Co-Registered Aerial Stereopairs from Low-Flying Aircraft for the Analysis of Long-Term Tropical Rainforest Canopy Dynamics

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Abstract

Ground-based censusing of tagged trees in permanent plots has been the standard research method for monitoring the long-term dynamics of tropical rainforest tree populations. This paper describes a method for quantifying the turnover and crown growth rates of tropical rainforest canopy trees over an 18-year period using a temporal sequence of large-scale aerial stereopairs. The stereopairs were co-registered using an array of control points that consisted of surveyed aerial targets and primary branch bifurcation points (BIPs) having the same persistent geometry and spatial coordinates in the crowns of selected canopy trees.

Six crown size classes were distinguished, and critical late stages in the life history of mature canopy trees were identified. The smallest crown size classes (<20 and 20 to 40 m^2) experienced more than 75 percent of the canopy tree mortality over the 18-year period. Of the canopy trees that survived, the mid-range 60- to 80-m^2 crown size class was identified as a critical late stage, having both the highest mean crown growth rate (2.42 m^2 yr^{-1}) among those trees that exhibited positive growth as well as the highest proportion of trees (47 percent) experiencing a reduction in crown size. The results demonstrate that high resolution, aerial stereophotography from low-flying aircraft can serve as a valuable tool for demographic research in tropical rainforest ecosystems.

Introduction

Tropical rainforest canopies represent complex assemblages of tree crowns competing for solar irradiance. The long-term dynamics of these assemblages are of interest because of their influence on the structure and function of tropical rainforest ecosystems (Connell *et al.*, 1984; Hubbell and Foster, 1990; Carey *et al.*, 1994). Most studies on the growth rates and turnover of tropical rainforest tree populations have involved ground-based monitoring of dbh (trunk diameters at breast height) in permanent plots (e.g., Lang and Knight, 1983; Lieberman and Lieberman, 1987; Manokaran and Kochummen, 1987; Whitmore, 1989; Herwitz and Young, 1994; Condit *et al.*, 1996). Trees are tagged and periodic stem reinventories are conducted for the quantification of survivorship, mortality, recruitment, and dbh growth increments. The standard trunk size for inclusion in such a demographic study is ≥10 cm dbh. This ground-based approach, however, does not provide a direct measure of the spatial and temporal patterns of crown development.

When considering how size differences may be an important factor determining the coexistence of canopy trees, most workers think in terms of dbh or tree height (Kohyama, 1993; Thomas, 1996). Projected crown areas are not often considered because of the difficulty of measurement. What is the long-term growth rate of canopy tree crowns? What is the relationship between survivorship probability and crown size? One of the major limitations of dbh measurements is that they do not provide any indication of reductions in crown area. What is the extent and frequency of long-term reductions in crown area caused by lateral shading and branch breakage? Sapwood has been suggested as an indicator of tree fitness because of its presumed positive correlation with the surface area of photosynthetically active foliage (Waring *et al.*, 1977), but there are several sampling limitations, including representativeness of tree cores and the number of trees that can be practically monitored over time by repeated sampling. Direct measures of changes in crown area from an aerial perspective would provide not only a meaningful growth index, but also would serve as a guide to tree fitness. Photogrammetric analysis of aerial stereophotographs from low-flying aircraft is the logical method for resolving individual canopy tree crowns and addressing these research issues.

Limitations that commonly face airborne studies in tropical rainforest sites include unfavorable cloud cover, few landmark features to use as ground control points, and a high density of canopy tree crowns that often confounds conventional photogrammetric procedures (Arp *et al.*, 1982). In most closed canopy forests, quantitative assessments of canopy tree crowns have been approximated by ground-based photography (Anderson, 1964; Turton, 1988; McIntire *et al.*, 1990) or ground-based surveying (Young and Hubbell, 1991; Sumida, 1995). This paper describes a method of co-registering and analyzing a temporal sequence of large-scale aerial stereopairs of a tropical rainforest stand for the direct measurement of canopy tree crowns. Recognizing the usefulness of long-term databases for testing models of forest dynamics

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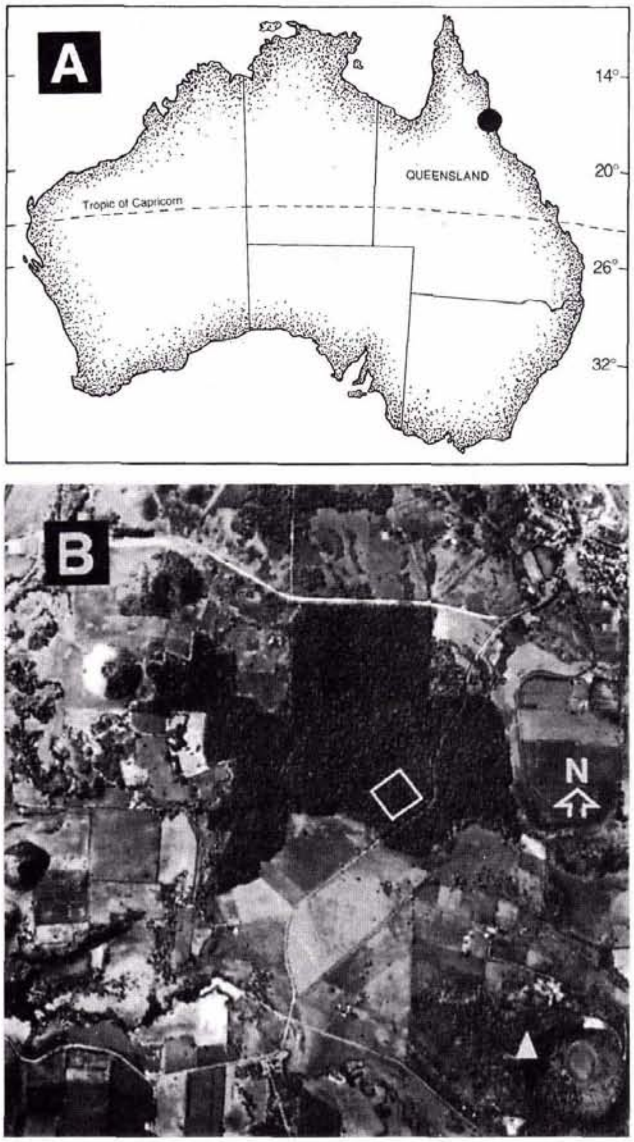

Figure 1. (A) Location of Atherton Tableland in northeast Queensland, Australia. (B) Aerial view of Curtain Fig Forest (CFF) surrounded by cleared land on the Atherton Tableland. The white outline in the CFF defines the 3.6-ha sample area. *The white triangle symbol in the southeastern* corner corresponds to the summit of Mount Quincan.

(Swaine *et al.*, 1987; Vanclay, 1989; Kohyama, 1993), the objective was to quantify long-term mortality, survivorship, and changes in projected crown area as a function of crown size. Our study tested the hypothesis that canopy tree death rates and growth rates are independent of crown size.

Study Site

The tropical rainforest selected for study was Queensland State Forest No. 452 located 700 m ASL on the Atherton Tableland in northeast Queensland, Australia (17°16'S, 145°35'E) (Figure 1). The stand is 258 ha in areal extent, and is locally referred to as the Curtain Fig Forest (CFF). With canopy tree heights ranging between 25 and 42 m (Myers and Benson, 1981; Herwitz, 1982), the structure of the CFF has a greater resemblance to lowland tropical rainforest than to montane rainforests. In the Australian physiognomic classification system (Webb, 1959), the CFF is considered a complex notophyll vine forest type (Myers, 1982; Turton, 1988) that is more generally defined as a submontane tropical rainforest.

In late July 1976, Myers and Benson (1981) conducted a series of overflights in a Cessna 182 for aerial photography of the CFF canopy. Stereopairs (1:2000 to 1:6000 scale) were obtained using Vinten and Hasselblad 70-mm cameras, and Kodak 2445 aerocolor negative film at flight heights of 500 to 800 m. Their objective was to assess the usefulness of large-scale aerial stereopairs for canopy tree species identification. The result was a set of high quality color prints and diapositives in which individual canopy tree crowns could be readily resolved.

At the time of the Myers-Benson overflights in 1976, ground control markers at the CFF site were not installed. The CFF, however, stands isolated as a protected forest island because of extensive clear-cutting on the Atherton Tableland. Unobstructed by the forest cover, the surrounding pasture and the paved road passing through the forest interior (Figure 1B) provide open sites for the installation of ground control markers. In addition, a 35-m-tall scaffolding tower stands above a section of the CFF canopy (Figure 2) in close proximity to the paved road. The tower was constructed by the CSIRO Division of Forest Research in 1984.

Materials and Methods

Our study involved replicating the Myers-Benson flight sequence over the same section of the CFF canopy 18-years

Figure 2. Ground-based view of above-canopy tower in the CFF study site.

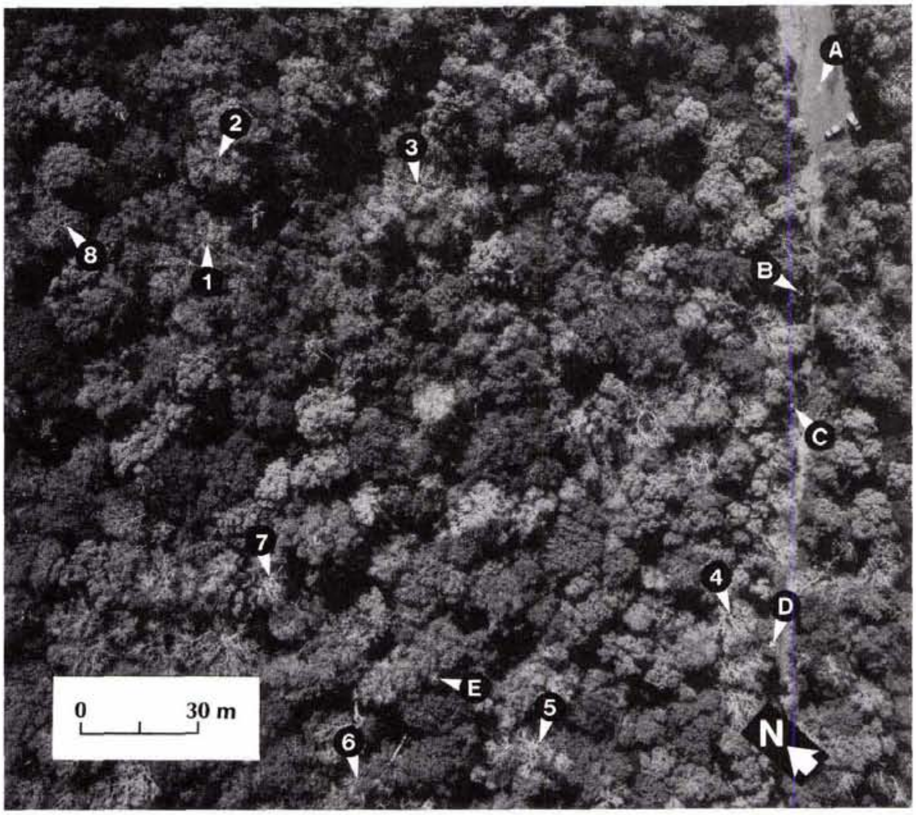

Figure 3. Close-up aerial view of a section of the CFF sample area from the 1994 overflight showing selected aerial targets (**A** to **E**) and primary branch bifurcation points (BIPs #1 to #8).

later in 1994 for the acquisition of a comparable set of aerial stereopairs. This was accomplished using a similar aircraft, a calibrated Wild RC8 aerial camera equipped with a 152.625-mm focal-length lens, and Kodak 2445 aerocolor negative film. The CFF canopy was photographed at the same time of year (late July) and at the same time of day (late morning). Flight departure was from the Mareeba Aerodrome located on the Atherton Tableland 10 km north of the CFF. Flight heights ranged from 229 to 458 m for the acquisition of stereopairs at scales ranging from 1:1500 to 1:3000. Flight lines into the prevailing southeasterly winds made it possible to fly at lower altitudes, maintain aircraft horizontally (tilt angle $<2°$), and obtain >50 percent overlap in the stereopairs. Coverage of each of the 23- by 23-cm images ranged from 12 to 24 ha. The section of the CFF canopy selected for tree crown analysis covered an area of 3.6 ha (Figure 1B).

Before the 1994 flight sequence, a topographic survey (± 5 cm accuracy) was conducted for the installation of ground-based aerial targets at defined *X*, *Y*, and *Z* metric coordinates in the Australian Map Grid (AMG, Zone 55). The starting reference point was the summit of nearby Mount Quincan (887.81 m ASL) located 1620 m from the CFF (Figure 1B). The survey proceeded to the CFF with the systematic emplacement of permanent spikes flush with the ground at open locations unobscured by the forest cover. The spikes were represented as aerial targets that consisted of white cross markers measuring 1 m in length. A total of 13 aerial targets were installed: five in the surrounding pasture, seven on the paved road, and one atop the above-canopy tower. Examples of these targets, labeled A through E, are shown in Figure 3.

Co-registering the Myers-Benson 1976 stereopairs with the 1994 set was the prerequisite for quantifying changes in the CFF canopy. The 1994 stereopairs were first stereorectified using a Leica BC1 stereoplotter and the installed aerial targets as the initial set of ground control points. The rectified 1994 imagery was then used to define the AMG image coordinates of shared primary branch bifurcation points (BIPs) that were present in the same position in the 1976 stereopairs. Eight BIPs having the same approximate dimensions as the aerial cross targets were selected and are identified in Figure 3. Co-registration was achieved using the shared BIPs as control points to rectify the 1976 imagery.

Primary branches, which are the woody appendages radiating directly from tree trunks, bifurcate into secondary branches at branch points (Morgan and Cannell, 1988; Pertunen *et al.*, 1996). Due to the apical growth of the leading shoots of trees, primary branches maintain the same position relative to the trunk from which they radiate. They do not become raised off the ground through time. This would only be the case for plants that grow from basal (not apical) meristems (Zimmerman and Brown, 1971). With a distinctive geometry involving branch diameters exceeding 10 cm, the BIPs of mature tropical canopy trees often maintain fixed spatial coordinates much like the crotches of divergent tree trunks. Secondary trunk lean or branch breakage would be exceptions to the condition of BIPs having fixed spatial positions. The selected BIPs had no evidence of these secondary changes, maintaining the same distinctive geometry and position within the tree crown.

Seven of the selected shared BIPs (1 through 7 in Figure 3) were in the crowns of the seasonally deciduous canopy tree species *Toona ciliata* F. Muell. In many tropical rainforests, foliage obscures the woody frames and BIPs of canopy trees from aerial view; however, in the CFF, the leafless condition of *T. ciliata* during the southern hemisphere winter months of July-August made it possible to use geometrically distinctive BIPs in the crowns of selected individuals that survived from 1976 to 1994. *Toona ciliata* (formerly *Toona australis*) of the Meliaceae family is a relatively common tree species in northeast Queensland (Francis, 1951) and in the CFF (Myers and Benson, 1981; Herwitz, 1993). When well developed canopy trees representing this species are in a leafless condition, their BIPs are clearly visible in large-scale aerial photographs. One of the selected BIPs (#8 in Figure. 3) was from the evergreen species *Aleurites moluccana* which is characterized by widely spreading crowns and aggregated clumps of foliage that do not fully obscure its primary branches.

Once the BIPs were selected, individual canopy tree crowns were distinguished on the basis of their color, texture, and 3D morphology. Crown perimeters were mapped by stereoviewing of the diapositives and by detailed examination of positive prints enlarged to 1:335 scale. Crowns that were only partially exposed and lacked well defined perimeters were not included. The crown perimeters and BIPs in each set of stereopairs were traced onto stable-base plastic transparencies overlying the enlarged prints, and then digitized into AutoCAD using a Summagraphics digitizing tablet. Using the shared BIPs as control points, the images were rectified in AutoCAD using a projective transformation, and the projected area and perimeter of each definable canopy tree crown were computed. The transformations were statistically significant at the 0.01 level.

The trees were grouped into six projected crown area size classes: (1) <20 m^2, (2) 20 to 40 m^2, (3) 40 to 60 m^2, (4) 60 to 80 m^2, (5) 80 to 100 m^2, and (6) >100 m^2. Our null hypothesis was that there was no difference between these size classes in terms of survivorship and crown growth rates. Mortality was quantified on the basis of crowns delimited in the 1976 imagery that could not be re-identified in the 1994 imagery. The change in the projected crown area of each canopy tree that survived from 1976 to 1994 was the basis for determining the rate of crown growth or crown reduction. Changes in crown area were computed in absolute units of m^2 and as percent changes from the tree's crown area in 1976. One-way ANOVAs were used to test for differences in crown growth among the six crown size classes. Pairwise comparisons of the six size classes were made using Duncan's multiple-range test. The spatial patterning of mortality, survivorship, and changes in crown area was represented by rebuilding the AutoCAD coverage into a format suitable for GIS mapping in ArcView (Version 3.0).

In 1976, a permanent 0.5-ha sample plot (50 by 100 m) was established close to the center of our 3.6-ha sample area for a ground-based inventory of trees ≥10 cm dbh (Stocker *et al.*, 1995). The results of the ground-based inventory were compared with our aerial inventory of canopy trees.

Results

Stand Characteristics

A total of 443 canopy trees were delimited in the 3.6-ha sample area in the 1976 aerial stereopairs (Figure 4). The forest floor was not visible in any of the stereopairs. The spaces between crowns evident in Figure 4 represent subcanopy assemblages in which individual tree crowns could not be distinguished. The stand density of canopy trees with crowns that could be clearly defined was thus equivalent to 123 trees ha^{-1}. This stand density is much less than the values

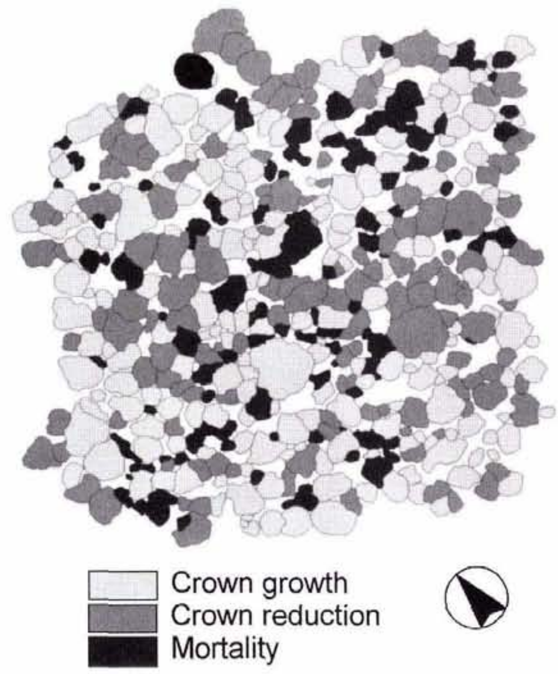

Figure 4. Map of projected crown areas of definable canopy trees in the CFF sample area in 1976 showing the spatial distribution patterns of mortality, positive crown growth, and reductions in crown area over the 18-year period 1976-1994.

commonly recorded for tropical rainforests from ground-based inventories. In most tropical rainforests, the stand density of trees ≥10 cm is >300 trees ha^{-1} (e.g., Herwitz, 1981; Lieberman *et al.*, 1985; Proctor *et al.*, 1988; Carey *et al.*, 1994; Condit *et al.*, 1996).

In the 0.5-ha permanent plot, the stand density of trees ≥10 cm dbh was 624 trees ha^{-1}. In the 1976 stereopairs, a total of 87 canopy trees were delimited in the same area, yielding a stand density of 174 trees ha^{-1}. These findings indicate that only 28 percent of trees ≥10 cm dbh had their crowns exposed in the upper canopy; the other 72 percent had crowns in a subcanopy position that could not be discerned in the stereopairs. Airborne remote sensing, thus, provided a means for quantifying the extent of full canopy exposure of tropical rainforest tree crowns in populations of stems measuring ≥10 cm dbh.

The projected crown perimeters were quite variable. Some crowns had very irregular perimeters due to deep indentations often associated with an abutting crown of a neighboring canopy tree. Others were more rounded and elliptic. The scatter of crown perimeters as a function of crown area increased most dramatically among canopy trees with crown areas exceeding 40 m^2 (Figure 5). This finding may be attributable to the complex life histories of canopy trees (Clark and Clark, 1992) involving branch breakage and asymmetric crown development (Young and Hubbell, 1991; Herwitz *et al.*, 1994).

Survivorship and Mortality

Survivorship over the 18-year period amounted to 74.5 percent of the 443 canopy trees delimited in the 1976 stereopairs. With a canopy tree stand density of 123 trees ha^{-1}, 25.5 percent mortality represents an average canopy tree

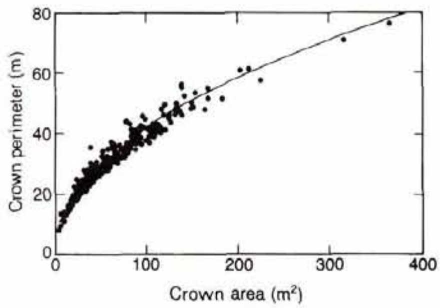

Figure 5. Relationship between crown perimeter and crown area based on condition of canopy trees delimited in 1976 stereopairs. Best-fit curve shown in relation to scatter of data points representing 443 canopy trees.

death rate of 31.4 trees ha^{-1}/18 yrs, which is equivalent to 1.74 trees ha^{-1} yr^{-1} or 1.4 percent yr^{-1}. At this rate of canopy tree turnover in the CFF, the average life expectancy of canopy trees would be approximately 71 years. This life expectancy is comparable to ground-based long-term assessments in other tropical rainforests. For example, in old growth forest on Barro Colorado Island in Panama, Putz and Milton (1982) estimated average life spans ranging from 79 to 122 years for trees ≥19 cm dbh. In a review of long-term inventories conducted in tropical forests, Phillips and Gentry (1994) reported a mean annual mortality rate of 2.0 percent yr^{-1}, with values ranging from 0.5 to 3.6 percent yr^{-1}.

The crown size class distributions of survivorship and mortality differed markedly (Figure 6). More than 75 percent of the canopy trees that died were in the smaller <20 m^2 and 20 to 40 m^2 size classes. Only 11.5 percent were in the ≥60 m^2 size classes. More than 35 percent of the survivors were in the ≥60 m^2 size classes. Large crown size was not positively correlated with the higher mortality probabilities;

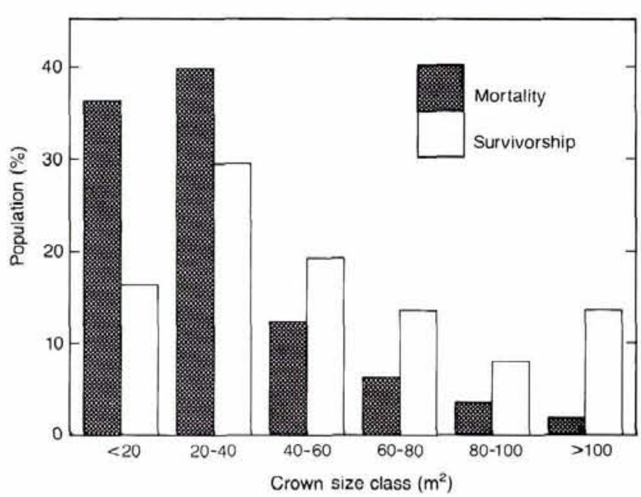

Figure 6. Size class population distributions expressed as a percentage of trees that died in the mortality grouping and as a percentage of trees that survived in the survivorship grouping over the 18-year period.

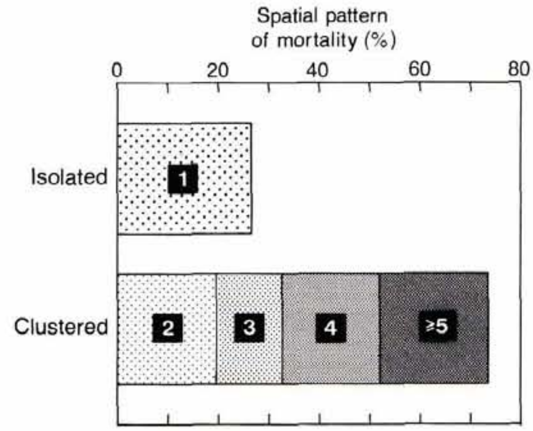

Figure 7. Bar graph showing the spatial pattern of mortality expressed as a percentage of the trees that died, and subdivided into the categories of spatially isolated mortality and spatially clustered mortality. The boxed numbers indicate the number of trees including neighbors that died in each mortality grouping.

rather, it was the smaller canopy trees, which were unable to fully expand their crowns, that had the higher death rates. This finding is contrary to the widely held view that tree death rates in tropical rainforest ecosystems are independent of tree size class for individuals ≥10 cm dbh (Clark and Clark, 1996).

Mortality had a clustered distribution pattern (Figure 4). Clustered mortality was defined as involving crowns in the 1976 imagery that either abutted each other at some point along their perimeter or were separated by a distance of <2 m. Of the 113 canopy trees that died, only 26.5 percent were spatially isolated from other trees that died. Most of these cases of isolated mortality involved trees in the smaller crown size classes (<20 and 20 to 40 m^2). The other 73.5 percent of the trees that died were part of a mortality cluster that involved groupings of other deceased neighboring canopy trees ranging in number from 2 to ≥5 individuals (Figure 7). Mortality clusters are suggestive of a tree toppling domino effect associated with high wind speeds or possibly a biological factor (e.g., root pathogens).

Wet season depressions over the Coral Sea often intensify into cyclones, subjecting northeast Queensland (including the Atherton Tableland) to a relatively high frequency of rainfall events associated with strong winds that cause treefall disturbances and branch breakage among canopy trees (Webb, 1958). The CFF was periodically subject to strong wind conditions during the period 1976 to 1994. In 1986, Northeast Queensland was most severely affected by Cyclone Winifred; however, its effects on the Atherton Tableland were limited, involving moderate canopy disturbance consisting of foliage removal and branch breakage on topographic highs (Unwin *et al.*, 1988; Turton, 1992). If wind-induced tree toppling was the cause of mortality in the CFF, then the mortality clusters would be oriented in a northwesterly direction in conformity with the prevailing southeasterlies on the Atherton Tableland (Herwitz and Slye, 1996). Most of the clusters were oriented in a northeast-southwest direction (Figure 4). Subdividing the 3.6-ha sample area into equal-sized directional quadrants revealed that 68.1 percent of the mortality was concentrated in the northeast and southwest quadrants,

Table 1. One-Way Analysis of Variance of Changes in Crown Area as a Function of Crown Size Class

	SS	df	MS	F	P
Crown growth (m^2 yr^{-1})					
Size class	56.25	5	11.25	7.65	<0.001
Error	282.48	192	1.47		
Crown growth (%)*					
Size class	86,999	5	17,400	2.63	<0.05
Error	1,271,610	192	6,623		
Crown reduction (m^2 yr^{-1})					
Size class	42.34	5	8.47	15.89	<0.001
Error	67.15	126	0.53		
Crown reduction (%)*					
Size class	1,908	5	382	1.08	NS
Error	44,628	126	354		

*Change in crown area expressed as a percentage of the crown area in 1976.

with only 13.3 percent in the southeast quadrant and 18.6 percent in the northwest quadrant. Wind disturbance was excluded as the cause of the mortality clusters.

Changes in Crown Area

The mean change in crown area of the 330 canopy trees that survived over the 18-year period was 7.7 ± 28.9 m^2 (± 1 SD). Expressed as a percentage of each tree's crown area in 1976, this change was 24 ± 78 percent. The wide range of variation is explained in part by the reduction in the crown area of 40 percent of the survivors, an unexpectedly large proportion. This relationship between long-term crown growth and crown reduction has not been previously quantified for a tropical rainforest ecosystem. As was the case for mortality, the trees that experienced crown reduction had clustered distribution patterns (Figure 4). More than 70 percent of the trees exhibiting crown reduction were located <2 m from a neighboring canopy tree that also experienced a reduction in crown area.

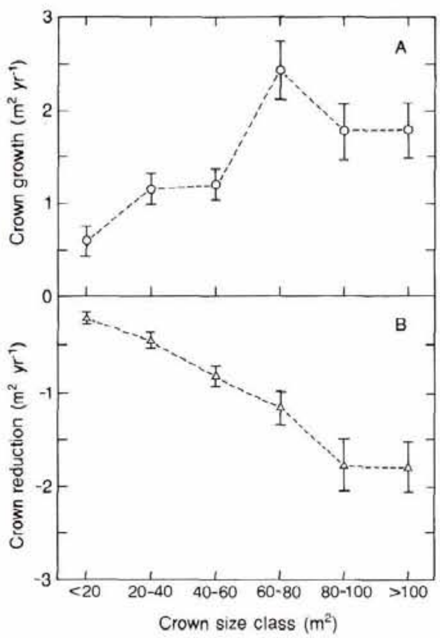

Figure 8. Mean changes in projected crown area (±1 standard error) shown for each crown size class over the 18-year period, expressed in absolute units of m^2 yr^{-1}, and subdivided into groupings of canopy trees with: (A) positive crown growth and (B) reductions in crown area.

Table 2. Duncan's Multiple-Range Test of Crown Size Class Differences in Mean Crown Growth Rate (m^2 yr^{-1})

Crown Size Class (m^2)	Crown Size Class (m^2)				
	<20	20-40	40-60	60-80	80-100
> 100	**	NS	NS	*	NS
80-100	**	NS	NS	*	
60-80	**	**	**		
40-60	NS	NS			
20-40	NS				

**P <0.01; *P <0.05; NS = no significant difference.

In absolute terms, the mean change in crown area of canopy trees with positive growth was 24.1 m^2/18 yrs. Expressed as a mean annual growth rate, this value is equivalent to 1.34 m^2 yr^{-1}. A positive correlation (r = 0.395; P <0.001) was found between mean annual crown growth rate and crown area, but the scatter and confidence limits were quite wide. The best-fit non-linear equation was $y = 0.056(x^{0.69})$, where y is the mean annual growth rate in m^2 yr^{-1} and x is the crown area in m^2. Examples of outliers at the extremes include one of the smallest canopy trees with a crown area of only 10 m^2 that grew at a rate of >5 m^2 yr^{-1}, and the largest canopy tree with a crown area of 365 m^2 that grew at a rate of 1.7 m^2 yr^{-1}.

The one-way ANOVA showed that the mean annual crown growth rates (m^2 yr^{-1}) of the different size classes differed significantly (F = 7.65; P <0.001) (Table 1). The general trend among surviving trees with positive growth was an increase in growth rate as a function of crown size (Figure 8A). The mean growth rates progressively increased from the <20-m^2 to the 40- to 60-m^2 size class, reaching a maximum mean growth rate of 2.42 m^2 yr^{-1} in the 60- to 80-m^2 size class. The rate declined slightly in the 80- to 100-m^2 and >100-m^2 size classes to values of 1.72 and 1.77 m^2 yr^{-1}, respectively. The growth rate of the 60- to 80-m^2 size class was the most significantly different from each of the other size classes (Table 2).

Expressed as a percentage of the crown area in 1976, the mean annual crown growth rate of surviving trees with positive growth was 3.30 percent yr^{-1}. In contrast to the absolute growth rates, the percentage growth rates followed the opposite trend. A negative correlation (r = −0.264, P <0.01) was found between percentage crown growth over the 18-year period and crown area. Therefore, the general trend among surviving trees with positive growth was a decrease in percentage crown growth rate as a function of crown size (Figure 9A). The best-fit equation was $y = 167.8(-29.4 \ln(x))$, where y is the percentage crown growth in m^2/18 yrs and x is the crown area in m^2. The smallest size class (<20 m^2) had both the highest variance and the highest mean value of 4.9 percent yr^{-1}. The mean annual percentage growth rate decreased to 1.4 percent yr^{-1} in the >100-m^2 size class. There was a slight deviation from the downward trend in the more vigorous 60- to 80-m^2 size class which had a mean percentage growth rate of 3.4 percent yr^{-1}. The one-way ANOVA showed that the mean percentage crown growth rates of the different size classes differed at the 0.05 level (Table 1).

The mean change in crown area for the 132 surviving canopy trees that experienced a reduction in their crown areas was −16.1 ± 16.5 m^2/18 yrs (± 1 SD). This value is equivalent to a mean annual crown reduction rate of −0.92

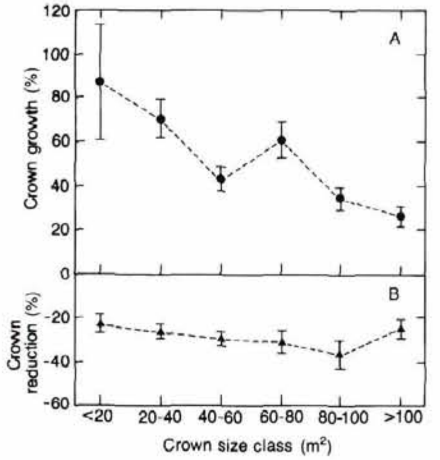

Figure 9. Mean changes in projected crown area (±1 standard error) shown for each crown size class over the 18-year period, expressed as percentages of the crown area in 1976, and subdivided into groupings of canopy trees with: (A) positive crown growth and (B) reductions in crown area.

$m^2\ yr^{-1}$. The crown reduction rate was lowest for the <20-m^2 size class ($-0.21\ m^2\ yr^{-1}$), increasing progressively through each successive size class to the highest mean reduction rate of $-1.81\ m^2\ yr^{-1}$ for the >100-m^2 size class (Figure 8B). A strong negative correlation ($r = -0.596$; $P < 0.001$) was found between crown reduction rate and crown area. The best-fit equation was $y = 2.14 + (-0.79 \ln(x))$, where y is the mean annual crown reduction rate in $m^2\ yr^{-1}$ and x is the crown area in m^2. A highly significant difference between size classes was indicated by the one-way ANOVA ($F = 15.89$, $P < 0.001$) (Table 1). Duncan's multiple-range test showed that the differences were significant in all but four of the pairwise combinations (Table 3).

Expressed as a percentage of each tree's crown area in 1976, the mean annual rate of crown reduction of surviving trees without positive growth over the 18-year period was -1.54 percent yr^{-1}. Unlike the other changes documented above, there was no significant difference between the percentage reductions of the six size classes (Figure 9B). Each size class had a mean value ranging between -1.2 and -2.0 percent yr^{-1}. The 80- to 100-m^2 size class exhibited the highest variance.

When considering the proportion of trees in each size class that experienced a reduction in crown area, there were no marked differences between size classes. Each size class

TABLE 3. DUNCAN'S MULTIPLE-RANGE TEST OF CROWN SIZE CLASS DIFFERENCES IN MEAN CROWN REDUCTION RATE ($M^2\ YR^{-1}$)

Crown Size Class (m^2)	Crown Size Class (m^2) <20	20-40	40-60	60-80	80-100
> 100	**	**	**	*	NS
80-100	**	**	**	*	
60-80	**	**	NS		
40-60	*	NS			
20-40	NS				

$**P < 0.01$; $*P < 0.05$; NS = no significant difference.

had between 32 and 47 percent of its population exhibiting a long-term reduction in crown area. The larger size classes ($>60\ m^2$) had 41 percent to 47 percent of its survivors experiencing crown reductions as compared with 32 percent to 42 percent in the <60-m^2 size classes. The <20-m^2 size class had the lowest proportion of survivors (32 percent) with crown reduction, while the 60- to 80-m^2 size class had the highest proportion (47 percent). The 60- to 80-m^2 size class, thus, appears to be a critical stage at which canopy trees separate into two categories: (1) *vigorous growth*, as evidenced by the highest absolute mean growth rates among trees with positive growth; and (2) *decline*, as evidenced by the highest proportion of individuals exhibiting crown reduction. Canopy trees that maximize vegetative growth with crown sizes of 60 to 80 m^2 will likely have the highest probability of attaining a larger stature and increasing their longevity.

Discussion

Past high-altitude airborne and satellite remote sensing studies of forest canopies have provided measures of a wide range of variables, including forest cover, canopy height, standing biomass, leaf area, productivity, and biochemical content (Vanclay and Preston, 1990; Johnson *et al.*, 1994; Peterson, 1996). With pixel sizes of ≥5 m, the focus has been on integrated measures of entire canopies, not individual tree crowns. Using multispectral satellite data too coarse to resolve individual crowns, Wu and Strahler (1994) estimated crown size and stand density by inverting a canopy reflectance model; the applicability of their procedure to tropical rainforest ecosystems, however, is limited because of their assumption of a simple fixed 3D shape for each crown. Geocoded multisensor databases assembled for a Costa Rican rainforest site were used for monitoring canopy temperature, water vapor returns to the atmosphere, and temporal changes in rainforest cover, and for constructing stereo perspectives of the topography (Luvall *et al.*, 1990; Welch *et al.*, 1990); but with the 5- to 10-m pixel resolution, only the largest canopy tree crowns could be distinguished. Neither satellite nor high-altitude aircraft imagery provide the necessary resolution for delimiting populations of co-occurring canopy trees in closed canopy forests.

Airborne laser altimetry, which provides a direct method for measuring canopy surface elevations, holds some promise (Nelson *et al.*, 1984; Jensen *et al.*, 1987). The upgraded instrument known as SLICER (scanning lidar imager of canopies by echo recovery) is capable of obtaining high accuracy, high resolution measurements, but the cross-track scanning of the laser beam produces only narrow swaths of canopy structure with laser footprints (cells) nominally 10 to 15 m in diameter (Harding *et al.*, 1994). The objective of most studies involving SLICER and other forms of laser altimetry, therefore, has been to characterize entire canopies, not individual canopy trees.

The procedures and results described in this paper demonstrate the usefulness of temporal sequences of large-scale aerial stereopairs from low-flying aircraft for distinguishing individual canopy trees, quantifying the long-term dynamics of their crowns, and identifying critical late stages in their life history. Large-scale aerial stereoimagery of forested ecosystems from past overflights that lack control points can be co-registered with more recent imagery in which ground control points have been established. The selection of shared persistent BIPs as secondarily defined control points for image co-registration is not limited to leafless deciduous trees, as evidenced by the usefulness of the evergreen species *Aleurites moluccana* with its widely spreading crowns and prominent primary branches. The use of BIPs, thus, may be applicable not only to seasonal tropical rainforests, such as the CFF, comprised of both evergreen and deciduous canopy tree species, but also to evergreen tropical rainforest ecosystems having canopy tree architectural designs characterized by primary branches unobscured by foliage.

In a preliminary analysis of Myers and Benson's 1976 stereopairs, Herwitz (1982) used road intersections in the cleared land surrounding the CFF as ground-based control points. The intersections were defined in land survey maps prepared by the Lands Department in the Queensland Survey Office. With our installation of ground-based aerial targets in closer proximity to the CFF sample area in 1994 and our use of shared BIPs, more precise registration of the 1976 stereopairs was obtained. The result was some of the most detailed long-term measurements of canopy tree turnover and crown growth ever recorded for a tropical rainforest ecosystem. No study has previously quantified tropical rainforest canopy dynamics from an aerial perspective over a comparable time period (18 years) with the same resolution of individual canopy tree crowns.

While many past studies of tropical rainforest dynamics have focused on the spatial and temporal variation of treefall gaps and post-disturbance regrowth (Brokaw, 1985; Denslow, 1987; Clark and Clark, 1992), our study documented the dynamism of canopy trees of varying crown size. A remarkably large proportion of canopy trees decreased in size, yet continued to survive. The 60- to 80-m^2 size class was identified as the critical stage at which canopy trees either exhibit the fastest crown growth rates or experience crown reduction. Other unexpected findings included the spatially clustered patterns of canopy tree mortality and crown reduction in the larger size classes, the positive correlation between absolute crown growth and crown area, and the strong inverse relationship between percentage crown growth as a function of crown size.

Unlike past studies that grouped tree populations by dbh size class, canopy tree groupings by crown size class is more representative of tropical rainforest canopy structure. Multitemporal imagery from low-altitude airborne remote sensing provides an important aerial reference that could contribute to the formulation of more meaningful models of tropical rainforest dynamics. It also has the potential to significantly increase our understanding of long-term interactions that may be occurring among neighboring canopy tree crowns.

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References

Anderson, M.C., 1964. Studies of the woodland light climate. I. The photographic computation of light conditions, *Journal of Ecology*, 52:27–51.

Arp, H., J.C. Griesbach, and J.P. Burns, 1982. Mapping in tropical forests: A new approach using the laser APR, *Photogrammetric Engineering & Remote Sensing*, 48:91–100.

Brokaw, N.V.L., 1985. Gap-phase regeneration in a tropical forest, *Ecology*, 66:682–687.

Carey, E.V., S. Brown, A.J.R. Gillespie, and A.E. Lugo, 1994. Tree mortality in mature lowland tropical moist and tropical lower montane moist forests of Venezuela, *Biotropica*, 26:255–265.

Clark, D.B., and D.A. Clark, 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest, *Ecological Monographs*, 62:315–344.

———, 1996. Abundance, growth and mortality of very large trees in neotropical lowland rain forest, *Forest Ecology and Management*, 80:235–244.

Condit, R., S.P. Hubbell, J.V. Lafrankie, R. Sukumar, N. Manokaran, R.B. Foster, and P.S. Ashton, 1996. Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots, *Journal of Ecology*, 84:549–562.

Connell, J.H., J.G. Tracey, and L.J. Webb, 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity, *Ecological Monographs*, 54:141–164.

Denslow, J., 1987. Tropical rainforest gaps and tree species diversity, *Annual Review of Ecology and Systematics*, 18:431–451.

Francis, W.D., 1951. *Australian Rain-Forest Trees*, Forestry and Timber Bureau, Commonwealth of Australia, Halstead Press, Sydney.

Harding, D.J., J.B. Blair, J.B. Garvin, and W.T. Lawrence, 1994. Laser altimeter waveform measurement of vegetation canopy structure, *Proceedings of the Geoscience and Remote Sensing Symposium*, Abstracts, 68:4, Pasadena, California.

Herwitz, S.R., 1981. Regeneration of selected tropical tree species in Corcovado National Park, Costa Rica, *University of California Publications in Geography*, 24:1–109, University of California Press, Berkeley, California.

———, 1982. *Tropical Rainforest Influences on Rainwater Flux*, unpublished Ph.D. Thesis, The Australian National University, Canberra, 263 p.

———, 1993. Growth rates of selected Australian tropical rainforest tree species under controlled conditions, *Oecologia*, 96:232–238.

Herwitz, S.R., and S. Young, 1994. Mortality, recruitment, and growth rates of montane tropical rainforest canopy trees on Mount Bellenden-Ker, northeast Queensland, Australia, *Biotropica*, 26:350–361.

Herwitz, S.R., R.E. Slye, and S.M. Turton, 1994. Lateral shading and the differential interception of angular direct-beam radiation among neighboring tropical rainforest canopy trees, *Selbyana*, 15:A–10.

Herwitz, S.R., and R.E. Slye, 1996. Three-dimensional modeling of canopy tree interception of wind-driven rainfall, *Journal of Hydrology*, 168:205–226.

Hubbell, S.P., and R.B. Foster, 1990. Structure, dynamics, and equilibrium status of older-growth forest on Barro Colorado Island, Panama, *Four Neotropical Forests* (A. Gentry, editor), Yale University Press, New Haven, Connecticut, pp. 522–541.

Jensen, J.R., M.E. Hodgson, H.E. Mackey, Jr., and W. Krabill, 1987. Correlation between aircraft MSS and LIDAR remotely sensed data on a forested wetland, *Geocarta International*, 4:39–54.

Johnson, L.F., C.A. Hlavka, and D.L. Peterson, 1994. Multivariate analysis of AVIRIS data for canopy biochemical estimation along the Oregon transect, *Remote Sensing of Environment*, 47:216–230.

Kohyama, T., 1993. Size-structured tree populations in gap-dynamic forest: The forest architecture hypothesis for the stable coexistence of species, *Journal of Ecology*, 81:131–144.

Lang, G.E., and D.H. Knight, 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest, *Ecology*, 64:1075–1080.

Lieberman, D., M. Lieberman, G.S. Hartshorn, and R. Peralta, 1985. Growth rates and age-size relationships of tropical wet forest trees in Costa Rica, *Journal of Tropical Ecology*, 1:97–109.

Lieberman, D., and M. Lieberman, 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982), *Journal of Tropical Ecology*, 3:347–358.

Luvall, J.C., D. Lieberman, M. Lieberman, G.S. Hartshorn, and R. Peralta, 1990. Estimation of tropical forest canopy temperatures, thermal response numbers, and evapotranspiration using an aircraft-based thermal sensor, *Photogrammetric Engineering & Remote Sensing*, 56:1393–1401.

Manokaran, N., and K.M. Kochummen, 1987. Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia, *Journal of Tropical Ecology*, 3:315–330.

McIntire, B.M., M.A. Scholl, and J.T. Sigmon, 1990. A quantitative description of a deciduous forest canopy using a photographic technique, *Forest Science*, 36:381–393.

Morgan, J., and M.G.R. Cannell, 1988. Support costs of different branch designs: Effects of position, number, angle and deflection of laterals, *Tree Physiology*, 4:303–313.

Myers, B.J., 1982. Guide to the identification of some tropical rainforest species from large-scale colour aerial photographs, *Australian Forestry*, 45:28–41.

Myers, B.J., and M.L. Benson, 1981, Rainforest species on large-scale color photos, *Photogrammetric Engineering & Remote Sensing*, 47:505–513.

Nelson, R., W. Krabill, and G. Maclean, 1984. Determining forest canopy characteristics using airborne laser data, *Remote Sensing of Environment*, 15:201–212.

Pertunnen, J., R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa, and J. Väkeva, 1996. LIGNUM: A tree model based on simple structural units, *Annals of Botany*, 77:87–98.

Peterson, D.L., 1996. Forest structure and productivity along the Oregon transect, *The Use of Remote Sensing in the Modeling of Forest Productivity* (H.L. Gholz, K. Nakane, and H. Shimoda, editors), Kluwer Academic Publications, Dordrecht, The Netherlands, pp. 173–218.

Phillips, O.L., and A.H. Gentry, 1994. Increasing turnover through time in tropical forests, *Science*, 263:954–958.

Proctor, J., Y.F. Lee, A.M. Langley, W.R.C. Munro, and T. Nelson, 1988. Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics, *Journal of Ecology*, 76:320–340.

Putz, F.E., and K. Milton, 1982. Tree mortality rates on Barro Colorado Island, *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes* (E.G. Leigh, Jr., A.S. Rand, and D. Windsor, editors), Smithsonian Institution Press, Washington, D.C., pp. 95–100.

Stocker, G.C., W.A. Thompson, A.K. Irvine, J.D. Fitzsimon, and P.R. Thomas, 1995. Annual patterns of litterfall in a lowland and tableland rainforest in tropical Australia, *Biotropica*, 27:412–420.

Sumida, A., 1995. Three-dimensional structure of a mixed broad-leaved forest in Japan, *Vegetatio*, 119:67–80.

Swaine, M.D., D. Lieberman, and F.E. Putz, 1987. The dynamics of tree populations in tropical forests: A review, *Journal of Tropical Ecology*, 3:359–366.

Thomas, S.C., 1996. Relative size at onset of maturity in rain forest trees: A comparative analysis of 37 Malaysian species, *Oikos*, 76:145–154.

Turton, S.M., 1988. Solar radiation regimes in a north Queensland rainforest, *Proceeding of the Ecological Society of Australia*, 15: 101–105.

———, 1992. Understorey light environments in a north-east Australian rain forest before and after a tropical cyclone, *Journal of Tropical Ecology*, 8:241–252.

Unwin, G.L., G.B. Applegate, G.C. Stocker, and D.I. Nicholson, 1988. Initial effects of tropical cyclone 'Winifred' on forests in north Queensland, *Proceedings of the Ecological Society of Australia*, 15:283–296.

Vanclay, J.K., 1989. A growth model for North Queensland rainforests, *Forest Ecology and Management*, 27:245–271.

Vanclay, J.K., and R.A. Preston, 1990. Utility of Landsat Thematic Mapper data for mapping site productivity in tropical moist forests, *Photogrammetric Engineering & Remote Sensing*, 56:1383–1388.

Waring, R.H., H.L. Gholz, G.C. Grier, and M.L. Plummer, 1977. Evaluating stem conducting tissue as an estimator of leaf area in four woody angiosperms, *Canadian Journal of Botany*, 55:1474–1477.

Webb, L.J., 1958. Cyclones as an ecological factor in tropical lowland rainforest, North Queensland, *Australian Journal of Botany*, 6: 220–228.

———, 1959. A physiognomic classification of Australian rain forests, *Journal of Ecology*, 47:551–572.

Welch, R., T.R. Jordan, and J.C. Luvall, 1990. Geocoding and stereo display of tropical forest multisensor datasets, *Photogrammetric Engineering & Remote Sensing*, 56:1389–1392.

Whitmore, T.C., 1989. Changes over twenty-one years in the Kolombangara rain forests, *Journal of Ecology*, 77:469–483.

Wu, Y., and A.H. Strahler, 1994. Remote estimation of crown size, stand density, and biomass on the Oregon transect, *Ecological Applications*, 4:299–312.

Young, T.P., and S.P. Hubbell, 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps, *Ecology*, 72: 1464–1471.

Zimmerman, M.H., and C.L. Brown, 1971, *Trees Structure and Function*, Springer-Verlag, New York.

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