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REPORT

Quantifying mortality of tropical rain forest trees using high-spatial-resolution satellite data

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Abstract

Assessment of forest responses to climate change is severely hampered by the limited information on tree death on short temporal and broad spatial scales, particularly in tropical forests. We used 1-m resolution panchromatic IKONOS and 0.7-m resolution QuickBird satellite data, acquired in 2000 and 2002, respectively, to evaluate tree death rates at the La Selva Biological Station in old-growth Tropical Wet Forest in Costa Rica, Central America. Using a calibration factor derived from ground inspection of tree deaths predicted from the images, we calculated a landscape-scale annual exponential death rate of 2.8%. This corresponds closely to data for all canopy-level trees in 18 forest inventory plots, each of 0.5 ha, for a mostly-overlapping 2-year period (2.8% per year). This study shows that high-spatial-resolution satellite data can now be used to measure old-growth tropical rain forest tree death rates, suggesting many new avenues for tropical forest ecology and global change research.

Keywords

Costa Rica, IKONOS, La Selva Biological Station, QuickBird, remote sensing, tree mortality rates, tropical rain forest.

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INTRODUCTION

The planet's biological systems are currently experiencing steadily increasing temperature and atmospheric levels of CO_2 and other greenhouse gases (Houghton *et al.* 2001; Root *et al.* 2003). The summed current and future effects of global climate change on forest systems are poorly understood, and even the directions of the expected ecological changes in many systems are controversial. A key factor for predicting and understanding forest responses to global climate change is measurement of tree mortality rates. For example, models that couple climate change with vegetation response predict increased tree death rates in tropical forests, leading to a positive feedback with CO_2-induced global warming (Jones *et al.* 2003). Global warming will cause upward shifts in forest life zones along mountain slopes (Enquist 2002), with increased tree mortality and disappearance of species at their lower temperature boundaries (Peñuelas & Boada 2003). One manifestation of massive global perturbations such as ENSO events are increased death rates over large areas of tropical forests (Condit *et al.* 1995; Nakagawa *et al.* 2000; Williamson *et al.* 2000). Forest fragmentation can lead to significant carbon loss caused by increased tree mortality along fragment borders (Laurance *et al.* 2000), which in turn is a positive forcing factor on atmospheric CO_2 levels.

Better knowledge of tree mortality responses to increasing temperature and greenhouse gases as well as changing land use patterns is of great interest in all forest systems. However, tropical rain forests (TRFs) are of special concern. TRFs contain a substantial fraction of terrestrial biodiversity (Reaka-Kudla *et al.* 1997), their soils and biomass account for a large percentage of the total world terrestrial carbon pool (Dixon *et al.* 1994), and they are estimated to account for roughly one-third of net primary productivity on land (Dixon *et al.* 1994).

The decadal-level trajectory of tree growth and mortality rates in these forests is controversial, and there is debate over the status of TRFs as carbon sources or sinks (reviewed in Clark 2003). There are several reasons for this controversy. There are few data from long-term permanent forest inventory plots in the tropics, and in some cases, methodological issues limit the use of those few data that do exist (Clark 2002). Existing forest inventory plots in old-growth TRF are few in number, limited in size, and almost always sited in a non-random fashion with little or no replication (Brown 1996; Clark & Clark 2000a; Keller *et al.* 2001). In addition, with only one exception that we are aware of (Clark *et al.* 2003a), published long-term data are at supraannual time steps, which severely limit the ability to relate annual forest response to annual climate events such as ENSO episodes.

What is needed to assess forest dynamics in this biome and its relation to global climate change is a way to measure forest growth and mortality rates over large areas of tropical forests at annual time scales (Clark *et al.* 2003b). High-spatial-resolution (≤1-m panchromatic, ≤4-m multispectral) commercial satellite data offer a potential solution to these problems. For example, 1-m resolution IKONOS (Space Imaging Corp., Thornton, CO, USA) satellite data from terra firme TRF have been used to measure tree crown sizes, to detect the effects of selective logging and to extend remote-sensing capacity to distinguish secondary forests from old growth; these data have also been shown to be correlated with key forest structural parameters such as plot biomass and total gap area (Asner *et al.* 2002; Clark *et al.* 2003b; Hurtt *et al.* 2003; Read 2003; Read *et al.* 2003). These studies have also suggested (Read *et al.* 2003) that it should be feasible to use high-spatial-resolution satellite data to measure TRF tree growth and survival.

In this paper, we show that it is now possible to measure TRF tree mortality rates using such high-spatial-resolution satellite data. Forest-level tree mortality is a key ecosystem variable, because it integrates the physiological and demographic responses of all trees in a given forest, and it directly links to stand biomass and overall structure. We suggest that the ability to measure tree mortality over large regions of TRF using satellite data will have extensive applications for tropical forest research, and that high spatial resolution satellite data will be a key tool for assessing the sensitivity of this biome to climate and land-use change.

METHODS

Study site

The study site was conducted at the La Selva Biological Station of the Organization for Tropical Studies (O.T.S.) in the Atlantic lowlands of Costa Rica (longitude 84°00′W, latitude 10°26′N, Fig. 1). We worked in a 600-ha section of old-growth forest that is classified in the Holdridge Life Zone system as Tropical Wet Forest (Hartshorn & Hammel 1994). La Selva's mean annual rainfall and temperature are *c.* 4300 mm and 26°, respectively (Organization for Tropical

Figure 1 View of a part of the study area for this research, old-growth Tropical Wet Forest at the La Selva Biological Station, Costa Rica. Note the uneven canopy with scattered emergents and numerous canopy gaps, and generally rolling terrain. Photo by Matthew L. Clark.

Studies: http://www.ots.duke.edu/en/laselva/metereological.shtml, Unpublished data). A detailed site description is given in McDade *et al.* 1994.

Data and image pre-processing

We used images from two commercial satellites. The IKONOS panchromatic image had 1.0 m nominal spatial resolution and was taken on 16 August 2000. The collection azimuth was 203.7° at an elevation of 59.9°, and the sun azimuth was 80.2° at an elevation of 65.1°. The QuickBird (DigitalGlobe, Longmont, CO, USA) panchromatic image had 0.7-m nominal spatial resolution and was acquired on 6 June 2002 (Fig. 2). The satellite azimuth was 155.5° at an elevation of 68.1°, and the sun azimuth was 93.8° at an elevation of 68.2°. For both satellites, the spectrum of light detected was 0.45–0.90 μm. We used ERDAS Imagine 8.4 software (ERDAS, Atlanta, GA, USA) to create a 1000-ha subset of each image; this subset included our *c.* 600-ha old-growth study area. We referenced the QuickBird image to the IKONOS image, which had previously been georeferenced to the La Selva grid system (see below) using the crowns of conspicuous emergents that were referenced to the La Selva grid (RMSE = 4.3 m, Clark *et al.* 2003b).

Because GPS works poorly in the understory of old growth at La Selva, the research station's grid system was used for georectification and ground-truthing. The grid is constructed on a 100 × 50 m spacing to decimetre accuracy (cf. Hofton *et al.* 2002) with permanent markers at the grid intersections. We georeferenced both satellite images to this grid system, and also used the La Selva Geographic Information System (GIS) database of permanent grid-point locations, trails, streams, soil types and elevation contours (Organization for Tropical Studies 2003) for orienting ourselves in the field and for stratifying sampling.

As one independent check on our geolocation, we chose 17 emergent trees with conspicuous crowns on the QuickBird image. These emergents were distributed throughout our study area and were not control points for the QuickBird georeferencing (Fig. 3). With a hand-held compass (precision ± 0.5°) and a slope-correcting laser range finder, we ground-surveyed the positions of the crown centres of these trees in La Selva grid coordinates. We then compared these measurements on the ground to the locations predicted from the georectified image. Crown centres were assumed to be above the centre of trunks for the ground measurements, and were visually estimated on the image. Previously georeferenced canopy-level trees under long-term demographic study (the TREES project, Clark & Clark 1992, 2000b) were used to assess the relation between crown area and trunk diameter. We used data from a network of 18 georeferenced 0.5-ha annually-censused forest inventory plots (part of the CARBONO project, Clark & Clark 2000a) to assess tree geolocation and mesoscale (1–100 km^2) tree mortality (Fig. 3). These plots were sited with a stratified random design to sample the main upland forest gradients of soil and topography (Clark & Clark 2000a), so that the data are generalizable to this

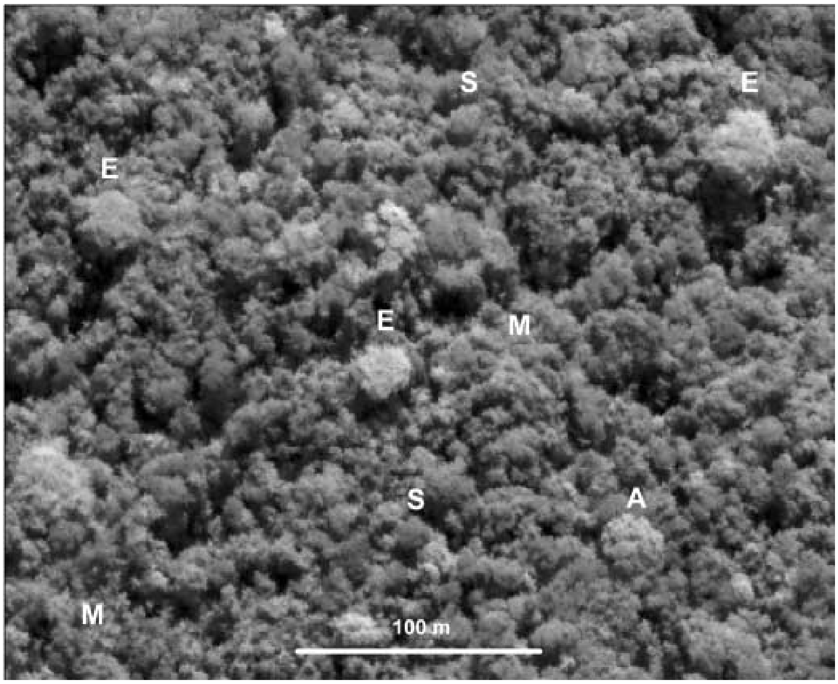

Figure 2 Old-growth Tropical Wet Forest at the La Selva Biological Station, Costa Rica. The image is 0.7-m resolution panchromatic data from the QuickBird satellite. The area shown is a subset of that shown in Figure 1. Isolated emergents (E) are clearly distinguishable, as are some smaller crowns that are clear because of local conditions (S). There are also areas where individual crown boundaries are not distinct (M). Dark areas are shadows, canopy gaps, or both. Crown A, which is particularly distinguishable from surrounding trees, is one of those selected for the allometry study.

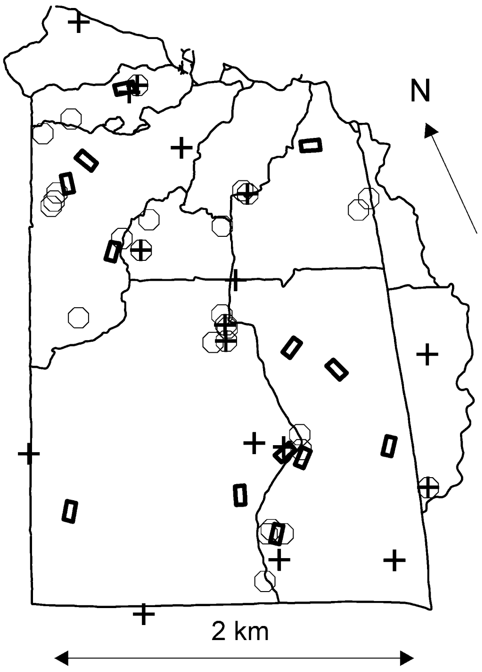

Figure 3 Study area at the La Selva Biological Station, Costa Rica. Rectangular figures are the 13, 0.5-ha forest inventory plots that were cloud-free in both satellite images and that were used to examine known tree mortality events. Crosses are the 17 emergents that were used to check the accuracy of georeferencing against independent ground surveys. Circles are the 27 distinctive crowns that were used to develop the relation between crown area and trunk diameter (there is some overlap between these two groups). Black lines are foot trails.

landscape. We used mortality data for all woody stems ≥10 cm in diameter above buttresses from the October 2000, 2001 and 2002 censuses.

Field and analysis methods

Tree allometry and geolocation

To develop allometric relations among imaged-derived and field-based measures of crown and trunk size, we selected 27 trees whose crowns were clearly distinguishable in the QuickBird and IKONOS images, and for which we had stem diameter measurements from the tree demography project (Fig. 3). For these individuals we measured in the field a Crown Area Index (CAI), as reported in Read *et al.* (2003) and Clark *et al.* (2003b). From the ground, we measured the length of the longest canopy axis of vertically-exposed crown, as well as the longest crown axis perpendicular to this axis. We defined CAI as the area of the 4-sided polygon formed by joining the endpoints of these axes. We subsequently digitized by hand the areas of these crowns in both the QuickBird and IKONOS images using the program ERDAS Imagine 8.4. These individuals also served as an additional independent check on geolocation accuracy and our ability to identify individual trees in images and in the field.

Mortality

To assess the relation between known georeferenced tree mortality events on the ground and the evidence in the images, we examined in the field every case of mortality for trees ≥30-cm diameter in 2000 or 2001 ($n = 27$ deaths) in the 13 forest inventory plots of 0.5 ha that were cloud-free in both images. We examined the canopy structure in the immediate vicinity of each dead tree, and also compared the IKONOS and Quickbird images at the predicted location of each dead tree.

To determine what percentage of mortality predicted from the images corresponded to mortality on the ground, we digitized all crowns in 11 plots of 0.5 ha that were selected to have high rates of crown disappearances based on comparison of the IKONOS and QuickBird images. We then located the canopy opening corresponding to each missing crown event on the ground, and assessed whether we could find evidence of a recent (≤2 years old) treefall or branchfall that could have caused the canopy opening. We could not unambiguously geolocate gaps in one plot because of the high local incidence of gaps and lack of distinctive emergents; we therefore discarded that plot, and report here data for the 10 plots that we could evaluate with certainty on the ground.

To determine landscape-scale estimates of tree mortality based on the satellite data, we selected 15, 50 × 100 m areas on the images using a random number table to define the corner coordinates in the La Selva grid system. Plots that fell on swampy or frequently-flooded terrain were discarded, because our focus and reference data were on non-swamp areas. Within each plot, all visually-interpreted crowns in the IKONOS image were digitized as a GIS layer. This layer was superimposed on the QuickBird image, and crowns present in the earlier-acquired IKONOS image but absent in the later QuickBird image were counted as mortality events.

Field work was carried out from January to April 2003. All trunk diameter measurements were made at breast height (*c.* 1.3 m) or above any buttresses or basal swellings (methods detailed in Clark & Clark 1999).

RESULTS

Geolocation and tree allometry

For the 17 emergents selected to have distinct crowns in the QuickBird image, the mean difference between the ground-based and image-based measurements of distances from crown centre to the nearest La Selva grid monument was

2.7 m (RMSE = 3.8 m). Thus both the IKONOS and QuickBird images were georeferenced to an accuracy considerably smaller than the diameter of many canopy-level tree crowns.

Indices of crown area measured from the ground were significantly related to the crown areas digitized on the two images (r^2 with IKONOS areas 0.46, r^2 with QuickBird areas 0.59; $n = 27$ and $P < 0.001$ in both cases). Trunk diameter was also closely related to all three measures of crown area:

(1) Stem diameter (mm) = 419.1 + (1.608 × Crown Area Index), $r^2 = 0.77$, $n = 27$, $P < 0.0001$
(2) Stem diameter (mm) = 437.9 + (0.811 × IKONOS area), $r^2 = 0.63$, $n = 27$, $P < 0.001$
(3) Stem diameter (mm) = 368.6 + (0.853 × QuickBird area), $r^2 = 0.77$, $n = 27$, $P < 0.001$

Both the ground-to-image location comparison for the 17 emergents as well as these consistent allometric relations show that the image geolocation was sufficiently accurate to locate specific individuals in the images and on the ground.

A significant constraint on these analysis was finding crowns that could be located unequivocally on the ground, and for which we could obtain accurate ground survey data. Because opening survey trails is not allowed at this reserve in old growth, we were restricted to trees that were close enough to grid markers to permit measurement of accurate slope-corrected distances with a laser range-finder (up to *c.* 30 m depending on understory conditions). The presence of crowns that were unequivocally identifiable both from the ground and in the images depended on factors such as local relief, the size of neighbouring crowns, local disturbance history, and the combination of satellite and sun angles. These totally distinct crowns that could also be identified and measured from the ground were a small subset of the total number of crowns in this image.

Mortality

Assessment of mortality events in annually-censused forest inventory plots

Upon examining in the field the 27 trees >30-cm stem diameter that died between October 2000 and 2002 in the forest inventory plots, we found canopy gaps caused by fallen trunks associated with 10 cases of mortality, and two cases where trees had died standing but had created large canopy gaps by branchfall. Canopy gaps potentially detectable by remote sensing had therefore been created in 44.4% (12/27) of the known mortality events. The other dead trees either died standing, leaving no canopy gaps or were under other canopies ($n = 13$), or could not be located unambiguously on the ground ($n = 2$).

From the images and the mapped positions of the dead individuals, we classified 17/27 = 63.0% of these crowns as having disappeared in the second satellite image (Fig. 4). The higher percentage of mortality detected in images (63.0%) compared with the ground data (44.4%) might be in part due the fact that our field work was carried out *c.* 10 months after the QuickBird image was taken, and field evidence of mortality could have been affected during that period.

Ground-validation of mortality predicted from satellite data

In the 10, 0.5-ha areas of the satellite images selected to show high rates of crown disappearance (=tree mortality), we classified 27 crowns as disappearing between images. On the ground, we were able to unambiguously locate 25 of these events with clear evidence for recent tree mortality (e.g. canopy opening and a recently fallen trunk, or a standing dead snag with branchfall opening a canopy gap). Of the remaining two cases, one was a branchfall, and for the other there was no evidence on the ground or in the canopy of a recent canopy opening. Based on these results,

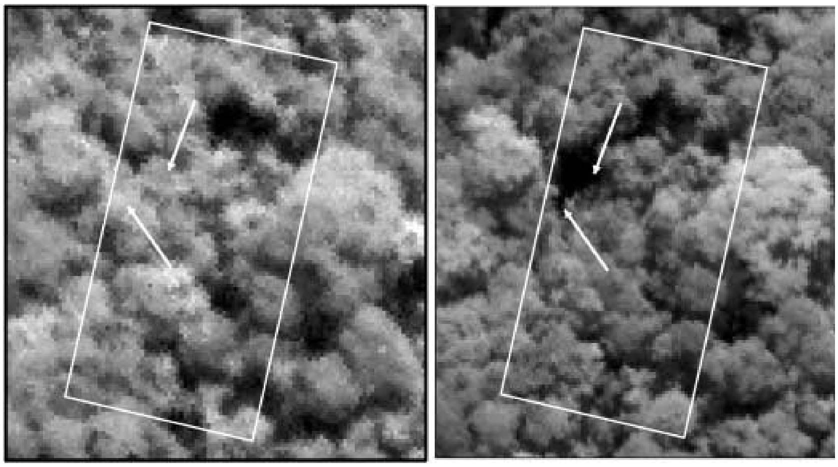

Figure 4 Ground verification of tree mortality in a permanent forest inventory plot (CARBONO Plot L6). The mapped locations of the two canopy-level trees known to have died between 2000 and 2002 in this plot are indicated by the end of the white arrows. Left image: IKONOS 1.0-m panchromatic data from 2000. Right image: 0.7-m panchromatic QuickBird 2002 data. Scale is shown by the 50 × 100 m forest inventory plot. In this case physical evidence of tree mortality (fallen trunks and canopy openings) was found for each tree during field work in 2003.

we calculated a calibration factor of 0.926 (25/27) to adjust image-based mortality rates for false positive classifications.

Estimation of landscape-scale tree mortality rates

Death rates estimated from the satellite images were very close to those measured on the ground (Table 1). The uncalibrated rate of landscape-scale exponential annual tree mortality estimated from all disappearing crowns in the 15 randomly-selected 0.5-ha plots was 0.030 per year (=3.0%), and the rate adjusted by the calibration factor described above was 0.028 per year. Death rates in the forest inventory plots over a largely overlapping time period were 0.023 per year for all stems ≥10-cm diameter, and 0.028 per year for trees ≥30-cm trunk diameter (Table 1).

Estimation of trunk diameters of recently dead trees

We attempted to predict the trunk diameters of trees that died between the two image dates by applying the crown area-trunk diameter allometry reported above (Equation 2), and using the digitized crown area in the IKONOS image of the trees that died in the 10, 0.5-ground validation plots as the independent variable. In the 2003 field work, we measured trunk diameters on the ground for all those stems where we could unambiguously identify the downed trunk of the dead individual. Contrary to the tight relationships in the allometry data, there was no relation between the measured and predicted trunk diameters ($r^2 = 0.005$, $n = 20$).

DISCUSSION

To our knowledge, this is the first paper showing that it is possible to use satellite-derived data to measure individual tree demographic processes in TRF. Our results thus confirm predictions that it should be possible to measure key components of TRF tree demography using high-spatial-resolution satellite data (Clark *et al.* 2003b; Read *et al.* 2003).

The correspondence between the satellite-based estimate of tree mortality and tree mortality measured in the forest inventory plots was very close (2.8 and 2.3% per year, respectively). This is particularly remarkable because the temporal and spatial domains of the datasets did not entirely overlap (Table 1), and 0.5-ha plot-level mortality rates at La Selva can vary up to almost 2-fold between years and up to 6-fold among plots within years (D.B. Clark *unpublished data*).

It appears contradictory that the satellite- and ground-based estimates of landscape-scale tree mortality were very similar, even though in the images we could only detect about two-thirds of the documented mortality in the forest inventory plots. We believe one explanation has to do with the trees sampled in the satellite-based estimate. For that estimate, we were able to distinguish 497 crowns in 7.5 ha of plots (Table 1), or a density of *c.* 66 stems per hectare. The forest inventory plots' data are based on all stems ≥10 cm in diameter, at an average stem density of 504 stems per hectare (Clark & Clark 2000a), so the number of crowns digitized for these plots from the satellite images corresponded to *c.* 13% of the stems ≥10 cm in diameter. Assuming that the digitized crowns corresponded to the largest stems, this would indicate that the trunk diameters for the digitized individuals were generally ≥300 mm (16.4% of the 2001 forest inventory plot sample had diameters ≥300 mm). Many of the crowns of trees <300 mm have little or no vertical illumination (Clark & Clark 1992), so their mortality would not be visible on the satellite images. However, several authors have reported that stand-level tree mortality rates are relatively independent of trunk diameter (Lieberman *et al.* 1985; Manokaran & Kochummen 1987; Swaine *et al.* 1987a). We hypothesize that this relative independence of mortality rates from trunk size accounts for the close correspondence between our satellite-based and whole forest-based mortality estimates. We do expect that mortality rates and their relation to diameter will vary somewhat according to differing environmental conditions (cf Barlow *et al.* 2003). For example, if we restrict the forest inventory plot mortality calculation only to canopy-level trees (>300-cm diameter), the space-based and ground-based mortality rates are identical to three decimals (Table 1).

Another apparent contradiction in our results is the very highly predictive relation between crown size and trunk diameter found in the allometric analyses, and the absolute

Table 1 Rates of tree mortality from 2000–2002 in upland old-growth Tropical Wet Forest at the La Selva Biological Station, Costa Rica. Satellite images and site selection as well as the forest inventory plots data are described in Methods. Annual exponential mortality m is calculated as $m = 1 - (N1/N0)^{1/t}$ where $N0$ = the number of individuals at time 0, $N1$ = the number of survivors at time 1, and t is the elapsed time in years (Sheil *et al.* 1995). The satellite-derived m was derived using a calibration factor of 0.926 (see text for explanation)

Data source	Time interval	t (years)	$N0$	$N1$	m
Satellite images	16/8/00–6/6/02	1.81	497	470	0.028
Forest inventory plots—stems ≥10-cm diameter	1/10/00–1/10/02	2.00	4362	4163	0.023
Forest inventory plots—stems >30-cm diameter	1/10/00–1/10/02	2.00	711	672	0.028

lack of correspondence between trunk diameter predicted from crown area and measured trunk diameter of recently dead trees in the high mortality plots. Here, we think non-random samples are a likely explanation. The trees selected for the allometry study were chosen to have very clearly delimited and distinctive crowns, so that we were 100% certain of their geolocation. We were successful in this, as shown by the tight allometric relationships and the low RMSE of the 17 emergents checked for geolocation. However, as Fig. 2 shows (see tree 'A'), these trees tended to have large, fully exposed crowns (mean digitized crown area 379 m^2 in the IKONOS image, $n = 27$), and were probably fast-growing (cf Clark & Clark 1999). In contrast, the trees that died in the high mortality plots had much smaller crowns on the average (55 m^2, $n = 27$), and were likely growing slowly prior to death (cf Swaine *et al.* 1987b). We hypothesize that fully exposed emergents have different crown area-trunk diameter allometries compared with soon-to-die, and generally much smaller, trees.

Given the potential global applications of the technique, we think further investigations in a diversity of TRF sites would be valuable. Studies at sites with ground data to validate and if necessary calibrate the satellite-derived mortality estimates will be particularly valuable. Given the vigour of TRF regrowth, the time interval between satellite images should be on the order of 1–2 years, so that ground evidence of mortality is still present.

A key research issue will be developing general crown area-trunk allometric equations that will allow prediction of ecosystem variables such as stand biomass and basal area. This will be challenging, because of the difficulty of geolocating smaller individual crowns on the ground (cf Fig. 2 'M'). Promising avenues for this research would be working at tower and canopy crane sites to obtain canopy access from above, incorporating high-resolution photography (cf Myers 1982), integrating these analyses with automated crown recognition programmes (Gougeon & Leckie 2003; Leckie *et al.* 2003), and extending the results with stand expansion factors (cf. Gillespie *et al.* 1992).

The sensors that produce remotely-sensed data, including satellite-based sensors, are constantly evolving towards increased spatial and spectral resolution. Here, we have shown that it is possible to evaluate TRF tree mortality rates using commercially-available satellite data at ≤1-m spatial resolution. As the spatial resolution of satellite imagery increases, an ever-increasing fraction of canopy trees will be measurable by these techniques. Satellite-based measurements of TRF tree mortality and growth will play an increasingly important role in our efforts to understand, measure, and monitor these endangered ecosystems and the dominant organisms in them, the canopy trees.

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REFERENCES

Asner, G.P., Palace, M., Keller, M., Pereira, R., Jr, Silva, J.N.M. & Zweede, J.C. (2002). Estimating canopy structure in an Amazon forest from laser range finder and IKONOS satellite observations. *Biotropica*, 34, 483–492.

Barlow, J., Peres, C.A., Lagan, B.O. & Haugassen, T. (2003). Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Letters*, 6, 6–8.

Brown, S. (1996). Tropical forests and the global carbon cycle: estimating state and change in biomass density. In: *Forest Ecosystems, Forest Management and the Global Carbon Cycle* (eds Apps, M.J. & Price, D.T.). Springer-Verlag, Berlin, pp. 135–144.

Clark, D.A. (2002). Are tropical forests an important carbon sink? Re-analysis of the long-term plot data. *Ecol. Appl.*, 12, 3–7.

Clark, D.A. (2003). Souces or sinks?: the responses of tropical forests to current and future climate and atmospheric composition. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* (in press).

Clark, D.A. & Clark, D.B. (1992). Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecol. Monogr.*, 62, 315–344.

Clark, D.A. & Clark, D.B. (1999). Assessing the growth of tropical rain forest trees: issues for forest modeling and management. *Ecol. Appl.*, 9, 981–997.

Clark, D.B. & Clark, D.A. (2000a). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For. Ecol. Manage.*, 137, 185–198.

Clark, D.B. & Clark, D.A. (2000b). Tree growth, mortality, physical condition, and microsite in old-growth lowland tropical rain forest. *Ecology*, 81, 294 and *Ecol. Archives*: http://www.esapubs.org/archive/ecol/E081/003/

Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. (2003a). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Nat. Acad. Sci. (USA)*, 100, 5852–5857.

Clark, D.B., Read, J.M., Clark, M.L., Murillo Cruz, A., Fallas Dotti, M. & Clark, D.A. (2003b). Application of 1-m and 4-m resolution satellite data to studies of tree demography, stand structure and land-use classification in tropical rain forest landscapes. *Ecol. Appl.*, (in press).

Condit, R., Hubbell, S.P. & Foster, R.B. (1995). Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.*, 65, 419–439.

Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C. & Wisniewski, J. (1994). Carbon pools and flux of global forest ecosystems. *Science*, 263, 185–190.

Enquist, C.A.F. (2002). Predicted regional impacts of climate change on the geographical distribution and diversity of tropical forests in Costa Rica. *J. Biogeogr.*, 29, 519–534.

Gillespie, A.J.R., Brown, S. & Lugo, A.E. (1992). Tropical forest biomass estimation from truncated stand tables. *For. Ecol. Manage.*, 48, 69–87.

Gougeon, F.A. & Leckie, D.G. (2003). Forest Information Extraction From High Resolution Images Using An Individual Tree Crown Approach. Information Report BC-X-396. Canadian Forest Service, Pacific Forestry Center, Victoria, British Colombia, Canada.

Hartshorn, G.S. & Hammel, B.E. (1994). Vegetation types and floristic patterns. In: *La Selva: Ecology and Natural History of a Neotropical Rain Forest* (eds McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S.). University of Chicago Press, Chicago, pp. 73–89.

Hofton, M.A., Rocchio, L.E., Blair, J.B. & Dubayah, R. (2002). Validation of Vegetation Canopy Lidar sub-canopy topography measurements for a dense tropical forest. *J. Geodynam.*, 34, 491–502.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X. *et al.* (2001). *Climate Change 2001: the Scientific Basis*. Cambridge University Press, Cambridge, UK.

Hurtt, G., Xiao, X., Keller, M., Palace, M., Asner, G.P., Braswell, R. *et al.* (2003). IKONOS imagery for the large scale biosphere–atmosphere experiment in Amazonia (LBA). *Remote Sens. Environ.* (in press).

Jones, C.D., Cox, P.M., Essery, R.L.H., Roberts, D.L. & Woodage, M.J. (2003). Strong carbon cycle feedbacks in a climate model with interactive CO2 and sulphate aerosols. *Geophys. Res. Lett.*, 30, 1479 (doi:10.1029/2003GL016867).

Keller, M., Palace, M.M. & Hurtt, G. 2001. Biomass estimation in the Tapajos National Forest, Brazil: Examination of sampling and allometric uncertainties. *For. Ecol. Manage.*, 154, 371–382.

Laurance, W.F., Delamonica, P., Laurance, S.G., Vasconcelos, H.L. & Lovejoy, T.E. (2000). Rainforest fragmentation kills big trees. *Nature*, 404, 836.

Leckie, D.G., Gougeon, F.A., Walsworth, N. & Paradine, D. (2003). Stand delineation and composition estimation using semi-automated individual tree crown analysis. *Remote Sens. Environ.*, 85, 355–369.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. (1985). Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.*, 73, 915–924.

McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (eds) (1994). *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago.

Manokaran, N. & Kochummen, K.M. (1987). Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *J. Trop. Ecol.*, 3, 315–330.

Myers, B.J. (1982). Large-scale color aerial photographs-a useful tool for tropical biologists. *Biotropica*, 14, 156–157.

Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T. *et al.* (2000). Impact of severe drought associated with the 1997–1998 El Nino in a tropical forest in Sarawak. *J. Trop. Ecol.*, 16, 355–367.

Organization for Tropical Studies (2003). *Geographic Information System*. http://www.ots.duke.edu/en/laselva/gis.shtml

Peñuelas, J. & Boada, M. (2003). A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biol.*, 9, 131–140.

Read, J.M. (2003). Spatial analyses of logging impacts in Amazonia using remotely sensed data. *Photo. Eng. Remote Sens.*, 69, 275–282.

Read, J.M., Clark, D.B., Venticinque, E.M., & Moreira, M.P. (2003). Application of merged 1-m and 4-m resolution satellite data to research and management in tropical forests. *J. Appl. Ecol.*, 40, 592–600.

Reaka-Kudla, M.L., Wilson, D.E. & Wilson, E.O. (eds.) (1997). *Biodiversity II: Understanding and Protecting Our Biological Resources*. Joesph Henry Press, Washington, DC.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. *Nature*, 421, 57–60.

Sheil, D., Burslem, D.F.R.P. & Alder, D. (1995). The interpretation and misinterpretation of mortality rate measures. *J. Ecol.*, 83, 331–333.

Swaine, M.D., Lieberman, D. & Putz, F.E. (1987a). The dynamics of tree populations in tropical forest: a review. *J. Trop. Ecol.*, 3, 359–366.

Swaine, M.D., Hall, J.B. & Alexander, I.J. (1987b). Tree population dynamics at Kade, Ghana (1968–1982). *J. Trop. Ecol.*, 3, 331–345.

Williamson, G.B., Laurance, W.F., Oliveira, A.A., Delamonica, P., Gascon, C., Lovejoy, T.E. *et al.* 2000. Amazonian tree mortality during the 1997 El Nino drought. *Conserv. Biol.*, 14, 1538–1542.

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