Quantifying the deciduousness of tropical forest canopies under varying climates

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Abstract. Deciduousness is an important functional attribute of tropical trees, reflecting climatic conditions. Precisely quantifying and mapping deciduousness in tropical forests will be necessary for calibrating remote sensing images which attempt to assess canopy properties such as carbon cycling, productivity, or chlorophyll content. We thus set out to assess the degree of canopy deciduousness in three moist, semi-deciduous tropical forests in central Panama. One site is a 6-ha research plot near the Atlantic coast of Panama, where rainfall is 2830 mm/yr. The second site is a 50-ha plot on Barro Colorado Island, near the center of the isthmus of Panama, where rainfall is 2570 mm/yr, and the final site is a 4-ha plot near the Pacific coast of Panama, where rainfall is 2060 mm/yr. At each site, a random sample of trees from all canopy species (those with individuals ≥ 30 cm DBH) were visited and scored for deciduousness three times during the 1997 dry season. The estimated peak fraction of deciduous individuals in the canopy at the wetter site was 4.8%, at the intermediate site, 6.3%, and at the drier site, 24.3%. The estimated fraction of crown area deciduous peaked at 3.6%, 9.7%, and 19.1% at the wet, medium, and dry sites respectively. The percentage of canopy species that was deciduous – 14%, 28%, and 41% – was much higher than the percentage of deciduous individuals, because not all individuals of deciduous species were deciduous. During the 1999 dry season, every individual of all the deciduous species was visited at the two drier sites, and the total number of deciduous trees observed closely matched the estimated numbers based on the smaller 1997 samples.

Keywords: Climate gradient; Deciduousness; Phenology; Tropical forest.

Abbreviation: BCI = Barro Colorado Island.

Introduction

Deciduousness is a key functional trait both for individual trees and for forest communities. Partial or full leaf loss during part of the year is an important ecosystem trait, since it indicates that forest productivity is seasonally reduced, and deciduousness may correlate with important ecosystem-level characteristics, such as tree height, biomass, and diversity. Since deciduousness changes canopy reflectance, it can be detected in satellite images (Reed et al. 1994; Bohlman et al. 1998), and thus could potentially be mapped over wide areas. Reflecting its importance in tropical ecosystems, deciduousness often provides a main axis for vegetation classification (Beard 1944; Hall & Swaine 1981; Box 1996): tropical dry forests are deciduous, wet forests are evergreen, and forests in between are called semi-deciduous. Deciduousness is thus an important and easy-to-measure indicator, and models of how tropical forests respond to future climatic changes (Steffen et al. 1996) might be calibrated by assessing how well they predict deciduous behavior under different climates.

This requires calibration sites, where deciduousness and climate are carefully measured, and despite the importance of this single character in forest classification and ecosystem function, there are very few quantitative estimates of deciduousness in tropical forests. The only indication of the degree of deciduousness typically reported is the fraction of species (e.g. Frankie et al. 1974; Reich 1995). Quantitative studies on the fraction of canopy cover lost during seasons of leaf fall are rare. We thus embarked on a straightforward effort to map and quantify deciduousness in three forests in central Panama. We sampled every canopy species for deciduous behavior, and then made a complete census of all deciduous species. The three sites, though close together, have different precipitation patterns, so we were able to quantify the relationship between climate and deciduousness.

Study sites

The study was carried out in lowland forests (< 200 m elevation) adjacent to the Panama Canal. Annual rainfall even in the driest sites in central Panama exceeds potential evapotranspiration and is ample to sustain tall, moist, high-biomass forest. There is a long dry season, though, running from mid-December until mid-April, during which many trees lose all their leaves (Leigh et al. 1982), and there is considerable variation across the isthmus in the length of the period when potential evapotranspiration exceeds precipitation (Fig. 1). At the Pacific side of the Canal, near Panama City, total annual rainfall is 2060 mm and the dry season lasts 129 days; at Barro Colorado in the center of the isthmus, rainfall is 2570 mm and the dry season 118 days; while near the Atlantic, rainfall is 2830 mm and the dry season is 106 days (Fig. 1). Condit (1998a) reported slightly different estimates for dry season duration, but based on an approximation for potential evapotranspiration (100 mm/month); here we use direct measurements of potential evapotranspiration (Fig. 1). All three sites have typical lowland-tropical temperature regimes, with a mean close to 27 °C throughout the year.

We have established three forest census plots across the isthmus, spanning this rainfall gradient. A 50-ha plot on the Smithsonian Tropical Research Institute's research reserve on Barro Colorado Island was set up in 1981 (Hubbell & Foster 1983, 1986, 1992; Condit et al. 1995, 1996a, c). Here we use data from the 1995 census of the plot. A 6-ha plot near the Atlantic coast at Fort Sherman was established in 1996, and a 4-ha plot near the Pacific, near the Cocoli River, was established in 1994. The latter two sites are on former US military installations.

Methods

All stems ≥ 1 cm diameter-at-breast-height (DBH) were identified to species, measured at breast height, and mapped, throughout all three plots. Condit (1998b) describes in detail the methods used. We are primarily interested in deciduousness of trees forming the upper canopy, since this is where leaf-loss would have the greatest impact on ecosystem function, and where it is visible remotely. In addition, understory species are seldom deciduous (Frankie et al. 1974; Wright 1991): to our knowledge, just one understory tree at Barro Colorado – *Erythrina costaricana* – is (Condit et al. 1996b). Thus, we only surveyed species which reached a DBH of 30 cm; we refer to these as canopy species. At Barro
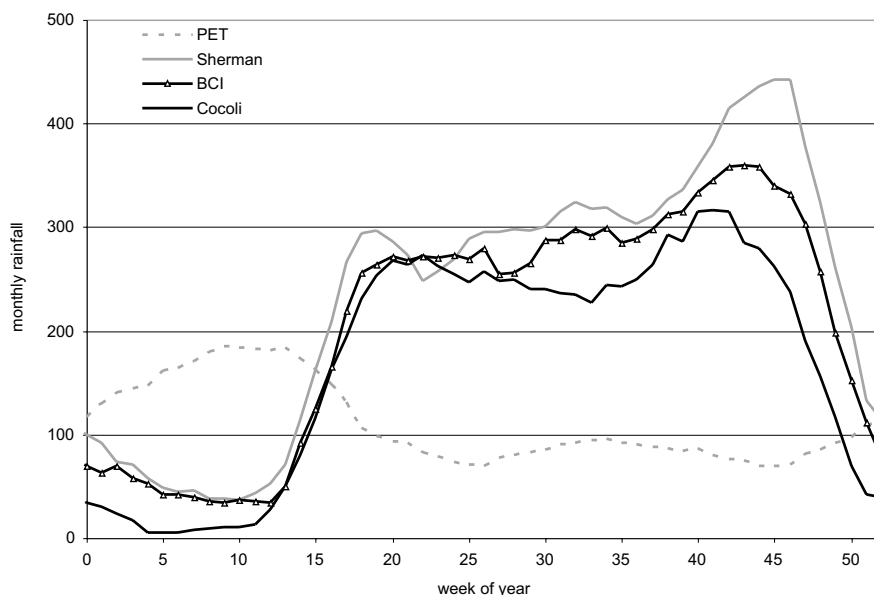
Fig. 1. Precipitation and potential evapotranspiration (PET) at the three plot sites. Both were calculated starting with weekly means over 12-25 yr, taking a 5-week running mean at each point, then adjusting to monthly by multiplying the weekly mean by 4.35 (the number of weeks in a month). One station is 6 km from the Sherman plot, the second is 1 km from the BCI plot, and the last is 4 km from the Cocoli plot. PET data are from Barro Colorado Island only. Dry season length was estimated as the interval each precipitation curve spent below the PET curve; for example, at Cocoli, precipitation rises above PET at week 15.8 and falls below at week 49.5, which works out to 129 days below PET. The difference between dry seasons is probably even more extreme than this indicates, because there is undoubtedly greater solar radiation and thus higher PET at the drier sites. (BCI data courtesy of the Smithsonian Environmental Sciences Program; Sherman and Cocoli data courtesy of the Panama Canal Commission.)

Colorado, 139 of the 144 canopy species in the 50-ha plot were censused; at Sherman, 64 of the 66 canopy species were censused; and at Cocoli, 34 of 39 species were censused. The species not censused included two palms at BCI and Cocoli (known to be non-deciduous), plus a few species having only a single individual in each plot.

For each species, three individuals ≥ 30 cm DBH at each plot were selected at random from the computer database, and each selected tree was visited during the last two weeks of January, 1997. For species which did not have three individuals, all individuals ≥ 30 cm DBH were censused. Subsequently at BCI, but not at the other two plots, additional individuals of common deciduous species were added to the census – up to seven trees ≥ 30 cm DBH, and seven additional trees 5-30 cm DBH. All selected trees were revisited during the last half of February and the last half of March, 1997, and then again in September, 1997. If a tree was found dead or the crown could not be observed due to lianas, it was removed from the list and another randomly selected tree chosen.

During the second half of March, 1999, we extended this approach by visiting every individual of all species recorded as deciduous at BCI or Cocoli during the 1997 surveys (but not at Sherman, where few trees were deciduous). Non-deciduous species were not checked, with two exceptions – *Jacaranda copaia* and *Tabebuia rosea* – which have been seen deciduous (but not during the 1997 census). All *Tabebuia* were visited, but we checked only 22 *Jacaranda* because it is extremely abundant and most had full crowns of leaves in March, 1999 (one of 22 was deciduous). One species, *Cavanilesia platanifolia*, was excepted from the Cocoli census in 1999, since it is abundant and always deciduous in the dry season. We saved time by omitting it, and assumed in the data analysis that all *Cavanilesia* were deciduous. Each tree visited was scored for leaf loss on a scale from 0 - 4:

4 = > 95% of leaves remaining;
3 = 65-95% of leaves remaining;
2 = 35-65% remaining;
1 = 5-35% remaining;
0 = < 5% remaining.

This semi-quantitative system is a typical approach for assessing phenology (Borchert 1980; Bullock & Solis-Magallanes 1990). Yellow or brown leaves were counted as missing. Leaves were considered missing if there were branches that had small branchlets but no leaves. Branches that were clearly rotting or had no small branchlets were considered dead and not counted as missing leaves. There were undoubtedly a few cases where recently dead branches or even trees were scored incorrectly as deciduous, but the September census proves that nearly all trees we censused were alive

(nearly every individual was scored as 3 or 4).

We tallied the fraction of trees in each category, 0 through 4, but we simplify most of our presentation by reporting all individuals with a score of 0 or 1 as deciduous (< 35% of leaves remaining), and all others as non-deciduous. Although this reflects an arbitrary division of a continuous scale (leaf loss) into discrete categories, we believe it most closely reflects everyday use of the term deciduous. We also report an estimate trees scoring 2, to indicate the number of individuals that were partially deciduous.

We report several alternate indices of forest deciduousness at each of the three plots: the fraction of canopy species that were deciduous, the fraction of individuals in the canopy that were deciduous, and the fraction of crown area that was deciduous. From the 1997 census, we had to estimate these fractions from small samples for each species, using the mean fraction of deciduous individuals per species in the samples, then weighting this by the abundance of each species in the entire plot. That is, let n_s be the abundance of species s, so $N = \Sigma_s n_s$ is the total abundance of all species, and let f_s be the fraction of deciduous individuals tallied in our sample for species s. An estimate of the total abundance of deciduous individuals in species s is thus $f_s n_s$, and the estimated fraction deciduous for the whole canopy is found by summing over all species. We call this the index of deciduousness:

$$\frac{\sum_s f_s n_s}{N}. \tag{1}$$

Deciduousness of crown area was calculated as well, based on allometric equations relating crown radius to DBH. Crown area refers to the area of the horizontal projection of each individual crown, based on the assumption that crowns are circular so their area is p times the radius squared. We have equations for 81 individual species (Bohlman et al. submitted); for species lacking the allometric data, a general equation based on data for all 81 species combined was used. We tallied the total crown area of each species in the canopy by summing all individuals alive in the main 1995 census, then used Eq. 1 and the 1997 sample to get total deciduous crown area. In 1999, since we checked every deciduous individual, we summed the crown area over each that was deciduous.

In 1999, we had a near-complete count of all deciduous individuals in the BCI and Cocoli plots at a single point in time. But trees that were dead, had badly broken crowns, or could not be observed due to liana cover (or occasionally stranglers), cause this to be an underestimate. At BCI during March, 1999, 720 trees were visited, but 118 could not be scored (43 definitely dead, 59 with lianas and some possibly dead, 16 with broken crowns). At Cocoli, 14 of 72 trees visited likewise could

not be scored. We made a simple assumption that the dead trees had been replaced by an equal number of others growing past 30 cm DBH since 1995, and that these and the ones with liana cover had a fraction of deciduous trees matching the fraction in those observed. For example, at BCI in March 1999, we scored 265 of 602 trees as deciduous. To account for the 118 individuals missed, we multiply 265 by 720/602, giving 317 deciduous trees. We report this as our 1999 BCI estimate and use a similar calculation for the Cocoli plot.

Error rates for the percentage of deciduous individuals in 1997 were calculated in a simple and approximate way. The total number of individuals sampled at one plot was taken as the sample size, and 95% confidence limits on the estimated percent deciduous (from Eq. 1) were taken from Sokal & Rohlf (1969). For example, at BCI during the March, 1997 census, 428 individuals $\geq$ 30 cm DBH were censused. The estimated percentage of the canopy that was deciduous was 6.3 %, and 95 % confidence limits on 6% of 421 – interpolated from Sokal and Rohlf's appendix – are ca. 4 - 9 %. This is a rough approximation of confidence limits, since it effectively assumes that the sample was statistically uniform (that is, that all species were identical). We did not calculate confidence limits on the percentage of crown area, since there was no obvious way to do so and the error would presumably be close to that for individuals. We did not calculate errors around the percent of species because we had complete lists of species in the plots – they were not samples. Neither did we calculate error for the 1999 census, since it was a near complete count of all deciduous individuals.

An index of deciduousness was calculated for each of the five census dates, including only those individuals observed deciduous at the time of the given census. In addition, we estimated the index by including all individual trees that were observed deciduous at least once. If trees are not synchronized in leaf loss, this number would be higher than the fraction deciduous during any single census. For example, if a third of the trees of a species are deciduous in January, a different third deciduous in February, and the last third deciduous in March, then we say that 100 % of the individuals of that species were deciduous at least once, while only 33% were deciduous at any one time. We could not make this calculation in 1999, since we had only one census that year.

Finally, the degree of deciduousness was calculated in different habitats within the 50-ha plot at Barro Colorado, following habitat definitions given in Condit et al. (1995, 1996ac). Each 20 m × 20 m quadrat was classified into one of the following regions: the swamp, a 1.2 ha region that is flooded with standing water most of the year; streamsides, regions within 20 m of small streams (1.9 ha); slopes, quadrats inclined by 7° or more (11.4

ha); and plateau, which is flat, non-flooded terrain. The plateau was subdivided into three sections: a 6.8 ha block in the eastern part of the plot that is $\geq$ 150 m above sea level, a 2.1 ha section of young forest, and a 24.8 ha western block that is < 150 m elevation. The remaining 1.8 ha of the 50-ha plot consist of quadrats with a mixture of habitats, and these were not used in analyses. The habitats differ in soil moisture because of a perched water table that meets the surface along the slopes; the high plateau is furthest from the water table and thus driest (Condit 1995, 1996a, c; Harms 1997).

Species names match those given in Condit et al. (1996b). Some of these names have now been revised, for example, the genera *Scheelia* and *Bombacopsis*, and eventually we will update Condit et al. (1996b) with a table showing old and new names for all changes. Here we use names reported earlier so that data from different reports on the BCI plot are compatible.

Results

Deciduous species

The fraction of canopy species recorded as deciduous followed the precipitation gradient, with the wet site at Fort Sherman having the fewest deciduous species and the drier Cocoli site having the most. At BCI, there were 37 species scored as deciduous at least once in 1997: 20 that had at least one individual scoring 0 and 17 more scoring a 1 but not 0. In 1999, two additional species were recorded as deciduous, bringing the total number of deciduous canopy species in the BCI plot to 39, or 28% of all the canopy species in the plot (Table 1). At Fort Sherman, 14.1% of canopy species were deciduous, and at Cocoli, 41.2% (Table 1). No 1999 census was done at Fort Sherman, and no new deciduous species were added in 1999 at Cocoli. Table 2 lists all the species recorded as deciduous.

The 12 most common deciduous species at BCI contributed more than 75% of all the deciduous trees in

Table 1. Number of deciduous species observed in each plot. The total number of species is based on all individuals $\geq$ 30 cm DBH alive during the 1994 census at Cocoli, 1995 at BCI, and 1996 at Sherman. The number of deciduous species includes all which had at least one deciduous individual during 1997 or 1999.

	Sherman	BCI	Cocoli
Total species in plot	66	144	39
No. of species censused	64	139	34
No. of deciduous species	9	39	14
% of species deciduous	14.1	28.1	41.2

Table 2. Fraction of individuals that was deciduous during four different censuses (January-March, 1997, and March, 1999) at three plots. The column 'any 97' gives the fraction of individuals that was deciduous in at least one of the 1997 censuses. Only species recorded as deciduous at least once, at one site, are included; blanks indicate a species was not present at the site (or had no individuals ≥ 30 cm DBH). If all entries at one plot are 0.00, the species was present (and censused) at the plot but not observed to be deciduous, while it was deciduous at another plot (for example, *Andira inermis* was recorded as deciduous at BCI, but not at Cocoli or Sherman). The number of individuals censused is given in parentheses at each site (in 1997, not all individuals were censused in every month, because some trees were added after January).

Species	Cocoli Jan 97	Feb 97	Mar 97	any 97	(N)	Mar 99	(N)	BCI Jan 97	Feb 97	Mar 97	any 97	(N)	Mar 99	(N)	Sherman Jan 97	Feb 97	Mar 97	any 97	(N)
Andira inermis	0.00	0.00	0.00	0.00	(2)	- - -	(0)	0.00	0.00	1.00	1.00	(1)	1.00	(1)	0.00	0.00	0.00	0.00	(2)
Astronium graveolens	0.00	0.00	0.33	0.33	(3)	0.00	(7)	0.20	0.20	0.20	0.40	(5)	0.31	(16)	- - -	- - -	- - -	- - -	- - -
Cavanillesia platanifolia	1.00	0.80	1.00	1.00	(5)	- - -	(0)	1.00	1.00	1.00	1.00	(5)	1.00	(17)	- - -	- - -	- - -	- - -	- - -
Ochroma pyramidale	0.00	0.00	1.00	1.00	(1)	0.00	(1)	0.00	0.00	0.50	0.50	(2)	0.00	(2)	- - -	- - -	- - -	- - -	- - -
Bombacopsis quinata	1.00	1.00	1.00	1.00	(1)	1.00	(1)	0.00	0.00	1.00	1.00	(1)	1.00	(1)	- - -	- - -	- - -	- - -	- - -
Bombacopsis sessilis	1.00	0.00	0.00	1.00	(1)	1.00	(1)	0.67	0.33	0.33	0.67	(3)	0.00	(3)	- - -	- - -	- - -	- - -	- - -
Pseudobombax septenatum	0.33	1.00	1.00	1.00	(5)	1.00	(9)	1.00	0.80	0.80	1.00	(5)	1.00	(6)	- - -	- - -	- - -	- - -	- - -
Spondias mombin	0.00	0.60	0.40	0.60	(5)	0.88	(8)	0.00	0.83	1.00	1.00	(6)	0.77	(13)	- - -	- - -	- - -	- - -	- - -
Spondias radlkoferi	0.00	0.00	0.00	0.00	(1)	- - -	(0)	0.00	0.67	0.67	0.67	(3)	0.91	(23)	- - -	- - -	- - -	- - -	- - -
Sterculia apetala	0.50	0.00	0.50	0.50	(2)	0.00	(2)	0.80	0.00	0.00	0.80	(5)	0.00	(14)	- - -	- - -	- - -	- - -	- - -
Tabebuia rosea	0.00	0.00	0.00	0.00	(1)	- - -	(0)	0.00	0.00	0.00	0.00	(3)	0.61	(18)	- - -	- - -	- - -	- - -	- - -
Zuelania guidonia	0.50	1.00	1.00	1.00	(2)	1.00	(2)	0.50	1.00	0.50	1.00	(2)	1.00	(2)	- - -	- - -	- - -	- - -	- - -
Apeiba membranacea	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.40	0.33	0.14	0.57	(7)	0.66	(79)	0.60	1.00	1.00	1.00	(5)
Aspidosperma cruenta	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.00	0.00	(3)	- - -	(0)	0.00	0.20	0.20	0.20	(5)
Cassipourea elliptica	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.00	0.00	(5)	- - -	(0)	1.00	1.00	1.00	1.00	(1)
Jacaranda copaia	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.00	0.00	(3)	0.05	(22)	0.20	0.20	0.00	0.40	(5)
Lonchocarpus latifolius	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.20	0.00	0.00	0.20	(5)	0.04	(24)	0.00	0.00	0.00	0.00	(1)
Trichospermum galeottii	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.00	0.00	(1)	- - -	(0)	1.00	1.00	1.00	1.00	(1)
Virola sebifera	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.00	0.00	(3)	- - -	(0)	0.25	0.25	0.00	0.25	(4)
Annona spraguei	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	- - -	1.00	1.00	(1)	- - -	(0)	- - -	- - -	- - -	- - -	- - -
Apeiba tibourbou	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.33	0.67	0.67	(3)	1.00	(3)	- - -	- - -	- - -	- - -	- - -
Ceiba pentandra	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.14	0.00	0.14	0.14	(7)	0.18	(28)	- - -	- - -	- - -	- - -	- - -
Cupania latifolia	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.33	0.33	(3)	0.00	(3)	- - -	- - -	- - -	- - -	- - -
Dipteryx panamensis	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.33	0.67	0.67	(6)	0.14	(28)	- - -	- - -	- - -	- - -	- - -
Ficus trigonata	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.25	0.00	0.00	0.25	(4)	0.00	(5)	- - -	- - -	- - -	- - -	- - -
Guapira standleyana	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.29	0.29	0.29	(7)	0.06	(35)	- - -	- - -	- - -	- - -	- - -
Guazuma ulmifolia	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.67	0.67	(3)	0.00	(18)	- - -	- - -	- - -	- - -	- - -
Hampea appendiculata	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.50	0.50	(2)	0.00	(2)	- - -	- - -	- - -	- - -	- - -
Hirtella americana	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	1.00	0.00	1.00	(1)	- - -	(0)	- - -	- - -	- - -	- - -	- - -
Hura crepitans	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.43	0.67	0.67	0.89	(9)	0.93	(67)	- - -	- - -	- - -	- - -	- - -
Myrospermum frutescens	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.50	1.00	1.00	1.00	(4)	1.00	(4)	- - -	- - -	- - -	- - -	- - -
Nectandra cissiflora	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.33	0.33	0.33	0.33	(3)	0.00	(2)	- - -	- - -	- - -	- - -	- - -
Ormosia macrocalyx	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.50	0.00	0.00	0.50	(2)	0.00	(2)	- - -	- - -	- - -	- - -	- - -
Platymiscium pinnatum	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.67	0.67	(3)	0.44	(25)	- - -	- - -	- - -	- - -	- - -
Platypodium elegans	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.33	1.00	1.00	(3)	0.86	(22)	- - -	- - -	- - -	- - -	- - -
Pterocarpus rohrii	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.33	1.00	1.00	(3)	0.60	(5)	- - -	- - -	- - -	- - -	- - -
Sapium aucuparium	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.83	1.00	1.00	1.00	(6)	1.00	(8)	- - -	- - -	- - -	- - -	- - -
Sapium spec.	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.50	0.50	(2)	0.00	(2)	- - -	- - -	- - -	- - -	- - -
Tabebuia guayacan	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.25	0.25	(4)	0.71	(17)	- - -	- - -	- - -	- - -	- - -
Trema micrantha	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.17	0.33	0.33	(6)	0.00	(5)	- - -	- - -	- - -	- - -	- - -
Triplaris cumingiana	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.67	0.67	0.67	(3)	0.33	(6)	- - -	- - -	- - -	- - -	- - -
Zanthoxylum belizense	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.25	0.00	0.00	0.25	(4)	0.00	(65)	- - -	- - -	- - -	- - -	- - -
Zanthoxylum panamense	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.00	0.50	0.33	(3)	0.22	(9)	- - -	- - -	- - -	- - -	- - -
Bursera simaruba	0.67	1.00	1.00	1.00	(3)	1.00	(7)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Cedrela odorata	0.00	1.00	1.00	1.00	(2)	1.00	(3)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Dalbergia retusa	0.00	0.80	0.80	1.00	(5)	0.33	(6)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Jacaranda caucana	0.00	1.00	1.00	1.00	(1)	0.00	(1)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Trichilia hirta	0.00	0.67	1.00	1.00	(3)	0.29	(7)	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Jacaratia spinosa	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	1.00	1.00	1.00	1.00	(1)
Matayba apetala	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0.00	0.20	0.20	0.20	(5)
Schizolobium parahybum	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	1.00	1.00	0.00	1.00	(1)

the forest (Table 3). At Cocoli, four species accounted for close to 73% of the deciduous individuals. At Sherman, two species accounted for nearly all deciduous trees (Table 3). At all three plots, canopy dominants were mostly non-deciduous. The four top ranking in terms of crown area (≥ 30 cm DBH) at Sherman – *Brosimum utile* (*Moraceae*), *Manilkara zapote* (*Sapotaceae*), *Vochysia ferruginea* (*Vochysiaceae*), and *Calophyllum longifolium* (*Guttiferae*) – were not deciduous. At BCI, the four top ranking were *Trichilia turberculata* (*Meliaceae*), *Quara-*

ribea asterolepis (*Bombacaceae*), *Hura crepitans* and *Tetragastris panamensis* (*Burseraceae*); only *Hura* was deciduous. Even at Cocoli, three of the top four ranks in crown area were non-deciduous – *Anacardium excelsum* (*Anacardiaceae*), *Calycophyllum candidissimum* (*Rubiaceae*), and *Scheelia zonensis* (*Palmae*); the highly deciduous *Cavanilesia platanifolia* ranked second in crown area at Cocoli.

Deciduousness of the canopy

The estimated fraction of the canopy that was deciduous followed the same trend, with Sherman being the least and Cocoli the most deciduous. But the fraction of deciduous individuals was much lower than the fraction of deciduous species. The estimated fraction of canopy individuals which were deciduous reached a peak of 4.8 % at Fort Sherman, in the February, 1997, census (Table 4). At BCI, the peak deciduousness in 1997 was 6.3 % (in March), and at Cocoli, 24.3 % (also in March). In March, 1999, deciduousness was slightly higher at BCI than in 1997, and slightly lower at Cocoli (Table 4), but the complete census closely confirmed the estimates from small samples in 1997.

The same trends were reflected by estimates of the fraction of total crown area that was deciduous. The estimated peak deciduousness of crown area in 1997 was 3.6 % at Sherman, 9.7% at BCI, and 19.1% at

Cocoli (Table 4) in 1997. Complete censuses in 1999 gave similar figures: 11.8% at BCI and 18.2% at Cocoli.

Estimates of deciduousness based on species, individuals, and crown area, differ for two reasons. First and foremost, not all individuals of deciduous species were deciduous (Table 2, Table 3). At BCI, in the 37 species recorded as deciduous in 1997, we censused 142 individuals. Of these, only 88 were recorded as deciduous at least once; the other 54 individuals in these deciduous species were never observed deciduous. At Sherman, 14 of 28 individuals of the deciduous species were not recorded as deciduous, and at Cocoli, five of 39 individuals were not.

Second, deciduous species had different average abundance and crown sizes than non-deciduous species. At BCI, 26% of the species were deciduous (Table 1), but these accounted for just 21% of the crown area and 16% of the individuals in the entire plot ($\geq$ 30 cm DBH). Three common deciduous trees in the BCI plot – *Hura*, *Cavanilesia*, and *Platypodium* – are large canopy emergents, with immense crowns but few small individuals in the plot (Condit et al. 1998), whereas several of the dominant non-deciduous species have narrow crowns (especially *Trichilia tuberculata*). At Sherman, 14% of the species were deciduous, and these accounted for 9% of the crown area and 14% of the individuals; deciduous species at Sherman all have small crowns, but were numerically quite common. At Cocoli, 41% of

Table 3. Dominant deciduous species. Number of deciduous trees $\geq$ 30 cm DBH in the three plots, during March, 1997 and March, 1999. The total number of individuals is based on the full plot censuses of 1994-1996. The 1997 estimates for deciduous individuals are based on small samples, extrapolating to the total number alive in the full census (from Eq. 1). The calculation for *Hura* provides an example: the 50-ha plot at BCI had (in the 1995 census) 77 individuals $\geq$ 30 cm DBH of *Hura*; that is not an estimate, all 77 of those trees were tagged and mapped. During the March census in 1997, we visited nine of those trees, and found six deciduous. The estimate 50.8 is 0.66 × 77. The 1999 figures are actual numbers of observed trees, with no estimate incorporated.

species	Family	Total individuals $\geq$ 30 cm DBH	Individuals deciduous (March 97)	Individuals deciduous (March 99)
Sherman				
Apeiba membranacea	*Tiliaceae*	8	8.0	- -
Aspidospermum cruenta	*Apocynaceae*	34	6.8	- -
BCI				
Hura crepitans	*Euphorbiaceae*	77	50.8	62
Platypodium elegans	*Leguminosae*	25	25.0	19
Platymiscium pinnatum	*Leguminosae*	33	22.1	11
Dipteryx panamensis	*Leguminosae*	28	18.8	4
Spondias radlkoferi	*Anacardiaceae*	26	17.2	21
Cavanilesia platanifolia	*Bombacaceae*	17	17.0	17
Apeiba membranacea	*Tiliaceae*	106	14.8	52
Spondias mombin	*Anacardiaceae*	14	14.0	10
Guazuma ulmifolia	*Sterculiaceae*	20	13.4	0
Tabebuia guayacan	*Bignoniaceae*	19	4.8	12
Tabebuia rosea	*Bignoniaceae*	21	0.0	11
Sapium aucuparium	*Euphorbiaceae*	8	8.0	8
Cocoli				
Cavanilesia platanifolia	*Bombacaceae*	29	29.0	- -
Pseudobombax septenatum	*Bombacaceae*	10	10.0	9
Trichilia hirta	*Meliaceae*	10	10.0	2
Bursera simarouba	*Burseraceae*	9	9.0	7
Spondias mombin	*Anacardiaceae*	11	4.4	7

the species were deciduous, but these accounted for just 22% of the crown area and 29% of the individuals. Two large-crowned deciduous *Bombacaceae* are abundant there (*Cavanilesia* and *Pseudobombax*), but they have many more smaller individuals than they do at BCI; in addition, Cocoli has common deciduous species with small crowns (*Trichilia hirta*, *Bursera*; Table 2). In terms of numerical abundance, Cocoli is dominated by the non-deciduous *Anacardium excelsum*.

Partial deciduousness

At all three forests, many trees scored 2 on the scale of deciduousness, with 35 - 65 % of leaves remaining. The peak fraction of individuals in this category in 1997 was 6.2 % at Sherman, 10.2 % at BCI, and 20.7 % at Cocoli. At BCI and Fort Sherman, these are higher than the fractions we defined as deciduous (scoring 0 or 1, with < 35 % of leaves remaining; Table 4). The fraction of canopy individuals that were fully deciduous – reaching a score of 0 – was 1.5 % at Sherman, 2.9 % at BCI and 20.9 % at Cocoli. Most of the deciduousness at any one time, especially at BCI and Sherman, was in trees which only dropped some of their leaves.

Habitats in the BCI plot

The different habitats of the BCI plot were not markedly different in deciduousness, with the single exception of the small patch of young forest. This 2.1 ha section had a peak in 1997 of 14.8 % of its individuals and 15.2 % of its crown area deciduous. The adjacent high plateau was 6.7 % deciduous in terms of individuals, 9.3 % in terms of crown area. The 1999 count of deciduous individuals confirmed this difference: 45 individuals were observed deciduous on the high plateau, and 16 in the young forest

(those are not estimates, but trees actually observed). These represent 7.7% and 14.0% of all canopy trees in each region (based on the 1995 census).

Smaller individuals

Some trees between 5 and 30 cm DBH were deciduous at BCI, but a lower fraction than among trees larger than 30 cm DBH. In 23 deciduous species, we censused some individuals < 30 cm DBH and some ≥ 30 cm DBH. In 16 of these, smaller trees had a lower fraction deciduous than larger trees, while in three species, larger trees had a lower fraction (four species had equal fractions). For all deciduous species combined, 88 of 142 individuals (61 %) above 30 cm DBH were recorded as deciduous during at least one census in 1997, whereas in the smaller DBH class, 32 of 75 (43%) were.

The total fraction of individuals and crown area between 10 and 30 cm DBH that was deciduous at BCI never exceeded 1%. This is partly because deciduous species have a lower percentage deciduousness in the smaller size class. But it is mostly because several of the prominent deciduous species at BCI – *Hura*, *Platypodium*, *Dipteryx*, and *Cavanilesia* – have populations consisting of very few small individuals (this is documented in detail in Condit et al. 1998).

Wet season census

In September, 1997, 572 individuals that had been censused during the dry season of 1997 (January-March) were revisited. Of these, 34 could not be observed (due to lianas, or having died). Only one individual was deciduous (a *Cavanilesia platanifolia*), and 12 more scored 2 on the deciduous scale. The remaining 525 trees scored 3 or 4.

Table 4. Fraction of deciduousness in the canopy at three plots. All entries refer only to trees ≥ 30 cm dbh. The 1997 figures are estimates from small samples, as calculated from Eq. 1; confidence limits (see Methods) are given in parentheses. The 1999 figures are based on near complete samples, but were adjusted upward slightly to account for trees not observed due to liana cover or mortality (see Methods).

		Sherman		BCI		Cocoli	
		Frequency	%	Frequency	%	Frequency	%
Individuals censused for deciduousness in 1997		201		421		69	
Individuals censused for deciduousness in 1999		0		720		72	
Total individuals in plot		516	100.00	4135	100.00	325	100
Deciduous individuals	Jan 97	13.7	2.7 (1-6)	158.6	3.8 (2-7)	42.3	13.0 (6-25)
	Feb 97	24.7	4.8 (2-11)	201.1	4.9 (3-8)	67.2	20.7 (11-33)
	Mar 97	18.8	3.6 (1-10)	261.1	6.3 (4-9)	78.8	24.3 (14-37)
	Mar 99	- - -	- - -	317	7.7	71	21.9
Total crown area (ha)		2.570	100.00	28.106	100.00	2.33	100
Deciduous crown area (ha)	Jan 97	0.056	2.2	1.450	5.2	0.243	10.4
	Feb 97	0.093	3.6	1.928	6.9	0.386	16.6
	Mar 97	0.066	2.6	2.729	9.7	0.444	19.1
	Mar 99	- - -	- - -	3.323	11.8	0.423	18.2
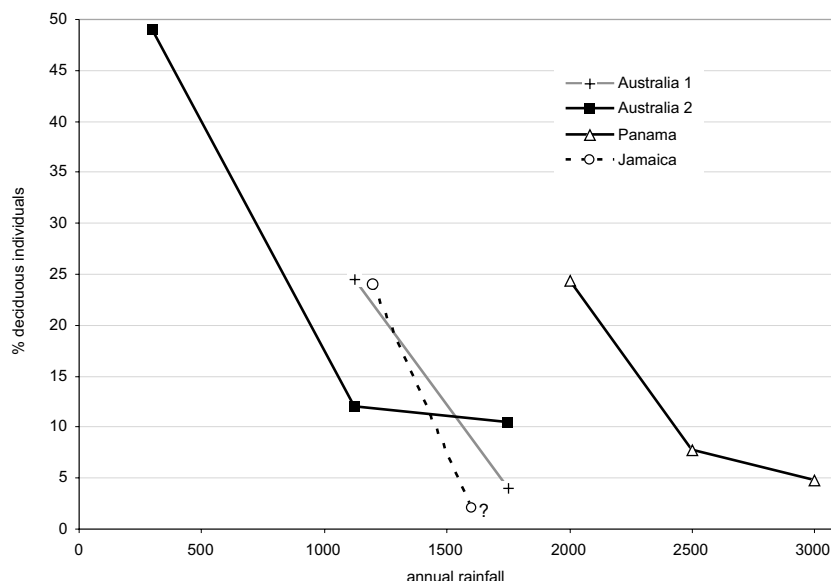
Fig. 2. Percent deciduous individuals recorded in various tropical forests. Site 1 in Australia is poor in nutrients, while site 2 is rich (both from Webb 1968). The Jamaican site is on limestone, and taken from Kelly et al. (1988); there is a question mark near the lower point because no exact figure was given for this site, only that one or two species were deciduous. Webb's data from Australia are also very poorly documented, with no dates, tree sizes, or sample sizes given. The Panama data are those presented in this paper.

Discussion

This is the most complete, quantitative assessment of deciduousness in a tropical forest that we know of. Other studies have tallied only the fraction of deciduous species in a flora, for example, Guanacaste in Costa Rica has 63 - 83 % deciduous tree species, La Selva has 15 %, and BCI has been reported to have 10 % (Frankie et al. 1974; Reich 1995; Wright 1991). Some tropical dry forests have essentially 100 % deciduous species (Bullock & Solis-Magallanes 1991), but others have some evergreen species (Sobrado 1991).

From the perspective of ecosystem function, the percent of species that are deciduous is not as important as the percent of the canopy that is deciduous. This is the index that would reflect seasonality in carbon cycling, primary productivity, or leaf area index; it is what would be detectable in aerial images of the canopy (Reed et al. 1994; Bohlman et al. 1998). We found that the percent of the canopy that was deciduous was much lower than the percent of species that was deciduous, at all three plots. At the wettest site, the peak deciduousness of crown area was 3.6 %, while 14 % of the species were deciduous. At BCI, crown area deciduousness reached 9.7 %, while 28 % of species were deciduous, The figure of 28 % for species is much higher than that given by Wright (1991) and Croat (1978), probably because we are only considering large trees; understory trees are seldom deciduous (Frankie et al. 1974; Wright 1991). At the driest plot, 19 % of the crown area but 41% of the

species were deciduous.

The gradient of deciduousness in our study matched the gradient of moisture, as predicted by physiological models, and as observed qualitatively, for example, in African forests (Hall & Swaine 1981; Veenendaal et al. 1996). Kikuzawa (1991, 1995) showed how a simple model of leaf value predicts increasing deciduousness in forests with longer periods unfavorable for growth. Deciduousness is usually taken to be an adaptation to reduce water stress during dry periods in the tropics (Borchert 1980, 1992; Reich 1984; van Schaik et al. 1993).

However, we must consider that some of the gradient in deciduousness in our samples is caused by differences in forest age, not climate. The Cocoli forest is clearly a younger forest than the other two, as the biggest *Anacardium* and *Cavanilesia* there are not nearly the size as those on BCI; it has probably regrown in 100 yr or less. In young forest near the canopy crane at Panama City (not far from Cocoli), evergreen species appear to be replacing deciduous ones as succession proceeds (J. Wright pers. comm.). On BCI, we estimated the small patch of young forest in the 5-ha plot to be about 15% deciduous, while the old part of the 50-ha plot (> 500 yr old) was 6 - 8 % deciduous. Thus, secondary forest at BCI is still less deciduous than secondary forest at Cocoli. We estimate that if the Cocoli forest remains undisturbed for three more centuries, its deciduousness will decline from its current level close of 20 - 25 % down to 12 - 15 %. These changes would be caused by a decline in the abundance of deciduous species,

especially *Cavanilesia* and *Pseudobombax*, during succession.

Geldenhuys (1993) did a precisely documented analysis of deciduousness at dry, subtropical sites in South Africa, where rainfall was about 1000 mm/yr. He reported that 13.8 % of the stems, 27.7 % of the basal area, and 28 % of the species were either deciduous or semideciduous. Kelly et al. (1988) reported that 24 % of the individuals, 37 % of the basal area, and 27 % of the species were deciduous in a dry tropical forest (1200 mm rainfall) in Jamaica. In both studies, though, the figures refer to the total number of individuals of deciduous species, not the number actually deciduous at one time.

Webb (1968) reported quantitative figures for the proportion of deciduous individuals in forests all over eastern Australia. In Fig. 2, we compare his results as well as those from Jamaica with ours. The driest site in Panama is much more deciduous than the Australian and Jamaican sites, which are slightly drier. Interestingly, if we are correct that Cocoli's forest will fall to 12 - 15 % deciduousness as it reaches maturity (and we made that estimate before seeing Webb's or Kelly's data), it would align quite reasonably with the high-nutrient site in Australia. BCI also has a rich soil (Leigh 1999), suggesting that perhaps BCI and Australian forests are similar in their deciduousness-climate relation. Data are far too sparse to pursue this now, but Mackey (1993) used Webb's data to construct a quantitative model predicting the occurrence of deciduous and semideciduous forest as a function of climate and soil in Australia. We are in a position to develop the same sort of model in both Central America and in Australia, once we develop common means for describing climate.

An intriguing feature of deciduousness in the Panama forests is its variation and inconsistency. Most species at all three plots, including the canopy dominants, were evergreen. Of the minority of species that were not evergreen, only some individuals were deciduous, and it was typical for individuals of a species to be deciduous at different times and to different degrees. There were also many individuals in both forest that were partly deciduous (35 - 65 % of leaves remaining), more than those we scored as deciduous. This variation has been described carefully in individual species (Borchert 1980) and may be typical of tropical trees in wet seasonal environments, where water availability in the soil varies from year to year and from site to site.

Because of the variation in the timing of deciduousness between species and between individuals, it is clear that we could have missed deciduous individuals and species that dropped leaves before or between our censuses. Still, we reiterate the point that what really matters at the ecosystem level is the deciduousness at any one moment, which is exactly what we censused. Although we may have missed individuals that were deciduous outside our censuses, our estimates of the degree of deciduousness at four points in time are unbiased. We are also certain that our censuses captured the peak deciduousness at each plot, or very nearly the peak, during February and March, toward the end of the dry season, when soil moisture is most limiting.

What we would like to do as a next step is test whether these differences in leaf loss can be detected using remote sensing. Seasonal changes in remotely-sensed data have been traced to tree phenology (Bohlman et al. 1998) but proving this connection will require quantitative estimates of deciduousness. Ultimately, it may be possible to assess deciduousness over wide spatial scales using remote-sensed data. If so, it would be possible to monitor changes through time in the degree of deciduousness. Models predicting how plant functional types change as climates change (Steffen et al. 1996) could be tested at large scales by observing shifts in the distribution and abundance of deciduous species, a major functional type of tropical trees.

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