Relationships between soil hydrology and forest structure and composition in the southern Brazilian Amazon

Jirka, Stefan1*; McDonald, Andrew J.1,6; Johnson, Mark S.2,3,6; Feldpausch, Ted R.1,5,6; Couto, Eduardo G.4,6 & Riha, Susan J.1,6

1Department of Earth and Atmospheric Sciences, College of Agriculture and Life Sciences, Cornell University, Bradfield Hall, Ithaca, NY 14853, USA; 2Department of Crop and Soil Sciences, College of Agriculture and Life Sciences, Cornell University, Bradfield Hall, Ithaca, NY 14853, USA; 3Department of Geography, Simon Fraser University, Burnaby, BC V5A 1S6, Canada; 4Faculdade de Agronomia e Medicina Veterinária, Universidade Federal de Mato Grosso, Cuiabá, MT 78060-900, Brazil; 5Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds, LS2 9JT, UK; 6E-mail addresses ajm9@cornell.edu; msj8@cornell.edu; nj2@cornell.edu; couto@ufmt.br; sjr4@cornell.edu

Abstract

Question: Is soil hydrology an important niche-based driver of biodiversity in tropical forests? More specifically, we asked whether seasonal dynamics in soil water regime contributed to vegetation partitioning into distinct forest types.

Location: Tropical rain forest in northwestern Mato Grosso, Brazil.

Methods: We investigated the distribution of trees and lianas ≥ 1 cm DBH in ten transects that crossed distinct hydrological transitions. Soil water content and depth to water table were measured regularly over a 13-month period.

Results: A detrended correspondence analysis (DCA) of 20 dominant species and structural attributes in 10 × 10 m subplots segregated three major forest types: (1) high-statured upland forest with intermediate stem density, (2) medium-statured forest dominated by palms, and (3) low-statured campinarana forest with high stem density. During the rainy season and transition into the dry season, distinct characteristics of the soil water regime (i.e. hydro-indicators) were closely associated with each vegetation community. Stand structural attributes and hydro-indicators were statistically different among forest types.

Conclusions: Some upland species appeared intolerant of anaerobic conditions as they were not present in palm and campinarana sites, which experienced prolonged periods of saturation at the soil surface. A shallow impermeable layer restricted rooting depth in the campinarana community, which could heighten drought stress during the dry season. The only vegetation able to persist in campinarana sites were short-statured trees that appear to be well-adapted to the dual extremes of inundation and drought.

Keywords: Biodiversity; Detrended correspondence analysis (DCA); Mato Grosso; Palm; Primary forest; Soil water; Tropical forest; White sand soil.

Abbreviations: DCA = Detrended correspondence analysis; LAI = Leaf area index; θ = soil volumetric water content.

Nomenclature: Ribeiro et al. (1999).

Introduction

Correlative studies that link the distribution of tropical forest types to environmental factors are common. Soil class (Harms et al. 2001; Duque et al. 2002; Svenning et al. 2004), soil texture (Laurance et al. 1999), flooding regime (Salo et al. 1986), slope angle (Duivenvoorden 1996; Clark et al. 1999), precipitation gradients (Pyke et al. 2001), and topography (Valencia et al. 2004) have all been found to covary with patterns in vegetation distribution. Evidence for explicit controls on tree distribution, however, is scarce and often confined to a particular species or set of species (e.g. Baker et al. 2003; Souza & Martins 2004). Establishing causal relationships is difficult since vegetation can affect soil properties as well as show preferences for specific edaphic site characteristics (Sollins 1998).

Soil hydrology is a component of the environment that could play a strong role in shaping tropical forest structure and composition. At one extreme, inundation of soil with water creates anaerobic conditions which can lead to anoxia and cell death in roots of maladapted species (Vartapetian & Jackson 1997). Impeded drainage, due to either topographic position (Vormisto et al. 2004) or soil type (Péliissier et al. 2001), has been shown to affect plant species distribution. For example, certain palm species grow preferentially in low-lying areas affected by poor drainage (Svenning 2001; Souza & Martins 2005) or seasonal inundation (Frangi & Lugo 1998). At the other extreme, limited water availability under drought conditions can lead to reduced plant growth (Baker et al. 2003), net biomass loss via increased tree mortality (Rolim et al. 2005), increased herbivory (Itioka & Yamauti 2004), and seedling death (Engelbrecht & Kursar 2003; Engelbrecht et al. 2005). Furthermore, prolonged drought may favor the growth of species adapted to dry conditions thereby altering...
previous investigations identified unique patches of vegetation within the study area (Jirka 2005). Broadly speaking, three distinct forest types were distinguished: (1) upland forest – the most common vegetation type – characterized by tall canopy, open understory, high biomass, and intermediate stem density, (2) campinarana vegetation characterized by short, scrubby trees, high stem density and low biomass, and confined to bleached sandy soils, and (3) palm-dominated forest with low stem density generally located in low-lying, seasonally inundated areas. Using the spectral signature of a 7-4-2 band-rendering from a 1997 LANDSAT TM satellite image to provide spatially explicit information on the location of sites with apparently different vegetation composition, we located five 10 m × 100 m transects and five 10 × 50 m transects to characterize each forest type and transitions between them (Table 1).

Vegetation sampling

For each transect, the diameter of all trees, woody vines (lianas), and palms ≥ 10 cm diameter at breast height (DBH) was measured at 130 cm above the ground or above buttresses and stilt roots when present. For basal palms (i.e., no stem at 130 cm), the number of leaves ≥ 2 m long was counted. To account for the smaller size classes, all trees, lianas, and palms from 1-10 cm DBH were measured in nested 2 m × 10 m subplots every 10 m along six of the transects. In four additional transects (henceforth microbasin transects) only lianas 1-10 cm DBH were measured in nested 2 m × 10 m subplots. The diameter of lianas was measured at 130 cm from the ultimate rooting point in order to avoid multiple measurements of the same liana individual that may have fallen from the canopy and re-rooted (Gerwing & Farias 2000). Trees were identified to species level when possible, and mapped on an X-Y grid system to the nearest 10 cm. Height to the top of the crown was measured using a hand-held hypsometer (Vertex III, Haglöf, Sweden) for

Fig. 1. Study location in Juruena county, Mato Grosso, Brazil. The 1400 ha study area outlined in dashed white line is situated within the 25,000 ha logging concession outlined in black on the LANDSAT image. The Juruena River is seen to the east of the study area.
all trees ≥ 4 m tall and by using measuring poles for all trees < 4 m tall. The hypsometer was calibrated to ambient temperature. Above-ground biomass was estimated using published allometric equations derived in Amazonia for the different life form classes as follows: all trees (Brown 1997), palms ≥ 10 cm DBH (Frangi & Lugo 1985), palms < 10 cm DBH and basal palms (Cummings et al. 2002), and all lianas (Gehring et al. 2004).

We measured leaf area index (LAI) in the middle of the dry season (July 2004) using a tripod mounted 5.1 megapixel Nikon D70 digital SLR camera in conjunction with an 8 mm Sigma 360° fisheye lens. Hemispheric photographs of the canopy were taken every 10 m along the center of each transect on uniformly cloudy days. The digital setup produces a cropped image with a 1/3 reduction in the field of view (i.e. 120° rather than 180°).

To overcome this problem, we took two photographs at each location, rotating the vertically-oriented camera on its tripod by 90° between photographs, and subsequently composited the two photos using Adobe Photoshop 6.0 (Adobe Systems Inc., CA, USA) to produce a 180° image. Each composite image was analysed for leaf area index (LAI) using the software Gap Light Analyzer Version 2.0 (Simon Fraser University, BC, Canada, and Institute of Ecosystem Studies, NY, USA). LAI was not measured in the microbasin transects.

### Soil properties and hydrology

We dug 12 pits to 80 cm depth to characterize the soils associated with each forest type. Soil samples were collected from each horizon and analyzed in the laboratory for particle size distribution, color, pH, and organic carbon (OC). Particle size analysis was carried out using the hydrometer method (Gee & Bauder 1986). Due to high concentrations of amorphous clays, samples were placed in a 1:1 solution of 1 N sodium hydroxide, NaOH, and sodium hexametaphosphate, (NaPO₄)₆, and placed on a slow shaker for 16 h to disperse aggregates. Dry soil samples were analyzed for color using a Minolta CR-4000 chromameter (Minolta, USA). Munsell hue was transformed to the same scale by adding ten to samples with higher hues (e.g. 2.5 Y +10 = 12.5 YR). Based on the work of Torrent & Barrón (1993), a modified redness index (RI) was calculated using Munsell hue, chroma and value:

$$RI = \frac{((20-hue) \times \text{chroma})}{\text{value}}$$ (1)

RI serves as a semiquantitative measurement of hematite.

Soil pH was measured by using a 1:2.5 soil : 0.01 M CaCl₂ solution with a combination electrode. Total carbon (TC) content was determined using dry combustion at 1400 °C with a total carbon analyzer (Jena Analytik AG, Jena, Germany). Since inorganic carbonates are not present in these acidic soils, TC is equivalent to organic carbon (OC).

Two types of instruments were used to monitor soil water dynamics: time domain reflectometry (TDR) and groundwater wells. TDR systems were used to measure volumetric water content (θ), with TECANAT® access tubes installed to a depth of 100 cm using a slurry backfill technique as recommended by the manufacturer (Anon. 2001) to eliminate air gaps between the tubes and the soil. We used a TRIME-FM3 meter coupled with a T3 probe (IMKO Micromodultechnik GmbH, Ettingen, Germany) to take measurements of volumetric water content at the following soil depth increments: 0-20, 10-30, 30-50, 50-70, 70-90, and 80-100 cm. Since the TRIME probe measures water content in an elliptical field, two measurements were taken at each depth increment and averaged to account for spatial variability in water content. We used the laboratory calibration for the TDR meter.

Groundwater wells were installed to at least 2.5 m deep, and were constructed of 5 cm diameter PVC tubing sealed at the bottom with plastic caps and with holes bored into the bottom 1 m of the tube to allow groundwater infiltration. TDR tubes and groundwater wells were installed in close proximity to allow for comparisons between measurements at each location. In total, 15 sites were established throughout the transects with paired TDR access tubes and groundwater wells. Measurements were taken weekly or semi-weekly from July 2004-August 2005. A 10-week gap in data collection occurred from mid-November 2004 to early
February 2005 due to technical difficulties. We also measured below canopy rainfall (throughfall) using four rain gauges (Pronamic, Silkeborg, Denmark) paired with event data loggers (Onset Computer Corp., MA, USA) installed in the microbasin transects. Here, we report average daily throughfall.

**Statistical analyses and interpretation**

We used multivariate techniques to relate vegetation distribution to seasonal hydrological dynamics and soil properties. Each transect was parsed into 10 × 10 m subplots. For each subplot, a data matrix was created and populated with information on aggregate stem density of trees (20 most abundant species) and lianas as well as stand structural characteristics (LAI and mean canopy height). Indirect gradient analysis was performed using detrended correspondence analysis (DCA; Hill 1979; Hill & Gauch 1980) in CANOCO 4.5 (Microcomputer Power, NY, USA) – debugged according to Oksanen & Minchin (1997) – to identify ecological groupings of species and structural characteristics (ter Braak & Šmilauer 1997). The detrending by segments procedure and down-weighting of rare species were used. Although the DCA did not exhibit a significant 'arch effect', we restricted our interpretation of DCA results to the first ordination axis because of the known distortions of the higher order axes in DCA (Pyke et al. 2001; McCune & Grace 2002). We conducted two separate ordinations using the following parameters: (1) absolute abundance of the 20 most frequently encountered tree species ≥ 1 cm DBH, absolute abundance of lianas ≥ 1 cm DBH, absolute abundance of trees < 10 cm DBH and ≥ 10 cm DBH, mean canopy height, and LAI; (2) absolute abundance of the 20 most frequently encountered tree species ≥ 10 cm DBH, absolute abundance of lianas ≥ 1 cm DBH, and mean canopy height. In the first ordination the microbasin transects were excluded while in the second ordination all transects were used. We only present results from the first ordination because of the greater resolution of vegetation sampling (i.e., all stems ≥ 1 cm DBH as well as LAI); however, the second ordination confirmed the classification of the microbasin transects as upland forest and resulted in a similar segregation of sample scores as the first ordination. Visual interpretation of DCA scatterplots was used to demarcate the divisions between forest types in ordination space so that each 10 × 10 m subplot was classified in an ecologically meaningful way. Summary statistics were calculated for each forest type by combining data for similarly classified subplots.

All statistical analyses besides DCA were calculated using the S-Plus 6.2 Statistical Package (Insightful Corp., WA, USA) and Minitab Statistical Software (Minitab 14, PA, USA). For the subset of 10 m × 10 m subplots with hydrological instrumentation and soil pits, hydrological and soil data were categorized into one of the three forest type based on their segregation in the DCA scatterplots. We derived hydro-indicator variables to describe hydrological characteristics at critical periods for plant survival and growth during the year (Table 2). Relationships between hydro-indicators and DCA axis loadings for subplots with hydrological data were then tested using Pearson correlations. We used one-way analysis of variance (ANOVA) to test for differences among forest types for both hydro-indicators and vegetation variables. Tukey multiple comparisons were used to test for significance of differences among means. Data were tested and shown to meet the assumptions of normality and equal variances.

**Results**

**Ordination of forest types and structural characteristics**

The DCA using the 20 most abundant tree species (Table 3) and lianas ≥ 1 cm DBH together with mean canopy height and LAI indicated the presence of three forest types (Fig. 2). Axis 1 (DCA-1) explained 28.7% of the variation in forest structure and composition, and had an eigenvalue of 0.275. Due to known distortions of higher order axes (McCune & Grace 2002), we did not analyse them further. DCA-1 described a transition from palm to upland to campinarana forest types. On the lower left of DCA-1 the palms *Euterpe oleracea*,

| Table 2. Description of hydro-indicator variables derived from soil volumetric water content and water table depth measurements. θ equals soil volumetric water content. |
|---|---|---|
| Hydro-indicator measurement | Ecological significance |
| 1 | Maximum depth to water table | Aerated rooting zone |
| 2 | # of days water table at surface | Anaerobic conditions throughout the profile |
| 3 | # of days water table above 40 cm | Anaerobic conditions below 40 cm |
| 4 | Water storage to 1 m August | Drought stress at height of dry season |
| 5 | Difference in above and below impeding layer on 16 March | Surface anaerobic conditions and root impedance at the height of the wet season |
| 6 | Difference in above and below impeding layer on 12 May | Surface anaerobic conditions and root impedance at the beginning of the dry season |
Socratea exorrhiza and Astrocaryum spec. along with the hardwood Inga spec. were tightly associated, while on the upper left of DCA-1 the palm Oenocarpus bataua dominated. The upland forest type near the center of the DCA scatterplot was associated with large canopy trees including Trattinickia burserifolia, morphospec. 1 (unidentified, Moraceae), Joannesia spec., and the palm Euterpe oleracea as well as an abundance of trees ≥ 10 cm DBH, tall canopy stature and high LAI. On the right of DCA-1, species typical of campinarana forest such as Peltogyne spp., members of Melastomataceae, Psychotria spec., Pseudobombax spec., Aspidosperma spec. and Zollernia spec. as well as an abundance of trees < 10 cm DBH and lianas formed a tight cluster. The transects were clearly differentiated in the DCA scatterplot of sample scores, enabling demarcation of forest types based on the above interpretation (Fig. 2b).

A total of 1241 trees and 185 lianas were found in the transects. Total above-ground biomass averaged across the transects was 161 Mg/ha. There were distinct differences in stand structure among forest types (Table 4) as well as the frequency of occurrence of the 20 most

Table 3. The 20 most frequently encountered taxa in targeted vegetation transects totaling 0.75 ha in northwestern Mato Grosso, Brazil. Frequency of occurrence in 10 m x 10 m subplots in each of three forest types classified by DCA scatterplot interpretation and total stems are shown. Bold numbers denote frequency > 0.15.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency</th>
<th>Total stems</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peltogyne spp.</td>
<td>0.400</td>
<td>157</td>
</tr>
<tr>
<td>Oenocarpus bataua</td>
<td>0.218</td>
<td>100</td>
</tr>
<tr>
<td>Melastomes*</td>
<td>0.364</td>
<td>72</td>
</tr>
<tr>
<td>Euterpe oleracea</td>
<td>0.255</td>
<td>59</td>
</tr>
<tr>
<td>Trattinickia burserifolia</td>
<td>0.200</td>
<td>40</td>
</tr>
<tr>
<td>morphospec. 1</td>
<td>0.109</td>
<td>39</td>
</tr>
<tr>
<td>Pseudobombax spec.</td>
<td>0.127</td>
<td>36</td>
</tr>
<tr>
<td>Licaria spec.</td>
<td>0.164</td>
<td>32</td>
</tr>
<tr>
<td>Oenocarpus bataua</td>
<td>0.236</td>
<td>27</td>
</tr>
<tr>
<td>Joannesia spec.</td>
<td>0.073</td>
<td>22</td>
</tr>
<tr>
<td>Astrocaryum spec.</td>
<td>0.055</td>
<td>20</td>
</tr>
<tr>
<td>Aspidosperma spec.</td>
<td>0.059</td>
<td>19</td>
</tr>
<tr>
<td>Meliosma spec.</td>
<td>0.182</td>
<td>17</td>
</tr>
<tr>
<td>Zollernia spec.</td>
<td>0.164</td>
<td>13</td>
</tr>
<tr>
<td>Bowdichia spec.</td>
<td>0.018</td>
<td>12</td>
</tr>
<tr>
<td>Attalea spec.</td>
<td>0.000</td>
<td>12</td>
</tr>
<tr>
<td>Diploptery purpurea</td>
<td>0.073</td>
<td>12</td>
</tr>
<tr>
<td>Amaioua spec.</td>
<td>0.000</td>
<td>11</td>
</tr>
<tr>
<td>Inga spec.</td>
<td>0.073</td>
<td>11</td>
</tr>
<tr>
<td>Psychotria spec.</td>
<td>0.000</td>
<td>10</td>
</tr>
</tbody>
</table>

* Melastomes were only identified to the family level but are included in the table because they were used as an indicator taxon in the DCA analysis.

Fig. 2. DCA scatterplot of (a) species and (b) samples in targeted vegetation transects using abundance of 20 dominant tree species, lianas and trees < 10 cm and trees > 10 cm, average canopy height, and LAI for 10 x 10 m subplots. Broken line demarcates forest types through visual interpretation. Open symbols indicate subplots with only vegetation data and filled symbols indicate subplots with vegetation data and hydrology data. Hydrology data were obtained from four additional upland sites located in microbasin transects. Key: Abbreviations are of species names given in Table 3. trees > 10: abundance of stems ≥ 10 cm DBH; trees < 10: abundance of stems < 10 cm DBH; height: mean canopy height; LAI = Leaf area index.
abundant species (Table 3). Liana, palm and small tree (< 10 cm DBH) stem densities and biomass were significantly different among forest types (Tukey multiple comparison, \( P < 0.05 \)). The palm forest had more than 4 \times the number of palm stems and palm biomass than the other two forest types. Characteristics of the campinarana forest included significantly higher stem densities of lianas and small trees (< 10 cm DBH), as well as a short-statured canopy and lower LAI than upland forest (Tukey multiple comparison, \( P < 0.05 \)). Although not statistically different, stem density and biomass of large trees (≥ 30 cm DBH) and total biomass were in the order upland > palm > campinarana forests. Liana biomass was low in all forest types, accounting for 1.7, 0.7 and 0.4% of total biomass in campinarana, palm and upland forests, respectively. Basal area of large trees in upland forest was 19.0 m\(^2\)/ha while in palm forest and campinarana it was only 8.6 and 3.8 m\(^2\)/ha, respectively. Basal area of palms was 1.7, 2.3, and 8.2 m\(^2\)/ha in campinarana, upland and palm forests, respectively. Soil variability

Chemical and physical characteristics of soils varied by forest type, but only clay content at 30-50 cm differed significantly among forest types (Table 5). In general, soil texture was the most defining characteristic with sand content throughout the profile in the order campinarana > upland > palm forests. Upland sites had the highest clay concentrations, especially for the 30-50 and 50-70 cm depths. Sand content in the upper horizons of campinarana areas were as high as 91% with the clay fraction as low as 4%. Palm and campinarana sites had low RI values, indicative of gleyed soils formed through the reduction, mobilization, and leaching of iron. The higher RI values for upland forest soils indicate that the upland sites are well-drained. Organic C contents and pH were similar across sites.

Soil profiles showed clear indications of the differing hydrologic regimes among forest types (Fig. 3). For the campinarana sites, the most distinguishing feature of the solum was the presence around 50 cm depth of a

![Image](image-url)
dense illuvial horizon, 2-4 cm thick, formed by an accumulation of humic material and iron oxides. Although other ecological surveys have described such ‘white’ sand soils in Amazonia (Duivenvoorden 1996; Laurance et al. 1999; Duque et al. 2005), to our knowledge none has described the presence of a shallow restrictive layer, classified as a concretion or induration according to USDA Soil Taxonomy (Anon. 1999). These soils are classified as Typic Kandiaquults due to the presence of aquic conditions as indicated by redoximorphic features in the soil profile (Anon. 1999). The impeding layer created a noticeably truncated rooting zone with a high concentration of roots in the top 20 cm. Strong motting below the layer indicated the presence of a seasonally-high water table. Sandy soils adjacent to areas with campinarana vegetation did not contain this impeding layer. Soils in palm-dominated areas were gleyed near the soil surface at the time of sampling during the dry season, indicating sustained anaerobic conditions at these sites. This was evidenced by one pit excavated in palm forest being water-logged below 40 cm during the height of the dry season. The palm and hardwood-dominated areas, unlike the campinarana, did not exhibit an impeding layer. Soils under hardwood vegetation had no evidence of redoximorphic features such as motting or gleying within the top 80 cm of the solum.

**Seasonal hydrological dynamics**

Vadose zone hydrology as characterized by soil volumetric water content and depth to water table showed marked seasonal dynamics which coincided with seasonality in rainfall (Fig. 4). In general, water storage (top 1 m of the soil profile) was in the order palm > upland > campinarana forests whereas depth to water table was in the order upland > campinarana > palm forests. Rainfall during the 2004-2005 wet season, remarkably low across the entire Amazon Basin (Hopkin 2005), totalled only 1588 mm from 1 October-30 April compared to 2271 mm for the same period in the previous year. This difference is reflected in measurements of both water storage and

![Fig. 4. Time series canopy throughfall (n = 4) and hydrological data (error bars represent ± 1 SE) by vegetation type for campinarana (n = 4), palm forest (n = 5), and upland hardwood forest (n = 6) from July 2004 through August 2005 showing (a) daily canopy throughfall, (b) depth to water table, and (c) water storage per 1 m soil depth in transects near Juruena, Mato Grosso, Brazil. A two and a half month gap in hydrology data collection is shown as the discontinuity in the upper](image)

<table>
<thead>
<tr>
<th>Table 5. Soil properties ± 1 SE in pits excavated in campinarana (n = 3), palm forest (n = 3), and upland hardwood forest (n = 6). Pits were classified based on their location in ordination space in the DCA scatterplot in Fig. 2.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depth-th (cm)</td>
</tr>
<tr>
<td>pH (in CaCl₂)</td>
</tr>
<tr>
<td>Campinarana</td>
</tr>
<tr>
<td>0-10</td>
</tr>
<tr>
<td>10-30</td>
</tr>
<tr>
<td>30-50</td>
</tr>
<tr>
<td>50-70</td>
</tr>
<tr>
<td>Palm forest</td>
</tr>
<tr>
<td>0-10</td>
</tr>
<tr>
<td>10-30</td>
</tr>
<tr>
<td>30-50</td>
</tr>
<tr>
<td>50-70</td>
</tr>
<tr>
<td>Upland</td>
</tr>
<tr>
<td>0-10</td>
</tr>
<tr>
<td>10-30</td>
</tr>
<tr>
<td>30-50</td>
</tr>
<tr>
<td>50-70</td>
</tr>
</tbody>
</table>

Redness index = [(20-hue) × chroma/value]. For upland forest, color information was not available in three pits in microbasin transects.
water table depth during the middle of the dry season. In both campinarana and upland forest, the water table was over 1 m deeper in July 2005 than in July 2004 whereas in palm forest it was only ca. 30 cm deeper. On the other hand, water storage decreased the most in palm forest across the same time interval. This discrepancy occurred since the water table was on average 85 cm deep in July 2004; thus, soil water content below 85 cm was saturated.

Water table position in upland forest was significantly deeper than in campinarana, but not in palm forest, every month of the year except November (Tukey multiple comparison, $P < 0.05$). Seasonal dynamics in soil volumetric water content among forest types, however, were similar despite textural differences (Fig. 5a). Two major features in seasonal $\theta$ dynamics at 100 cm depth were apparent: (1) palm sites were always wetter due to landscape-level influences on drainage patterns, and (2) the recharge of campinarana soils at depth was delayed due to the low conductivity of the restrictive layer at 50 cm (Fig. 5b).

The hydro-indicator variables were significantly different among sites (Tukey multiple comparison, $P < 0.05$) (Table 6). The maximum water table depth (hydro-indicator 1) was not reached until the beginning of the wet season, despite the onset of rainfall events (Fig. 4). The duration of a water table at the soil surface (hydro-indicator 2) in the palm forest was two-fold longer than in campinarana while in upland forest all sites except one never experienced inundating conditions at the surface. At 40 cm depth (hydro-indicator 3), the same trend was observed, although the duration of saturation at this depth compared to the soils surface was nearly twice as long for both the palm forest and campinarana. Water storage (hydro-indicator 4) was at a minimum at the end of the dry season in August for both years, with a significant reduction from 2004 to 2005 due to lower overall rainfall. Surface saturation caused by impeded drainage was evident in campinarana; $\theta$ at 10 cm was 22% greater than at 60 cm at the height of the wet season (hydro-indicator 5). By the beginning of the dry season (hydro-indicator 6) in campinarana, however, water was depleted from upper horizons which were drier relative to deeper horizons. In palm and upland forests there were little or no differences between $\theta$ at 10 and 60 cm, irrespective of seasonality. Correlations between DCA-1 axis loadings and hydro-indicators showed that a significant percentage of forest stand structure and species composition was attributable to the derived hydro-indicators, especially water storage at the height of the dry season and depth-wise $\theta$ contrasts at the middle and end of the wet season (Table 6).

**Table 6.** Hydro-indicators in campinarana ($n = 4$), palm ($n = 5$), and upland ($n = 6$) forests. Hydro-indicators are described in Table 2. Variables with the same letter are not statistically different at $P < 0.05$ using a Tukey multiple comparison. Pearson correlation coefficients between the hydro-indicators and DCA axis 1 scores are shown in the right columns of the table. Values of statistical significance are: * $= P < 0.05$; ** $= P < 0.01$; *** $= P < 0.001$. $\theta$ equals soil volumetric water content.

<table>
<thead>
<tr>
<th>Hydro-indicator</th>
<th>Units</th>
<th>Campinarana</th>
<th>Palm</th>
<th>Upland</th>
<th>DCA-1 w/o MB transects</th>
<th>DCA-1 all transects</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>cm</td>
<td>266.5 ± 60.0b</td>
<td>277.8 ± 50.4b</td>
<td>632.7 ± 81.0a</td>
<td>−0.118</td>
<td>−0.036</td>
</tr>
<tr>
<td>2</td>
<td>days</td>
<td>22.3 ± 8.2ab</td>
<td>46.8 ± 14.9a</td>
<td>0 ± 0b</td>
<td>−0.44</td>
<td>−0.239</td>
</tr>
<tr>
<td>3</td>
<td>days</td>
<td>46.3 ± 16.1ab</td>
<td>81.0 ± 15.0a</td>
<td>0 ± 0b</td>
<td>−0.459</td>
<td>−0.309</td>
</tr>
<tr>
<td>4</td>
<td>mm</td>
<td>150.0 ± 20.1b</td>
<td>247.4 ± 17.2a</td>
<td>192.1 ± 7.2b</td>
<td>−0.785 **</td>
<td>−0.812 ***</td>
</tr>
<tr>
<td>5</td>
<td>$\theta$</td>
<td>22.5 ± 3.1a</td>
<td>5.4 ± 4.6b</td>
<td>−2.5 ± 3.1b</td>
<td>−0.661 *</td>
<td>−0.676 **</td>
</tr>
<tr>
<td>6</td>
<td>$\theta$</td>
<td>−9.9 ± 5.0a</td>
<td>−6.7 ± 2.0a</td>
<td>−11.0 ± 3.6a</td>
<td>0.043</td>
<td>−0.080</td>
</tr>
</tbody>
</table>
Discussion

Differences in hydrologic regime and soils among forest types

The distribution of dominant tree species and the structural attributes of vegetation in this landscape appear to be strongly affected by soil hydrology as mediated by landscape position and intrinsic edaphic properties. We observed consistent differences in soil hydrology between forest types at ecologically critical stages as demonstrated by the hydro-indicators. Two principal factors responsible for the partitioning of vegetation emerged from this analysis: (1) the duration of surface saturation and (2) confinement of roots to surface horizons due to the presence of a shallow restrictive layer at campinarana sites. Species tolerance for anaerobic conditions under surface saturation, which can lead to anoxia and cell death, vary from hours to many days (Vartapetian & Jackson 1997). Saturated surface conditions were observed at both palm and campinarana sites, albeit for different reasons, but not at upland sites. The landscape position of palm forest sites, which occupy low-lying convergence zones, leads to an accumulation of water from contributing upland areas so that by the middle of the wet season the water table is at or near the surface. Campinarana sites, on the other hand, were located on gently sloping upland positions but experienced inundated surface conditions during periods of prolonged rainfall due to poor internal drainage from the presence of an impeding layer at 50 cm depth (Fig. 3). Upland forest sites were generally located on sloping upland positions and soil profiles there displayed features indicating they were well-drained. High variability in water table depth at upland sites suggests that the factor confining species to upland forest was probably intolerance of anaerobic conditions at the soil surface. This conclusion is supported by Pelissier et al. (2001) who determined that the duration of surface saturation superseded surface water deficit as the predominant factor controlling tree species distribution in a tropical forest in French Guiana.

Both campinarana and palm forest experienced prolonged surface saturation, but only campinarana sites had the shallow impeding layer which limited rooting at depth (pers. obs.). Reductions in root development and plant growth due to high penetration resistance are well-documented in crop plants (Beemster et al. 1996; Rosolem et al. 2002). Although we did not quantify penetration resistance in the campinarana soils, no roots were observed below the impeding layer at 50 cm indicating that vegetation was unable to access deep water, which is fundamental to drought tolerance in seasonally dry areas of Amazonia (Nepstad et al. 1994). Thus, species typical of palm forest, though tolerant of surface saturation, were likely excluded from campinarana sites due to the inability to acquire water at depth.

Differences in vegetation composition and stature among forest types

Plant communities found in the different forest types were markedly different. Palm forest, composed of distinct palm assemblages in different areas of the study site, was dominated by flooding-tolerant species such as *Euterpe oleracea*, *Socratea exorrhiza*, *Astrocaryum* spec., and *Oenocarpus bataua* (Table 3). The ability of members of Arecaceae to flourish under flooded conditions is well-documented in Neotropical forests (Svenning 2001; Souza & Martins 2004; Boll et al. 2005; Souza & Martins 2005). The dominant palm assemblage included *Euterpe oleracea*, *Socratea exorrhiza* and *Astrocaryum* spec. and was located in low-lying convergence zones. *Oenocarpus bataua*, which shows strong gap-dependent recruitment due to high light requirement during the juvenile phase (Svenning 1999), dominated in an area transitioning into campinarana vegetation. At the edge of low-statured campinarana, light penetration through the canopy is relatively high due to low LAI (Table 4) and lack of overstory species, thereby creating areas favorable for establishment of *Oenocarpus bataua*.

Campinarana was dominated by short, scrubby trees and bushes such as *Peltogyne* spp., *Pseudobombax* spec., *Amaioua* spec., *Psychotria* spec., and melastomes. Although we did not identify Melastomataceae beyond the family level, the low frequency of melastomes in palm and upland forests relative to campinarana at our study area (Table 3) enabled us to use them as an indicator species for campinarana vegetation. Likewise, members of Melastomataceae have been used as bio-indicators for the distribution of vascular plants in Peruvian and Colombian Amazonia (Tuomisto et al. 2003; Duque et al. 2005). We encountered the palm *Attalea* spec. in a mono-dominant stand among campinarana vegetation. Other members of *Attalea* are known to grow in clumps in disturbed areas in Brazilian Atlantic rain forest (Souza & Martins 2003), and they also exhibit high occurrence rates close to parent trees due to limited fruit dispersal (Pimentel & Tabarelli 2004). Campinarana sites shared structural and floristic characteristics with *caatinga* forests in Venezuelan Amazonia (Coomes & Grubb 1996). The short-statured forests there grow on seasonally water-logged, bleached sandy soils and are dominated by short, thin-boled trees with physiological adaptations to water stress such as sclerophyllous leaves.

Upland sites which did not experience extended anaerobic conditions were dominated by large canopy trees such as *Trattinickia burserifolia*, *Joannesia* spec., *Diplotropis purpurea*, morphospec. 1 and *Licaria* spec.
The generalist palm *Euterpe oleracea* was also found in upland forest indicating its ability to adapt to a wide spectrum of environmental conditions. Despite a deep aerated rooting zone in upland sites, adverse conditions for plant growth were still encountered in the form of drought stress in this seasonally dry area of Amazonia as evidenced by low soil moisture status to 100 cm at the height of the dry season. Mechanisms for ameliorating water stress by large trees may include hydraulic redistribution (Oliveira et al. 2005b) as well as increased use of deep water (Oliveira et al. 2005a).

Water status also affected structural attributes of dominant vegetation in all three forests. There was a progression in forest stature, biomass and LAI in the order upland > palm > campinarana forests. Dominant vegetation growing in campinarana substrate endured less than ideal growing conditions, including dual extremes of inundation and drought stress and was typified by short, scrubby trees and a relatively high density of small lianas. In palm sites, root growth below 50 cm was uninhibited but extended periods of surface inundation precluded large canopy trees intolerant of anaerobic conditions. Upland sites were essentially released from hydrological growth constraints and had the highest values for tree height, biomass and LAI. However, values for total biomass in upland forest were somewhat lower than values reported for other Amazonian forests (Laurance et al. 1999; Keller et al. 2001; DeWalt & Chave 2004), which may be explained by our targeted selection of sites transitioning from palm or campinarana to upland hardwood forest. Overall, liana biomass was only ca. 1 Mg/ha, which is generally low for Amazonia (Gerwing & Farias 2000) but approximates liana biomass found in southwestern Amazonia at savanna-tropical rain forest transition sites (Cummings et al. 2002). The high density of small lianas we found in campinarana forest with a limited zone for root development is consistent with studies suggesting that liana densities peak in forests with low precipitation (i.e., low plant available water) (Schnitzer & Bongers 2002).

Significant differences in soil water regime among distinct forest types indicate that soil hydrology impacts the distribution of vegetation in this landscape. The underlying ecophysiological mechanisms responsible for controlling distribution were likely related to species-specific responses to inundation (Parolin 2002) and drought (Burslem et al. 1996; Poorter & Hayashida-Oliver 2000; Ashton et al. 2006), particularly during the seedling phase since seedlings are more susceptible to fluctuating environmental conditions than adult trees (Coomes & Grubb 2000; Bunker & Carson 2005). Other factors beyond the scope of this study may have affected vegetation distribution in this forest including botic factors such as dispersal limitation, competition, and predation (Wright 2002; Münzbergová & Herben 2005), and abiotic factors such as nutrient availability (Hall et al. 2004), light availability (Bunker & Carson 2005), and topographic variation (Itoh et al. 2003; Yasuhiro et al. 2004).

**Conclusions**

This study provides a quantitative analysis of the relationship between soil hydrology and vegetation zonation in a tropical rain forest in southern Amazonia. Gross differences in soil hydrology at the height of the wet season and transition into the dry season influenced the forest type distribution in this landscape. Soil hydrological differences were primarily attributable to topographic position in palm forest and intrinsic edaphic characteristics in campinarana. Ecological mechanisms maintaining vegetation zonation with respect to soil water regime may include seedling establishment and survival, differential species tolerance of extreme hydrological events, and species competitive advantage. Further investigation into the ecophysiological traits of the species associated with these hydrologic environments will improve understanding of how vulnerable these influences on biodiversity are to external drivers like climate change and deforestation.

**Acknowledgements.** This work was funded by the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (ND-11) which is a project of the U.S. National Aeronautic and Space Administration. Tim Fahey gave valuable comments on the manuscript and Johannes Lehmann provided guidance for the overall project objectives. Elielton de Souza and Benedito Andrade along with numerous other technicians were instrumental in collecting field measurements. We thank Rohden Lignea Ltda. for allowing us access to the research site. This work was also supported by a U.S. National Science Foundation IGERT Program at Cornell University small grant to Stefan Jirka.

**References**


Hill, M.O. 1979. *DECORANA: A FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging*. Cornell University, Ithaca, NY, US.


Yasuhiko, K., Hirofumi, M. & Kihachiro, K. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island,


Yasuhiko, K., Hirofumi, M. & Kihachiro, K. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island,