

AMAZONIAN FORESTS AT THE EDGE: CANOPY PHENOLOGY, WATER-USE AND FLAMMABILITY OF SEASONALLY-DRY, EVERGREEN FORESTS

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One of the great paradoxes of tropical ecology is presented by the large areas of forests with evergreen canopies that grow where severe, seasonal drought should provoke plants to shed their leaves. For example, the forest near Paragominas, in the eastern Amazon, has just experienced 4 months with only 60 mm of rainfall, and yet it is lush and green, and shows little sign of drought stress. Forests such as this, which remain lush and green despite severe periods of drought, are common along eastern and southern Amazonia, where it is difficult to find forests that shed their leaves during dry seasons, even though dry seasons are very harsh.

One important element of this paradox is the widely held assumption that moist tropical forests are, in general, very shallow-rooted, and perched on a sterile subsoil that is virtually devoid of nutrients. It is these shallow root systems that quickly absorb the nutrients in rainwater, and the nutrients released from decomposing leaf litter that falls on them. It is in large part because of these shallow root systems that some scientists have declared that moist tropical forests are extremely fragile ecosystems, with their nutrients found mostly in their living biomass.

This assumption has remained unchallenged and untested for so long. It is very difficult to study what happens beneath the soil, particularly beyond 50 to 100 cm depth. We believe that tropical forests are assumed to be shallow-rooted because no one has bothered to look. And if we are right, and forests such as those in eastern Amazonia occupy many meters of soil, instead of many centimeters, then we must rethink how fragile these forests really are, how they process water, where they store carbon, and how they absorb and cycle nutrients. In sum, we must rethink the ecology of moist tropical forests.

About 7 years ago, we decided to test the assumption that moist tropical forests have shallow root system in the eastern Amazonian cattle and timber town of Paragominas, in northeastern Amazonia, ca. 300 km southeast of Belem. In Paragominas, an average of 5 months out of each year receive <50 mm of rain (Fig.1) compared to about 120 mm of water lost to evapotranspiration).

This is a very severe pattern of seasonal drought, and yet it is very common along the agricultural frontier of Amazonia, that is concentrated along the eastern and southern margins of the region. But average patterns of rainfall hide the considerable year to year variation in precipitation patterns, particularly in eastern Amazonia and northeastern South America generally, because rainfall in these regions is strongly influenced by the El Nino Southern Oscillation (ENSO). This climatic anomaly occurs when the surfacewaters of the southern Pacific Ocean warm up, changing the patterns of air circulation such that some regions receive more rain than usual while other regions receive much less rain than usual. Eastern Amazonia and Northeastern S. America receive muchless rainfall than usual. In Paragominas, the influence of ENSO on annual rainfall (Fig.2) can be seen in this graph; the columns with hatch marks are the years of ENSO, and demonstrate that rainfall can be less than half of the average during these events. Incidentally, a very strong ENSO is forming right now, and ENSOs in general have increased during the last 10 years or so.

In the Paragominas region, tall, dense, evergreen forests perched on deeply-weathered, kaolinite-dominated, Oxisols (Latosolos), have been replaced over large areas by cattle pastures. Many of these cattle pastures have been degraded through over grazing and subsequently reformed through tilling, fertilization and replanting with new forage grasses such as *Bracharia brizantha* (brachiarão). Other pastures have been degraded and abandoned.

Our study site, located on the Fazenda Vitoria, 7 km from Paragominas, provides us with an opportunity to ask ecological questions about primary forests at the same time that we ask how land-use--in this case forest conversion to cattle pasture--changes the ecology of this forest. In this study, we not only tested the assumption that amazonian forests have shallow roots, but we compared the root distribution and the root function between primary forest and the degraded pastures that are rapidly replacing these forests. This forest and pasture are located adjacent to one another, on the same soil and at the same topographical position, allowing us to make direct, before and after comparisons of these two ecosystems. The areas called capoeiras, are secondary forests, that have regrown on abandoned pastures.

The simplest response to our test of the assumption that moist tropical forests are shallow-rooted is: false!. As example, a clump of soil was removed from the bottom of a 12m deep soil shaft, and live, fine roots were growing through it. Of a total of 6 metric tons per hectare of fine roots that we found in the primary forest, 10% of these roots were found below 1 meter depth; some fine roots were found as deep as 18 meters depth in the primary forest! Fine roots in the abandoned pasture were also deeply distributed, but were more sparse at depth than roots in the primary forest (Fig.3).

To understand the role of deep roots in absorbing water from the soil to keep the leaf canopy green and lush during the 5-month dry season, we excavated deep soil shafts, and installed water sensors and plexiglass tubes in the walls of these shafts for to follow root dynamics with a root periscope. We excavated 5 shafts in the primary forest and 3 shafts in the pasture, and installed Time Domain Reflectometry sensors 1.5 meters into

the walls of the shaft (to prevent the shaft air from interfering with the soil moisture that was being measured). These sensors were backfilled, then used to measure volumetric soil water content (cm^3 water / cm^3 soil) every month (Fig.4).

To make these measurements, we connected the sensors to a Tektronix cable tester, which sends a radio signal along the length of two steel rods in the sensor. The speed at which this radio signal returns along the sensor is a function of the water content of the soil. Hence, TDR can be used to make instantaneous, repeated measurements of soil water. TDR measures the total amount of water in the soil, which is far greater than the amount of water that is held at tensions that are accessible to plants.

To estimate the amount of plant-available water that corresponded to each TDR reading, we determined the moisture retention curves of the soil at various depths in the soil shafts, and thereby calculated the soil water content at which soil water potential was equal to -15 bars. We discovered, however, that some of the sensors registered values that were below this permanent wilting point. We therefore defined the minimum water content to which plants could dry the soil as the minimum of either the lowest TDR reading during a 4-year period, or the -15 bar soil water content. Having defined this minimum water content at which moisture was available to plants, we were able to calculate plant-available water (PAW) as the difference between the TDR reading and this minimum water content.

When we calculate PAW integrated for 2-meter depth intervals in the degraded pasture, the primary forest and a secondary forest capoeira that grew up on an abandoned pasture, we find (Fig.5), several interesting features. a) First, we see that deep soil water was depleted in both the capoeira and primary forest during the dry season of 1991, and was not replenished until the wet season of 1994. In other words, it did not rain enough in 1992 or 1993 to completely replenish the PAW to its maximum level in the forests, although the rain was sufficient to replenish PAW in the pasture. These data show that interannual droughts, such as those associated with ENSO events (as in this case) are manifested deep in the soil with very few symptoms in the aerial portion of the

forest. Deep-rooted ecosystems are buffered against the effects of severe seasonal drought, but this buffering capacity can be lost, or exceeded during particularly severe dry periods, or when rains during the wet season are insufficient to replenish the water lost through evapotranspiration. These data also indicate that the forests absorb more water from the soil to supply evapotranspiration than does the pasture, and/or, that the forests capture more incoming rain on their foliage and stems (as interception) than the pasture did, allowing less rainfall to reach the ground. Both of these phenomena were apparently at work in Paragominas. b) We also see that PAW in each of the three ecosystems, and in each of the four depth intervals, declined during periods of drought, as is expected, and that most of the change in PAW occurred below 2 m depth. In other words, most of the water absorbed by plants during the dry season of 1992 came from below 2 meters depth. These data show that both the forest and pasture ecosystems of Paragominas depend upon deep roots to absorb soil water to depths of at least 8 meters to maintain water-dependent process (such as evapotranspiration and photosynthesis) during dry seasons of several months duration.

TDR-based estimates of PAW can be used to estimate evapotranspiration for each of these ecosystems. If we add reductions of PAW (measured with TDR) to rainfall, (or subtract increases of PAW from rainfall), we can estimate the amount of water leaving the ecosystem as water vapor via transpiration of plants and through evaporation from plant and soil surfaces, i.e., evapotranspiration (ET). We must also correct this calculation for those times when soil moisture exceeds the field capacity of the soil, and can leave the 8-meter soil profile via drainage, i.e., via the flow of water out of the soil profile through the force of gravity. We calculated drainage for these TDR data using estimates of the soil water content at field capacity derived from water retention curves. We estimated drainage from the profile using Darcys law, which applied only when the deepest TDR reading (at 8 meters depth) registered soil water content above field capacity.

ET was consistently higher in the forest than in the pasture, especially in the dry season, but was virtually indistinguishable between the primary forest and secondary forest (capoeira). In other words, after 15 years of regrowth, the capoeira had already recovered the hydrologic functions of the primary forest. But the pasture released less water vapor to the atmosphere than the forest presumably because of (a) higher albedo than the forest (as measured by ABRACOS) and (b) lower green leaf area during the dry season than the forest, as discussed below.

During the 4-year study period, drainage did not occur from the forests for all of 1992 and 1993, because of incomplete recharge of soil moisture during these dry years. An average of 0.9 mm/day of water drained from the pasture during the 4-yr period. Hence, when forests are converted to pastures, much more water drains to the water table and to streams and rivers, increasing the risk of erosion and flooding.

So it appears that the canopy of the forest is lush and green and transpiring, even during the peak of the dry season. But is the canopy experiencing drought stress? The trees have retained their leaves, but have they retained all of them? To address this question, we climbed up into the canopy--every month for two years--to measure the drought stress in the leaves and the shedding and production of leaves on marked branches. This work required a five-man team spending 3 days each month, arriving in the forest at 4:00 am, clipping leaves and measuring pre-dawn leaf water potential using a pressure chamber, then, later the same day, climbing the same trees to visit marked branches and record new leaves produced, and old leaves shed since the previous reading. We monitored leaf water potential and leaf phenology in this way for 12 species of trees and lianas in each of the three ecosystems: primary forest, secondary forest, and degraded pasture.

The results of this study, shown here for the peak of the 1992, El Nino dry season, show (Fig.6) a tight relationship between the depletion of PAW, the reduction of leaf area, and the increase in drought stress (decrease in leaf water potential). By the end of this dry period, the primary forest had lost 15% of its leaf area, while the pasture had lost

45%. If the pasture leaf area is weighted according to the relative importance of the species studied, then the reduction in leaf area climbs to 70% (because the dominant grasses lose virtually all of their green leaf area during the dry season). Although the drought-induced reduction of leaf area in the forest is less than in the pasture, the pressure chamber data show that the forest trees and lianas were experiencing greater drought stress than the pasture plants. In particular, three species of understory trees, *Lecythis idatimon*, *Rinorea guianensis*, and *Tachigalia myrmecophilia*, displayed pre-dawn leaf water potentials in October of 1992 of -2.5 to -3 Mpa! The tagged branches of these species show that these understory species underwent virtually no leaf shedding in response to drought stress, which is expected for trees growing in the shade, where leaf longevity should be high to compensate for the considerable expense of constructing leaves with little sunlight. We do not know, however, if such a precipitous increase in the tension of the xylem sap in understory trees would be followed up in short order by leaf abscission or tree mortality.

Drought-induced leaf shedding is a vitally important topic in the seasonally-dry tropics. In eastern Amazonia, primary forests extend like giant fire breaks through the landscape, preventing the spread of escaped agricultural fires. By absorbing water stored in a very large volume of soil, these forests are able to maintain a lush, green leaf canopy that prevents all but 2-3% of incoming solar radiation from reaching the forest floor. In the deep shade of the primary forest understory, the leaves, twigs and other fine fuels that might sustain a forest fire remain damp, and impossible to ignite. If the water stored deep in the soil is depleted, however, drought stress develops in trees, and leaf-shedding begins. As leaves are shed, more solar radiation penetrates to the forest floor, drying the fine fuel layer. Eventually, sufficient leaves have been shed by the canopy to allow the fine fuel layer to dry enough to be set on fire. At this point, the primary forest loses its function as a giant fire break through the landscape.

Using field measurements of the rate at which the fine fuel layer dries sufficiently to be ignited in forest, secondary forest, and pasture ecosystems (Uhl and Kaufman, 1990,

Ecology 71(2): 437-449), we estimated those days during which each of these ecosystems could be set on fire during the ENSO dry season of 1992. Pastures can be ignited within one day of a rain event in Paragominas, while secondary forests, which lose more leaf area in response to drought than primary forests, require 8-10 days without rain to dry sufficiently to catch fire. Primary forests only catch fire when deep soil moisture is depleted, and drought-induced leaf-shedding has taken place. We estimate that just prior to the November rain event of 1992, the primary forests of Paragominas lost sufficient leaf area to become susceptible to fire. In fact, ranchers of this region reported fires entering their primary forests late in October of this year. In contrast, the highly flammable pasture and secondary forests of the region were susceptible to fire for several weeks during this dry season.

It is very difficult to study the rainfall regime at which eastern Amazonian forests become susceptible to fire. We have therefore begun an experiment to exclude rainfall from a patch of forest with the goal of determining how much drought is necessary to provoke enough leaf shedding for these forests to catch fire, and what physiological processes accompany the onset of this drought. In this rainfall exclusion experiment, we monitor leaf phenology, leaf water stress, and leaf conductance of trees that are experimentally dried down vs. trees that are in the control forest. We are now in the process of excluding 50% of rainfall from a one-hectare study forest. We are just at the beginning of this experiment, and we welcome graduate students and researchers who wish to conduct studies within this experiment.

The studies we have described so far are from a single forest. How wide-spread is the phenomenon of deep rooting forests in Amazonia? To answer this question, we have developed a model of the minimum rooting depth of Amazonian forests together with Gustavo Negreiros. In this model, we use 1160 soil texture profiles from around Amazonia to generate a map of the amount of water that can be stored in the soil at tensions that are available to plants, and we assume that this texture doesn't change with depth. We then superimpose on this soil map, within a geographical information system,

a map of monthly rainfall obtained from DNAE for >400 weather stations across Amazonia. Then, assuming that the forests of Amazonia are using about 3.5 mm of water per day to supply evapotranspiration, we estimate the soil depth that these forests must absorb water from to supply this evapotranspiration.

More than 70% of the forest clearing in Amazonia has taken place within the zone of deep-rooting forests. And yet, it appears that forests can have deep roots even if deep roots are not necessary to maintain water uptake. For example, in Manaus, in the Ducke Reserve, we have found roots to 9 meters depth, although the amount of roots at depth was less than in Paragominas. In Santana do Araguaia, there is less rainfall than in Paragominas, and the amount of roots at depth was greater than in Paragominas.

What other function might deep roots serve other than to absorb water from the soil? Certainly there aren't sufficient nutrients at depth to be absorbed by roots? In fact, the deep soils in Paragominas contain K and Ca in forms that are available to plants. We could not detect available phosphorus in deep soils using Melich 2. But the total pool of P at depth is very large. Perhaps some portion of this large unavailable pool of P is, in fact, available to plants, particularly if these plant roots are infected by mycorrhizal fungi. To assess the potential of phosphorus uptake by deep roots via mycorrhizal fungi, we determined root infection rates by fungal hyphae in the primary forest, secondary forest and pasture. This work, conducted in collaboration with Valter Mendes and Elizabeth Cheng (Embrapa-Amazônia Oriental), shows that roots are infected with mycorrhizal (vesicular/arbuscular) at all depths, and infection rates are higher in the pasture and capoeira than in the primary forest. Hence, it appears that deep fine roots may help plants absorb nutrients, and not just water. We would therefore not expect deep-rooting to be restricted to the seasonally-dry portions of Amazonia.

We would like to close this lecture by examining the question of deep root system recovery. How is it that the secondary forest, after a mere 15 years, had recovered the hydrologic functions of the primary forest? Can root systems actually repenetrate to 8 meters depth and beyond in such a short period of time following pasture abandonment?

To address this question, we determined the identify of roots found during our excavation of the deep soil shafts, and found that the secondary forest had one third as many morphospecies of roots at depth as did the primary forest. And the secondary forest had about one third as many species above the ground, as well. It therefore appears that this secondary forest can quickly recover deep root systems. One of the secondary forest species found at depth was *Davilla kunthii*, “cipo de fogo”. When we excavated individual plants of this species, we found that by the time this cipo reaches a height of one meter, its root system has penetrated to 8-10 meters depth!. Hence, cipo de fogo appears to recover its belowground structure before it recovers its aboveground structure. Teresa Restom, who did these excavations, has conducted a study of cipo de fogo and cipos in general, and found that this species is responsible for 4% of evapotranspiration in the secondary forest.

The rapid recovery of deep root systems in secondary forests may be related to leaf cutter ants. The density of leaf cutter ant nests explodes following deforestation in Amazonia and across Latin America. In Paragominas, the density of nests increases nearly 40-times when primary forest is converted to pasture, then abandoned. This high density of nests in the secondary forest (>2 per hectare), which cover roughly 100m² per nest, appears to facilitate root penetration. The channels and chambers excavated by the cutter ants allow root to penetrate quickly to great depths, as we discovered during excavation of cipo de fogo root systems. But the nests also soften the soil that is not excavated. The resistance to penetration (Fig.7) of this soil is much lower than the soil that is not influenced by the nest, and the density of roots in this soil is much higher. This work, which is the PhD dissertation of Paulo Moutinho, reveals that cutter ants may have a strongly beneficial effect on secondary forests.

In summary, the ecology of Amazonian forests growing where rainfall is seasonal can only be understood by looking deep beneath the ground. For it is through the uptake of water stored deep in the soil that these forests can retain their leaves during dry seasons of many months. And it is because these forests can retain their leaves when it is very dry

that they can maintain deep shade in the understory, preventing the spread of fires that escape from agricultural lands. The fact that these deep roots are infected with mycorrhizal fungi suggests that they may also contribute to the nutrition of the forests. In some aspects, these studies reveal that the Amazonian forest is less fragile than we thought it was. 90% of this forests phosphorus stock is found in the soil, not in the biomass. And 15 years after pasture abandonment, secondary forests have recovered the deep soil hydrologic functions of the primary forest, facilitated, apparently, but an unlikely agent: the leaf cutter ant.

Understanding of these deeply rooting forests is critical, because it is these forests that are being converted to pasture. If the frequency of ENSO events continues to increase, or if the reduction in rainfall that is predicted by climate models of deforestation in Amazonia begins to appear, than large portions of the forests of eastern and southern Amazonia could begin to catch fire, with tremendous losses of timber, wildlife, carbon and hydrologic functions at stake.

***AS FIGURAS ESTÃO NO FINAL DA PUBLICAÇÃO**

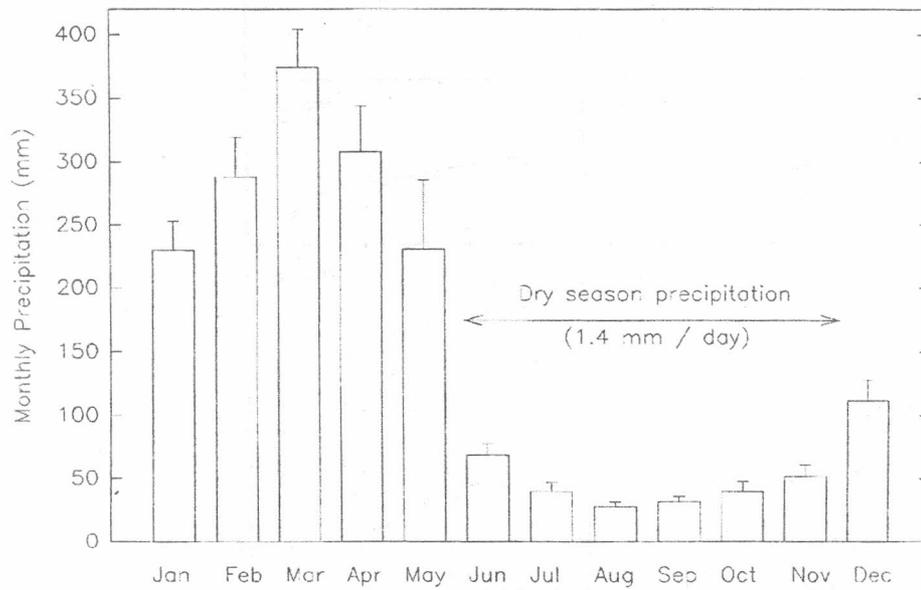


Figure 1: Average monthly precipitation (mm) and standard error bars for Paragominas, Para, Brazil from 1973 to 1993. Average daily precipitation during the dry season (June to November). From JIPP et al., in press.

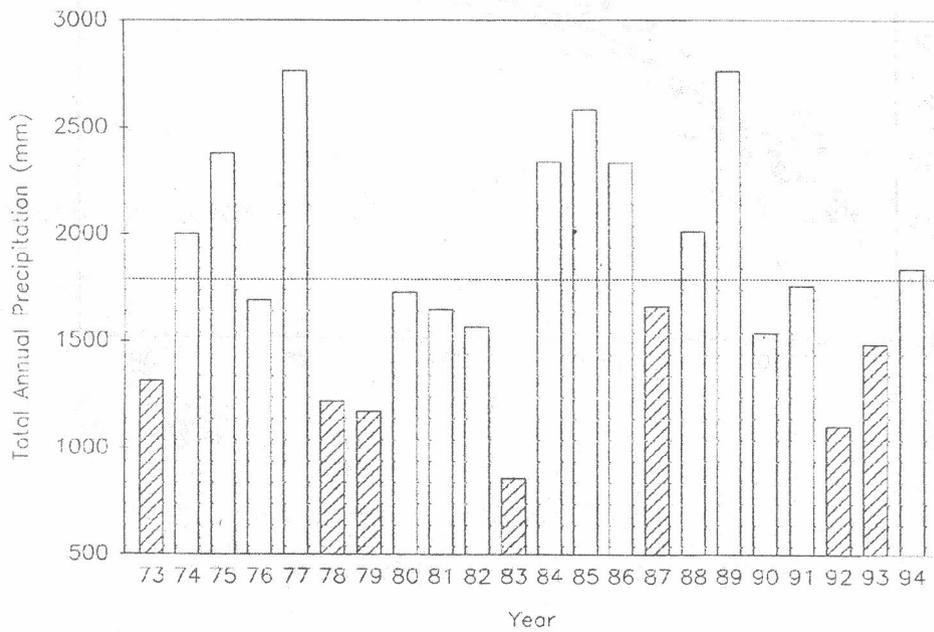


Figure 2: Annual precipitation totals in Paragominas since 1973. Dashed horizontal line is the 22 year average (1805mm). Cross-hatching indicates ENSO influence. From JIPP et al., in press.

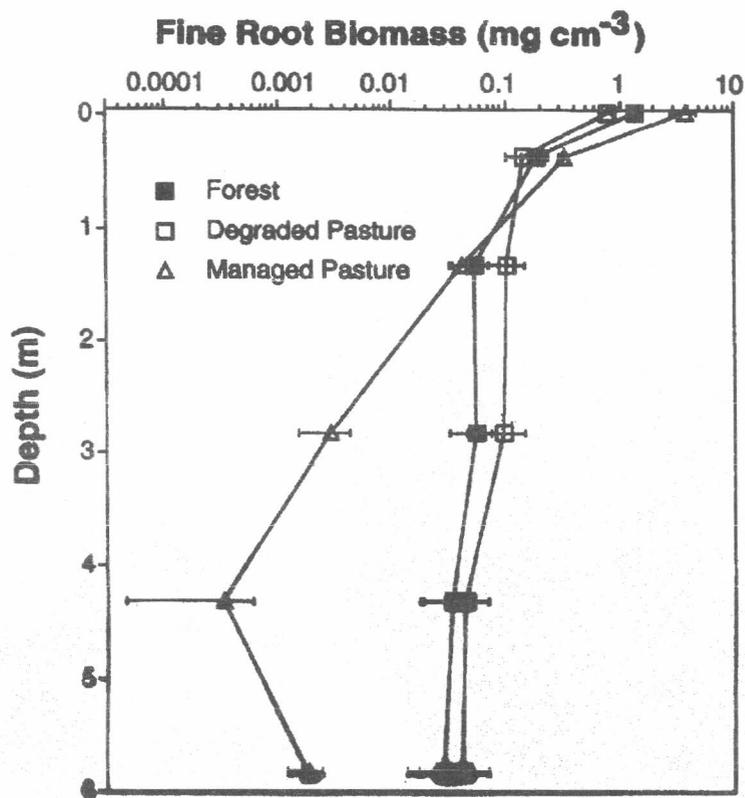


Figure 3: Vertical profile of live fine-root biomass (diameter < 1mm) in adjacent mature forest and man-made pastures near Paragominas, eastern Amazonia. Points are means, and bars are one standard error of the mean from 1.5kg soil samples taken at each sampling depth in 36 auger borings in the forest, 17 in the degraded pastures, and 6 in managed pastures. From NEPSTAD et al., 1994.

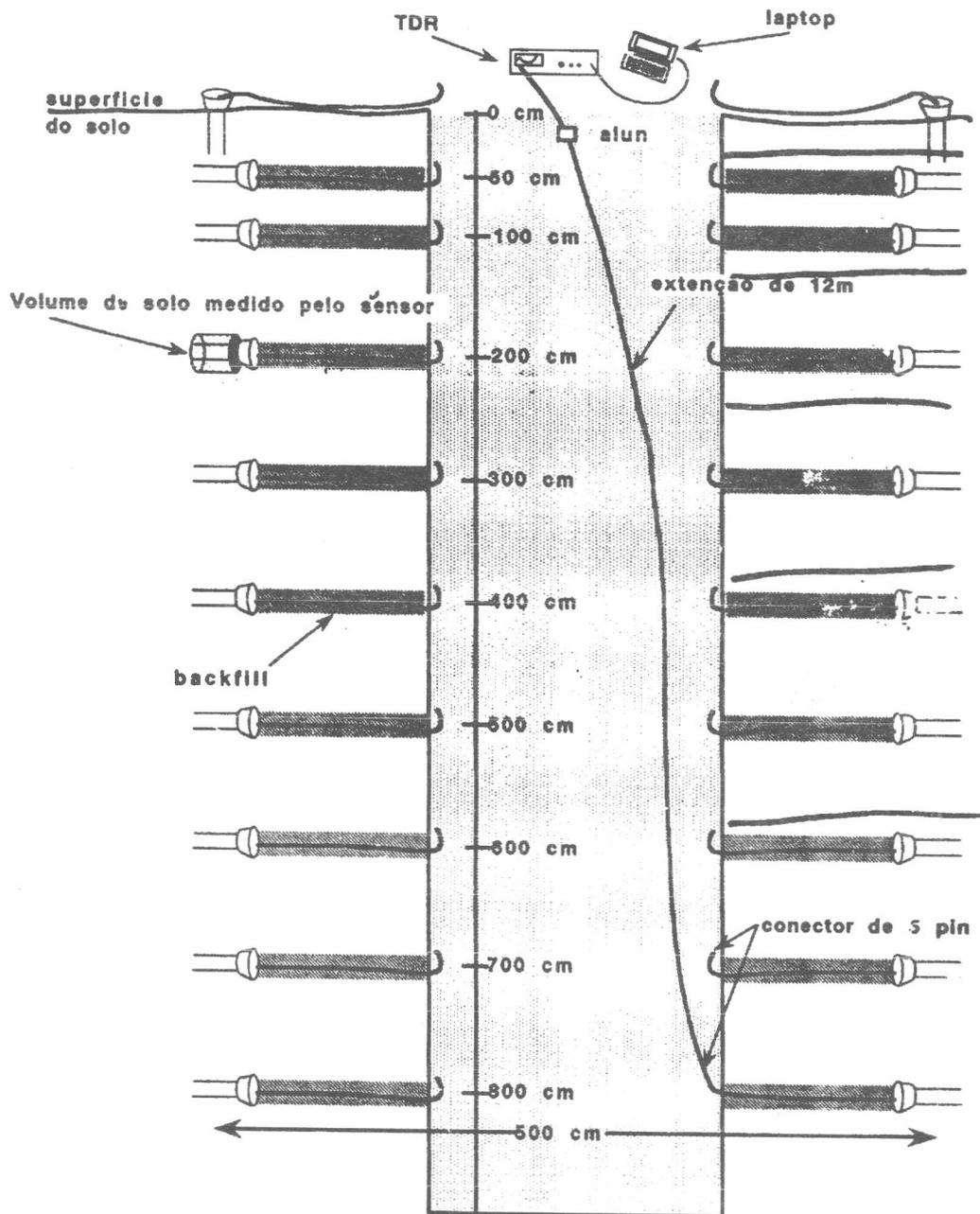


Figure 4: Schematic design of the TDR sensors distribution in the walls of a shaft.

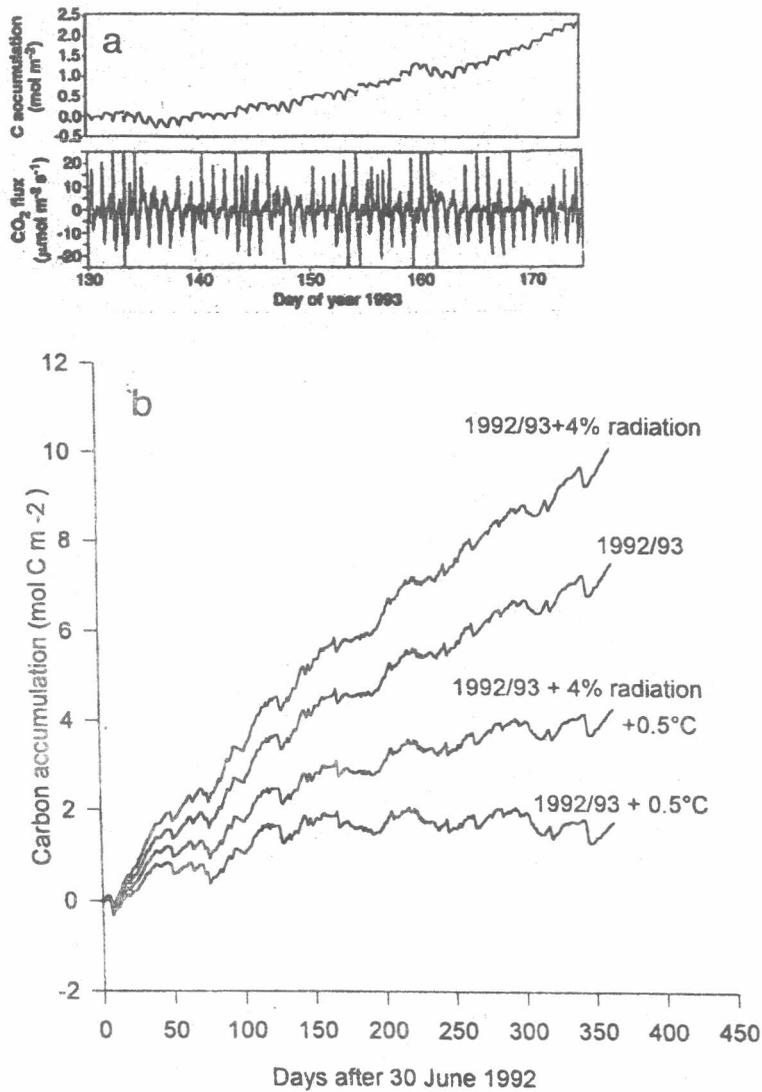


Figure 1. (a) Measured and (b) modelled accumulation of carbon at Reserva Jaru, an undisturbed tropical rain forest in Brazil. (a) shows the data obtained with the eddy covariance sensor, (b) shows the sensitivity of the accumulation rate to temperature and radiation (from Grace *et al* 1995 *Science* 270, 778-780)

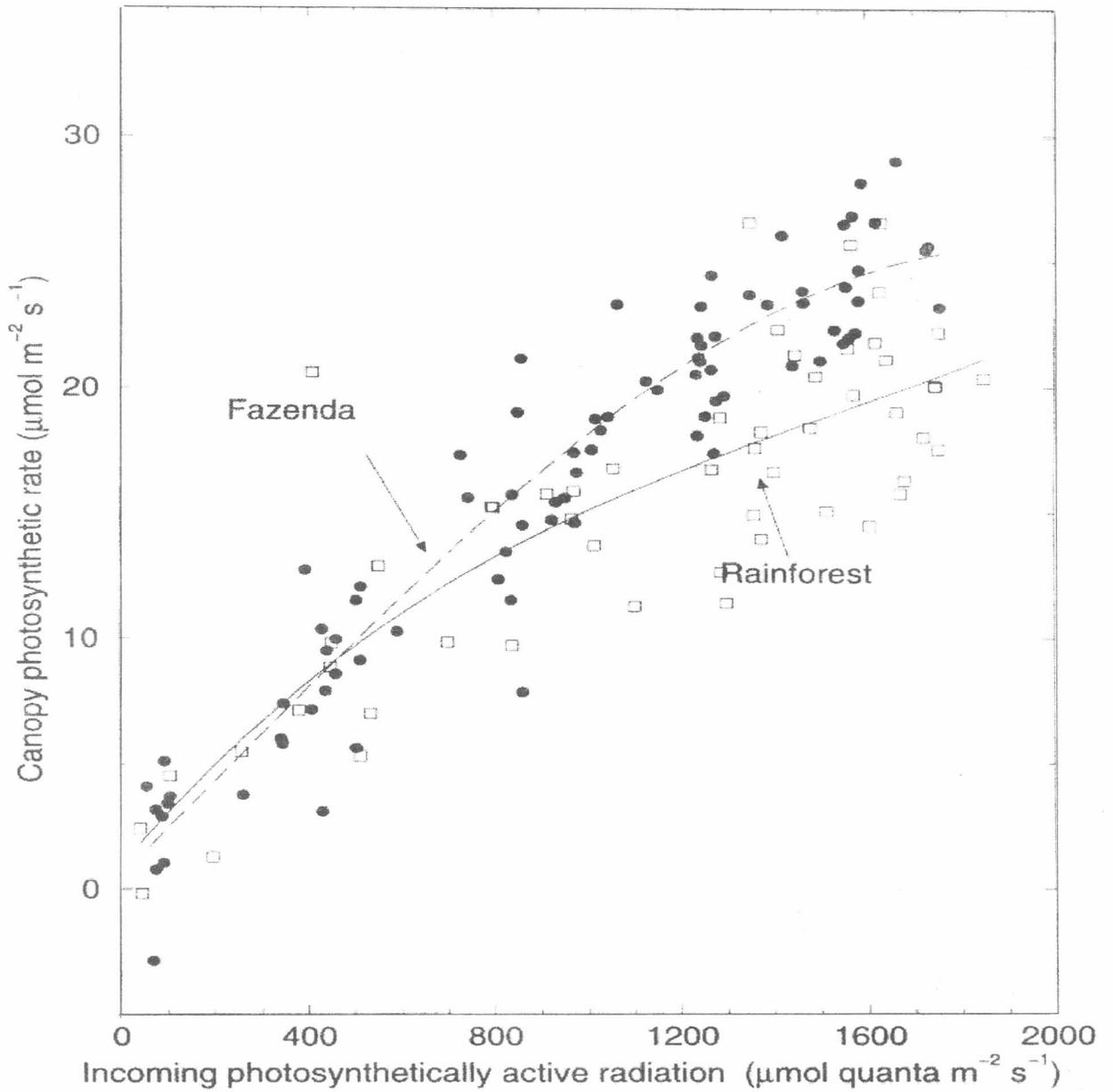


Figure 2. The ecosystem photosynthetic response curve for rain forest and cattle pasture (Fazenda), obtained from observations on 11 consecutive days in May 1993, towards the end of the wet season (from Grace *et al.*, 1997 submitted for publication).

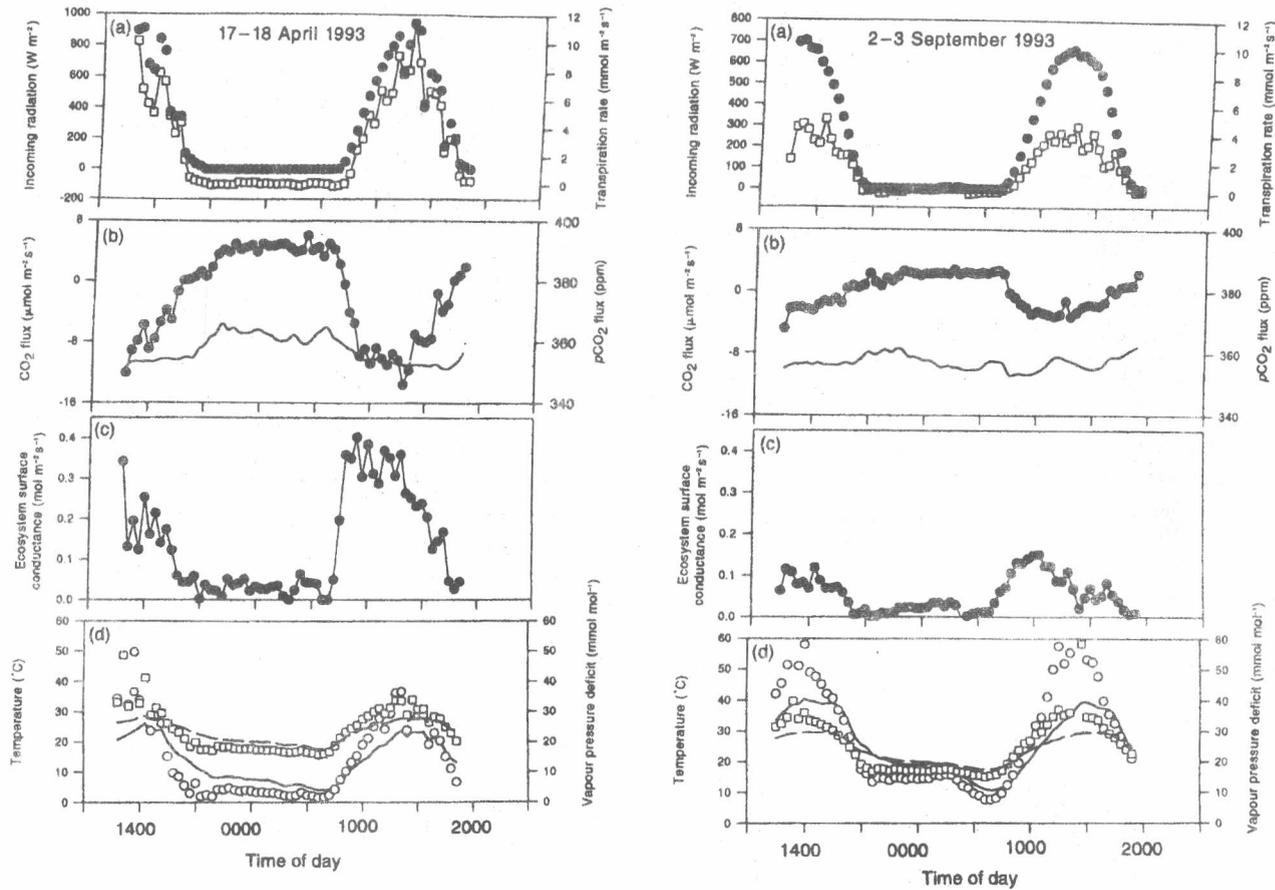


Figure 3. Water vapour and carbon dioxide fluxes over cerrado *sensu stricto* in the wet season (April) and the dry season (September). Symbols: ● is incoming solar radiation in (a), CO₂ flux in (b) and ecosystem surface conductance in (c); □ is transpiration rate in (a) and canopy-to-air vapour pressure deficit in (d); ○ is canopy temperature; solid line in (d) is air temperature and broken line is the saturation humidity deficit. From Miranda *et al.*, (1997).

Fig. 4

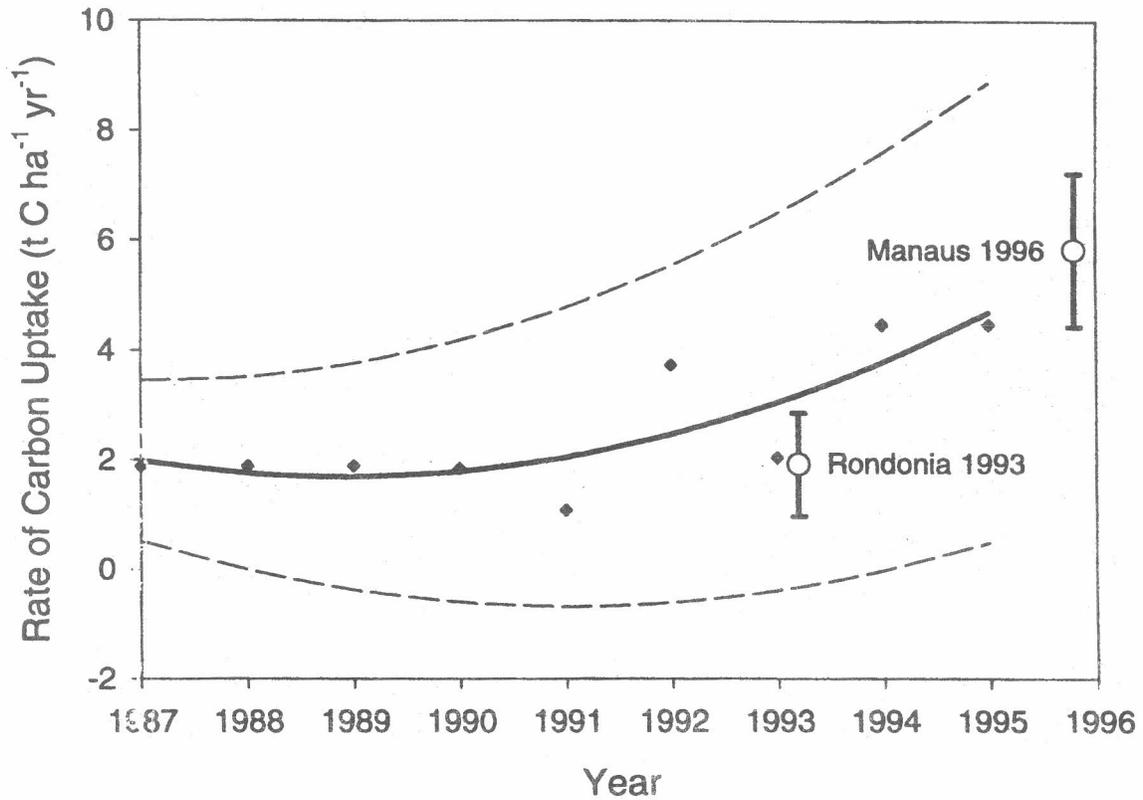


Figure 4. Estimated rates of carbon accumulation in biomass in three-hectares of forest plot near to Manaus since 1986, as determined from the mean of sample plot data. The values obtained from eddy covariance measurements in Jaru Rondonia 1993 and Manaus 1996 are shown for comparison (from Malhi, Higuchi, Nobre, Grace, Ribeiro, Perreira, Scott, Filho & Culf 1997, submitted for publication).

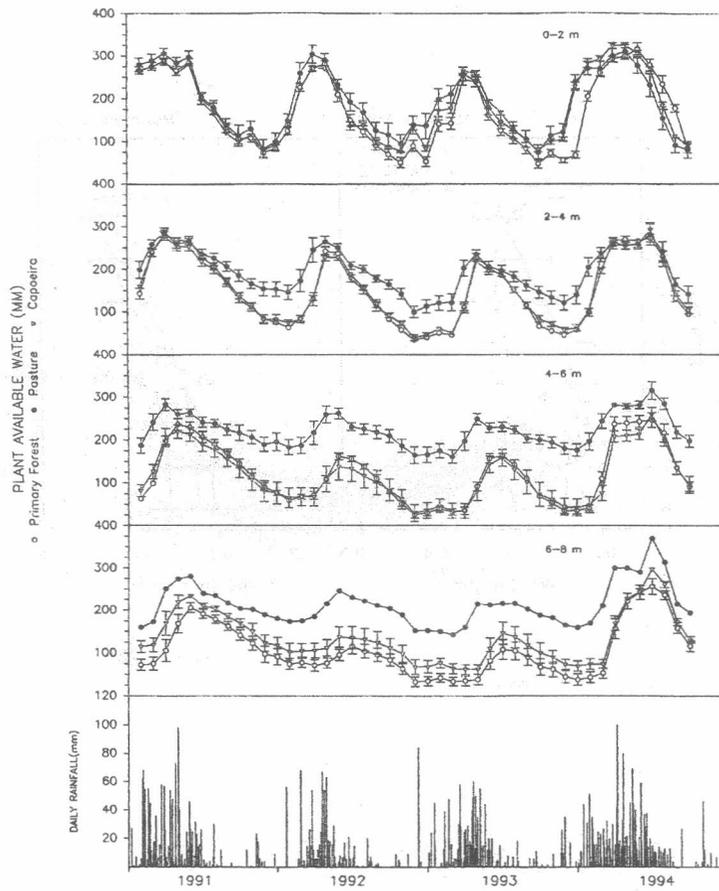


Figure 5: Stocks of average monthly (1991-1994), plant-available water (TDR measures) at the surface and at depth in the experimental site of Paragominas. From JIPP et al., in press.

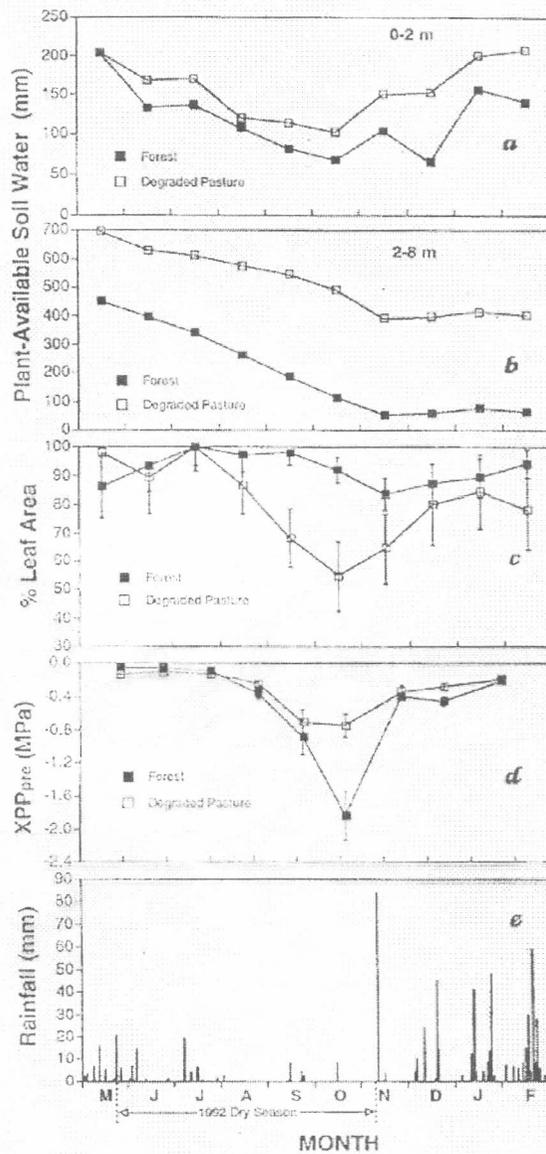


Figure 6: Plant available-soil water (PAW), leaf area, predawn water potential of leaves (mean from many species) and average monthly precipitation (mm) for Paragominas, Para, Brazil from 1992/1993.

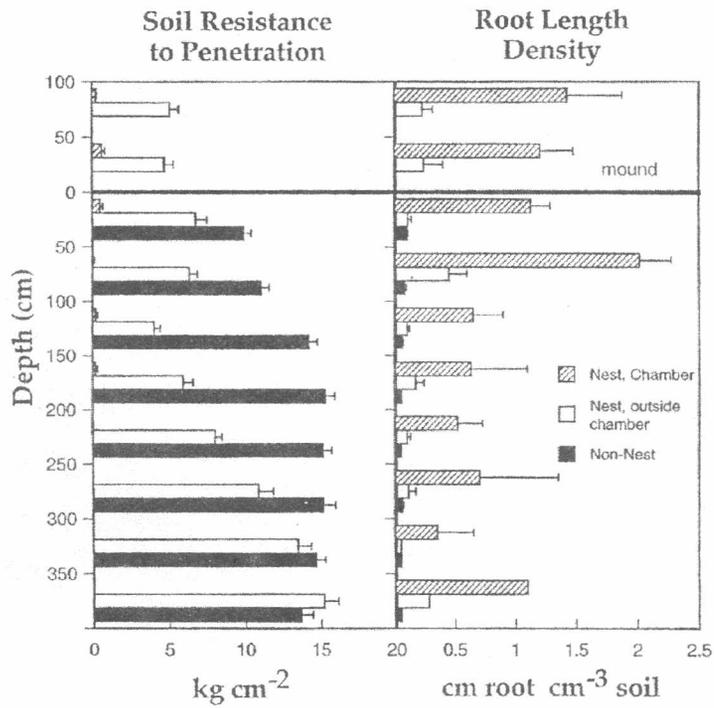


Figure 7: Effects of cutter ant (*Atta sexdens*) nests on soil resistance to penetration and root length density in secondary forest at Paragominas, Para, Brazil. From JIPP et al., in press. Data are from Paulo Moutinho PhD thesis, Campinas, São Paulo.