

RELATIONSHIP BETWEEN LIDAR METRICS AND ABOVEGROUND BIOMASS IN CLOSED-CANOPY NEOTROPICAL FORESTS

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ABSTRACT

Previous studies have shown that canopy metrics from lidar data are highly correlated with aboveground biomass in a variety of closed-canopy forests, however the generality of these site-specific relationships has remained untested. In this study, we compare relationships between lidar canopy metrics and forest structural summaries from a tropical wet forest site in Costa Rica and across a series of tropical moist forest field sites in Panama. We found that in both regions lidar metrics were strongly correlated with forest structural summaries including mean stem diameter, basal area and aboveground biomass. We also showed that the relationships differed between these regions unless deciduousness of canopy trees in Panama was considered. Adjusting for leaf-drop removed statistically significant differences between the two regions in the relationships between a lidar metric and both mean stem diameter and basal area. The relationships between lidar metrics and aboveground biomass, however, remained significantly different between the two study areas because of different general allometric relationships used to estimate aboveground biomass in tropical wet forests and tropical moist forests. Future efforts should continue to examine climatic factors that may influence the generality of the relationships between lidar metrics and forest structural characteristics, and address the dearth of allometric data on the very large trees that can dominate the biomass of primary tropical forests.

1 INTRODUCTION

Aboveground biomass (the total amount of oven-dried biological material present above the soil surface in a specified area) estimates in forest ecosystems are critical for carbon dynamics studies at multiple scales. These estimates provide initial conditions for ecosystem and biogeochemical models (e.g., Foley et al., 1996; Friend et al., 1997; Hurtt et al., 1998; Potter, 1999) that simulate the exchange of carbon and energy between the atmosphere and forest canopies through time. In addition, knowledge of forest carbon stocks are necessary for carbon flux estimates from deforestation, land cover change, and other disturbances (e.g., Houghton, 1991).

Changes in vertical canopy structure typically accompany changes in aboveground biomass in forest ecosystems. For example, as forests recover from past disturbance events, there are often changes in both the horizontal and vertical distribution of forest structure that are associated with an overall increase in

aboveground biomass (Aber, 1979; Bormann and Likens, 1979; Oliver and Larson, 1990; Richards, 1996). Additionally, variability in environmental conditions (e.g., climatic, edaphic) and disturbance regimes may result in differences in the spatial distribution of aboveground biomass and vertical canopy structure (e.g., Clark and Clark, 2000; Laurance et al., 1999; Lieberman et al., 1996; Yamakura et al., 1996). For example, in nutrient poor areas, forests typically are lower-stature and contain less aboveground biomass than in nutrient rich areas (Kimmins, 1997; Oliver and Larson, 1990).

Lidar (**light detecting and ranging**) remote sensing has proven to be an efficient tool for the characterization of forest structure in a variety of forest environments (Drake et al., In press; Magnussen et al., 1999; Means et al., 1999; Nelson et al., 1988). Because lidar instruments sample the vertical distribution of canopy (e.g., leaves and branches) and ground surfaces (Blair and Hofton, 1999; Dubayah and Drake, 2000; Dubayah et al., 2000; Harding et al., 2001) and because of ecological and

biomechanical links between biomass and vertical structure (Franco and Kelly, 1998; Givnish, 1986; King and Loucks, 1978; O'Neill and DeAngelis, 1981; Oohata and Shinozaki, 1979), recent studies have found a strong correlation between lidar metrics and aboveground biomass (Drake et al., In press; Lefsky et al., 1999; Means et al., 1999; Nelson et al., 1988).

However, the relationships that have been developed between lidar metrics and aboveground biomass (e.g., Means et al. 1999, Drake et al. In press) are site specific and there have been no attempts to compare relationships developed in areas with different environmental conditions. Global terrestrial biomass estimates from future spaceborne lidar instruments such as the Vegetation Canopy Lidar (Dubayah et al., 1997) and the Ice, Cloud, and Land Elevation Satellite (Schutz, 1998) depend on an examination of the generality of these relationships in different regions and biomes.

In this study we examine the relationship between lidar metrics and aboveground biomass in closed-canopy Neotropical forest areas with different environmental conditions. We focus on a tropical wet forest (sensu Holdridge et al., 1971) area in Costa Rica, and on a tropical moist forest area in Panama that receives 50-75% less rainfall on average. First we test for differences in the relationships between lidar metrics and forest structural characteristics such as basal area and aboveground biomass at the two study areas. We also explored other factors (e.g., environmental characteristics) that could help explain any differences in the relationships at the two study areas.

2. METHODS

Field data

Data collected as a part of different ongoing field studies at two Central American study area was used in this study. The first study area is the La Selva Biological Station in the Atlantic lowlands of northeastern Costa Rica (McDade et al., 1994). La Selva is a 1540 ha research facility that is comprised of a mixture of primary and secondary tropical forest, agroforestry, and current or abandoned pasture areas. This area receives approximately 4200 mm rainfall per year (OTS, 2001; Sanford Jr. et al., 1994) and is classified as "tropical wet forest" according to the Holdridge classification method (Holdridge et al., 1971).

The second study area is centered on the Isthmus of Panama along the Panama Canal. This area spans a precipitation gradient ranging from approximately 2000 mm rainfall per year on the Pacific coast of Panama to 3000 mm rainfall per year on the Atlantic side (Condit et al., 2000; Pyke et al., In press) and is classified as lowland "tropical moist forest" (Holdridge et al., 1971). Within this broad area, we focus on a series of 1 ha plots distributed throughout this precipitation gradient (Pyke et al., In press), and on the 50 ha research site on Barro Colorado Island (Condit, 1998).

In the Costa Rica study area, field data were collected in eighteen 0.5 ha primary forest plots (Clark and Clark, 2000), and 3 secondary forest areas of 14, 22 (Guariguata et al., 1997; Nicotra et al., 1999) and 31 (Pierce, 1992) years since abandonment as of March 1998. In addition, published data for 6 agroforestry plots (Menalled et al., 1998) were included.

At the Panama study area, field data from nineteen 1 ha research plots near the Panama Canal (Pyke et al., In press) were used in this study. Four of these sites are mature secondary forests, and the rest are primary forest (Table 1). The remaining field data in Panama were from the 50 ha plot on Barro Colorado Island (BCI, Condit 1998). The 50 ha plot was first divided into 50 1 ha square plots. Next, the spatial correlation length of the lidar metrics used in this study (metrics discussed below) was determined to be approximately 90 m so every other 1 ha plot was discarded to maintain relative independence of the independent variable in the regression analysis. This left a total of 25 1 ha plots from BCI in a checkerboard pattern.

Table 1. Forest structural summaries for all field data used in this study.

Study Site	Land Cover Type	Number of Sites	Mean QMSD (cm)	Mean Basal Area (m ² ha ⁻¹)	Mean Estimated AGBM (Mg ha ⁻¹)
BCI, Panama	Primary Forest	25	28.16	26.27	286.77 *
Panama Canal Plots	Primary Forest	15	26.69	25.23	257.73 *
	Secondary Forest	4	24.35	26.89	277.91 *
La Selva Biological Station, Costa Rica	Primary Forest	18	20.76	23.6	160.5**
	31 yr Secondary Forest	1	22.24	26.71	147.7**
	22 yr Secondary Forest	1	12.85	22.05	129.4**
	14 yr Secondary Forest	1	10.46	14.28	78.5**
	Agroforestry	6	9.03	14.48	34.3

* Estimated aboveground biomass (Mg/ha) using general equation for tropical moist forests (Brown 1997)
 ** Estimated aboveground biomass (Mg/ha) using general equation for tropical wet forests (Brown 1997)

In all forest plots at both study areas, stem diameters were measured in a marked location either at breast height or, when necessary, above buttressing (see methods in Clark and Clark, 2000; Condit, 1998). Stem diameter measurements were used to estimate aboveground biomass values for each measured tree using general allometric equations (Brown, 1997) for tropical wet forests (Equation 1) at the Costa Rica study area, and for tropical moist forests (Equation 2) at the Panama study area. Stem diameters were also used to calculate quadratic stem diameter and basal area for each plot.

$$\text{Equation 1. } \text{AGBM}_s = 21.297 - 6.953(\mathbf{D}) + 0.740(\mathbf{D}^2)$$

Where **D** is the stem diameter in cm, and **AGBM_s** is the estimated oven-dried AGBM for the stem in kg

$$\text{Equation 2. } \text{AGBM}_s = \exp(-2.134 + 2.530 \cdot \ln(\mathbf{D}))$$

Where **D** is the stem diameter in cm, and **AGBM_s** is the estimated oven-dried AGBM for the stem in kg

Plot-level values of estimated aboveground biomass were then calculated by summing all estimated stem-level aboveground biomass values and converting to standard units (Mg/ha). Sixteen plots at the Panama study area contained stems whose diameters were larger than the maximum diameter used to develop the original allometric equation (Equation 2), therefore, only plots that contained stems within this regression range (<150 cm) were used in the regression analysis comparing lidar metrics with EAGB. However, all plots were used in the regression analysis involving lidar metrics and QMSD or basal area.

Lidar data

Lidar data were collected over both study areas in March 1998 using the Laser Vegetation Imaging Sensor (LVIS, Blair et al., 1999; Dubayah et al., 2000). LVIS is an airborne scanning laser altimeter that measures the roundtrip time for pulses of near-infrared laser energy to travel to the surface and back. The incident energy pulse interacts with canopy (e.g., leaves and branches) and ground features and is reflected back to a telescope on the instrument. Unlike most other laser altimeters, LVIS digitizes the entire time-varying amplitude of the backscattered energy (in 30 cm vertical bins). This yields a “waveform” or profile related to the vertical distribution of intercepted surfaces from the top of canopy to the ground within each 25 m footprint (Blair et al., 1999; Dubayah and Drake, 2000; Dubayah et al., 2000). LVIS scanned across a swath of approximately 1 km with a 50% overlap of footprints across swath, and contiguous along-track footprint spacing. At both study areas, only LVIS footprints that were entirely coincident with field plots were included.

The lidar metric that is used in this study is the height of median energy (HOME). HOME is calculated by first identifying the location of the median of the entire signal (i.e. above the noise level), including the energy from both canopy and ground surfaces (Drake et al., In press). This location is then referenced to the ground (the center of the last Gaussian pulse) to derive a height. Plot-level means for HOME were then calculated for all shots that fell within each plot.

Adjustment of lidar HOME for deciduousness in Panama

When the lidar flights occurred in late March 1998, the Panama study area was at the end of its dry season and leaf loss from canopy-forming trees was extensive in some areas. As a result, more of the lidar energy was able to penetrate through the upper canopy, thereby reducing the lidar HOME metric relative to the Costa Rica study area. To compensate for this effect, a proportional adjustment to the HOME metric was made based on the estimated fraction of crown area that was deciduous (FCAD).

The first step was to linearly interpolate between data points for precipitation and the fraction of crown area deciduous as listed in Condit et al. (2000). The relationship (Equation 3) was then used to interpolate FCAD from average precipitation values for

all Panama field plots. Lidar HOME was then proportionally adjusted in these Panama plots by the fraction of crown area deciduous using the relationship in Equation 4.

$$\text{Equation 3. } \mathbf{FCAD} = -0.02 * \mathbf{Rainfall} + 60.27$$

where **Rainfall**=mm/yr and **FCAD**= fraction of crown area deciduous (developed from Condit et al. 2000)

$$\text{Equation 4. } \mathbf{HOME}' = \mathbf{HOME} / (1 - \mathbf{FCAD})$$

where HOME= lidar height of median energy (m) and **FCAD**= fraction of crown area deciduous

Data analysis

A linear regression analysis was used to develop relationships between plot-level averages of lidar HOME and field-derived QMSD, basal area and EAGB for each study area. For each forest structural characteristic (e.g., QMSD), an analysis of covariance (ANCOVA) was then performed to test for significant differences in the slope and intercept of the relationships (Zar, 1996) developed for each site. This process was used for both the normal and deciduous adjusted HOME metrics.

3. RESULTS AND DISCUSSION

Lidar HOME vs. estimated aboveground biomass

The lidar metric HOME is highly correlated with estimated aboveground biomass (EAGB) in both study areas (Figure 1). In the Panama study area, the R^2 value is 0.66 for plots whose tree diameters are all within the range of the general allometric equation (Equation 2), and 0.82 for all Panama plots, with RMSE values of 31.52 Mg/ha and 39.10 Mg/ha respectively. For the Costa Rica relationship, the R^2 value is 0.89 and the RMSE is 22.54 Mg/ha.

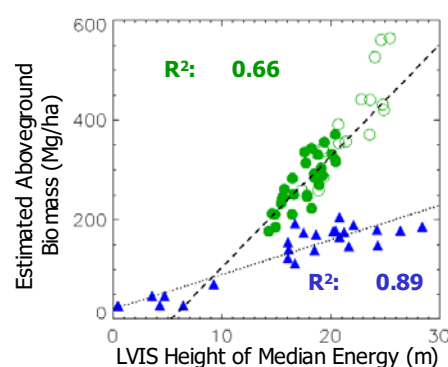


Fig 1. Regression analysis for lidar height of median energy (m) vs. plot-level allometrically-estimated aboveground biomass (Mg/ha) for study areas in Panama (circles, dashed line, upper left R^2) and Costa Rica (triangles, dotted line, lower right R^2). The open circles in the Panama regression relationship indicate plots that contain stems whose diameters are larger than the original distribution sampled to develop the allometric equation (equation 2) and were not included in the regression analysis.

However, there is a great deal of divergence between the relationships for the two study areas (Figure 1). The slope is much greater in the Panama relationship (22.33) compared to the Costa Rica relationship (6.33). The Panama regression equation also has a negative intercept, probably the result of only sampling within relatively high biomass areas. An analysis of covariance (ANCOVA) shows that the slopes and intercepts of these two equations are significantly different ($p < 0.01$).

Lidar HOME vs. basal area and QMSD

Lidar HOME is strongly correlated with quadratic mean stem diameter (QMSD) in both study areas (Figure 2a). The level of variation in QMSD explained by the HOME metric (i.e., the R^2 value) is approximately 92% in the Costa Rica study area compared to 66% in the Panama study area. However, the RMSE in Panama (1.89 cm) is somewhat lower than the value from the Costa Rica relationship (2.09 cm). HOME is also strongly correlated with basal area in both areas (Figure 2b). In this case the level of variation explained is approximately equal for both areas (~70%).

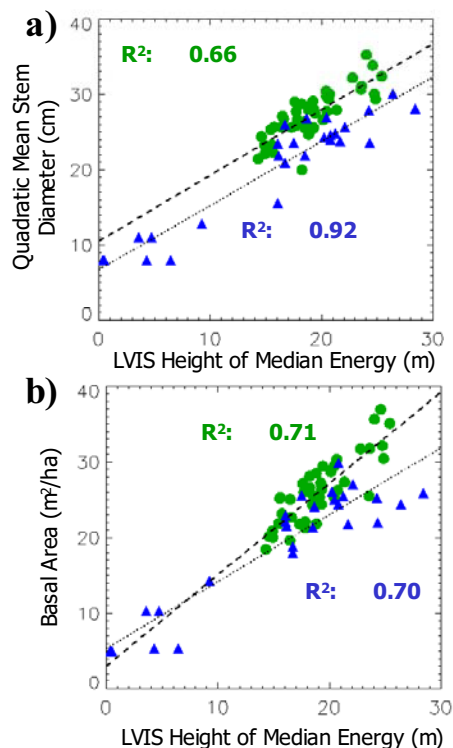


Fig. 2. Regression analysis for lidar height of median energy (m) vs. **a)** plot-level quadratic mean stem diameter (cm) and **b)** plot-level basal area (m^2/ha) for study areas in Panama (circles, dashed line, upper left R^2) and Costa Rica (triangles, dotted line, lower right R^2).

The relationships between lidar HOME and QMSD (Figure 2a) and between HOME and basal area (Figure 2b) are not as divergent at the two study areas as were the relationships between HOME and EAGB (Figure 1). The slopes of the relationships between HOME and QMSD are similar at both

sites, and were not found to be significantly different ($p=0.55$) in an ANCOVA analysis. Intercepts for the HOME-QMSD relationships, however, were found to be significantly different ($p < 0.01$), indicating that the relationships are not equivalent between study sites. Similarly, both the slopes and the intercepts of the HOME-basal area relationships were found to be significantly different between the two study areas, however the y-intercept term in the Panama linear regression relationship was not significantly different from zero ($p=0.19$).

There are two possible reasons for differences in the HOME-basal area and HOME-QMSD relationships between study areas. First, tree diameters could be larger for a given tree height on average at Panama. An analysis of the relationship between stem diameter and stem height from both Panama (based on allometry from BCI in Bohlman et al., In review) and La Selva supports this trend (Drake et al., In review). It is possible that this individual-level relationship could influence the plot-level relationships between lidar HOME and either basal area or QMSD. A second possible explanation is that the drier conditions at Panama resulted in more leaf loss, which in turn lowered lidar HOME values. The HOME metric is determined by the vertical distribution of canopy elements (e.g., leaves and branches), therefore a reduction in leaf abundance of canopy-forming trees in drought-deciduous areas (Condit et al., 2000) would allow more energy to penetrate further into the canopy, thereby lowering the HOME value. We therefore next examine the effect of this deciduousness on the relationship between HOME and forest structural summaries.

Deciduous-adjusted HOME vs. basal area and QMSD

The relationships are much more similar between the two study areas after the proportional adjustment of HOME for the effect of leaf loss of canopy trees (Figure 3a and b). The slope and the intercept from both HOME'-QMSD relationships are not significantly different using an ANCOVA test ($p=0.85$ and 0.21 respectively). Similarly, the difference in slope from the HOME'-basal area relationships in the two study areas is smaller and not significantly different ($p=0.06$). The intercepts in the HOME'-basal area relationships were found to be significantly different ($p < 0.01$) however where the data cover the same range of HOME' and basal areas, the two point clouds now overlap more completely and appear similar (Figure 3b).

Thus, proportional adjustment of lidar HOME metrics by simple fraction of crown area deciduous values eliminated much of the difference between HOME-basal area and HOME-QMSD relationships at both Costa Rica and Panama plots. The minor remaining differences may be the result of small differences in diameter vs. height relationships in both study areas (discussed above) or a difference in the ranges of conditions studied combined with a modest nonlinearity in the underlying causal relationship. In either case, leaf loss in canopy trees at the end of the dry season in Panama was responsible for much of the difference between relationships in these two tropical regions that we found with unadjusted lidar data.

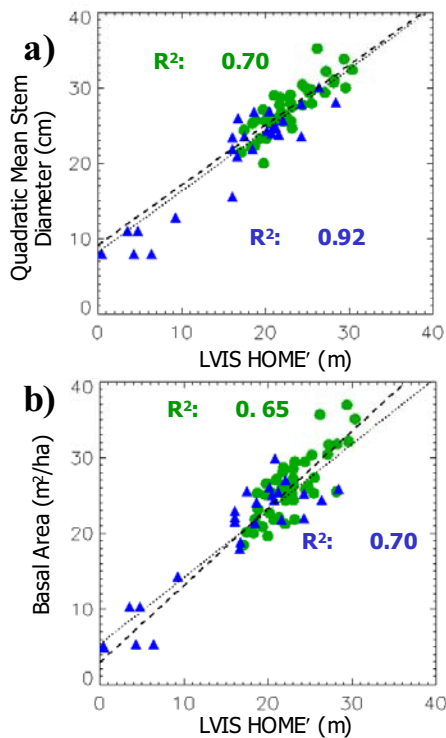


Fig 3. Regression analysis for deciduous-adjusted lidar height of median energy (m) vs. **a)** plot-level quadratic mean stem diameter (cm) and **b)** plot-level basal area (m^2/ha) for study areas in Panama (circles, dashed line, upper left R^2) and Costa Rica (triangles, dotted line, lower right R^2).

Deciduous-adjusted HOME vs. estimated aboveground biomass

The proportional adjustment of lidar HOME did not affect the strength of the relationship between HOME and EAGB at both study areas (Figure 4). The R^2 and the RMSE stayed approximately the same (66% and $\sim 31 \text{Mg}/\text{ha}$ respectively) after HOME values were adjusted. However, although the adjustment did slightly reduce the slope of the Panama relationship (from 22.33 to 21.46), the relationships from the two study areas were still significantly different in both slope and the intercept ($p < 0.01$, from ANCOVA).

The differences in relationships between HOME' and EAGB for the two study areas are most likely the result of using different allometric equations to estimate aboveground biomass from stem diameter in each area. At nearly the same total basal area, Panama sites are calculated to have much larger biomass than nearly all similar sites in Costa Rica (Table 1). This is despite having only minor differences in HOME'-QMSD (Figure 3a) and HOME'-basal area (Figure 3b) relationships after adjustment for leaf loss. As a result, sites at Panama and Costa Rica with nearly identical basal areas and HOME' values may have very different EAGB values.

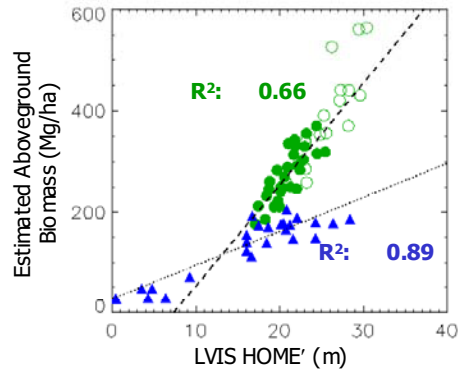


Figure 4. Regression analysis for deciduous-adjusted lidar height of median energy (m) vs. plot-level allometrically-estimated aboveground biomass (Mg/ha) for study areas in Panama (circles, dashed line, upper left R^2) and Costa Rica (triangles, dotted line, lower right R^2). The open circles in the Panama regression relationship indicate plots that contain stems whose diameters are larger than the original distribution sampled to develop the allometric equation (equation 2) and were not included in the regression analysis.

4. CONCLUSIONS

Our results show that relationships between a simple lidar metric (height of median energy) and directly measured forest structural characteristics, such as basal area and QMSD, are nearly identical at both Costa Rica and Panama study areas after accounting for the extensive leaf loss of canopy-forming trees in Panama during the study period (Figure 3a and b). There is still a subtle difference in the HOME'-basal area relationships from the two study areas that could be attributable to differences in the individual-level diameter vs. height allometric relationships for the two sites. Nevertheless, these results illustrate that the same lidar metric, HOME, is strongly correlated with basal area and QMSD. In addition, the relationships appear to be general across both tropical wet and tropical moist forest life zones.

The relationships between lidar metrics and allometrically estimated aboveground biomass are significantly different, however, for these two study areas. Although adjustment for leaf loss slightly improved the agreement between the two site-specific relationships, the two different allometric equations (Equations 1 and 2) used to estimate aboveground biomass lead to significant differences at both study areas.

An assessment of the applicability of these general allometric equations vs. locally-derived allometric equations (cf. Keller et al., In Press) would be beneficial because remotely sensed estimates of biomass (and carbon) are ultimately dependent on allometric relationships. We therefore join with other authors (Brown et al., 1995; Clark and Clark, 2000) who have called for more destructive sampling, especially of sparsely sampled large trees, in different tropical life zones to more rigorously assess the robustness of general allometric equations. Ultimately, this will allow for better broad-scale, remotely sensed aboveground biomass estimates.

Assuming that the general allometric equations used in this study are reasonably accurate, these results have significant implications for how global observations from future spaceborne lidar instruments (e.g., VCL) should be used to produce global estimates of terrestrial aboveground biomass. Our results show that it will likely be necessary to develop unique relationships between lidar metrics and aboveground biomass in different bioclimatic life zones.

Future work in other tropical and extra-tropical forest environments may reveal that it is possible to develop a relatively simple algorithm or model to estimate terrestrial aboveground biomass globally from a suite of lidar and climatic metrics. In more open tropical woodlands, it is likely that additional lidar metrics such as canopy top height and a canopy cover index will be necessary to estimate aboveground biomass accurately. We also expect that the fusion of lidar data with high spatial and temporal satellite imagery will further extend the utility of these data.

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REFERENCES

Aber, J. D., 1979. Foliage-height profiles and succession in Northern hardwood forests. *Ecology*, 60: 18-23.

Blair, J. B., and Hofton, M. A., 1999. Modeling laser altimeter return waveforms over complex vegetation using high-resolution elevation data. *Geophysical Research Letters*, 26: 2509-2512.

Blair, J. B., Rabine, D. L., and Hofton, M. A., 1999. The Laser Vegetation Imaging Sensor (LVIS): A medium-altitude, digitization-only, airborne laser altimeter for mapping vegetation and topography. *ISPRS Journal*

of Photogrammetry and Remote Sensing, 54: 115-122.

- Bohlman, S. A., Condit, R., O'Brien, S. T., Foster, R. B., and Hubbell, S. P., In review. Using species-specific allometric equations to predict canopy structure on Barro Colorado Island, Panama.
- Bormann, B. T., and Likens, G. E. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.
- Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Ferreira, C. A. C., and Victoria, R. A., 1995. Uncertainty in the biomass of Amazonian forests: An example from Rondonia, Brazil. *Forest Ecology and Management*, 75: 175-189.
- Brown, S. 1997. Estimating biomass and biomass change of tropical forests: A primer. *UN-FAO Forestry Paper 134*, Rome, Italy.
- Clark, D. B., and Clark, D. A., 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management*, 137: 185-198.
- Condit, R. 1998. *Tropical Forest Census Plots*. Springer-Verlag, Berlin, Germany.
- Condit, R., Watts, K., Bohlman, S. A., Perez, R., Foster, R. B., and Hubbell, S. P., 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. *Journal of Vegetation Science*, 11: 649-658.
- Drake, J. B., Dubayah, R. O., Clark, D. B., Knox, R. G., Blair, J. B., Hofton, M. A., Chazdon, R. L., Weishampel, J. F., and Prince, S., In press. Estimation of tropical forest structural characteristics using large-footprint lidar. *Remote Sensing of Environment*.
- Drake, J. B., Knox, R., Dubayah, R., Clark, D., and Condit, R., In review. Aboveground biomass estimation in closed-canopy Neotropical forests using lidar remote sensing: Factors affecting generality of relationships. *Global Ecology and Biogeography*.
- Dubayah, R., Blair, J. B., Bufton, J. L., Clark, D. B., JaJa, J., Knox, R. G., Luthcke, S. B., Prince, S., and Weishampel, J. F. 1997. The Vegetation Canopy Lidar mission. Pages 100-112. *Land Satellite Information in the Next Decade II: Sources and Applications*. American Society for Photogrammetry and Remote Sensing, Bethesda, MD.
- Dubayah, R. O., and Drake, J. B., 2000. Lidar remote sensing for forestry. *Journal of Forestry*, 98: 44-46.

- Dubayah, R. O., Knox, R. G., Hofton, M. A., Blair, J. B., and Drake, J. B., 2000. Land surface characterization using lidar remote sensing. Pages 25-38 in M. J. Hill and R. J. Aspinall, eds. *Spatial Information for Land Use Management*. Gordon and Breach Science Publishers, Australia.
- Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A., 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles*, 10: 603-628.
- Franco, M., and Kelly, C. K., 1998. The interspecific mass-density relationship and plant geometry. *Proceedings of the National Academy of Sciences, USA*, 95: 7830-7835.
- Friend, A. D., Stevens, A. K., Knox, R. G., and Cannell, M. G. R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling*, 95: 249-287.
- Givnish, T. J., 1986. Biomechanical constraints on self-thinning in plant populations. *Journal of Theoretical Biology*, 119: 139-146.
- Guariguata, M. R., Chazdon, R. L., Denslow, J. S., Dupuy, J. M., and Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecology*, 132: 107-120.
- Harding, D. J., Lefsky, M. A., Parker, G. G., and Blair, J. B., 2001. Laser altimeter canopy height profiles: Methods and validation for closed-canopy, broadleaf forests. *Remote Sensing of Environment*, 76: 283-297.
- Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T., and J. A. Tosi, J. 1971. *Forest Environments in Tropical Life Zones: A Pilot Study*. Pergamon Press, New York, NY.
- Houghton, R. A., 1991. Tropical deforestation and atmospheric carbon dioxide. *Climatic Change*, 19: 99-118.
- Hurt, G. C., Moorcroft, P. R., Pacala, S. W., and Levin, S. A., 1998. Terrestrial models and global change: challenges for the future. *Global Change Biology*, 4: 581-590.
- Keller, M., Palace, M., and Hurt, G. C., In Press. Biomass estimation in the Tapajos National Forest, Brazil: Examination of sampling and allometric uncertainties. *Forest Ecology and Management*.
- Kimmins, J. P. 1997. *Forest Ecology: A Foundation for Sustainable Management*. Prentice-Hall, Inc., Upper Saddle River, NJ.
- King, D., and Loucks, O. L., 1978. The theory of tree bole and branch form. *Radiation and Environmental Biophysics*, 15: 141-165.
- Laurance, W. F., Fearnside, P. M., Laurance, S. G., Delamonica, P., Lovejoy, T. E., Rankin-de Merona, J., Chambers, J. Q., and Gascon, C., 1999. Relationship between soils and Amazon forest biomass: A landscape-scale study. *Forest Ecology and Management*, 118: 127-138.
- Lefsky, M. A., Harding, D., Cohen, W. B., Parker, G., and Shugart, H. H., 1999. Surface lidar remote sensing of basal area and biomass in deciduous forests of eastern Maryland, USA. *Remote Sensing of Environment*, 67: 83-98.
- Lieberman, D., Lieberman, M., Peralta, R., and Hartshorn, G. S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, 84: 137-152.
- Magnussen, S., Eggermont, P., and LaRiccia, V. N., 1999. Recovering tree heights from airborne laser scanner data. *Forest Science*, 45: 407-422.
- McDade, L. A., Bawa, K. S., Hespeneide, H. A., and Hartshorn, G. S., eds. 1994. *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago.
- Means, J. E., Acker, S. A., Harding, D. J., Blair, J. B., Lefsky, M. A., Cohen, W. B., Harmon, M. E., and McKee, W. A., 1999. Use of large-footprint scanning airborne lidar to estimate forest stand characteristics in the Western Cascades of Oregon. *Remote Sensing of Environment*, 67: 298-308.
- Menalled, F. D., Kelty, M. J., and Ewel, J. J., 1998. Canopy development in tropical tree plantations: A comparison of species mixtures and monocultures. *Forest Ecology and Management*, 104: 249-263.
- Nelson, R., Krabill, W., and Tonelli, J., 1988. Estimating forest biomass and volume using airborne laser data. *Remote Sensing of Environment*, 24: 247-267.
- Nicotra, A. B., Chazdon, R. L., and Iriarte, S. V. B., 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology*, 80: 1908-1926.
- Oliver, C. D., and Larson, B. C. 1990. *Forest Stand Dynamics*. McGraw Hill, New York.

- O'Neill, R. V., and DeAngelis, D. L., 1981. Comparative productivity and biomass relations of forest ecosystems. Pages 411-449 in D. E. Reichle, ed. *Dynamic properties of forest ecosystems*. Cambridge University Press, Cambridge.
- Oohata, S., and Shinozaki, K., 1979. A statical model of plant form— Further analysis of the pipe model theory. *Japanese Journal of Ecology*, 29: 323-335.
- OTS, Organization for Tropical Studies 2001 La Selva Biological Station: Meterological data (1957-2001), Available at: <http://www.ots.duke.edu/en/laselva/>
- Pierce, S., 1992. La Selva Biological Station history: colonization/landuse/deforestation of Sarapiquí, Costa Rica. M.S. thesis, Colorado State University. Fort Collins, CO.
- Potter, C. S., 1999. Terrestrial biomass and the effects of deforestation on the global carbon cycle - Results from a model of primary production using satellite observations. *Bioscience*, 49: 769-778.
- Pyke, C. R., Condit, R., Aguilar, S., and Lao, S., In press. Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*.
- Richards, P. W. 1996. *The Tropical Rain Forest: An Ecological Study*. Cambridge University Press, New York.
- Sanford Jr., R. L., Paaby, P., Luvall, J. C., and Phillips, E., 1994. Climate, geomorphology and aquatic systems. Pages 106-119 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. University of Chicago Press, Chicago.
- Schutz, B. E., 1998. Spaceborne laser altimetry: 2001 and beyond. in H. P. Plag, ed. *Book of Extended Abstracts, WEGENER-98*. Norwegian Mapping Authority, Honefoss, Norway.
- Yamakura, T., Kanzaki, M., Itoh, A., Ohkubo, T., Ogino, K., Chai, E., Lee, H. S., and Ashton, P. S., 1996. Forest structure of a tropical rain forest at Lambir, Sarawak with special reference to the dependency of its physiognomic dimensions on topography. *Tropics*, 6: 1-18.
- Zar, J. H. 1996. *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, NJ.