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Estimating Canopy Structure in an Amazon Forest from Laser Range Finder and IKONOS Satellite Observations[1]

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ABSTRACT

Canopy structural data can be used for biomass estimation and studies of carbon cycling, disturbance, energy balance, and hydrological processes in tropical forest ecosystems. Scarce information on canopy dimensions reflects the difficulties associated with measuring crown height, width, depth, and area in tall, humid tropical forests. New field and spaceborne observations provide an opportunity to acquire these measurements, but the accuracy and reliability of the methods are unknown. We used a handheld laser range finder to estimate tree crown height, diameter, and depth in a lowland tropical forest in the eastern Amazon, Brazil, for a sampling of 300 trees stratified by diameter at breast height (DBH). We found significant relationships between DBH and both tree height and crown diameter derived from the laser measurements. We also quantified changes in crown shape between tree height classes, finding a significant but weak positive trend between crown depth and width. We then compared the field-based measurements of crown diameter and area to estimates derived manually from panchromatic 0.8 m spatial resolution IKONOS satellite imagery. Median crown diameter derived from satellite observations was 78 percent greater than that derived from field-based laser measurements. The statistical distribution of crown diameters from IKONOS was biased toward larger trees, probably due to merging of smaller tree crowns, underestimation of understory trees, and overestimation of individual crown dimensions. The median crown area derived from IKONOS was 65 percent higher than the value modeled from field-based measurements. We conclude that manual interpretation of IKONOS satellite data did not accurately estimate distributions of tree crown dimensions in a tall tropical forest of eastern Amazonia. Other methods will be needed to more accurately estimate crown dimensions from high spatial resolution satellite imagery.

Key words: *allometry; Amazon; biomass; Brazil; canopy dimensions; forest canopy; IKONOS; laser; LIDAR.*

SPATIAL VARIATION IN THE BIOPHYSICAL STRUCTURE OF TROPICAL FORESTS is key to determining their physiological function, biomass distribution, and role in biogeochemical processes (Kuppers 1989, Montgomery & Chazdon 2001). Most previous studies have focused on measurements of stem diameter and/or forest canopy height (Brown *et al.* 1995, Clark & Clark 2000, Keller *et al.* 2001). Some of these efforts have described the vertical distribution of forest canopy strata, such as understory, mid-canopy, and emergent trees (Song *et al.* 1997, Montgomery & Chazdon 2001). Only a few studies have provided detailed quantitative information

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on tree crown dimensions in tropical forests (Dawkins 1963, Wadsworth 1997).

Interest in tropical forest crown diameter, area, and depth estimates has increased for several reasons. First, information on canopy roughness is needed for land–atmosphere and mesoscale meteorological models (Chen & Coughenour 1994, Dirmeyer & Shukla 1994, Betts *et al.* 1997). Along with tree height, estimates of crown shape are useful for determining canopy roughness. Second, estimation of photosynthetically active radiation absorption (APAR) by canopies is routinely employed for estimating net primary productivity of forests (Field *et al.* 1995, Bondeau *et al.* 1999). The newest APAR models employ spatially specific, three-dimensional representations of the canopy, and thus they require inputs of crown area or diameter and depth (Myneni & Asrar 1993, Asner & Wessman 1997). Third, forest gap probability models benefit from spatial information on crown area, which is needed to constrain simulations of treefall dynamics (Blackburn & Milton 1996, Song *et al.* 1997, Moorcroft *et al.* 2001). Fourth, remote sensing theories and models often employ information on crown dimensions. Advanced photon transport models used for interpreting satellite data require quantitative information on crown diameter, area, and depth (Li *et al.* 1995, Myneni *et al.* 1997, Kynazikhin *et al.* 1998).

Crown dimension data could also be used to improve canopy allometric equations employed in forest biomass studies (Alves & Santos 2002). Knowledge of the spatial distribution of crown shape could improve landscape- and regional-scale estimates of carbon stocks in tropical forests. Crown area and diameter also may allow species identification and other inferences needed for tree demographic studies (Meyer *et al.* 1996). Finally, crown structural data could be used to improve timber harvest plans by aiding in tree selection and by excluding damaged trees.

Measurements of tree crown diameter, area, or depth are notoriously difficult to acquire, especially in tall, humid tropical forests. The options for collecting these measurements have traditionally been limited to laborious survey methods resulting in much error. Recently, more efficient methods such as field-based laser range finder systems have been used to quickly collect estimates of tree crown height, diameter, and depth (Williams *et al.* 1994, Law, Kelliher *et al.* 2001, Law, Thornton *et al.* 2001, Treuhaft *et al.* 2002). These newer field-based approaches, however, have not been tested in tropical forest ecosystems. They also have not provided estimates of crown area, owing to the difficult task of measuring diameters along multiple, horizontal crown axes per tree.

The IKONOS satellite (Space Imaging Corp., Thorton, Colorado) was launched into low earth orbit in September 1999. IKONOS provides the first operational meter-scale resolution observations of earth for use by the civilian sector. The instrument has a panchromatic band (400–700 nm) with *ca* 0.8 m spatial resolution, as well as four multispectral bands (450, 550, 680, and 800 nm), each with *ca* 4 m spatial resolution. The panchromatic imagery in particular may provide an opportunity to measure tree crown diameters and areas from the spaceborne vantage point. This satellite provides observations directly comparable to ground-based measurements; yet no studies have provided this comparison in tropical forests. If successful, IKONOS would provide measurements over a spatial extent otherwise unachievable in field research and forest management efforts (Franklin *et al.* 2001). While aerial photographs have been used in studies of forest canopy structure and forestry applications (Swellengrebel 1959, Green 2000), they are not readily available for many parts of the world, especially in remote humid tropical regions. IKONOS and other new-generation satellite sensors could provide access to tree structural characteristics anywhere in the world (Bradshaw & Spies 1992, Blackburn & Milton 1996, Brandtberg 1999, Sommerfeld *et al.* 2000, Pitkänen 2001, Shugart *et al.* 2001).

We report on a study to assess the value of the field laser and IKONOS satellite data for measuring tree crown dimensions in a lowland tropical forest of the eastern Amazon, Brazil. We carried out a detailed field study of tree crown height, diameter, and depth using a handheld laser range finder and stratified sampling criteria based on the tree stem diameter at breast height (DBH). We also quantified differences in crown shape between different tree size classes. We then compared the field-based measurements of crown diameter and area to those estimated via manual interpretation of panchromatic IKONOS satellite imagery.

MATERIALS AND METHODS

SITE DESCRIPTION.—The study was conducted at the Fazenda Cauaxi in the Paragominas Municipality of Para State, Brazil, in the eastern Amazon (3°43.878′S, 48°17.438′W). The climate of the Cauaxi region is humid tropical with annual precipitation averaging 2200 mm (Costa & Foley

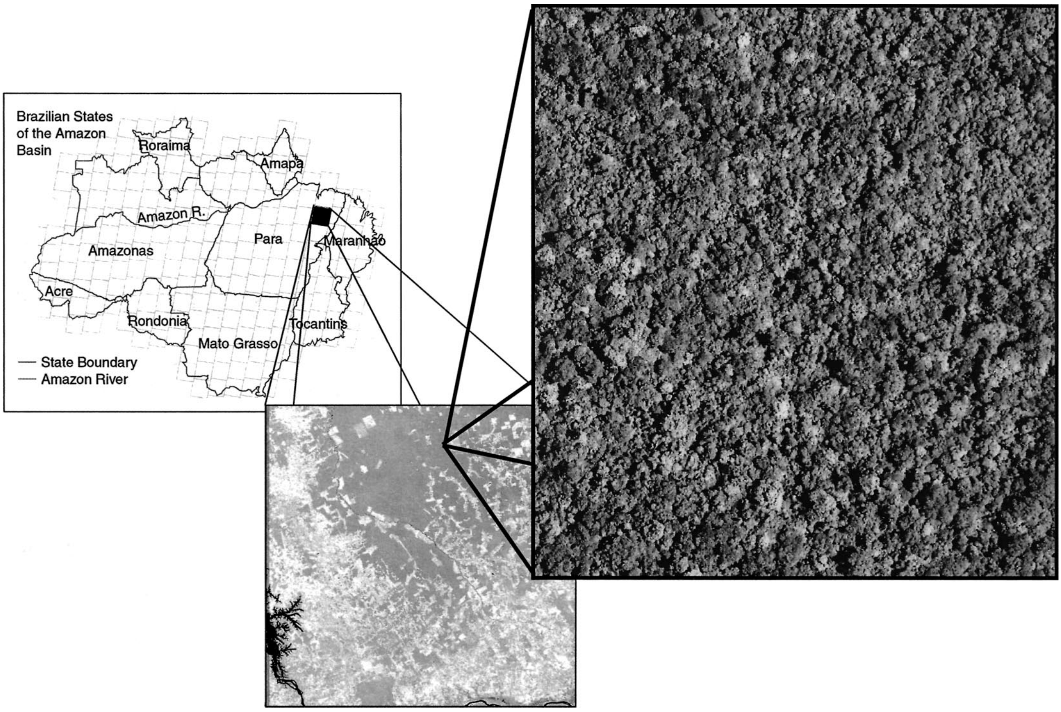

FIGURE 1. The study area was located in the state of Para, Brazil in the eastern Amazon basin. Landsat 7 image shows location of study site relative to heavy deforestation in the region of Maraba and Paragominas. Panchromatic IKONOS satellite image of study is shown at *ca* 0.8 m spatial resolution.

1998). A dry season extends from July through November (generally <50 mm/mo). Soils in the area are classified mainly as dystrophic yellow latosols according to the Brazilian system (RADAMBRASIL 1983). The topography is flat to mildly undulating, and the forest is classified as tropical dense moist forest (IBGE 1988).

A forest site of *ca* 50 ha was selected for field and satellite measurements (Fig. 1). The most common upper canopy species found at the site were *Manilkara huberii*, *Manilkara paraensis*, *Protium pernevatum*, *Dinizia excelsa*, *Piptadenia suaveolens*, *Licania* spp., *Astronium lecointei*, *Eschweilera odorata*, and *Parkia* spp. Stand basal area was *ca* 57 m^2/ha for trees greater than 10 cm DBH (Pereira *et al.* 2002).

FIELD MEASUREMENTS.—Line transects of 500 m length were spaced at 50 m intervals crossing the study plot (N = 20). Fourteen of these transects were randomly selected for surveys of DBH, tree height, and crown dimensions. DBH measurements were collected for 2171 individuals encountered with DBH > 20 cm (measured 1.3 m above ground or above buttresses) within 10 m to either side of each transect. For 300 selected trees, we collected additional crown dimension measurements including top-of-crown height, bottom-of-crown height, and crown width along the estimated longest axis. Crown depth was estimated as the difference in tree height from the top to bottom of crown. These measurements were collected using a handheld laser range finder (Impulse-200LR, Laser Technology Inc., Englewood, Colorado), which measures distance and calculates heights via an angular measurement simultaneously taken from a clinometer integrated into the instrument (Law, Kelliher *et al.* 2001, Law, Thornton *et al.* 2001, Treuhaft *et al.* 2002). A detailed description of the instrument is provided in Williams *et al.* (1994).

To compare field studies to satellite estimates of tree dimensions, it was necessary to weight the data set according to the relative frequency of the individual DBH class in the original 2171 tree sample as discussed above. We employed a stratified sampling procedure to select the 300 trees for crown measurements and to balance the number of samples across tree size classes. Since there are many smaller trees and fewer larger trees in most forests, such a selection process was developed

TABLE 1. *Tree characteristics derived from the field-based laser range finder measurements of a forest in Para, Brazil (eastern Amazon). Data were weighted based on known* in situ *sampling biases, as described in Methods. For each canopy variable, superscript letters indicate mean and median values that are statistically different at* $P < 0.05$ *level using ANOVA and Mann-Whitney rank sum test, respectively.*

	Mean	Standard Deviation	Median	Lower Quartile	Upper Quartile	Skewness	Min	Max
DBH (cm)								
Understory	27.1^{a}	1.4	24.0^{a}	21.7	30.0	6.7	20.0	58.0
Dominant	40.6^{b}	3.0	36.0^{b}	26.0	50.0	4.7	20.0	172.0
Super Dominant	84.2^{c}	5.1	80.0^{c}	58.8	114.0	2.5	20.0	192.0
All	37.4	3.4	30.0	23.8	44.0	6.5	20.0	172.0
Tree Height (m)								
Understory	21.4^{a}	0.9	20.9^{a}	18.6	23.0	1.5	10.9	36.5
Dominant	25.3^{b}	1.5	27.0^{b}	20.9	31.0	−3.2	9.2	48.8
Super Dominant	46.1^{c}	7.1	46.0^{c}	36.9	48.8	−12.7	29.0	55.8
All	23.6	1.7	23.9	19.8	30.0	−0.6	9.2	55.8
Crown Diameter (m)								
Understory	8.0^{a}	1.0	7.6^{a}	5.6	9.0	1.1	2.0	17.0
Dominant	11.6^{b}	1.4	10.9^{b}	7.8	14.0	1.5	1.0	31.0
Super Dominant	19.9^{c}	1.9	16.9^{c}	13.7	26.0	4.9	8.8	40.7
All	10.6	1.6	9.0	7.4	12.9	3.1	1.0	40.7
Crown Depth (m)								
Understory	5.7^{a}	1.1	4.8^{a}	2.9	7.9	2.2	1.9	13.4
Dominant	7.3^{b}	1.3	6.0^{a}	4.7	9.0	3.1	0.6	27.0
Super Dominant	11.6^{c}	1.3	11.8^{b}	7.7	15.8	−0.6	4.4	19.5
All	6.9	1.3	5.9	4.0	8.9	2.2	0.6	27.0

based on Keller *et al.* (2001). We measured all 2171 tree DBHs, and a random number generator was used to determine if crown measurements would be collected and recorded. The selection process was based on the following tree size classes: DBH 20–40 cm (10% sampled), DBH 40–60 cm (20% sampled), DBH 60–80 cm (30% sampled), DBH 80–100 cm (50% sampled), and greater then DBH 100 cm (100% sampled). Selected individuals were classified into understory, dominant, or super-dominant tree classes. This procedure produced a nearly uniform distribution of diameters across 10 cm DBH classes from 20 to 100 cm.

SATELLITE OBSERVATIONS.—The IKONOS satellite data were acquired on 2 November 2000, from an orbital altitude of 680 km. The data from a 600 x 600 m block of undisturbed forest, including the 50 ha area surveyed in the field, were analyzed in a combined image processing (IDL, Research Systems Inc., Boulder, Colorado) and geographic information system (ArcInfo, ESRI, Redlands, California) environment. Each crown center was manually identified in the 0.8 m panchromatic image provided by IKONOS. Crown area was estimated by manually tracing a polygon around each apparent crown (Fig. 2a). A total of 1675 tree crowns was identified, and their areas were digitally calculated. All polygons were then analyzed for maximum crown diameter. We developed an automated routine to find the longest crown axis for each polygon, and the length of this maximum axis was recorded (Fig. 2b).

RESULTS AND DISCUSSION

FIELD MEASUREMENTS.—Both mean and median values of DBH, tree height, crown diameter, and crown depth are provided in Table 1. The data were often, but not consistently, non-normally distributed; therefore, we highlight the comparisons of only median values in the text but provide all

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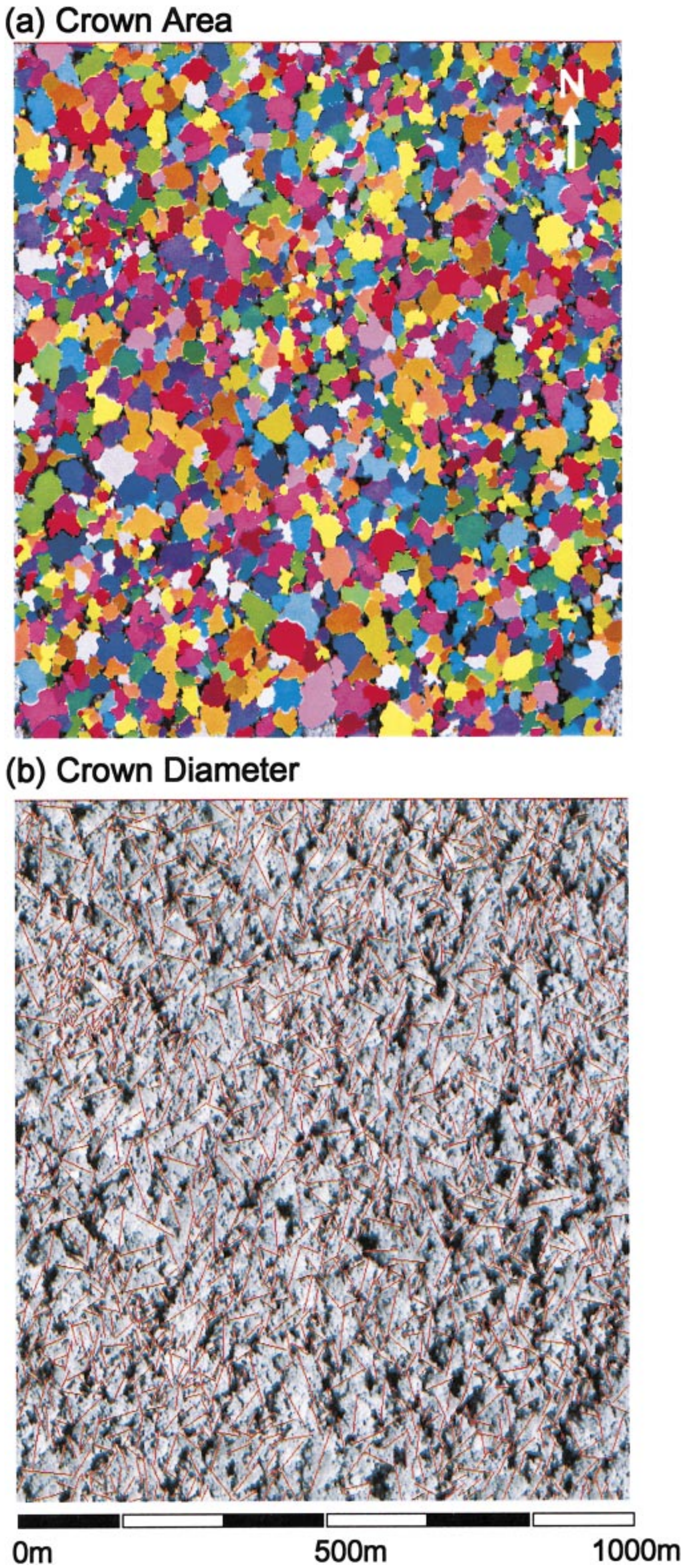
FIGURE 2. (a) Tree crown area delineated in 1675 polygons. (b) Tree crown diameter along longest axis of each crown area polygon.


(a) Crown Area
N
(b) Crown Diameter
0m
500m
1000m

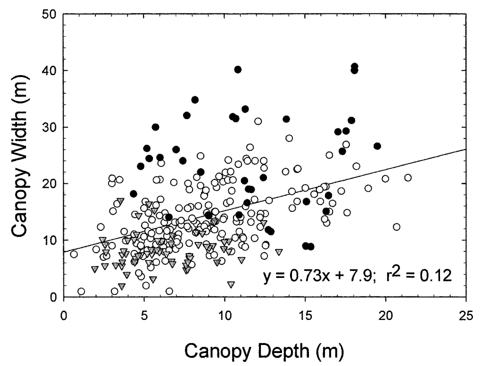


FIGURE 4. Relationship between crown diameter and depth for understory (gray diamonds), dominant (white circles), and super-dominant (black circles) tree classes. Regression is for all classes combined.

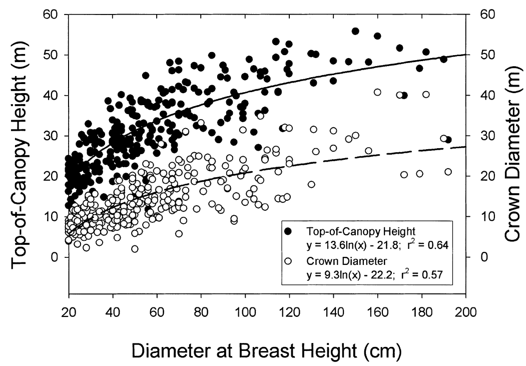


FIGURE 3. Relationships between tree stem diameters at breast height (DBH) and either top-of-canopy height or crown diameter.

statistical results in Table 1. The median height of all trees sampled was 23.9 m, and median DBH was 30.0 m. Median crown diameter was 9.0 m, nearly one-third that of tree height. Crown depth measurements had a median value of 5.9 m, or about 25 and 65 percent of the median tree height and crown diameter, respectively.

Median (and mean) tree height and DBH were almost always significantly different among the field classifications of understory, dominant, and super-dominant classes (Table 1; Mann–Whitney rank sum tests on medians and ANOVA on means, $P < 0.05$). Median tree heights for understory, dominant, and super-dominant classes were 20.9, 27.0, and 46.0 m, respectively. The shortest and tallest trees measured were 9.2 and 55.8 m, respectively, corresponding to stem DBH values of 20 cm (the lower limit of our survey) and 192 cm. Median DBH values were 24.0, 36.0, and 80.0 m for understory, dominant, and super-dominant classes, respectively. Tree height was well predicted by DBH (hgt = 13.6*ln(DBH) − 21.8; R^2 = 0.64; Fig. 3), displaying the natural-log relationship typical of canopy allometric studies (Clark & Clark 2000).

Crown diameters and depths also increased with increasing canopy class (Table 1). Median crown diameters for understory, dominant, and super-dominant classes were 7.6, 10.9, and 16.9 m, respectively. The narrowest crown was 1.0 m, and the widest crown was 40.7 m. Crown diameter was also well predicted by DBH using a natural-log relationship (dia = 9.3*ln(DBH) − 22.2; R^2 = 0.57; Fig. 3).

Median crown depths were 4.8, 6.0, and 11.8 m, respectively (Table 1), but the understory and dominant classes were not significantly different. Crown depth was positively correlated with crown diameter, although the relationship was statistically weak ($R^2 = 0.12$, $P < 0.05$; Fig. 4). The tallest trees in the forest—super dominants—had significantly flatter crowns (diameter ≫ depth) than other tree classes. Super-dominant trees on average were 72 percent larger in the horizontal than in the vertical direction (Table 1). In contrast, the smallest tree class—understory—had diameters that were only 39 percent larger than their crown depths. This is a common observation in tropical forests, where the tallest trees harvesting the most light at the top of the canopy tend to have crowns of greater width than depth. Mid-canopy and understory trees harvest light from smaller incidence angles, and they must compete for canopy openings, both of which reduce crown diameter relative to depth (Mulkey *et al.* 1996).

Satellite vs. field measurements.—Based on manual interpretation of IKONOS data (Fig. 2b), estimates of crown diameter had a median value of 16.1 m, with a minimum of 3.2 m and maximum of 39.8 m (Table 2). This median was 78 percent higher than that of the field measurements (Table 1), although the maximum canopy diameters from each method were nearly equal (field: 40.7 m vs. satellite: 39.8 m). Satellite-derived estimates of crown diameter were significantly higher than from all field-based measurements (Mann–Whitney rank sum, $P < 0.01$), but were not higher than the medians from the dominant and super-dominant classes alone (Mann–Whitney, $P > 0.05$).

Cumulative frequency distributions of crown diameters derived from IKONOS and field laser data are shown in Figure 5. Kolmogorov–Smirnov

TABLE 2. *Tree crown diameter and area statistics from IKONOS satellite imagery of a forest in Para, Brazil (eastern Amazon).*

	Crown Diameter (m)	Crown Area (m^2)
Mean	16.4	124.8
Standard Deviation	8.2	125.1
Median	16.1	105.1
Lower Quartile	10.2	41.2
Upper Quartile	20.4	196.1
Skewness	0.65	1.57
Min	3.2	5.9
Max	39.8	699.1
N	1675	1675

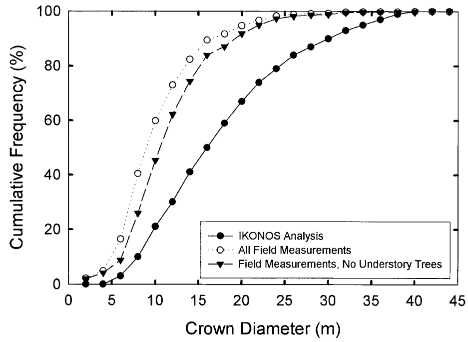


FIGURE 5. Cumulative frequency (%) histograms of tree crown diameter (m) derived using IKONOS, field laser measurements, and field measurements not including understory trees.

tests (Sokal & Rohlf 1995) indicated that field and IKONOS distributions were significantly different ($P < 0.01$). The distribution of satellite-based estimates appeared biased toward larger trees. Over 40 percent of all trees surveyed had crown diameters less than 10 m, but IKONOS estimates indicated only *ca* 20 percent at this threshold. Furthermore, IKONOS estimates showed that roughly 20 percent of the trees had crown diameters greater than 25 m, but field measurements indicated only 5 percent of this size or larger.

Removal of the understory trees from the field data did not change the statistical comparison to the IKONOS-based distribution (Kolmogorov–Smirnov test, $P < 0.01$). It did, however, result in a significant shift in the distribution of field-based measurements (Fig. 6). Whereas 60 percent of all trees surveyed had crown diameters less than or equal to 10 m, the distribution without understory trees showed that only 44 percent of trees were less than or equal to 10 m.

Crown areas from the IKONOS imagery displayed very high spatial variability (Fig. 2a). Subsequently, the median crown area was 105.1 m^2, with minima and maxima of 5.9 and 699.1 m^2, respectively (Table 2). For comparison, the field-based crown diameter data were used to model crown area. Assuming a circular shape for each crown (area = πr^2), the median value was 63.6 m^2 for field measurements. The satellite-based crown area results thus were 65 percent higher than the modeled field-based estimates, a somewhat smaller difference in comparison to the crown diameter results from the two methods. This was likely due to the assumption of circular crowns in the modeled field data. Because the crowns were far from circular (Fig. 2a), this assumption would result in an overestimate of area since the field measurements were made of the long axis in each crown.

Errors in manual interpretation of IKONOS data.—We identified at least three causes for the observed difference between field and IKONOS crown diameter distributions. Manual interpretation of IKONOS imagery missed many small crowns and probably merged groups of smaller crowns as single larger crowns. Additionally, the manual approach probably aggregated smaller understory crowns to larger crowns in the canopy. Insufficient spatial resolution of the imagery accounts for part of this confusion, as does variability in apparent shadows within and between tree crowns as seen from above (Asner & Warner in press). The field measurements, however, were not

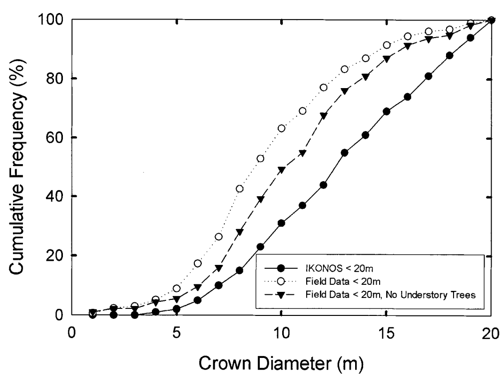


FIGURE 6. Comparison of cumulative frequency histograms for tropical tree crown diameters under 20 m: IKONOS (black circles); field data without understory trees (white circles); and all field data for crowns less than 20 m diameter (black diamonds).

spatially continuous, and thus the field study could have missed some larger tree crowns in the area. Nonetheless, the stratified sampling and frequency correction of the field data should have minimized this source of error. Field-based crown diameter measurements also require a subjective estimate of the longest crown axis. It is therefore plausible that we consistently underestimated crown diameters in the field.

It is difficult to assess the true accuracy of either the laser range finder or IKONOS satellite results; however, we believe that the tendency of the IKONOS results to produce many larger tree diameters and areas than the field measurements indicates that manual interpretation of the satellite image was biased. Methods based on a more quantitative analysis of crown brightnesses and shape in the IKONOS data may yield more accurate results. For example, new approaches are being developed to automatically delineate individual tree crowns and quantify forest structure from high spatial resolution imagery (St-Onge & Cavayas 1997, Wulder *et al.* 2000, Franklin *et al.* 2001). Moreover, even higher spatial resolution sensors, such as Quickbird (DigitalGlobe, Longmont, Colorado) with 0.6 m spatial resolution, may improve space-based analyses of crown diameter, area, and spacing in tropical forests. The complex stratification of tropical forest canopies, however, will continue to challenge any such studies.

CONCLUSIONS.—We used a handheld laser range finder to estimate tree crown height, diameter, and depth in a lowland tropical forest in the eastern Amazon, Brazil. These measurements were compared with measurements of tree stem diameter at breast height (DBH). We found significant relationships between DBH and both crown diameter and tree height derived from the laser measurements. We also quantified changes in crown shape between tree height classes. Field-based laser methods proved highly efficient for collecting data on tree height and crown dimensions. Typically, the limiting steps in field data collection were the DBH measurement and the crown diameter estimate, as the laser method was highly efficient for height estimation. Laser range finders are easy to operate and readily available from commercial vendors.

We compared measurements of tree crown diameter collected using the laser range finder and high-resolution, panchromatic IKONOS satellite data. The satellite observations overestimated the frequency of larger crowns. The median crown diameter values of the two methods differed by 78 percent. The estimates based on manual interpretation of the IKONOS data likely missed many small crowns and confused groups of smaller crowns for single larger crowns, contributing to the overestimate of crown diameters and the subsequently biased distribution of results. IKONOS-based measurements were also likely to have underestimated the number of understory trees.

The IKONOS method employed here was only effective for accurate estimates of crown diameter for the largest super-dominant trees (Table 1; Fig. 5). Super-dominant trees are of great value to loggers. For example, crown diameter estimates and frequency counts for large trees may help to identify effects of past logging well after the ground scars from the harvest are made invisible to common analyses of multispectral remote sensing data (Stone & Lefebvre 1998, Asner *et al.* 2002).

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LITERATURE CITED

ALVES, L. F., AND F. A. M. SANTOS. 2002. Tree allometry and crown shape of four tree species in Atlantic rain forest, southeast Brazil. J. Trop. Ecol. 18: 245–260.

ASNER, G. P., M. KELLER, R. PEREIRA JR., AND J. C. ZWEEDE. 2002. Remote sensing of selective logging in Amazonia: Assessing limitations based on detailed field observations, Landsat ETM+, and textural analysis. Remote Sens. Environ. 80: 483–496.

———, AND A. S. WARNER. Canopy shadow in the LBA IKONOS satellite archive: Implications for multispectral studies of tropical forests and savannas. Remote Sens. Environ. In press.

———, and C. A. Wessman. 1997. Scaling PAR absorption from the leaf to landscape level in spatially heterogeneous ecosystems. Ecol. Model. 103: 81–97.

Betts, R. A., P. M. Cox, S. E. Lee, and F.I. Woodward. 1997. Contrasting physiological and structural vegetation feedbacks in climate change simulations. Nature 387: 796–799.

Blackburn, G. A., and E. J. Milton. 1996. Filling the gaps: Remote sensing meets woodland ecology. Global Ecol. Biogeogr. Let. 5: 175–191.

Bondeau, A., D. W. Kicklighter, and J. Kaduk. 1999. Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. Global Change Biol. 5: 35–45.

Bradshaw, G. A., and T. A. Spies. 1992. Characterizing canopy gap structure in forests using wavelet analysis. J. Ecol. 80: 205–215.

Brandtberg, T. 1999. Automatic individual tree based analysis of high spatial resolution aerial images on naturally regenerated boreal forests. Can. J. For. Res. 29: 1464–1478.

Brown, I. F., L. A. Martinelli, W. W. Thomas, M. Z. Moreira, C. A. C. Ferreira, and R. A. Victoria. 1995. Uncertainty in the biomass of Amazonian forests—An example from Rondonia, Brazil. For. Ecol. Manage. 75: 175–189.

Chen, D. X., and M. B. Coughenour. 1994. GEMTM—A general model for energy and mass transfer of land surfaces and its application at the FIFE sites. Agric. For. Meteorol. 68: 145–171.

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

Costa, M. H., and J. A. Foley. 1998. A comparison of precipitation datasets for the Amazon basin. Geophys. Res. Let. 25: 155–158.

Dawkins, H. C. 1962. Crown diameters: their relation to bole diameter in tropical forest trees. Commonwealth For. Rev. 26: 318–333.

Dirmeyer, P. A., and J. Shukla. 1994. Albedo as a modulator of climate response to tropical deforestation. J. Geophys. Res. Atmos. 99: 20,863–20,877.

Field, C. B., J. T. Randerson, and C. M. Malmstrom. 1995. Global net primary production: Combining ecology and remote sensing. Remote Sens. Environ. 51: 74–88.

Franklin, S. E., M. A. Wulder, and G. R. Gerylo. 2001. Texture analysis of IKONOS panchromatic data for Douglas-fir forest age class separability in British Columbia. Int. J. Remote Sens. 22: 2627–2632.

Green, K. 2000. Selecting and interpreting high-resolution images. J. For. 98: 37–39.

IBGE. 1988. Mapa de vegetaçao do Brasil. Ministerio da Agricultura, Brasilia, Brasil.

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

Kuppers, M. 1989. Ecological significance of aboveground architectural patterns in woody plants: A question of cost–benefit relationships. Trends Ecol. Evol. 4: 375–379.

Kynazikhin, Y., J. V. Martonchik, R. B. Myneni, D. J. Diner, and S. W. Running. 1998. Synergistic algorithm for estimating vegetation canopy leaf area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data. J. Geophys. Res. 103: 32,257–32,275.

Law, B. E., F. M. Kelliher, D. D. Baldocchi, P. M. Anthoni, and J. Irvine. 2001. Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. Agric. For. Meteorol. 110: 27–43.

———, P. Thornton, J. Irvine, S. Van Tuyl, and P. Anthoni. 2001. Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Global Change Biol. 7: 755–777.

Li, X., A. H. Strahler, and C. E. Woodcock. 1995. A hybrid geometric optical–radiative transfer approach for modeling albedo and directional reflectance of discontinuous canopies. IEEE Trans. Geosci. Remote Sens. 33: 466–480.

Meyer, P., K. Staenz, and K. I. Itten. 1996. Semi-automated procedures for tree species identification in high spatial resolution data from digitized colour infrared aerial photography. J. Photogram. Remote Sens. 51: 5–16.

Montgomery, R. A., and R. L. Chazdon. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology 82: 2707–2718.

Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala. 2001. A method for scaling vegetation dynamics: The ecosystem demography model. Ecol. Monogr. 71: 557–585.

Mulkey, S. S., R. L. Chazdon, and A. P. Smith. 1996. Tropical forest plant ecophysiology. Chapman and Hall, New York, New York.

Myneni, R. B., and G. Asrar. 1993. Radiative transfer in 3-dimensional atmosphere vegetation media. J. Quant. Spectros. Rad. Trans. 49: 585–598.

———, R. R. Nemani, and S. W. Running. 1997. Estimation of global leaf area index and absorbed PAR using radiative transfer models. IEEE Trans. Geosci. Remote Sens. 35: 1380–1393.

Pereira, R., Jr., J. C. Zweede, G. P. Asner, and M. Keller. 2002. Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. For. Ecol. Manage. 168: 77–89.

Pitkänen, J. 2001. Individual tree detection in digital aerial images by combining locally adaptive binarization and local maxima methods. Can. J. For. Res. 31: 832–844.

RADAMBRASIL. 1983. Levantamento de Recursos Naturais, vols. 1–23. Ministerio das Minas e Energia, Departamento Nacional de Produçao Mineral, Rio de Janeiro, Brasil.

Shugart, H. H., L. Bourgeau-Chavez, and E. S. Kasischke. 2001. Determination of stand properties in boreal and temperate forests using high-resolution imagery. For. Sci. 46: 478–486.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York, New York.

Sommerfeld, R. A., J. E. Lundquist, and J. Smith. 2000. Characterizing the canopy gap structure of a disturbed foresting using the Fourier transform. For. Ecol. Manage. 128: 101–108.

Song, B., J. Chen, P. V. Desanker, D. D. Reed, G. A. Bradshaw, and J. F. Franklin. 1997. Modeling canopy structure and heterogeneity across scales: From crowns to canopy. For. Ecol. Manage. 96: 217–229.

Stone, T. A., and P. Lefebvre. 1998. Using multi-temporal satellite data to evaluate selective logging in Para, Brazil. Int. J. Remote Sens. 19: 2517–2517.

St-Onge, B. A., and F. Cavayas. 1997. Automated forest structure from high resolution imagery based on directional semivariogram estimates. Remote Sens. Environ. 61: 82–95.

Swellengrebel, E. J. G. 1959. On the value of large-scale aerial photographs in British Guiana forestry. Emp. For. Rev. 38: 54–64.

Treuhaft, R. N., G. P. Asner, B. E. Law, and S. Van Tuyl. 2002. Forest density profiles from the quantitative fusion of radar and hyperspectral data. J. Geophys. Res. 107: 29–46.

Wadsworth, F. H. 1997. Forest production for tropical America. USDA, Forestry Service, Washington, D.C.

Williams, M. S., W. A. Bechtold, and V. J. LaBau. 1994. Five instruments for measuring tree height: An evaluation. South. J. Appl. For. 18: 76–82.

Wulder, M., K. O. Niemann, and D. G. Goodenough. 2000. Local maximum filtering for the extraction of tree locations and basal area from high spatial resolution imagery. Remote Sens. Environ. 73: 103–114.