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APPLICATION OF 1-M AND 4-M RESOLUTION SATELLITE DATA TO ECOLOGICAL STUDIES OF TROPICAL RAIN FORESTS

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Abstract. Understanding the current status of the world's tropical rain forests (TRF) can be greatly advanced by global coverage of remotely sensed data at the scale of individual tree crowns. In 1999 the IKONOS satellite began offering worldwide 1-m panchromatic and 4-m multispectral data. Here we show that these data can be used to address diverse aspects of forest ecology and land-use classification in the tropics.

Using crowns of emergent trees as control points, we georeferenced a 600-ha subset of IKONOS 1-m and 4-m data from an August 2000 image of the La Selva Biological Station, Costa Rica (root mean square error = 4.3 m). Crown area measured on the image was highly correlated with crown area for the same tree measured from the ground. Using a 1988 aerial photograph as a baseline, all trees >1 m diameter in a long-term study that died over the ensuing 12-year period, and that could be located in the photograph, were detected as missing in the IKONOS image ($N = 7$). Crown growth for large trees visible on both images averaged 12 m^2/yr ($N = 16$). We thus demonstrate that IKONOS imagery can provide data on four variables necessary for doing demographic research: tree size, location, mortality, and growth.

Stand basal area, estimated aboveground biomass, and percentage of the canopy >15 m tall for 18 0.5-ha permanent forest inventory plots in old growth were all highly significantly correlated with different indices derived from the IKONOS data.

We used summary statistics from the original IKONOS data as well as derived indices to characterize nine areas with well-documented land-use histories. Secondary forests were clearly separable from the other sites. One of the secondary forests was 40 years old, suggesting that IKONOS data can be used to detect significantly older secondary forest than is possible with coarser resolution satellite data. The selectively logged forest was distinguishable by measuring the size of the largest crowns on the 1-m image. This suggests a range of applications for detecting and quantifying biomass degradation due to selective logging and edge effects.

Satellite data at 1-m and 4-m resolution make possible a truly global approach to fine spatial resolution remote-sensing studies of TRF ecology and land use.

Key words: Costa Rica; fine spatial resolution data; forest biomass; high-resolution satellite data; IKONOS; QuickBird; remote sensing; selective logging; tropical land use; tropical rain forest; tropical secondary forests.

Introduction

Tropical rain forests (TRF) play important roles in global nutrient cycles and net primary productivity, and they also contain a significant proportion of all terrestrial biodiversity. There are two broadly defined types of issues concerning these forests for which better research tools are urgently required. One class of issues can generally be termed ''ecological.'' Here the key questions are rates and direction of change of tropical forests in terms of stand turnover, net primary productivity (NPP), biomass, nutrient stocks, and biodiversity. In many ways these are questions about tree demography. What are the historical and current rates of tree growth, recruitment, and mortality? What are the factors affecting these processes? Given increasing global temperature and CO_2 concentrations, a reasonable expectation is that significant changes are underway in all of these processes. Additional factors that are leading to major changes in some TRF areas are massive regional defaunation (Redford 1992, Peres and Zimmerman 2001), forest fragmentation effects (Laurance et al. 1997), and local climate change due to deforestation (Lawton et al. 2001).

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A second class of TRF issues concerns land use. These are not basic science questions, but rather are related to natural resource management. Fundamental issues include the rates of selective logging, deforestation, secondary forest regrowth, reforestation via tree plantations, and the resulting extent and configuration of forest cover of different types.

This distinction of TRF issues is fairly arbitrary, and the issues and processes of interest may overlap, such as changes in old-growth forest structure and function as a result of regional deforestation. However, it is generally true that the ecological questions in TRF have been addressed by terrestrial ecologists, whereas as land-use questions have been dealt with primarily by geographers and remote-sensing scientists. This is partially due to the research tools available. TRF ecologists frequently use sparsely sampled, fine-scale forest inventory plot data over decadal time scales, whereas geographers and remote-sensing scientists address land-use questions primarily using intensively sampled, coarse-scale remotely sensed data.

Forest inventory plots that can provide data for assessing the current and future dynamics of the world's tropical forests are few and sparsely distributed in space. For example, a pioneering meta-analysis of TRF dynamics was based on only 25 sites with a median plot size of 1 ha (Phillips et al. 1994). Because the few existing plots are rarely sited in a statistically based and fully documented design, biases due to nonrandom plot locations are a significant concern (Brown and Lugo 1992). For example, in one study a subjectively located plot was shown to overestimate landscape-scale forest basal area by >100%, (Clark and Clark 2000*a*). In addition, the establishment and maintenance of TRF inventory plots is constrained by problems of access: physical inaccessibility of many areas; socioeconomic inaccessibility due to factors such as epidemic disease and war; and political inaccessibility that can arise from national research policies of tropical nations.

The existing plot network also poorly samples very large trees (in TRF, usually arbitrarily defined as ≥60 or ≥70 cm diameter above buttresses). Very large trees, although few in number, are important components of forest biomass. For example, in one Neotropical lowland forest, trees >70 cm in diameter were <1% of all stems but contributed >14% of the estimated aboveground biomass (Clark and Clark 2000*a*). Because extremely large plots are required to study the demography and ecology of very large trees, the demographics of this structural guild remain poorly known.

Remote sensing provides a way to increase the size of areas sampled as well as to improve the statistical design of sampling. Aerial photography, for example, can be used over small landscapes to measure many aspects of TRF canopy tree ecology, including species identity, mortality, survivorship, and crown growth (Myers 1982, Herwitz et al. 2000, Trichon 2001). However, for cost and logistical reasons, it is unlikely to be a practical tool for obtaining complete coverage of representative TRF areas. To address ecological questions at larger scales, remotely sensed data with global coverage are needed, at a resolution fine enough to detect individual tree location, survivorship, and growth (Gougeon and Leckie 2003).

For addressing land use and some vegetation structural questions, a wide variety of space-borne and airborne sensors have been used in the tropics (Brondizio et al. 1996, Dimyati et al. 1996, Asner 2000, Peralta and Mather 2000, Lannom et al. 2001, Read and Lam 2002) and elsewhere (Green et al. 1994, Chen and Cihlar 1996, Fassnacht et al. 1997, Seixas 2000). There is usually an inverse relationship between spatial ground resolution resolved by the sensor and the extent covered by the imagery (Lillesand and Kiefer 2000, Key et al. 2001). There are two land-use classes that are of considerable ecological and practical interest and that have traditionally been difficult to map from satellite data: older secondary forests (forests regenerating from complete removal of forest cover; cf. Corlett 1994), and logged forest where there has been selective removal of commercially valuable trees (see e.g., Palubinskas et al. 1995, Steininger 1996, 2000, Stone and Lefebvre 1998, Asner et al. 2002*a*). Space-borne sensors that are commonly used for ecological studies, such as the Landsat Thematic Mapper sensors with spatial resolution of 30 m, are sensitive to forest structure differences of young secondary vegetation, but cannot help distinguish older second growth or selectively logged forest without extensive fieldwork or a priori knowledge of the study area (Moran et al. 1994, Steininger 2000, Drake 2001).

Until recently, the majority of remotely sensed, fine spatial resolution (≤ about 5 m) data were derived from airborne sensors. These sensors (e.g., high-resolution aerial photographs and other multispectral sensors) have been found to be useful for many forestry and ecological applications, and will continue to be important for site-specific studies (Caylor 2000, Green 2000). Airborne sensor data have been used for studies involving mapping of vegetation and land cover (Bowers et al. 1995, Schlesinger and Gramenopoulos 1996, Treitz and Howarth 2000, Read et al. 2001, Shugart et al. 2001), measures of vegetation canopy structure (McIntyre et al. 1990, Herwitz et al. 1998, Preston et al. 1999), identification of tree species and measures of tree densities (Vooren and Offermans 1985, Leckie and Gougeon 1999, Preston et al. 1999, Key et al. 2001), and biophysical measures of forest parameters (St.-Onge and Cavayas 1997, Fernandes et al. 2002).

Many studies using fine spatial resolution sensor data have incorporated texture or other forms of spatial measures to extract more information from the data. This is because as spatial resolution increases, ground objects tend to be represented by several pixels, and thus the spatial characteristics of imagery become increasingly important with respect to spectral information

(St.-Onge and Cavayas 1997). Texture measures have been particularly useful in tropical, temperate, and boreal systems for describing land cover and vegetation based on structure, age, biomass and other biophysical characteristics (e.g., Cohen et al. 1990, St.-Onge and Cavayas 1997, Shugart et al. 2000, Treitz and Howarth 2000, Franklin et al. 2001, Hudak and Wessman 2001, Read 2003).

The launches of the commercial IKONOS and QuickBird satellites in 1999 and 2001, respectively (see the Digital Globe and the Space Imaging web pages),[7,8] made possible the acquisition of fine spatial resolution (submeter panchromatic to 4-m multispectral) data on a by-demand basis. Studies using IKONOS data have demonstrated that these data probably have applications similar to those of fine spatial resolution airborne imagery. Hurtt et al. (*in press*) reviewed current applications of IKONOS imagery in Amazonian research, which include studies of land cover, forest structural characteristics, detection and quantification of logging activities, fine-scale heterogeneity in vegetation, biophysical and biochemical changes in vegetation, and mapping of agriculture and agroforestry. The ability of these sensors to resolve single tree crowns (Read et al. 2003) and to enable measurements of crown sizes (Asner et al. 2002*b*) could make it possible to detect older secondary forests, with larger tree crowns than those in younger forest, as well as logged areas, which may have fewer large crowns than unlogged old growth.

In this paper, we report initial results from research applying 1-m panchromatic and 4-m multispectral IKONOS data to several of the issues in forest ecological research just described. This research was carried out at the La Selva Biological Station in Costa Rica, where the breadth and detail of existing georeferenced data on land-use history and structure and function of old growth and secondary forest are currently unique for a TRF site. We used these detailed ground data to evaluate the potential of the IKONOS data for landscape-scale (e.g., 10^2–10^4 ha) studies of tropical tree growth and death rates, and for studies of old-growth tropical forest structure and forest dynamics (e.g., biomass, texture, gap extent). We also used IKONOS data to characterize selectively logged areas and secondary forests of differing ages. We show that 1-m and 4-m resolution space-borne sensor data hold great promise for addressing many questions related to the structure, function, and distribution of tropical forests.

Methods

Study area.—The study area was the La Selva Biological Station, located in the Atlantic lowlands of Costa Rica at ~35–150 m elevation. La Selva is classified as Tropical Wet Forest in the Holdridge Life Zone system (Hartshorn and Hammel 1994). This evergreen forest has an average annual rainfall of ~4000 mm and a mean temperature of 26°C (Sanford et al. 1994). We used field data from old-growth forest, selectively logged forest, and secondary forests, as we will describe (Figs. 1 and 2).

Satellite data.—We used IKONOS satellite (Space Imaging processing level: standard geometrically projected) multispectral (4-m pixels) and panchromatic (1-m pixels) data for a 53 km^2 area of mixed land-use history at the La Selva Biological Station. The panchromatic data contain one coarse spectral band of quantized radiance measured between 0.45 and 0.90 μm. The relatively finer spectral resolution multispectral data consisted of four bands: blue (0.45–0.52 μm), green (0.51–0.60 μm), red (0.63–0.70 μm), and near-infrared (0.76–0.85 (bands 1–4, respectively). The data were acquired on 16 August 2000 and were georectified using Ground Positioning Satellite (GPS) data and previously georeferenced points (n = 68), nearest neighbor resampling, and the WGS-84 geoid (a reference systems for GPS positioning). This transformation was used to planimetrically adjust the original UTM-projected IKONOS product to measured ground reference points (also in UTM). The original IKONOS image geolocation error was ~50 m. The overall root mean square error (RMSE) of this rectification was 3.4 m, but the error was not uniformly spread across the image due to limited possibilities for accurate control points in the roadless old-growth area (which also contains the most topographic variation in the scene).

For studies on tree growth and death rates and plot-based studies of old growth, we used a subset of the image that covered ~600 ha; this smaller image was rectified as we will describe. Because we were working at the scale of individual tree crowns, we required a high degree of geolocational accuracy in the IKONOS imagery. This was difficult to obtain in our old-growth study area, which is roadless and has no human structures to serve as landmarks. In addition, the old growth is relatively tall evergreen TRF, with few large gaps that could be used as a reference. Because our previous efforts to use GPS in this environment were problematic, we decided to georeference the image using the positions of emergent tree crowns that were distinctive on the IKONOS image (cf. Read et al. 2003), and whose locations we could survey into La Selva's grid system. This grid system, based on a 50 × 100 m spacing with permanent monuments, was installed using optical leveling techniques and is planimetrically accurate to several decimeters (Hofton et al. 2002). Our control-point trees were selected from the IKONOS image to be particularly distinctive in relation to local canopy topography, and to be <25 m from a grid point to minimize surveying errors. In the field, triangulation with other distinctive crowns as well as with canopy gaps was used to ensure that the correct tree had been located.

[7] URL: ⟨www.digitalglobe.com⟩
[8] URL: ⟨www.spaceimaging.com⟩

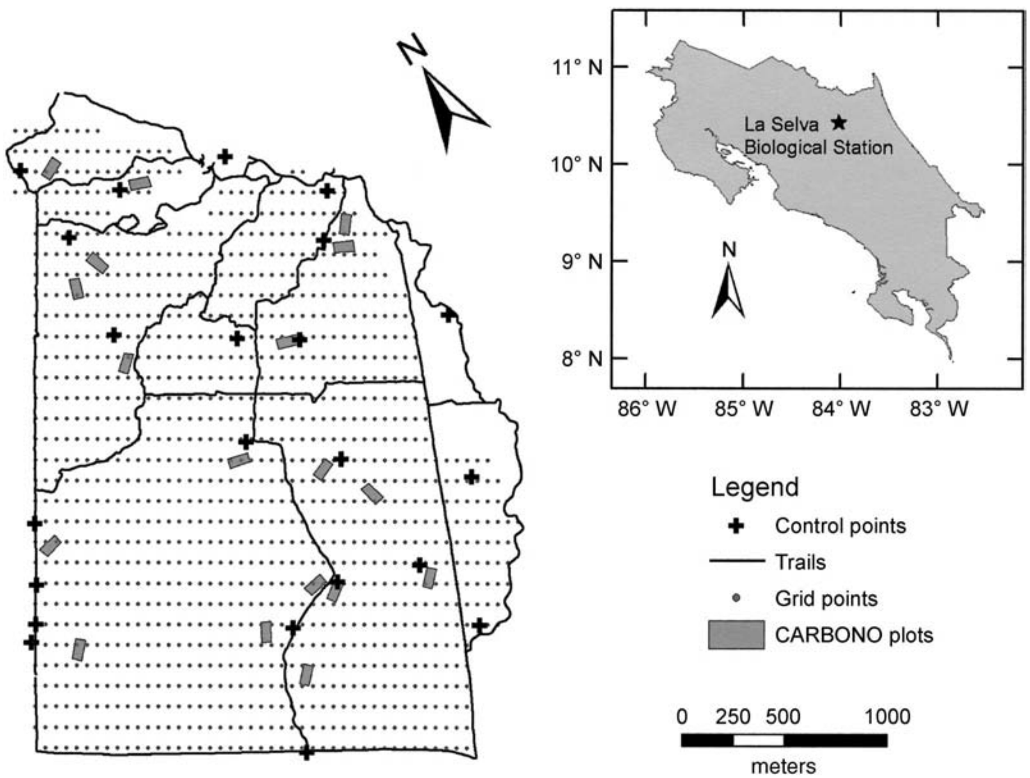

FIG. 1. The core old-growth study area at the La Selva Biological Station, Costa Rica. Gray rectangles are the 18 0.5-ha CARBONO forest inventory plots, black crosses are the 22 control points used for the georectification of the IKONOS image of this area, gray dots are monument locations in the 50 × 100-m station grid system, and black lines indicate trails.

If there was any doubt about the correct location of a tree (and there were many such cases), we did not use that individual. We are confident that all of our control points were correctly located, given that RMSE of the final rectification was 4.3 m. Additional evidence supporting this point will be given.

Ground data.—We used several existing data sets in our analyses. One consisted of trees in a long-term demographic study of ~3400 individuals of 10 species (the TREES project; Clark and Clark 1992, Clark and Clark 2000*b*). The study is based on annual evaluation of growth, survival, stem condition, and crown illumination index. All individuals are georeferenced to the La Selva grid system; they are distributed over ~330 ha of old-growth forest. Here we used data on stem size and location, survivorship, and crown illumination index. To evaluate the detection of mortality, we used mortality and geolocation data for all 17 trees >1 m diameter that were known to have died between 1988 (the date of an aerial photograph to be described) and the 2000 overflight.

A second data set comes from an ongoing study of carbon flux and storage (the CARBONO Project). A network of 18 0.5-ha plots was established using a stratified random design to insure nonbiased plot location among three edaphic categories: flat inceptisol sites, flat ultisol sites, and steep ultisol sites (Clark and Clark 2000*a*). Plot corners were georeferenced to La Selva grid coordinates. In each plot, all stems ≥10 cm diameter (at breast height or above buttresses) have been mapped and identified, and growth, survival, and recruitment of all stems are measured annually (September–October). Estimated aboveground biomass (EAGB) of each stem is calculated using Brown's (1997) tropical wet forest equation. Here we use data on plot basal area and EAGB from the September–October 2000 census to compare with various statistics derived from IKONOS data.

Canopy topography is also mapped annually in all 18 plots. At every 5-m grid intersection in each plot (N = 231 points), a clinometer is used to identify the highest vegetation 90° above the observer. The height to that top vegetation is measured with a 15-m measuring rod; heights >15 m are treated as one class. We use measurements made during June–August 2000; thus, these ground data were mostly taken within 8 weeks of the IKONOS overflight. Here we use the variable ''percentage of high canopy,'' defined as the percentage of the 231 points in each plot at which the highest vegetation reached >15 m height.

Crown size and growth.—To assess the relationship between ground-based measures of tree crown size and those from IKONOS data, we calculated an index of crown area for 30 trees whose location we could es-

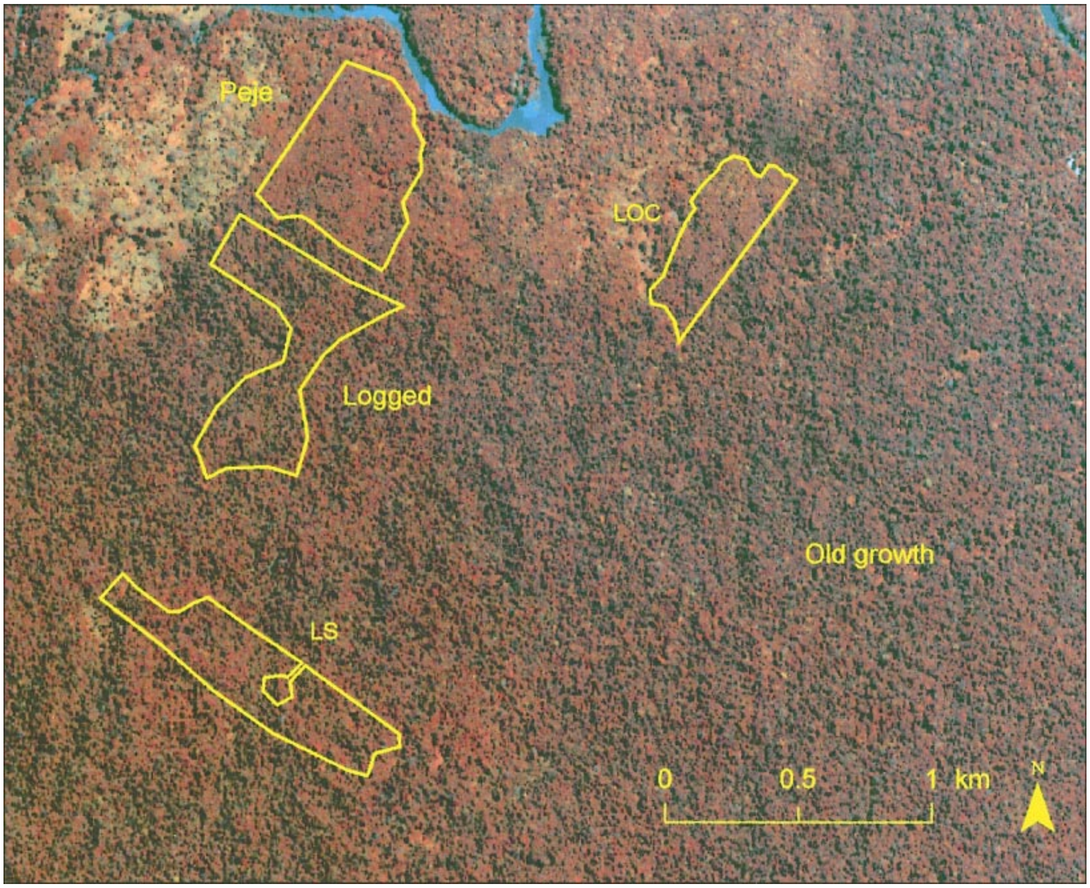

FIG. 2. Some of the areas studied for land-use detection at the La Selva Biological Station, Costa Rica. The image is from 4-m resolution multispectral IKONOS data, bands 4:2:1. Site names and characteristics are listed in Table 1, except for old growth. Secondary forest areas are lighter red and have smoother canopies. Note that the area selectively logged prior to 1982 (''Logged'') is not visually distinct from the old-growth area at this scale.

tablish unambiguously in the field. From the ground, we measured the longest canopy axis of vertically exposed crown, as well as the length of the longest crown axis perpendicular to this axis. Crown Area Index (CAI) was defined as the area of the four-sided polygon formed by joining the end points of these axes. We also calculated the same index on the 1-m IKONOS image by manually digitizing the axes over study tree crowns, using the image analysis program ERDAS Imagine 8.4 (ERDAS 1999).

To assess the potential of IKONOS data for studying recruitment into size classes visible on the image, we measured crown growth for a sample of canopy-level and emergent trees over a 12.5-year period. Crown edges were manually digitized and crown areas were derived from a 1-m colorized image transformation derived from merging the 1-m panchromatic and 4-m multispectral IKONOS data (August 2000) using bands 1, 2, and 3. Colorizing was achieved using the Resolution Merge function in ERDAS Imagine image processing software (ERDAS 1999), which uses a forward–reverse principle components transform (Chavez et al. 1991). The area for these same crowns was also manually digitized from a February 1988 color aerial photographic print. The spatial resolution of the original color negative is unknown. The print was scanned at 300 dots per inch (dpi), stored at 2-m resolution, and georeferenced in UTM to a RMSE of 16.2 m (Organization for Tropical Studies, *unpublished data*). We selected 20 individual trees that were unambiguously identifiable in both images. The geolocation of these 20 crowns was assessed on both images by measuring distances to two or more additional distinctive crowns; acceptable geolocation agreement was considered to be ≤5 m difference among crowns over distances of up to 300 m.

Land-use detection.—To evaluate the applicability of IKONOS data to detecting land-use history via differences in forest structure, we made use of La Selva's GIS land-use history coverage, as well as aerial photographs from 1966, 1971, 1976, 1983, and 1988 (OTS, *unpublished data*). We selected three sites of secondary forest (cf. Corlett 1994) of differing ages, one partially deforested area where many remnant trees were left,

TABLE 1. Study sites at La Selva, Costa Rica, for analysis of land-use history detection.

Name	Description	Area (ha)
LOC	secondary forest, 18 yr old	15.6
Peje	secondary forest, 21 yr old	28.5
SHO	secondary forest, 40 yr old	5.7
LS	partially deforested regenerated pasture, 21 yr old	25.8
Logged	selectively logged at unknown intensity prior to 1982	29.1
CES	old growth, old alluvial soil	20.1
CCL	old growth, old alluvial soil	7.8
SHA	old growth, residual soil	15.6
CC	old growth, residual soil	22.7

Notes: Site names refer to adjacent La Selva trails. Soil concepts follow Clark et al. (1998). Age of secondary forests refers to approximate time from pasture abandonment until year 2000, as determined from aerial photographs (Organization for Tropical Studies, *unpublished data*). Secondary forests are areas where the original forest cover was essentially completely removed and where subsequent forests developed almost entirely from immigration by off-site propagules (following Corlett 1994).

one area selectively logged prior to 1982, and four areas of old-growth forest (Table 1, Fig. 2). The four old-growth forest areas were selected to be of comparable size and topography as the other sites, and none of the areas is crossed by major streams. For these analyses, we used the quantized radiance 1-m panchromatic and 4-m multispectral IKONOS data, a Normalized Difference Vegetation Index (NDVI) image derived from a contrast of the red and infrared bands of the quantized radiance multispectral data ((Band 4 − Band 3) ÷ (Band 4 + Band 3)), as well as derived texture images. ''Texture'' was calculated as the standard deviation of the digital numbers in a $n \times n$ pixel moving window centered on a target pixel, where n was 3, 5, or 7 pixels. Areas with high texture values represent areas with relatively more local spectral variation in the IKONOS data than lower texture areas. For both original and texture data, we derived descriptive statistics of the data for each of the nine areas in Table 1 (maximum, minimum, mean, range, and standard deviation). We then used Principal Components Analysis (PCA) to reduce each of the original and 3×3, 5×5, and 7×7 texture analysis data sets from 20 (multispectral: five statistics × four bands) or five (panchromatic or NDVI statistics) variables to two principal component scores. We also did all of these analyses using the IKONOS data from each of the 18 0.5-ha old-growth plots.

RESULTS

Application of IKONOS data to demographic studies of large trees

For tree demographic studies, there are minimally four variables that must be measurable: individual tree location and size, and death and recruitment events (entry into a minimal size class). The value of a demographic study is greatly increased if a measure of individual growth is also obtainable. In these sections, we demonstrate that IKONOS data are sufficient to establish individual tree locations of large trees, to detect tree mortality, and to measure crown size and growth. Thus, demographic studies based on data derived from satellite images are now feasible for the ecologically important subset of large canopy trees in tropical rain forest.

Identification of individual crowns and image rectification.—The RMSE of the final IKONOS image rectification was 4.3 m, which is considerably less than half of the crown diameter of a large canopy tree in this forest. As a further assessment of the accuracy of the rectification, we selected 15 canopy or emergent trees from the TREES study. The centers of the stems of these trees were measured in the field relative to the La Selva grid (LSG) coordinate system. Individuals were selected to span the study area and to have roughly circular crowns that were distinct on the IKONOS image. Mean distance from the visually estimated crown center point on the IKONOS image (LSG coordinate system) to the mapped stem center location on the TREES data layer was 11.5 ± 3.6 m (mean ± 1 SD) and 5.3 ± 2.3 m for the original and final rectifications, respectively (cf. Fig. 3). This analysis, plus the RMSE of the final rectification, as well as the consistent relation between ground-based and image-derived size metrics, are three independent confirmations that we could reliably identify individual crowns on the image and subsequently in the field.

Crown size and growth.—The trees selected for this analysis had Crown Area Indices (CAIs) on the IKONOS image of ~200–700 m^2. Ground-based and image-derived measures of CAI were highly correlated:

$$\text{CAI}_{(\text{ground})} = 0.62\ \text{CAI}_{(\text{image})} + 80.6\ \text{m}^2$$

($N = 30$, $r^2 = 0.64$, $P < 0.001$; data not shown). $\text{CAI}_{(\text{ground})}$ was also correlated with the crown area derived by digitizing crown edges on the image:

$$\text{digitized crown area} = 1.37\ (\text{CAI}_{(\text{ground})}) + 56.2\ \text{m}^2$$

($N = 27$, $r^2 = 0.52$, $P < 0005$). This correlation was somewhat lower than that between the CAI polygons measured on the ground and on the image, probably because it was easier to select four pixels to determine two axes than to exactly follow crown edges in the

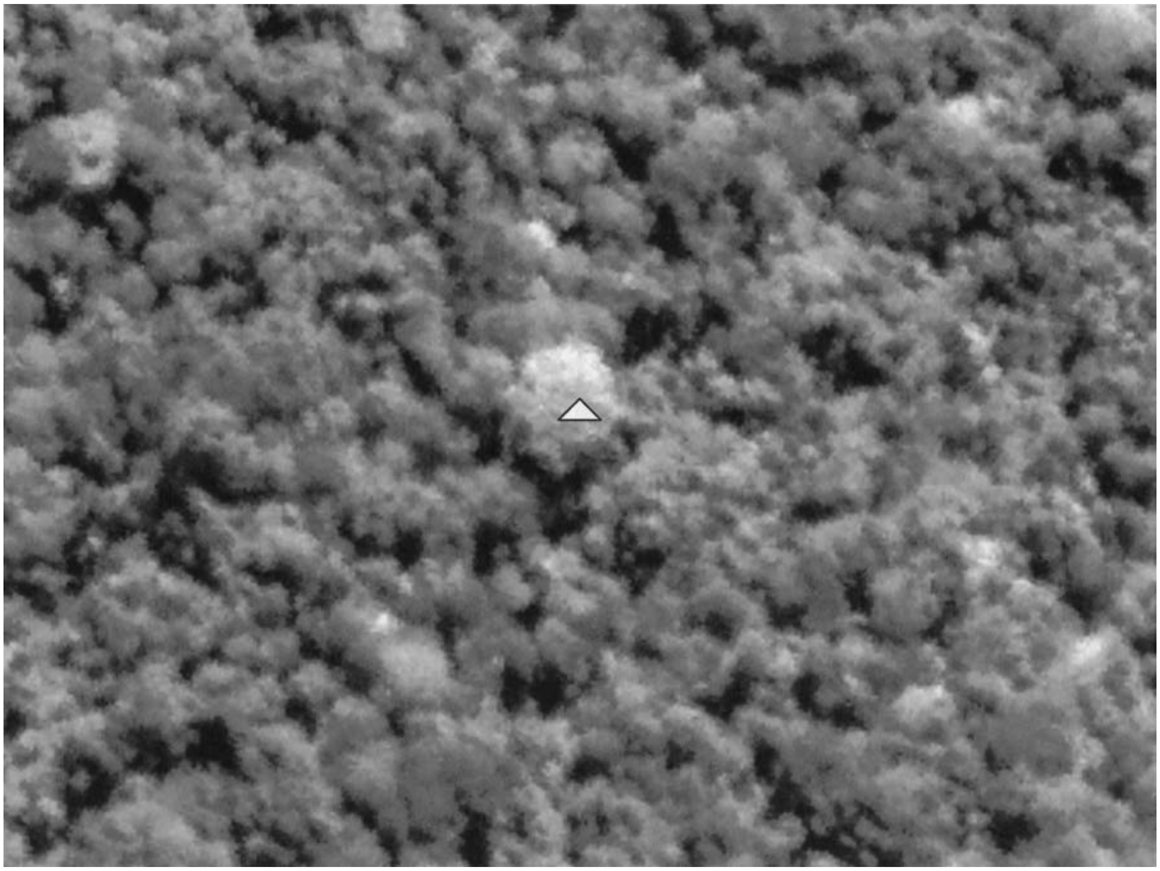

FIG. 3. An emergent *Hymenolobium mesoamericanum* Lima (Papilionaceae), typical of the emergent trees used for geo-rectification control points and crown morphology studies. Notice the absence of nearby emergent crowns that could cause problems identifying this individual from the ground. The triangle indicates the location of this individual in an existing GIS coverage of trees under demographic study. The image is from 1-m resolution panchromatic IKONOS data.

image. Indeed, there were three individuals for which entire crown edges were too indistinct to digitize. Not surprisingly, the digitized crown area was larger than the CAI polygon area because crowns tend toward circularity. Overall, these results indicate that it is possible to derive crown size measurements from satellite data that are consistently correlated with similar measurements taken in the field, although the relationship may be confounded by unexposed parts of the crown and shadows in the image, or by obscured sections of the crown as seen from the ground.

The 20 crowns selected for growth analysis averaged 570 m^2 per crown in the 1988 photograph and 669 m^2 in the 2000 image. For the 80% of crowns that increased in area (cf. Fig. 4), the mean increase was 12 m^2/yr over the 12.5-yr interval. Crowns that decreased in area (20% of individuals) averaged a loss of 8.3 m^2/yr. Individuals that lost crown area were almost twice as large in 1988 as the trees that increased crown area ($\bar{X}$ = 885 m^2 vs. 491 m^2 in 1988; Wilcoxon rank sum test, $P < 0.05$). This is consistent with the ontogeny of very large tropical trees, which frequently lose crown area for an extended period before dying and falling to the ground (Oldman 1983; D. B. Clark, *unpublished data*).

Individual tree mortality.—Because we had only one image from this new satellite, we could not make an image-to-image test using only IKONOS data to detect individual tree mortality. Instead, we used the digitized 1988 color photograph as the baseline. In the digitized photo, we looked for the 17 individuals in the TREES project that had initial diameters >1 m and that died after 1988 but before the 2000 IKONOS overflight. We were unable to unambiguously locate 10 of these crowns on the 1988 photograph, but we could identify the seven remaining individuals based on triangulation to other large trees and using the TREES maps. For these seven trees that were known to have died and could be located on the 1988 photograph, all were unambiguously missing on the IKONOS image (Fig. 5), using the same criteria of triangulation from distinctive crowns on that image.

Old-growth stand structure, canopy structure, and their relation to IKONOS imagery

We used ground data to characterize the physical structure of plots in old-growth forest, and then ex-

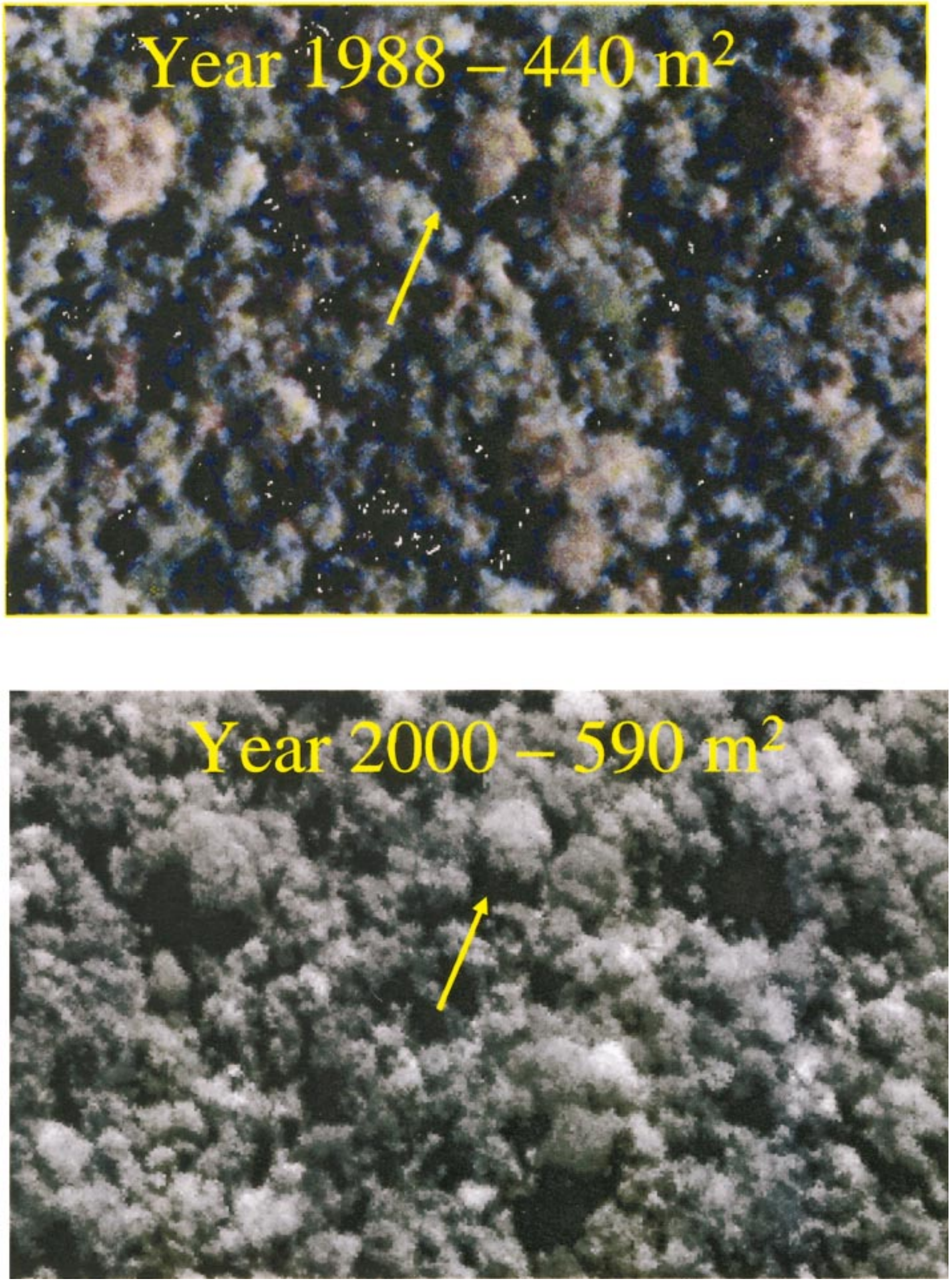

FIG. 4. Growth of a canopy tree crown over 12.5 years at the La Selva Biological Station, Costa Rica. The image from 1988 is a color aerial photograph; the year 2000 image is 1-m resolution panchromatic IKONOS data. Geolocation was verified using the relative position of other emergent trees in both images; note the three large trees forming the vertices of an approximate equilateral triangle pointing down, with the target tree in the middle of the axis approximately parallel to the *x*-axis. This tree crown grew 150 m^2, which was very close to the median growth for all crowns that increased in area.

amined the relationship between the physical structure of the vegetation in the plots and various aspects of the IKONOS data. We show here that the satellite data are correlated to a surprising degree with the ground data, even within the limited range of structural variation present in old-growth tropical rain forest on the upland soils at La Selva.

Old-growth structural characteristics.—Basal area in the 18 old-growth reference plots varied >60%, from 17.4 to 28.4 m^2/ha ($\bar{X}$ = 22.7 m^2/ha), whereas estimated aboveground biomass (EAGB) of stems ≥10 cm diameter varied from 108 to 196 Mg/ha ($\bar{X}$ = 155 Mg/ha). The percentage of plot area with canopy >15 m tall was similarly variable, ranging from 24% to 90%

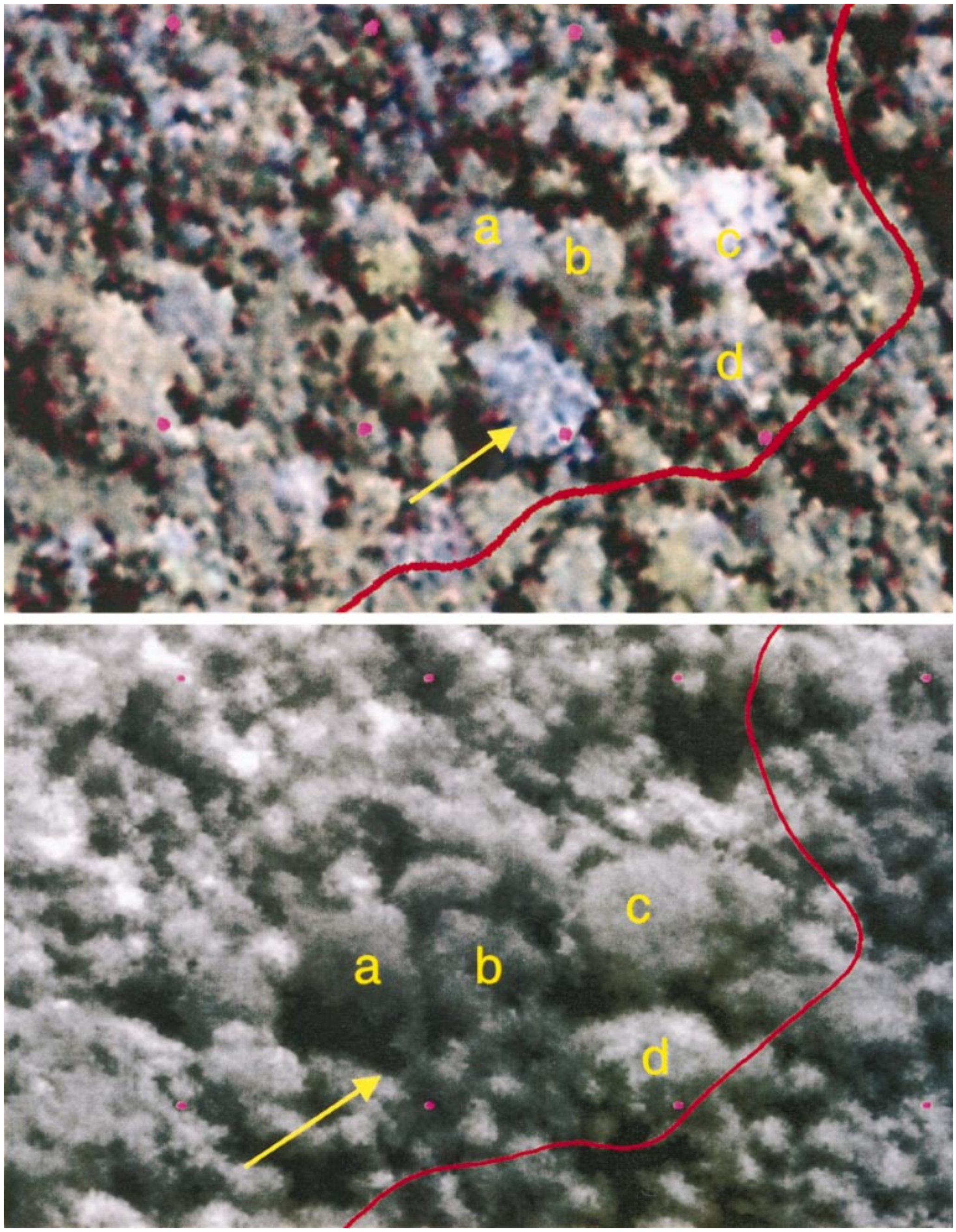

FIG. 5. Documentation of death of a canopy emergent at the La Selva Biological Station, Costa Rica. The upper image is a color aerial photograph from 1988; the lower image is IKONOS 1-m resolution panchromatic data from 2000. Notice the relative positions of crowns a–d, and the large light blue crown present in 1988 but missing in the 2000 image. This tree was under long-term observation in the TREES tree demography study. It was a 106 cm diameter *Lecythis ampla* Miers (Lecythidaceae) that died in 1990.

among the 18 plots ($\bar{X}$ = 59%). Plot basal area and EAGB were strongly correlated with the percentage of canopy >15 m tall ($r^2 = 0.779$ and 0.786, respectively, $P < 0.0001$, $N = 18$). Thus, there was substantial variance in stand basal area and biomass over this old-growth terra firme landscape at the scale of 0.5-ha units, and this variation was strongly correlated with the amount of high canopy present, a variable potentially detectable by IKONOS imagery.

Relationships between IKONOS data and forest structure.—We analyzed the relationship between descriptive statistics (maximum, minimum, mean, range, SD) of the 1-m panchromatic and of the blue, green, red, and near-infrared bands from the 4-m multispectral

TABLE 2. Pearson's correlation coefficients (r) between statistics of IKONOS 1-m resolution panchromatic data and structural variables for 18 0.5-ha plots in upland old-growth tropical rain forest, La Selva, Costa Rica.

Data†	Basal area‡	EAG biomass§	High canopy‖
Original mean			0.67[b]
3 × 3 mean		−0.61[a]	−0.67[b]
3 × 3 PCA2		−0.65[b]	−0.68[b]
5 × 5 mean		−0.59[a]	−0.66[b]
5 × 5 PCA2	−0.73[b]	−0.79[c]	−0.78[c]
7 × 7 mean			−0.64[b]

Notes: Due to the large number of correlations, only correlations with $P < 0.01$ are shown; significance levels are: [a] $P < 0.01$; [b] $P < 0.005$; [c] $P < 0.0005$. $N = 18$ plots for all correlations.

† Original, nontransformed image data; PCA2, second principal component score from original IKONOS data; 3 × 3, texture analysis (see *Methods*) of original data at 3 × 3 block size; 3 × 3 PCA2, second principal component of 3 × 3 texture data; 5 × 5 and 7 × 7, the same as 3 × 3.

‡ Measured as plot basal area (m^2/0.5 ha).

§ Estimated aboveground biomass (see *Methods*).

‖ Percentage of 231 sample points per plot with canopy heights >15 m.

TABLE 3. Pearson's correlation coefficients (r) between statistics of IKONOS 4-m resolution multispectral data and structural variables for 18 0.5-ha plots in upland old-growth tropical rain forest, La Selva, Costa Rica.

Data†	Basal area‡	EAG biomass§	High canopy‖
Original band 3 mean			0.62[a]
Original band 4 max			0.59[a]
Original band 4 mean	0.61[a]	0.61[a]	0.60[a]
3 × 3 band 2 max			−0.63[a]
3 × 3 band 2 range		0.61[a]	0.71[b]
3 × 3 PCA2		−0.64[b]	−0.71[b]
5 × 5 band 1 min	−0.69[b]	−0.70[b]	−0.62[a]
5 × 5 band 4 min	−0.63[a]	−0.65[b]	
5 × 5 PCA2	0.67[b]	0.71[b]	0.69[b]
7 × 7 band 4 min	−0.60[a]	−0.66[b]	−0.63[b]

Notes: Bands 1–4 were analyzed separately for all analyses except the PCA. Due to the large number of correlations, only correlations with $P < 0.01$ are shown; significance levels are: [a] $P < 0.01$; [b] $P < 0.005$. $N = 18$ plots for all correlations.

† Original, nontransformed data; PCA2, second principal component scores from original statistics (using four bands × five statistics = 20 variables); 3 × 3, texture analysis (see *Methods*) of original data at 3 × 3 block size; 3 × 3 PCA2, second principal component of 3 × 3 texture data; 5 × 5 and 7 × 7, the same as 3 × 3; max, maximum; min, minimum.

‡ Plot basal area (m^2/0.5 ha).

§ Estimated aboveground biomass (see *Methods*).

‖ Percentage of 231 sample points per plot with canopy heights >15 m.

data (bands 1–4, respectively), and plot basal area, estimated aboveground biomass (EAGB), and percentage of canopy >15 m tall (the percentage of 231 sample points per plot with canopy heights >15 m). We did the same analyses with 3 × 3, 5 × 5, and 7 × 7 texture images (see *Methods*), as well as with the first two principal components of the original image data and of the texture image statistics. We did similar analyses with a Normalized Difference Vegetation Index image derived from the multispectral data, but found no significant relations and do not present those results.

The panchromatic data were more frequently correlated with measures of forest structure than were the multispectral data (Tables 2 and 3). Of the 84 possible correlations between band statistics and forest structure variables for the panchromatic data, 11 (13%) were significant at $P \leq 0.01$, but there were only 21/264 significant correlations with the multispectral data (8%). The structural variable most frequently correlated with some aspect of the IKONOS data was the percentage of high canopy per plot. The strongest correlation was between EAGB and the second principal component from the 5 × 5 panchromatic texture data (Fig. 6). This single texture variable accounted for >62% of the variance in EAGB among these old-growth plots, and the relationship was reasonably linear across the range of biomass (Fig. 6).

Determination of land-use history

We compared PCA statistics of the IKONOS data for the sites shown in Table 1 using the original panchromatic and multispectral data, the derived NDVI data, and 3 × 3, 5 × 5, and 7 × 7 texture images for these data. The first principal component of the NDVI 3 × 3 texture data explained the highest percentage of variance (74.8%; 92.7% including axis 2). The first PCA axis of these data separated the three true secondary forest sites (cf. Corlett 1994) from the other six sites, including the selectively logged area and the partially deforested regenerated pasture (Fig. 7).

In contrast to the true secondary forest areas, the selectively logged area was not clearly distinguishable

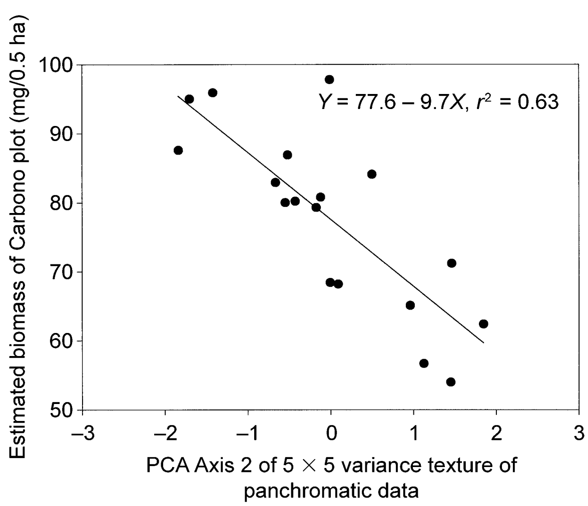

FIG. 6. Estimated aboveground biomass in 18 0.5-ha old-growth plots at the La Selva Biological Station, Costa Rica, and the second principal component axis score derived from a 5 × 5-cell variance texture analysis of 1-m resolution panchromatic IKONOS data. See *Methods* for details of texture analysis.

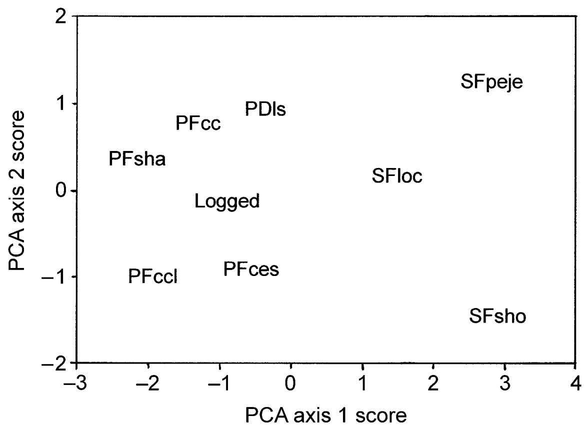

FIG. 7. The first two principal component values for nine areas of secondary forest (SF), partially deforested pasture (PD), selectively logged forest (Logged), and upland old-growth forest (PF) at the La Selva Biological Station, Costa Rica. Site codes follow Table 1. Data for the PCA were summary statistics (maximum, minimum, mean, range, and standard deviation) from a 3×3 texture image derived from an NDVI image of each area.

from the old-growth sites on the original (Fig. 2) or texture images. In the statistical analyses, the position of the logged area varied considerably, from being the most extreme value along one PCA axis to merging within the old-growth forest areas (Fig. 6). To look for direct IKONOS evidence of logging effects, we analyzed the maximum detectable crown sizes on the 1-m IKONOS image for 20 0.5-ha rectangular areas (50×100 m) from both the selectively logged area and the nearest old-growth forest in the original La Selva property, where we are confident that no logging at any intensity has occurred. Mean maximum crown diameter per 0.5-ha area was 19.6 m in old growth and 14.9 m in the selectively logged area (Wilcoxon rank sum test, $P < 0.003$). Because crown area scales with the square of the radius, this represents a >70% difference in mean crown areas of the largest trees between old growth and the area that was selectively logged ≥20 years ago. Thus, although neither superficial visual evaluation nor statistical summaries of the IKONOS data consistently distinguished selectively logged forest from old growth, it in fact was readily separable simply by the size of the largest tree crowns present, as manually interpreted from the IKONOS imagery.

DISCUSSION

Tropical tree demographic studies based on satellite data

Our results show that it is possible to use IKONOS data to geolocate individual emergent trees to subcrown accuracy, and to measure crown size, crown growth, and individual tree mortality. Thus, studies of the growth and death rates of large TRF trees based solely or principally on satellite data are now feasible. The percentage of canopy trees that it will be possible to study in this way will not be known until consecutive IKONOS or QuickBird images are available for a site, and the requisite image analyses and field verifications are done. Although many tree crowns in addition to isolated emergents are clearly visible in the panchromatic data (cf. Fig. 3), it is difficult to locate these trees on the ground with total certainty. When these canopy-level trees die, however, their absence should be detectable by examining sequential images (cf. Fig. 5). Field verification of a new treefall gap at the predicted location would validate these observations. By focusing satellite-based tree mortality studies over long-term forest inventory plots, it will be possible to determine what percentage of total canopy tree mortality is detectable via remote sensing at fine spatial resolution.

One caveat here is that we did not examine the effects of changing resolution on our measurements of growth and death. We used an aerial photograph of unknown resolution (but visually no better and perhaps lower than IKONOS; cf. Figs. 4 and 5), scanned at 300 dpi and stored at 2-m resolution, and compared this to IKONOS 1-m data. Future studies will probably compare QuickBird 0.7 m data to the IKONOS 1-m data. How these differences affect measured growth rates remains to be determined.

To rectify the IKONOS image to subcrown accuracy in a roadless area, we were aided by the presence of a 100×50-m grid. In similar work in Brazil (Read et al. 2003), we achieved similar results using GPS to map distinctive crowns along roads and logging patios. In areas with neither roads nor a grid, distinctive crowns along watercourses are useful, because GPS will usually work on open water. Successive rectifications may be necessary, using distinctive crowns bordering sites where GPS is possible, such as roads, logging clearings, large gaps, and watercourses, and working from open areas inward. As a last resort in roadless areas, single-rope techniques (ter Steege 1998) can be used to elevate GPS receivers high into the crowns of distinctive emergents.

Here we showed that crown growth rates of large canopy trees averaged ~12 m^2 per yr, which is also 12 pixels of panchromatic IKONOS data. In addition, numerous studies on tropical forest dynamics show that exponential death rates of ~2% per year for trees ≥10 cm diameter are common (Phillips et al. 1994). These two facts suggest that rates of tree growth and mortality can be measured with relatively short intercensus intervals using fine-resolution satellite imagery. Although significant advances in studying tree growth and death rates over large spatial scales are now possible using manual digitization (see *Conclusions*), additional progress will come as automated crown identification and mensuration techniques improve (cf. St.-Onge and Cavayas 1997, Hill and Leckie 1999, Gougeon and Leckie 2003).

Fine spatial resolution satellite data for studies of forest structure and land use/land-use change

We found that the percentage of high canopy as well as plot basal area and aboveground biomass from old-growth forest inventory plots were all highly significantly correlated with some aspects of the IKONOS data. It is of particular interest that the relationship with estimated aboveground biomass (Fig. 6) was linear and nonsaturating over the range of biomass sampled here. Also, in almost all PCAs, the secondary forest sites were clearly distinguishable from old-growth forest. Both of these results contrast with most previous work with Landsat or radar data (reviewed in Drake 2001).

These relationships occurred at different spatial scales and with different spectral bands, depending on the variable and habitat analyzed. We hypothesize that the reasons for differing results are related to properties of the characteristic elements of these forests, particularly mean canopy height, mean crown size and crown size distributions, and mean gap size and gap size frequency distributions. All of these variables vary substantially across any TRF successional gradient, and also across most mesoscale old-growth landscapes. For example, the variance in percentage of high canopy found here in old growth was 24–90% at the 0.5-ha scale, and this was highly correlated with estimated aboveground biomass per plot ($r^2 = 0.786$, $N = 18$, $P < 0.001$). Such variations in forest structure would cause variations in texture and spectral data. Our research was not designed to separate these variables, and further study over a range of natural and managed habitats will be needed to isolate these effects as well as any threshold effects. Although we expect that any given IKONOS–habitat relationship will vary among habitats due to differences in crown sizes, canopy heterogeneity, and gap regimes, and also with scene lighting and atmospheric conditions, our work clearly shows the potential for using IKONOS data for improved landscape estimation of a range of old-growth and secondary forest variables.

It is intriguing that the 40-year-old secondary forest site was just as distinguishable from old growth as the younger sites (Fig. 7). If this finding is confirmed in other tropical forest landscapes, IKONOS data could be used for much more accurate assessments of older tropical secondary forest than is currently possible over large areas.

IKONOS data have previously been used to assess impacts of recent selective logging in TRF (Read et al. 2003). Our results here extend that work, showing that it is possible to detect canopy changes due to selective logging that occurred at a minimum of 20 years previously. Landscape-scale biomass degradation, due to either selective logging (Brown et al. 1994) or direct edge effects in fragmented habitats (Laurance et al. 1997), is a major issue in TRF. Satellite data at the 1–4 m scale can now be used to quantify the existence and extent of biomass degradation due to the removal or death of large canopy trees for the vast areas of tropical forest where viewing conditions allow for at least sporadic data collection.

Conclusions

Panchromatic and multispectral satellite data at ≤4 m resolution now offer the possibility of doing research that was previously only possible by ground-based studies or using airborne sensors. Studies based on fine spatial resolution satellite data will face few of the problems of access due to physical, socioeconomic, and political factors that complicate ground-based research in much of the tropics. Cloud cover, however, remains a significant factor limiting access in many regions, particularly during rainy seasons. We have shown here that satellite data at the 1–4 m spatial scale can be applied to a variety of major ecological and land-use questions in tropical forest landscapes. We believe that this scale of resolution, essentially the canopy tree crown scale, is one at which collaborations between ecologists, remote-sensing scientists, and geographers are likely to be very productive (cf. Asner et al. 2002*b*; Read et al. 2003, Hurtt et al., *in press*). These interactions will become even more fruitful as high-resolution satellite imagery is further developed. New sensors with ever-increasing resolution, both spatially and spectrally, will continue to be launched. For example, only two years after the launch of IKONOS, the QuickBird satellite is now offering 70-cm resolution panchromatic and 2.8-m multispectral data. The potential scope of ecological and land-use research in TRF using passive optical sensing will continue to increase for the foreseeable future. A truly global comparative analysis of TRF structure and function based on currently available fine spatial resolution satellite data is now possible.

Finally, tree-crown-level satellite data now make feasible the monitoring of TRF productivity and dynamics in a globally representative network of sites. Satellite-based monitoring of these sites could be thought of as an extremely cost-efficient way to rapidly extend the spatial extent and statistical power and sensitivity of ground-measured plots. Consider that the total amount of tropical rain forest that is inventoried on an annual time step is probably on the order of 100–1000 ha. At current image prices, for U.S. $150 000 per year, one person using manual digitization could annually inventory canopy emergents in an area at least 1000 times larger than the area currently censused, with considerably less investment than current supra-annual ground censuses. The location and extent of such measurements could be tailored to greatly expand the geographic representation of ground-measured TRF plots, which will continue to be the keystone upon which all global evaluations of TRF condition rest. Given the enormity and ubiquity of known and likely negative impacts of global changes on TRF productivity and biomass, such a large-scale monitoring effort using fine spatial resolution satellite data is well justified on both scientific and economic grounds.

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