 136.2	81.1 ± 104.8	142.9 ± 155.1	368.8	446.0 ± 306.4	102.8 ± 7.9	287.6 ± 41.5	836.4	221.7 ± 53.6	115.7 ± 60.0	230.4 ± 76.5	567.8	192.6 ± 90.4	94.0 ± 43.7	95.3 ± 27.3	381.9	105.8 ± 53.1	44.0 ± 19.1	171.7 ± 54.7	321.5
5-10 cm	92.8 ± 23.3	30.3 ± 27.5	43.3 ± 18.0	166.4	132.5 ± 44.6	50.5 ± 12.0	85.2 ± 41.9	268.2	216.2 ± 103.8	75.1 ± 25.3	209.7 ± 104.1	501.0	161.4 ± 94.5	68.2 ± 39.7	88.1 ± 78.3	317.7	102.9 ± 53.0	53.8 ± 29.6	164.9 ± 72.7	321.6
10-20 cm	90.6 ± 39.4	36.5 ± 19.2	42.7 ± 26.8	169.8	119.0 ± 49.5	40.5 ± 8.8	73.6 ± 15.9	233.1	92.0 ± 41.0	74.2 ± 58.0	98.1 ± 69.0	264.3	148.5 ± 55.7	52.0 ± 13.4	73.9 ± 33.4	274.4	193.6 ± 129.7	79.1 ± 38.8	181.9 ± 86.5	454.6
20-30 cm	62.7 ± 37.8	18.2 ± 13.0	28.0 ± 26.6	108.9	35.5 ± 16.8	33.0 ± 22.3	18.1 ± 17.3	86.6	62.8 ± 30.9	38.6 ± 29.3	34.8 ± 51.5	136.2	99.0 ± 91.3	28.1 ± 11.2	38.2 ± 23.3	165.3	140.7 ± 56.3	36.8 ± 25.4	75.1 ± 42.6	252.6
30-40 cm	34.3 ± 12.1	7.9 ± 2.5	16.0 ± 10.9	58.2	20.6 ± 22.2	4.7 ± 8.2	3.8 ± 6.8	29.1	27.5 ± 23.0	12.1 ± 4.6	9.6 ± 12.4	49.6	75.3 ± 95.2	24.4 ± 23.2	35.9 ± 16.2	135.6	57.8 ± 31.0	27.8 ± 30.6	37.8 ± 27.7	123.4
40-50 cm	33.2 ± 17.0	6.6 ± 6.6	14.9 ± 27.1	54.7	4.0 ± 5.3	2.0 ± 3.4	0.0 ± 0.0	6.0	25.7 ± 30.0	8.7 ± 15.5	3.8 ± 5.6	38.2	44.7 ± 58.6	7.1 ± 3.8	30.4 ± 32.5	82.2	44.9 ± 34.4	14.4 ± 16.2	18.2 ± 11.0	77.5
Total	1070.8	363.2	722.0	2156.0	3567.5	417.9	676.4	4661.8	1333.3	532.2	938.2	2804.7	1220.0	499.6	873.9	2593.6	1246.8	371.5	882.5	2500.8

Table 4. Depth of the surface root mat for each 100 m^2 plot in the sample transect (Values for each plot are average from 50 sample points)

		Surface mat cm	
Forest type	Site	$\bar{x}$	s.d.
	0	12.1	6.6
	10	15.7	4.2
Bana	20	14.5	6.3
	30	18.7	6.2
	40	18.9	5.6
	50	15.5	5.1
transition	60	17.5	6.0
	70	18.1	5.8
	80	12.9	6.6
	90	24.1	9.6
Caatinga	100	24.6	6.8
	110	25.3	5.9
	120	33.0	9.2
	130	30.5	10.6
transition	140	19.6	6.0
	150	21.7	10.3
	160	35.9	10.8
	170	22.5	8.0
	180	22.1	7.6
Tierra firme	190	25.8	11.7
	200	23.4	8.3
	210	31.9	16.5

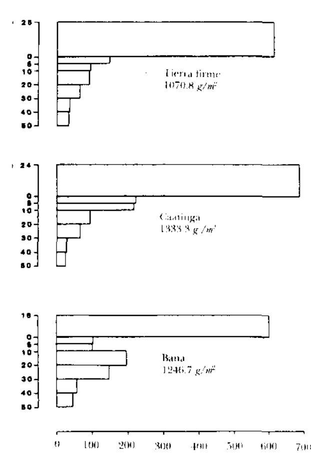

Figure 3. Vertical distribution of < 1 *mm* roots for tierra firme, caatinga, and bana forest types (Average values based on five transect pits in each forest type)

There is no obvious general trend in fine root biomass that reflects the nutrient status of the soils along this transect. The ratio of fine root biomass to total root biomass distribution in all three forest types indicates that soil nutrients in the forest types has little effect on either total biomass or fine root biomass. The distribution of fine roots within the profile, however, is somewhat different between forest types. A strong nutrient availability gradient from the surface down is probably the reason that most roots are distributed near or above the soil surface. This vertical nutrient gradient has been quantitatively demonstrated for all three forest types (Stark & Spratt 1977, Klinge & Herrera 1978).

In tierra firme forest 57%, in caatinga 44%, and in bana 38% of roots <5 *mm* diameter are in the surface root mat (Table 5). This surface mat concentration may be partially related to the nutrient content in the forest soils: the most phosphorus rich forest soil (bana) supports least fine root biomass in the surface mat. If most soil phosphorus in this forest type is in organic form then it is not surprising that fine roots are distributed in the "O" horizon rather than as a surface mat. The distribution of fine roots throughout the soil profile in bana forest is probably a response to the widely fluctuating water table; the excessively well drained Spodosols create a drought situation when three or more days without rain occur (Sobrado & Medina, 1980).

Table 5. Percent of small diameter roots within the uppermost 20 *cm* of mineral soil inclusive of the surface root mat

	Root Diameter Classes			
	Surface		Surface + 20 *cm*	
Forest type	< 1 *mm*	< 5 *mm*	< 1 *mm*	< 5 *mm*
Tierra firme	57%	57%	88%	90%
Tierra firme/Caatinga	79%	69%	98%	97%
Caatinga	52%	44%	91%	92%
Caatinga/Bana	41%	48%	82%	85%
Bana	48%	38%	80%	82%

In all forest types, most of the <5 *mm* root biomass is located near the surface or above the mineral soil. In bana forest 82%, in caatinga forest 92%, and in tierra firme forest 90% of these roots are in the surface mat and uppermost 20 *cm* of the mineral soil. The trend is similar for roots <1 *mm* diameter. The extreme case is the tierra firme/caatinga transition zone. In this zone 79% of roots <1 *mm* are in the surface mat alone. The extreme concentration of fine roots above the mineral soil indicates that most of the available nutrients must be cycled via forest litter and perhaps nutrient runoff.

Aboveground/belowground allometric equations

Basal area of tree stems for each 100 m^2 subplot was measured, calculated and converted to m^2 per hectare. Basal area was weakly correlated with total root biomass but not with <1 *mm* root biomass. A logarithmic transformation of the root biomass data was used because these data are not normally distributed. The basal area/root biomass equations (where R = ln [root biomass] in $Mg\ ha^{-1}$, and B = basal area $m^2\ ha^{-1}$) are:

$$R = 3.7029 + 0.0182, (r = 0.39, p < .04)$$

$$R < 1\ mm = 2.5468 + 0.0124\ B,\ (r = 0.00, n.s.)$$

Stem volume for each 100 m^2 subplot was calculated and converted to m^3 per hectare (Table 6). This was weakly correlated with total root biomass but not with < 1 *mm* root biomass for transect subplots. The stem volume root biomass equations (where R = ln [root biomass] in $Mg\ ha^{-1}$, and V = volume of stems > 5 *cm* diameter in $m^3\ ha^{-1}$) are:

$$R = 3.8857 + 0.0005\ V,\ (r = 0.32, p < .08)$$

$$R < 1\ mm = 2.5661 - 0.0065\ V,\ (r = 0.00, n.s.)$$

The low correlation coefficients indicate that neither stem volume nor basal area is an appropriate independent variable for estimating root biomass using the pooled values of all forest and forest transition types sampled on the transect. This is not surprising given the differences in aboveground physiognomy of the different forest types and the lack of difference in root biomass. As a correlation variable total root biomass performs better than fine root biomass. However, neither is very well correlated with the measured aboveground characteristics.

Table 6. Basal area and stem volume of forest stands along the 210 *m* transect that traversed three forest types and associated transition zones

Transect Site #	Forest Type	Basal Area ($m^2\ ha^{-1}$)	Volume $m^3\ ha^{-1}$
1	Bana	12.06	96.6
10	Bana	8.20	63.3
20	Bana	5.32	34.7
30	Bana	15.80	136.9
40	Bana	15.96	187.8
50	Transition	24.07	297.5
60	Transition	19.80	253.9
70	Transition	32.89	511.2
80	Caatinga	24.05	411.3
90	Caatinga	28.43	434.5
100	Caatinga	33.38	619.9
110	Caatinga	35.02	726.0
120	Caatinga	35.08	754.9
130	Transition	14.90	285.2
140	Transition	14.01	307.1
150	Transition	31.12	730.1
160	Transition	25.22	538.1
170	Tierra Firme	8.84	159.8
180	Tierra Firme	41.12	1105.3
190	Tierra Firme	24.01	508.2
200	Tierra Firme	12.47	245.0
210	Tierra Firme	37.63	926.2

Hermann (1977) found that aboveground correlations are best for highly stratified sites, that is, individual stands. To further examine the viability of aboveground/belowground correlation I subdivided the transect into the respective forest types and tested for correlations according to forest type. This approach yielded no significant correlations for either total root biomass or fine root biomass when compared with basal area or stem volume. The small number of observations per forest type is probably the main reason that no significant correlations were found on the basis of stratification by forest type.

Conclusions

The root biomass of all three forest types is remarkably concentrated near and above the surface of the mineral soil. This trend is extreme in the caatinga/tierra firme transition forest where 99% of the total root biomass is in the uppermost 20 *cm* of soil and above the surface of the soil in the form of a dense root mat. The concentration of roots near or above the soil surface indicates the extremely low nutrient status of these forest soils as well as the importance of litter as a source of available nutrients.

Fine root biomass distribution is similar to that of total root biomass distribution. Most roots are concentrated near or above the soil surface. Of the three forest types, bana forest root biomass is most deeply distributed in the soil profile. This may be in response to water stress that occurs during the dry season in these excessively well drained Spodosols.

Weak correlations are shown for total root biomass and basal area and for total root biomass and stem volume. Fine root biomass was not correlated with either of the two aboveground measures. There were no significant aboveground/belowground correlations when the forest was stratified according to forest type. This is probably due to the small sample size of each forest type.

The aboveground characteristics of basal area and stem volume vary according to forest type along this transect. However, root biomass appears to be independent of the aboveground characteristics of these mature forests. The distribution of roots by depth varies somewhat according to forest type. Perhaps root biomass has reached an upper limit given the extremely nutrient poor status of the forest soils. This upper limit (of ~ 50 - 60 $Mg\ ha^{-1}$) is exceeded only in transitional forest areas such as the caatinga/tierra firme transition where a relatively nutrient rich runoff appears to result in even greater root biomass.

Acknowledgements

I thank C. Damasio, G. Gomez, D. Gomez, and I. Guapo for their assistance with root extraction and separation. C. Uhl and K. Clark provided valuable comments on the sampling design. P. Zinke, J. McBride, R. Robichaux and S. Molden made suggestions for improvement of earlier drafts of this paper, and K. McElwain and M. Nelson typed the draft and prepared the figures.

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