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RELATIONSHIPS BETWEEN FREQUENCY OF GROUND EXPOSURE AND FOREST COVER IN A MANGROVE ISLAND ECOSYSTEM

BY

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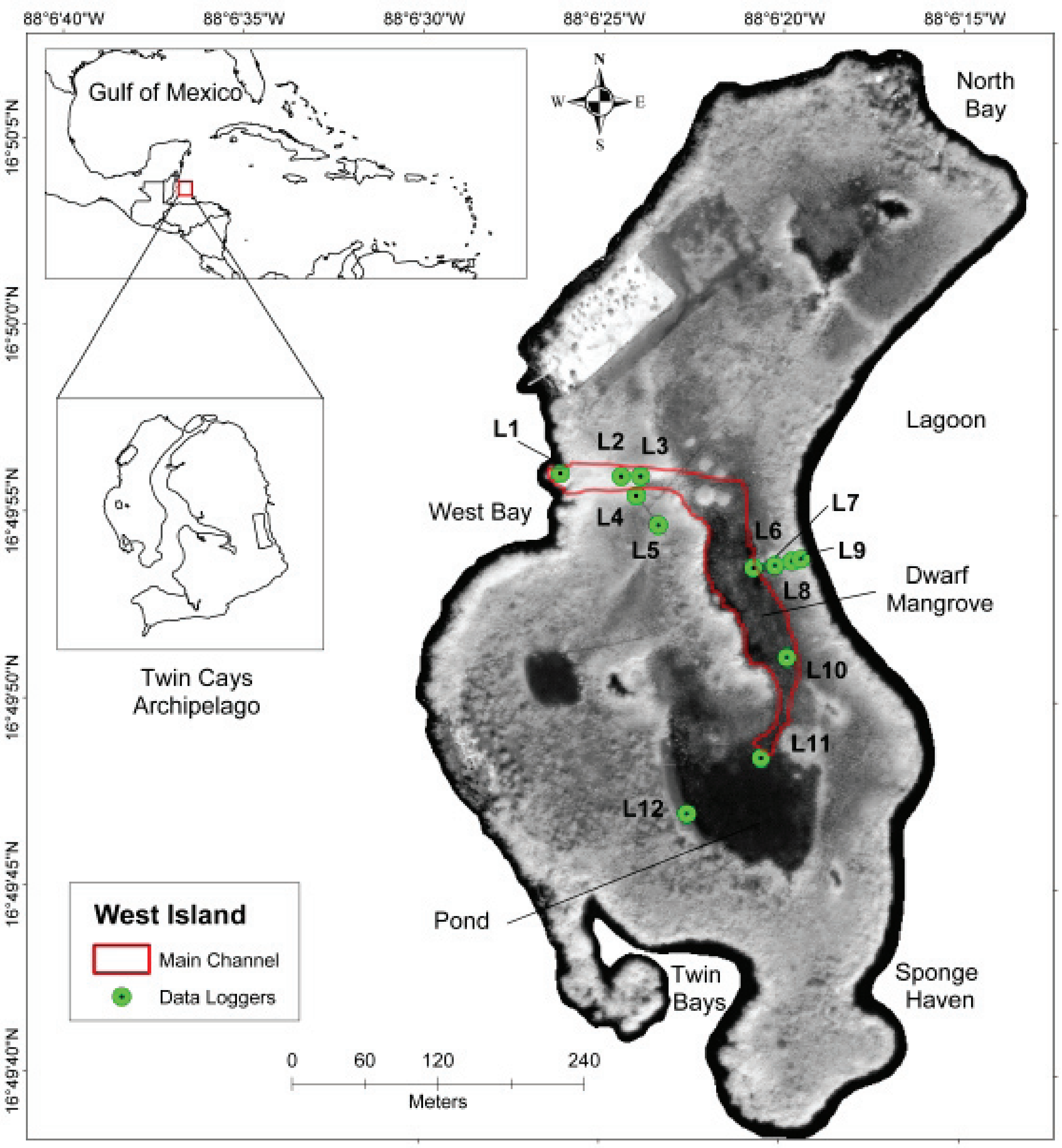

Figure 1. Geographical location of the study site in West Island, Twin Cays, Belize, Central America. Sampling stations (i.e., 12 water level data loggers, L1 – L12, shown as points in the study area map) were located along the main channel of the island. Tidal forcing enters the western side of the island and continues all the way to the pond. The spatial extent of the area of analysis included up until L10.

RELATIONSHIPS BETWEEN FREQUENCY OF GROUND EXPOSURE AND FOREST COVER IN A MANGROVE ISLAND ECOSYSTEM

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ABSTRACT

In mangrove forests, as in all intertidal systems the hydroperiod is of great importance to the vitality of mangrove forests. Despite the importance of inundation and drying periods in tidal ecosystems, spatially-explicit measurements of frequency of ground exposure to air (the drying period) and its effect on mangrove forest cover have rarely been quantified. An eight-month long study was conducted of the tidal regime along a main channel in an overwashed island mangrove forest off the coast of Belize, Central America. Cumulative frequency distribution of tidal data were integrated within a geographic information system to model the spatial extent of ground exposure, and forest cover was estimated using the normalized difference vegetation index (NDVI). Empirical relationships between forest cover and exposure were quantified along seven cross sections, and along 23 transects. On average, exposure accounted for 43% of the variance in NDVI along cross sections. Composite data results for 23 transects showed a positive linear response of NDVI to exposure along both right ($R^2 = 0.31$) and left ($R^2 = 0.14$) banks, with no response in the upper channel area. On average, exposure accounted for 33% of the variance in NDVI on the right bank, and for 13% of the variance on the left bank. At a local scale, NDVI highest responses in the right bank ranged from $R^2 = 0.44$ to $R^2 = 0.71$. Landscape variability in NDVI vs. ground exposure relationships may be due to confounding effects from interactions with other biological and physical variables such as: microbial mats, wind, sun shadows, spatial heterogeneity in topography, rainfall, canopy structure, root density and distribution.

INTRODUCTION

Mangrove forests are distributed throughout tropical and subtropical regions of the world. Globally, mangroves once occupied 75% of tropical coastlines, but due to rapid coastal development, just 25% of the world's tropical coastlines now support mangroves (Rönnbãck, 1999). Mangrove wetlands are one of the most productive aquatic ecosystems covering 240 x 10^5 km^2 of subtropical and tropical coastline characterized by high number of primary producers, diversity of microhabitats, complex multispecies

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interactions, and intensive exchange of organic matter and organisms within and outside the ecosystem (Day et al., 1989; Twilley et al., 1992).

Hydrologic events are among the determinant processes in the establishment and maintenance of wetland ecosystems (Mitsch and Goesselink, 1993). The reverse is also true, with ecological processes critical in determining the hydrological balance (Hughes et al., 1998). Because of this intimate relationship, quantification of hydrological parameters is of paramount importance in order to predict and manage change in wetland environments. Environmental changes affecting wetland hydrology include: both long-term and gradual changes (e.g., climate change and projected sea-level rise), sudden changes from natural disturbances (e.g., hurricanes) and human interference (e.g., hydraulic modification of tidal flow).

In intertidal systems, hydroperiods (i.e., the temporal pattern of inundation and exposure to air) influence water temperature, salinity, water oxygenation, and nutrient flows (Van Diggelen, 1991; Heley et al., 1992; Gosselin and Chia, 1995; Leuschner et al., 1998). Tidal inundation affects levels of water-logging, pH, redox potential in soil and water, and vegetation zonation (Vince and Snow, 1984; Armstrong et al., 1985; Van Diggelen, 1991; Pennings and Callaway, 1992; Bockelman et al., 2002). Hydroperiods affect plant communities not only through length, but also through depth of inundation (David, 1996; Newman et al., 1996; Baldwin et al., 2001; Steven and Toner, 2004).

Research in the Caribbean has described many of the mechanisms determining nutrient availability in nutrient-poor mangrove systems (Feller, 1995; Downing et al., 1999; Feller, 2002; Feller et al., 2003; Lovelock et al., 2004). Nevertheless, a great deal of uncertainty still exists about changes in the rate and volume of nutrient subsidies being delivered to these systems from natural (i.e., tidal sources, atmospheric deposition) or anthropogenic disturbances within the hydrologic regime of the mangrove system itself. Additionally, the impact that hydroperiod may have on growth patterns and the spatial distribution of mangrove forest in the neotropics is not well understood.

In this study it is hypothesized that with a higher frequency of ground exposure to the air (referred here as FOGE), resulting from periodic changes in water elevation, higher values of an index of mangrove forest cover will be found at the local and landscape spatial scales. It is assumed that in the process of de-watering during the tidal flux, roots biochemistry and soil aerobic processes are increased thus enhancing plant growth. On the other hand, in areas that are not routinely dewatered and have limited flushing, the effect of high/low temperature and salinity can be enhanced creating a detrimental environment for roots, thus reducing overall plant growth as represented in zones of stunted or ‘dwarf’ mangrove. These dwarf habitats are usually found in the interior of overwash mangrove islands as well as coastal mangrove systems.

Ground exposure and its effect on mangrove forest growth and spatial patterns has been rarely studied in tidal systems, especially in mangrove ecosystems with high spatial variability as found in the offshore islands of Belize (Rodriguez and Feller, 2004). The effect that drying periods and their spatial and temporal variability might have on mangrove structure and function is a critical factor that could explain the present spatial heterogeneity of mangrove communities on these islands. Few studies have experimentally addressed the causes of zonation in mangrove forests (Chapman, 1976; Smith, 1992; Ellison and Farnsworth, 2001).

The general understanding is that tidal regimes, with particular emphasis on the inundation period, impact other environmental conditions that influence growth, sediment flushing, and nutrient subsidies. These changes potentially alter patterns and rates of growth in mangrove plants. For example, if tidal flow into a mangrove forest is limited, reduced or inhibited, residence time of water in the hinterland increases, which may lead to higher water temperatures and salinity (due to evaporation) in the summer and diminished aeration of the substrate and nutrient replenishment. These factors have been correlated with reduced primary production in mangroves (McKee, 1995). In contrast, if flow into a mangrove forest is increased, enhanced flushing will moderate temperatures, flush the soil, and deliver fresh supplies of nutrients from the surrounding open water. As water reaches the interior of the island faster and more frequently, the soil surfaces and the upper root structures of the mangroves are regularly dewatered. As water finds less resistance and a greater hydraulic gradient, such conditions increase, enhancing plant growth. In Twin Cays, Belize, a differential annual growth was observed in *Rhizophora mangle*, represented by a greater distance in leaf scars, in response to increased water volumes resulting from mangrove clearing for survey lines development by the year 1992. Separation between leaf scars increased from an average of 0.91 cm yr^{-1} before survey line development to an average of 2.8 cm yr^{-1} after such hydrological disturbance. The production of elongated internodes and frequent lateral branches indicates vigorous growth conditions in *Rhizophora mangle* as has been shown by Gill and Tomlinson (1991). This type of measurement can provide a long record of how anthropogenic changes in the hydrology of the system can alter primary production and growth patterns.

Previous research on the hydrology and hydrogeology of an overwashed mangrove forest (Urish and Wright, 1990; Wright and Urish, 1990; Urish, 1991; Wright et al., 1991) has shown the complexity of tidal dynamics as it interacts with dense mangrove root systems. The fieldwork was accomplished at a location where there has been recent anthropogenic impact on intertidal dynamics. Previous research in mangrove ecology suggests that frequency and extent of surface flows affect mangrove tree growth and density (Woodroffe, 1995). In the past, some studies have concentrated on inundation frequency and sediment transport (Bockelman et al., 2002; Doyle, 2003; Bryce et al., 2003) and others have focused on restoration (Ball, 1980; Elster, 2000).

In this paper a spatially explicit model is developed to determine empirical relationships between frequency of ground exposure to air (i.e., drying as opposed to flooding) and forest cover in an intertidal mangrove island. Characterizing the spatial heterogeneity of such hydrological-plant interactions is a crucial step to the mechanistic understanding of some of the abiotic factors that determine the spatial distribution of mangrove forests communities in the Caribbean region.

METHODS

Study Site

This study was conducted in the West Island of Twin Cays (Fig. 1), a peat-based, 92-ha archipelago (16°50'N, 88°06'W) of off-shore mangrove islands just inside the crest of the barrier reef of central Belize, approximately 12 km from the mainland. The Smithsonian Institution's Marine Field Station on nearby Carrie Bow Cay, approximately 5 km from the study site, provided boats, laboratory, living accommodations, and logistical support during the fieldwork (Rützler et al., 2004). Twin Cays is built on a carbonate substrate made up of a dense limestone formed by finger corals and mollusk fragments overlaid by 8 to 12 m of peat that has accumulated over the past 8000 years BP. Twin Cays receives no terrigenous inputs of freshwater or sediments (Macintyre et al., 2004). The shoreline gradient is intertidal, but physiognomically varied and interrupted by tidal creeks that bring water into the interior area of the island flats and shallow ponds.

The vegetation is dominated by *Rhizophora mangle* L. (red mangrove) with lesser amount of *Avicennia germinans* L. (black mangrove), and *Laguncularia racemosa* (L.) Gaertn.f. (white mangrove). This paper will focus on the *Rhizophora mangle* L. within the tidal zone. Forests on West Island are characterized by a tree-height gradient, which parallels other gradients, such as productivity and tidal flushing. The tree-height gradient can be subdivided into three zones. From the sea to landward, the seaward-most zone is a narrow fringe of uniformly tall red mangrove trees (5-6 m). Next is a transition zone (2-4 m tall), where all three mangrove species are present, followed by a zone of uniformly stunted, dwarf red mangrove trees (~1.5 m), which form vast stands in the interior of West Island (Rodriguez and Feller, 2004). Since 1991, approximately 15 surveying tracks, 1-2 m wide and 100-400 m long, have been cut into the island's interior to explore its potential for private development. Although the proposed developments were aborted, the channels formed by the survey tracks have changed the flow patterns in the island providing a more rapid and frequent renewal of ocean water.

The climate of Twin Cays is characterized as tropical with an annual rainfall of about 180 centimeters (Walker 1973), and with a relative "dry" season from March to June where the rainfall averages about 50% that of the other months. The average annual air temperature is 27º C, ranging from 24º C in January to 29º C in June, with a humidity averaging about 78%. The seawater temperature outside the islands changes from 23º C in winter months to 31º C in the summer (Rützler and Ferraris 1982; Wright et al. 1991). Ponds in the interior of the island may reach temperatures as high as 40º C.

Tidal Data

A network of water level monitoring stations was used to determine the tidal dynamics interior to West Island (Fig. 1). Approximately 124,000 tidal elevation data points were collected at 30 minute intervals from 12 automatic water depth recorders (Ecotone Remote Data Acquisition Systems) between January 14 and August 18, 2003. A datum of Lower Low Water (LLW) was used. Mean Higher High Water (MHHW) was equal to 0.1968 m. All recorders continually monitored at 30-minute intervals the surface water depth or the groundwater elevation (i.e., where water drops below the surface). The recorders were surveyed to a common datum of Mean Lower Low Water (MLLW), computed as the mean of the lowest of the low water elevations of a daily tidal cycle (NOAA, 2005). For the estimation of the spatial extent of land flooding and exposure in the interior of West Island, one must consider the chances of tidal water elevation during a sampling period (i.e., in this case from January – August 2003) being less than elevation at which the ground is exposed. Frequency analysis of water elevation at the twelve data stations provided a statistical approach to compute probabilities of exposure during the 8-month sampling period.

Topography Data

The topography of the island interior was determined using standard land surveying techniques with an automatic level (Wolf and Ghilani, 2006). The data were then used to produce a topographic map with a 0.2-foot contour interval, with measurements later converted to the international metric system (Urish and Wright, 1990; Urish, 1991). The original map was drawn by Urish (1991) from approximately 1200 data points located along 22 transects, using an automatic level to an accuracy of ± 0.01 ft (± 0.30 cm) and then field checked for veracity. All measurements are related vertically to a MLLW datum as defined by the U. S. National Oceanographic and Atmospheric Administration (NOAA, 2005). Horizontal locations were established by global positioning system (GPS) measurements. Initially, an arbitrary datum was used to establish a common datum for all vertical measurements. The datum was later converted to MLLW, as a more extensive tidal record was determined for the local area. It should be recognized that while this record is useful, it is based only on an eight-month record, not the 19- year record prescribed by NOAA for long-term stations. No useful long-term station exists in the region to provide a reliable correlation for the extrapolation of a more extended tidal record.

Geospatial Models

Geospatial analysis of frequency of exposure and forest cover modeling consisted of the following steps: First, the topographic paper map with 0.2 foot-contour lines from survey data (Urish and Wright, 1990; Urish, 1991) was converted to a digital layer and co-registered to an IKONOS image acquired in 2003. Second, contour lines were digitized from this new coverage and used as input to ArcGIS-3D analyst to model the topographic surface with a triangular irregular network (TIN). A new polygon layer extending as far as the highest surveyed height was digitized and used as boundary layer in the creation of the TIN surface. The boundary polygon covered an area of approximately 91,509 m^2. This TIN was subsequently transformed to a digital elevation model (DEM). Thiessen polygons were computed to determine the most likely areas related to the data at each of the 12 data logger stations. Thiessen-weighted average involves a weighting factor that is proportional to the fraction of the drainage basin represented by each data logger. This spatial weighting approach has been extensively used in hydrology in the analysis of rainfall data distributed unevenly in space, and it is also a well-defined application of proximity models in GIS.

Modeling the frequency of ground exposure at the landscape scale was based on the interpolation of 260 points extracted from the previously created DEM layer from the topographic map produced by Urish (1991). These points were digitized within the boundary layer using a grid layer of 20 x 20 m cell size (ArcInfo Workstation, ESRI, Inc) overlaid on the DEM. This systematic sampling scheme produced a density of sampling points equal to approximately 28 points per hectare. In addition to elevation data, other attributes were added to this new point data layer including: (i) percentages for frequency of exposure and flooding derived from cumulative distribution functions corresponding to the 12 depth recorders placed along the channel, and (ii) vegetation index values derived from image analysis of satellite data. Interpolation of frequency of ground surface exposure values from the 260 digitized sampling points was done using Inverse Distance Weighting (IDW) and kriging interpolator algorithms from Geostatistical Analyst (ArcGIS 9.2, ESRI, Inc). The IDW method assumes a distance decay function using a linearly weighted set of sample points, so the influence of a point declines with increasing distance from that point. The Krigging method includes the autocorrelation of the values of the input points, and the creation of a surface of predicted variance (Bailey and Gatrell, 1995; Isaaks and Srivaastava, 1989; O'Sullivan and Unwin, 2002).

Different vegetation indices (VIs) from multispectral remotely sensed data have been developed and used to quantify biological and physical parameters (Schultz and Engman, 2000; Liang, 2004). In this study, forest cover estimates were derived from IKONOS (Space Imaging, Inc.) satellite data acquired in 2003. From this multispectral (blue, green, red, and near-infrared bands), high spatial resolution (1m pixel) imagery, the Normalized Difference Vegetation Index (NDVI) for the study site was derived. NDVI is a vegetation index widely used in various applications. NDVI responds to changes in biomass (Tucker, 1979), chlorophyll content (Buschman and Nagel, 1993), photosynthetic activity (Sellers, 1985), leaf area index (Asrar et al., 1984; Myneni and Williams, 1994; Sellers et al., 1994; Franklin et al., 1997), foliar loss and damage (Vogelman, 1990), phenology (Justice et al., 1985), and canopy water stress (Liang, 2004). NDVI is defined by the following equation:

$$NDVI = \frac{\rho_{NIR} - \rho_R}{\rho_{NIR} + \rho_R} \tag{1}$$

where, ρ_{NIR}, ρ_R represent the reflectance of near infrared and red bands, respectively. The range is theoretically between –1 and 1, but in practice the value of ρ_R is hardly ever larger that the one for ρ_{NIR}, which reduces the range to [0…1], with 0.1 representing very low plant cover and 0.7-1.0 maximum plant cover. Image processing was done with ERDAS IMAGINE 8.7 (Leica Geosystems GIS and Mapping, LLC).

To quantify FOGE-NDVI relationships along the main channel two sets of analysis were carried out: In the first analysis, cross sections of the channel were extracted from the DEM along seven transects having an average length of 99 m. Sampling points averaged 13 per transect and were located approximately 5 – 10 m apart. NDVI was extracted and then regressed against FOGE values taken at each sampling point. The second analysis consisted of using twenty-three transects digitized along areas modeled following a GIS suitability analysis for optimum placement of transects. From this suitability model three predicted co-occurring classes were extracted: (1)

Low FOGE-Low NDVI, (2) Medium FOGE-Medium NDVI, and (3) High FOGE-High NDVI. The second analysis provided an in-depth quantification of differences between the right and left banks (i.e., going in a northerly direction) as well as the upper section, the area close to the entrance of the channel. In the upper section of the channel, transects averaged 106 m in length, and the average number of sampling points was 52 per transect. In the left bank, transects averaged 58 m in length, and 30 sampling points per transect. In the right bank, transects averaged 48 m in length, and 25 sampling points per transect (Fig. 2). NDVI was extracted and then regressed against FOGE values taken at each sampling point.

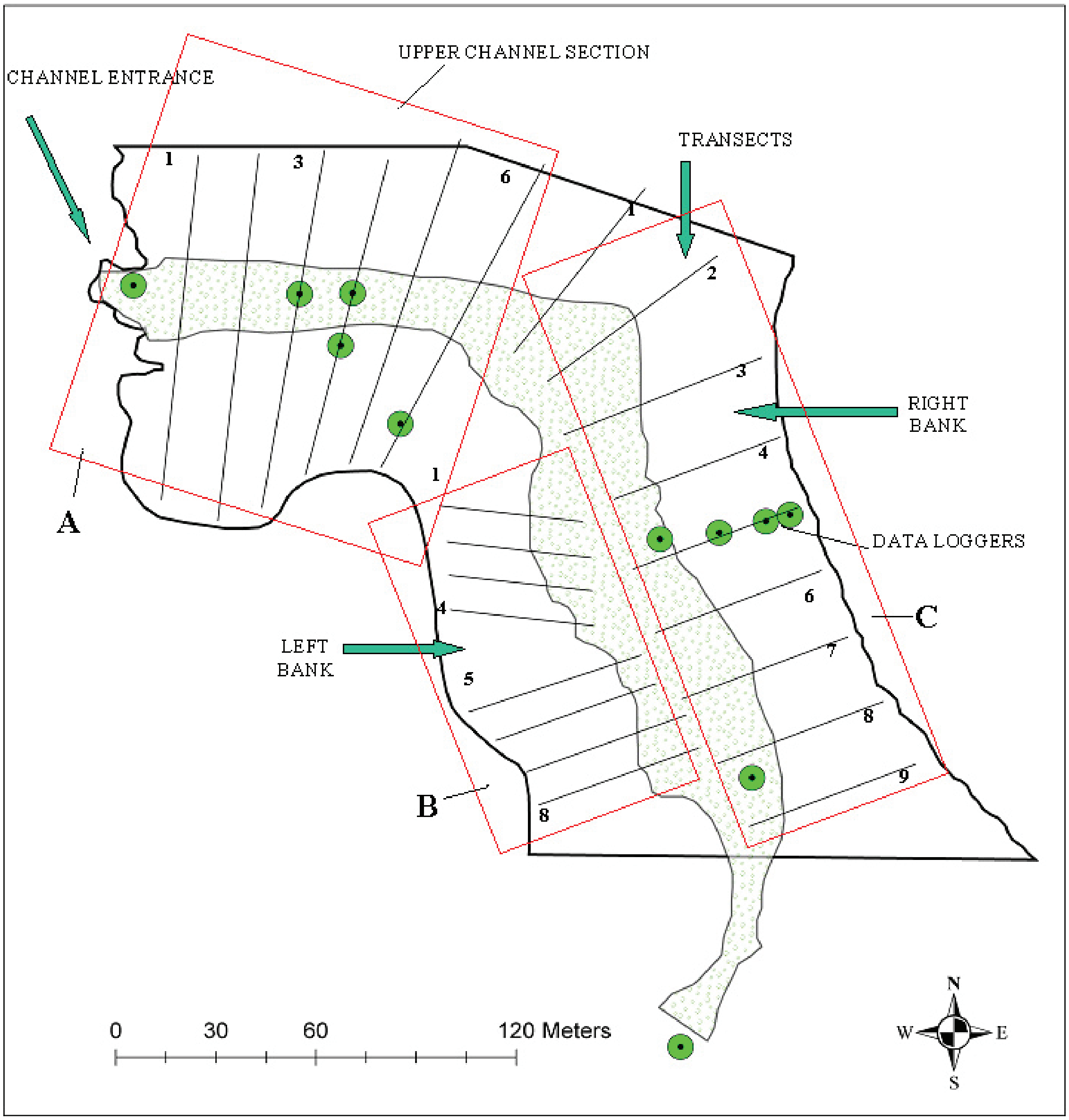


Figure 2. Location of three groups of transects (A, B, and C) digitized in the upper section, left and right banks along the main channel of West Island. Location of these 23 transects was based on GIS modeling of co-occurring combinations of NDVI and frequency-of-ground-exposure (FOGE), i.e., low, medium, and high. Values of FOGE and NDVI were extracted along these transects using the tool ‘extract values to point’ from Spatial Analyst (ArcGIS 9.2, ESRI, Inc).

A frequency analysis approach was followed to define the nonexceedence probability, which is the probability that the corresponding value of the random variable will not be exceeded in any one-time period (McCuen, 1998). This scale extends from 0.01% to 99.99%. A frequency curve provides a probabilistic description of the likelihood of occurrence or nonoccurrence of the variable. Thus, a cumulative frequency distribution (cfd) function (Langbein 1960; Bedient and Huber 1992; Ott 1995) was computed for time-series data for each of the twelve data logger locations. This information in combination with topography data provided the means to calculate exposure or flooding at other locations points used for the interpolation process. Cumulative frequency values were obtained by ranking n tidal elevations values according to their size and by giving the smallest elevation the rank $m = 1$. The percentage of all events less than or equal to each tidal elevation value is given by the formula:

$$Fi = \frac{m}{n+1} * 100\% \qquad (2)$$

where Fi is the cumulative percentage frequency of the variable, or the percentage of days with a tidal elevation equal or less than a particular daily tidal elevation having rank m. The percentage frequency of past events is taken as the probability (also in percent) of future events. The data were not partitioned in weekly or monthly intervals, and therefore, resulting values from this analysis were considered an annual representation of probability events.

Statistical Methods

Regression analysis was used to determine the contribution of frequency-of-ground-exposure to the overall prediction of NDVI. The test of significance (F-test) from the regression determined whether the relationship between independent and dependent variables was large enough to be measurable. We estimated overall local and scale relationships by regressing NDVI vs. FOGE data extracted along a total of 30 transects using SYSTAT 8.0 (SPPS, Inc). Landscape-scale relationships were estimated with the entire interpolated surfaces and remote sensing derivatives using the GRID module from Arc/Info software version 9.1 (Environmental Systems Research Institute, Redlands, CA).

RESULTS

Tidal Dynamics

Asymmetry of tidal spatial displacement within the island was evident from the cumulative frequency distribution analysis of water elevation (Fig. 3). Previous dye studies (Urish et al., In press) have shown a very complex tidal movement as water reaches the southern pond. This tidal asymmetry has also been shown to occur in mangrove creek systems where it is dominated by the interaction of tidal hydrodynamics and the intertidal storage effect of the mangrove swamps and salt flats (Bryce et al., 2003).

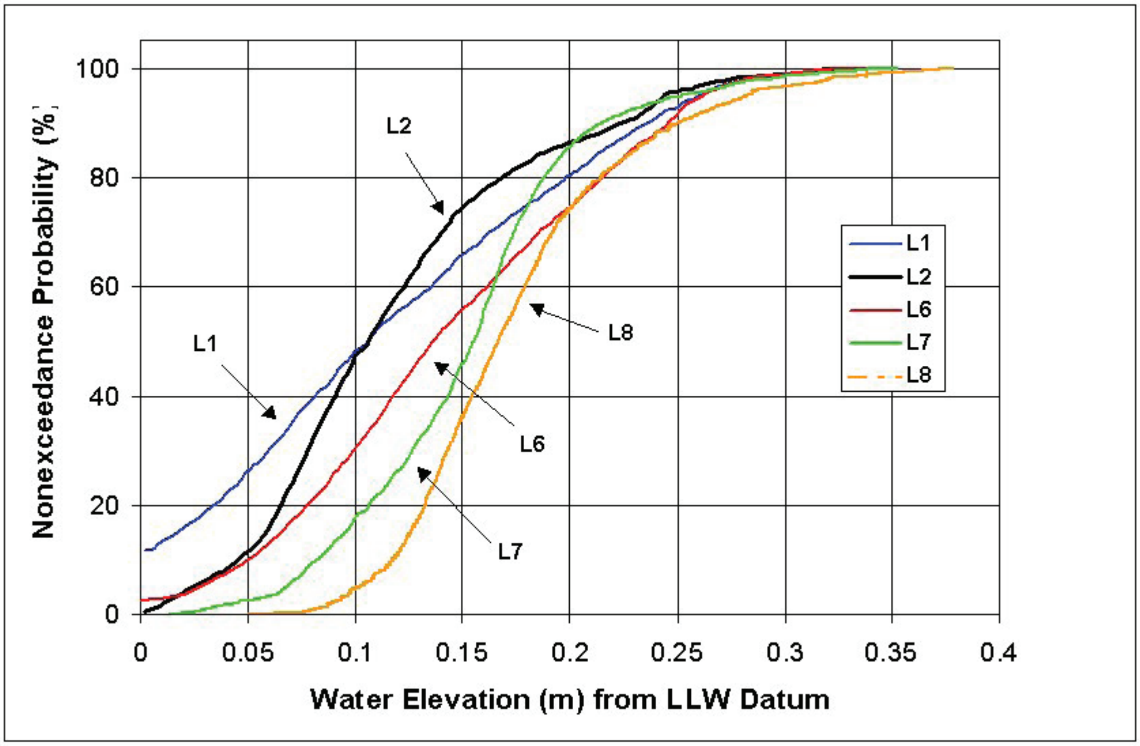


Figure 3. Cumulative distribution functions for some of the sampling stations showing the progression of tidal movement as one moves from the entrance (L1) towards the interior of the island (L8). The nonexceedance probability is the cumulative percentage frequency of the variable, or the percentage of days with a tidal elevation equal or less than a particular daily water elevation. The percentage frequency of past events is taken as the probability (also in percent) of future events. **Interpretation:** going up from 0.2 m in the x-axis to the curves and across will find ~39% chance of daily tidal elevations <= than 0.2 m at station L8; ~ 50% at L7, 48% at L6, ~ 78% at L2, and ~ 68% at L1.

The tide at Twin Cay at the coastline is micro-tidal with a mean range of 20 cm between MLLW and MHHW, and is a mixed semi-diurnal type (Kjerfive et al., 1982). During the 8-month period from January –August 2003 there was a measured extreme water level range of 50 cm at station L1 at the channel entrance. Once the tidal wave enters the tangled root system of the mangrove forest, the sinusoidal tidal signal changes to a highly asymmetric pattern, with the rising tide displaying a much steeper slope than the falling tide. The amplitude is attenuated and the highs and lows of the tidal signal lag the open lagoon water tide. Typical tidal signals for the lagoon and two inland stations, stations L2 and L6 some 50 meters and 192 meters (see Fig. 1 for location) from the channel entrance at L1, illustrate the magnitude of this effect. As the tidal wave moves through the mangrove root complex the tidal amplitude is reduced to 23% of the original signal at the shoreline (station L1) at L2 and 12% at L6. It can be expected that every 2 to 3 years a hurricane of sufficient magnitude will cause storm surges that will temporarily flood the entire island.

The flooding tide reverses course twice daily, and then flows back to the lagoon, all the while dispersing within the swamp waters of the mangrove. A hydrologic water budget analysis complemented by temperature and salinity measurements indicates that in the dry period during February to May, with a high evapotranspiration rate, the net flow is inland with respect to the interior pond, whereas during the rainy period the net flow is to the lagoon (Wright et al. 1991). This effect is illustrated for the shallow waters of the most remote interior pond, some 400 meters from the lagoon connection. In June the temperature of the water reaches 40 ^{o} C and the salinity increases to 42 ppt, inducing greater stress on the mangrove, whereas in January as a result of colder weather and greater rainfall water temperature falls as low as 25 ^{o} C, with a salinity of only 5 ppt. The combination of these factors along with the greatly reduced tidal flushing, is seen as a likely reason for the sparse vegetation and dwarf growth in this pond area. In contrast, vigorous growth is seen in the mangrove areas subject to more direct flooding by fresh seawater and a greater wetting period with only moderate seasonal variation in temperature and salinity. This same environmental stress occurs at the shallow fringe areas of the system.

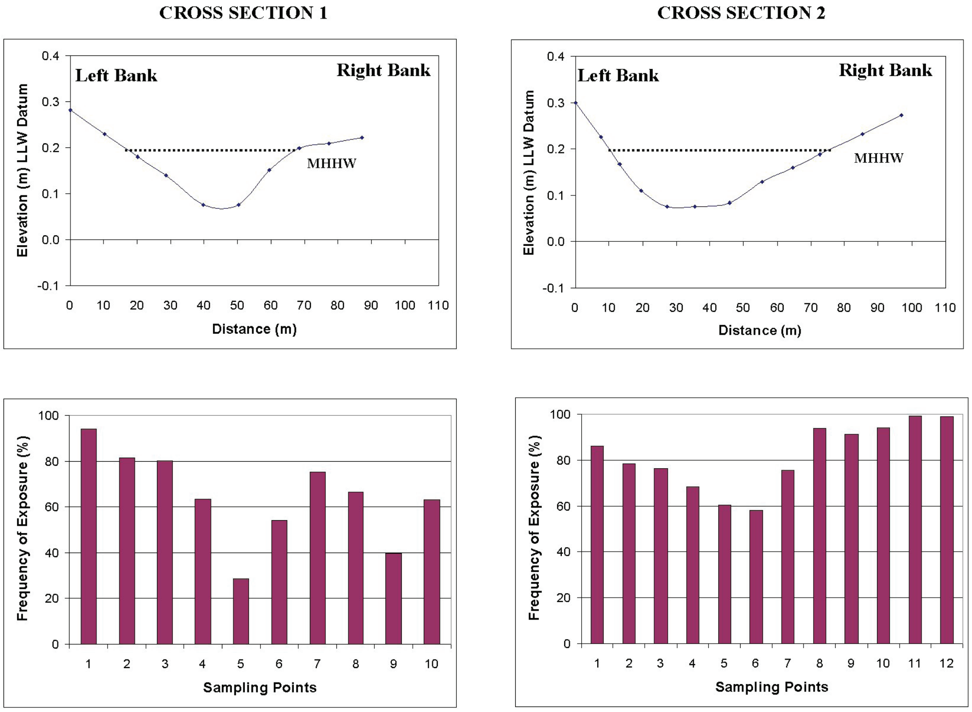
Frequency of Ground Exposure and Forest Cover

The spatial distribution of FOGE along the entire channel area, calculated from kriging interpolation, showed good agreement with ground truth of present physical characteristics, i.e., low percent exposure in areas dominated by dwarf mangrove vegetation. These are also areas where flooding remains the longest because of increased channel depth. The vegetation index for 2003 shows a clear distinction between dwarf zones (i.e., low NDVI ~ 0.2) and areas of intense growth (i.e., NDVI > 0.6) along the banks of the channel. Relationships between annual FOGE and NDVI were scale-dependent (i.e., entire channel vs. channel cross sections), and indicated that localized hydrodynamic-plant interactions must be taken in consideration even though the system is quite homogenous in *Rhizophora* mangrove stands. Regression analysis of raster surfaces of annual frequency of ground exposure and NDVI showed a positive trend ($Y_{NDVI} = 0.261 + 0.21_{exposure}$; RMSe = 0.188; Chi-Square = 1901.58) for the entire surveyed area. High spatial variability in this trend is reflected in the Chi-Square value.

Results along elevation cross sections (Fig. 4a, b) showed a temporal and spatial variability of annual FOGE values across different sections of the channel. Topography in the upper channel, cross sections 1 and 2 (Fig. 4a), is relatively shallow, with relatively high FOGE (i.e., > 80%) along both transects. In the middle channel, cross sections 3 and 4 (Fig. 4b), FOGE is very high in the banks of the channel and very low in the center. Bank slopes are steeper and plant cover increases with higher elevation. In the lower channel, cross sections 5, 6, and 7 topographic features vary but frequency of ground exposure continues to be high in the banks of the channel.

FOGE-NDVI relationships in these seven cross sections differed along the channel. For example, in the upper channel area (cross sections 1 and 2), NDVI decreased with exposure, with the highest exposure effect ($R^2 = 0.69$) on the right bank of the channel. In the middle channel, (cross sections 3 and 4) we found quite a different

(A) UPPER CHANNEL



(B) MIDDLE CHANNEL

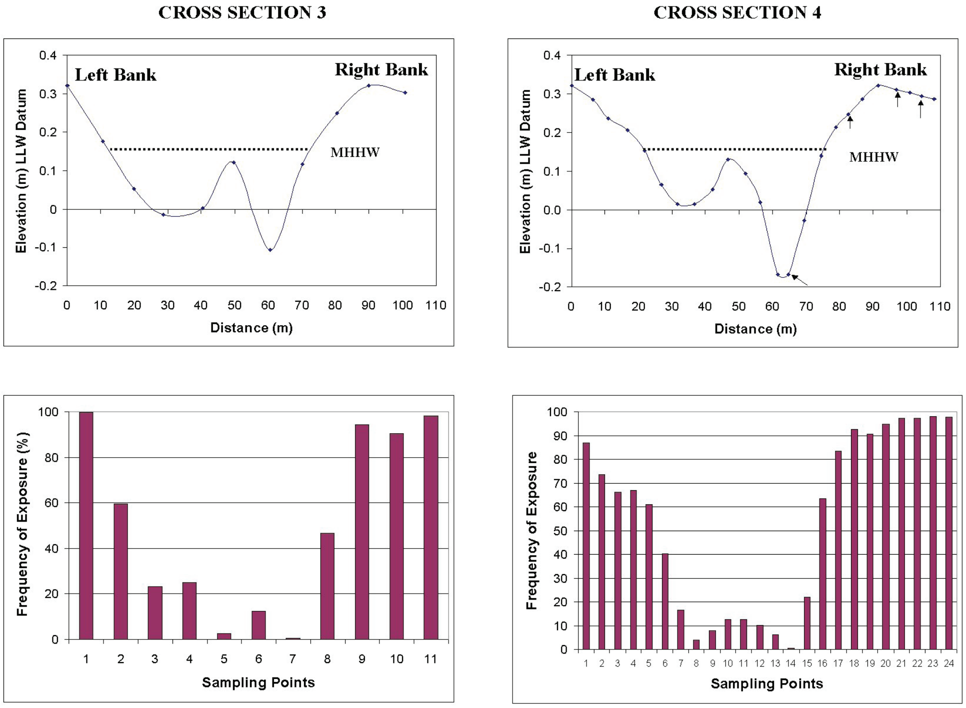


Figure 4. Cross sections of topographic elevations and their corresponding frequency of ground exposure (FOGE) along the upper (A) and middle (B) regions of the main channel in West Island, Twin Cays, Belize. Elevations are referenced to the Lower Low Water (LLW) Datum (i.e., the plane of reference to the mean lower low water elevations (MLLW)). Up-pointed arrows in cross section 4 show the location of four of the twelve data loggers (i.e., L6-L9) used in tidal sampling.

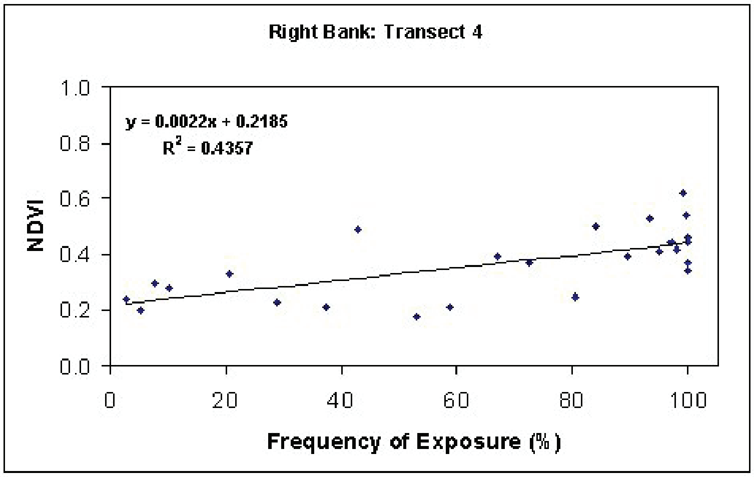
story. Here, NDVI increased with exposure on both sides of the channel, with the highest exposure effect ($R^2 = 0.98$) on the right bank in cross section 3. Finally in the lower channel (cross sections 5, 6, and 7), linear relationships between exposure and NDVI ranged from $R^2 = 0.27$ to $R^2 = 0.89$, with a distinct positive exposure effect on the right bank and negative exposure effect on the left bank of the channel. Because of the small sample size used in this regression analysis, it was important to do a second analysis of the data to see if the significance and variability in the relationships was more systematic throughout the entire channel.

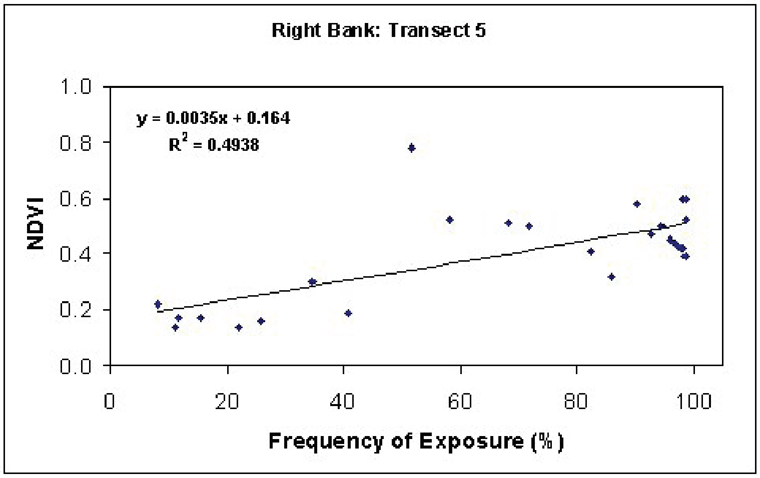
Analysis of a more intensive sampling scheme using 23 transects showed a clearer picture of the spatial pattern in the relationships between FOGE and NDVI along the main channel. For example, along the right bank, a positive linear trend was quite consistent with the highest regression coefficients found in transects No. 4, 5, and 6 ($R^2 = 0.44$; $R^2 = 0.49$; $R^2 = 0.71$, respectively (Fig. 5). Along the left bank, the response was also positive but less strong and more variable. The highest regression coefficients in the left bank were found in transects No. 1, 4, and 8 ($R^2 = 0.24$; $R^2 = 0.17$; $R^2 = 0.31$, respectively (Table 1). In the upper channel area, no NDVI response to exposure effects was found at all. Analysis of the composite data (Fig. 6) confirmed the differential responses of NDVI to changes in frequency-of-ground-exposure along three different sections of the channel, that is, no trend in the upper region, and a linear trend along the right and left banks of the middle and lower sections of the channel.

DISCUSSION

Results in this study of empirical relationships between states of ground exposure in the wetland's hydroperiod cycle and an a remotely sensed index of mangrove forest cover (i.e., NDVI) in Belize showed distinct spatial patterns in forest cover responses as one moved from the coastline toward the interior of the island. Nearby the entrance of the channel, where mangrove trees are exposed more directly to a daily flushing, on average, NDVI did not respond to changes in ground exposure. This response was a good indicator that other biological and physical factors (i.e., water depth, flooding regime, nutrient inputs, etc) may be affecting plant growth in this zone of the channel. Further down the channel next to the dwarf zone, NDVI positive responses to increases in frequency of ground exposure differed along the right and left banks, which may reflect environmental factors particular to each bank (i.e., tidal velocity, wind effect, channel width, etc.). For example, along the left bank, abundant microbial mats are found, wind is stronger, and sun shadows are prevalent. Furthermore, the spatial variability in NDVI-Exposure responses in the upper, middle, and lower regions of the channel could be explained if we take in consideration the differences in bottom topography and tidal patterns that occur along the channel.

Spatial variability at the local and landscape levels found in this study may also be due to some of the scale problems associated with hydrology (Harvey 1997; Bugmann 1997; Schulze 2000), which include: spatial heterogeneity in topography (i.e., slope), intensity and seasonality of rainfall, evapotranspiration characteristics of





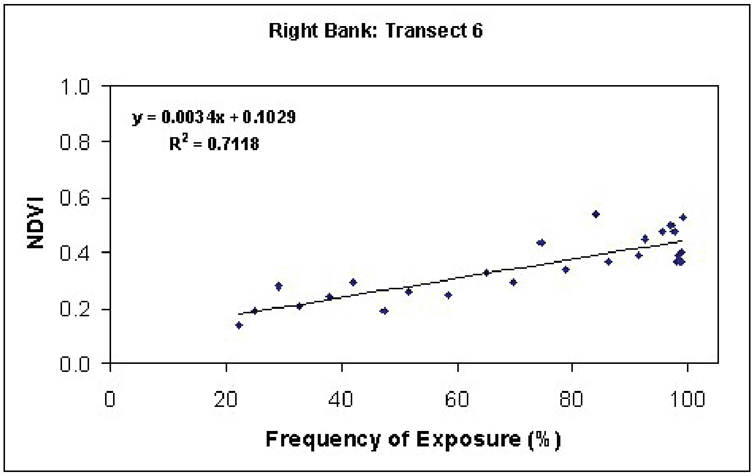


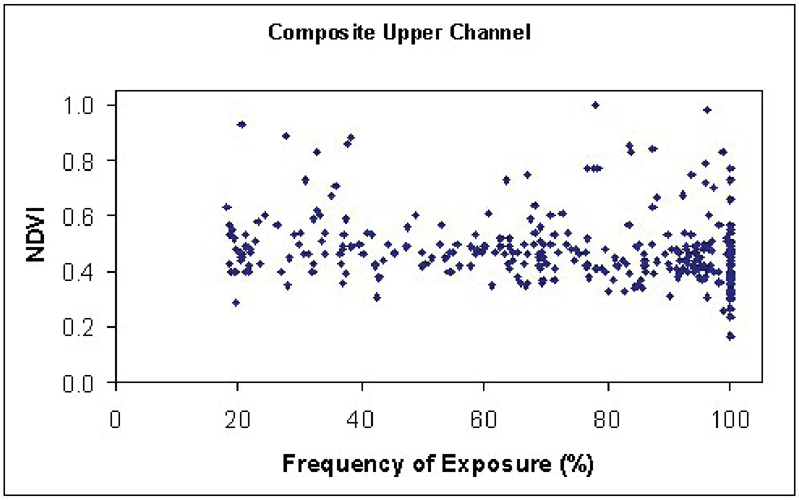
Figure 5. Results of linear regression analyses for best NDVI vs. frequency-of-ground exposure (FOGE) relationships along a number of transects in the right bank along the main channel in West Island, Twin Cays, Belize. Shown are the results along transects 4, 5, and 6 (see Fig. 2, area C, for transect location). Coefficient of variation for transects 1, 2, 3, 7, 8, and 9 ranged from 0.00 to 0.42 (See Table 1).

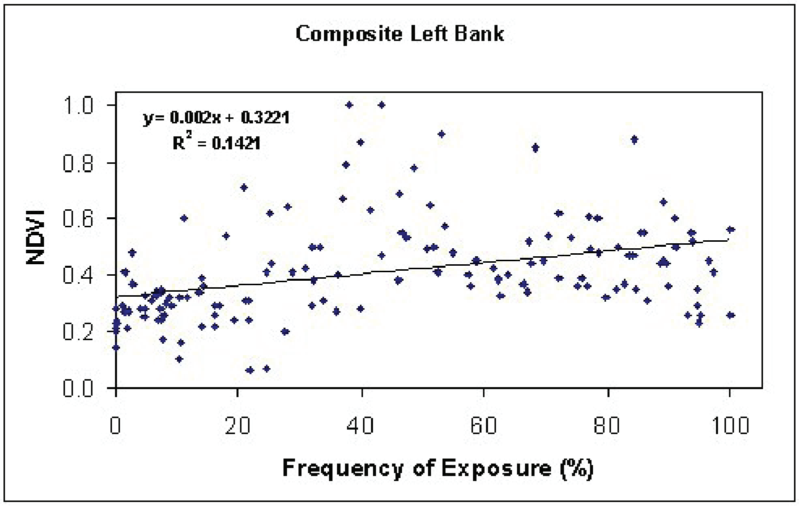
Table 1. Linear regression equations of relationships between a normalized vegetation index (NDVI) and frequency of ground exposure (FOGE) along left and right banks of the main channel in West Island in Twin Cays, Belize.

River Bank	Transect #	Slope of regression line	Y-Intercept of line	R^2
Right	1	-0.0026	0.6583	0.1632
	2	0.0000	0.4302	0.0001
	3	0.0016	0.2748	0.1776
	4	0.0022	0.2185	0.4357
	5	0.0035	0.1640	0.4938
	6	0.0034	0.1029	0.7118
	7	0.0020	0.2212	0.3776
	8	0.0028	0.2761	0.4185
	9	0.0026	0.1749	0.1718
Left	1	0.0038	0.2704	0.2442
	2	0.0026	0.2957	0.1700
	3	0.0014	0.3493	0.0570
	4	0.0017	0.3167	0.1660
	5	0.0002	0.4445	0.0022
	6	-0.0012	0.4791	0.0546
	7	0.0005	0.3892	0.0203
	8	0.0029	0.2846	0.3090

the forest, leaf area index, canopy structure, and root distribution and density. The other factor that needs consideration is the non-linearity response from plant systems due to microclimate differences (Bugmann 1997), and when under different moisture stress conditions. Moreover, intermittent, periodic and stochastic processes are noted differently according to the characteristics and interactions between types of scales (Schulze 2000). Furthermore, since annual values integrate diurnal and seasonal effects it is suspected that weekly, monthly, and seasonal effects of frequency of exposure may also be significant on NDVI but are not addressed in this paper. Variability in water quality, water surface and root temperature, and salinity are also factors of particular importance in the understanding of tidal fluxes and mangrove growth as well and should be addressed in future investigations. Furthermore, a synthetic approach integrating geospatial and simulation modeling of the mangrove system should be a priority in further long-term studies.

These results have important implications on the understanding of the mechanics of nutrient distribution and spatial heterogeneity in intertidal mangrove systems like Twin Cays. The frequency of ground exposure as a part of the hydroperiod, and NDVI as a measurable index of growth are factors that relate to, and can integrate past research including: nutrient limitations (Feller 1995); maintenance of soil fertility gradients (Feller





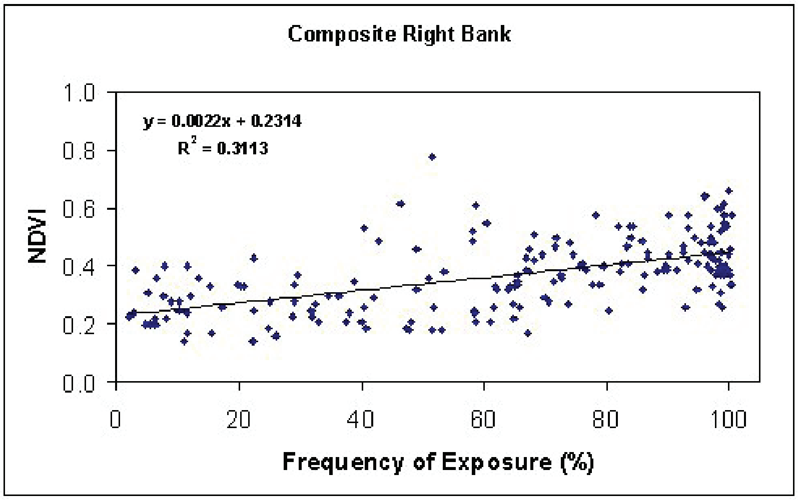


Figure 6. Results of linear regression analyses for composite data of NDVI vs. frequency-of- ground exposure (FOGE) relationships along twenty-three transects in the upper channel area, left bank, and right bank of the main channel in West Island, Twin Cays, Belize.

et al. 2003); nutrient effects on metabolic rates (Feller et al. 1999), and on growth, tissue quality, and nutrient cycling (Feller 1995; McKee 1995) in mangrove forests in the neotropics.

Further quantification of temporal patterns (i.e., weekly, monthly, seasonal) in tidal ground exposure in relation to likewise spatial distribution and temporal NDVI patterns could help determine more precisely the effects of tidal regimes on indices of growth in overwashed mangrove forests in the Caribbean.

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