Leaffall Phenology in a Subtropical Wet Forest in Puerto Rico: From Species to Community Patterns

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ABSTRACT

Leaffall phenology is an important periodical event in forests, contributing to mobilization of organic matter from primary producers to soil. For seasonal forests, leaffall periodicity has been related to rainfall regime and dry season length. In weakly seasonal forests, where there is no marked dry season, other climatic factors could trigger leaf shed. In this study, we aimed to determine if other climatic variables (wind speed, solar radiation, photosynthetic photon flux density [PPFD], day length, temperature, and relative humidity) could be better correlated with patterns of litter and leaffall in a weakly seasonal subtropical wet forest in Puerto Rico. Leaffall patterns were correlated mainly with solar radiation, PPFD, day length, and temperature; and secondarily with rainfall. Two main peaks of leaffall were observed: April–June and August–September, coinciding with the periods of major solar radiation at this latitude. Community leaffall patterns were the result of overlapping peaks of individual species. Of the 32 species analyzed, 21 showed phenological patterns, either unimodal (16 species), bimodal (three species), or multimodal (two species). Lianas also presented leaffall seasonality, suggesting that they are subject to the same constraints and triggering factors affecting trees. In addition to solar radiation as a main determinant of leaffall timing in tropical forests, our findings highlight the importance of interannual variation and asynchrony, suggesting that leaffall is the result of a complex interaction between environmental and physiological factors.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: climate seasonality; lianas; litterfall; Luquillo Experimental Forest; solar radiation; subtropical wet forest; weakly seasonal forests.

LEAFFALL IS ONE OF THE MOST IMPORTANT PERIODICAL EVENTS IN FORESTS. It constitutes around 65 percent of total litterfall (Vogt *et al.* 1985) and as such represents an important contribution to the mobilization of organic matter from primary producers to decomposers, soil fauna, and soil organic matter pools (Vitousek & Sanford 1986, Lawrence 1996). Characterization of leaffall phenology is therefore fundamental for the study of forest dynamics. Additionally, leaffall phenological patterns are important to distinguish plant functional types (Chapin *et al.* 1996). In turn, characterization of plant communities and ecosystems in terms of functional types has proved to be an insightful approach to the study of the relation between biodiversity and ecosystem functioning (Naeem & Wright 2003), and the effects of climate change on plant communities (Díaz & Cabido 1997). Thus, characterization of leaffall patterns as well as a better understanding of factors determining leaffall timing and spatial synchrony will be useful in tackling central issues such as forest dynamics, biodiversity–ecosystem relation, and climate change.

For seasonal forests, leaffall periodicity has been mainly related to environmental factors, such as rainfall regime—specifically the relative severity of the dry season. In deciduous forests with a marked dry season, leaffall is a mechanism for water conservation. If subject

to the same environmental pressures, one can expect that the majority of species in a strongly seasonal forest will respond in similar ways, having for example, consistent peaks of leaf shed that coincide with the dry season. Therefore, patterns of leaffall at the community level are the result of the conjunction of individual species adaptations to deal with the same problem, that is, water deficit (van Schaik *et al.* 1993). In contrast, in weakly seasonal forests, there is rarely a proper dry season. In such forests, environmental factors other than rainfall, together with internal (*i.e.*, developmental, physiological, and phylogenetic) factors may determine phenological patterns of leaf shed (Borchert 1980, Osada *et al.* 2002). If internal factors play a more important role in determining leaf-shed phenology in weakly seasonal forests, we would expect their plant communities to present a variety of species-specific leaf-shed patterns, among which an important proportion of species would have aseasonal patterns of leaffall. Moreover, when observed at the community level, all these patterns would generate an aseasonal pattern. However, several studies have shown seasonal patterns of leaffall both for specific species and communities in weakly seasonal forests (*e.g.*, Odum & Pigeon 1970, Medway 1972, Frankie *et al.* 1974, Kunkel-Westphal & Kunkel 1979, Putz & Windsor 1987, Lowman 1988, Burghouts 1993, Lawrence 1996, Xiao *et al.* 2006). Therefore, other environmental conditions instead or in addition to rainfall could trigger leaf shed in these forests. Many authors (*e.g.*, Longman & Jenik 1974, Wright & Cornejo 1990, van Schaik *et al.* 1993, Wright & van Schaik 1994) have pointed out that for

aseasonal or weakly seasonal forests, solar radiation and the concomitant increase in photosynthetic activity can be more important in determining leaf-shed patterns than rainfall.

Our study was conducted in a subtropical wet forest in Puerto Rico where a strong dry season is absent or mild and therefore leaf shed is less likely to be the result of water stress. We hypothesized that other climatic variables, such as solar radiation, photosynthetic photon flux density, and temperature are more closely correlated with leaffall patterns than rainfall. To test this, we analyzed the temporal variation of leaf litter production during 1 yr (Nov 2002–Nov 2003) for specific species and the whole community, and correlated these patterns with several climatic variables such as rainfall, wind speed, solar radiation, photosynthetic photon flux density, and temperature. Additionally, we present a classification of the most abundant plant species in the forest studied according to the leaffall patterns observed.

METHODS

STUDY SITE.—The study was carried out in a subtropical mountain wet forest (elevation ranges: 300–600 m) in northeastern Puerto Rico (18°20′ N, 65°49′ W) near El Verde Field Station, in the Luquillo Experimental Forest (LEF). It is a mature forest with a past land-use history characterized by selective wood logging and small-scale farming (mainly coffee and plantain) (Thompson *et al.* 2002). Hurricanes and droughts are main features of the natural disturbance regime of this forest (Zimmerman *et al.* 1995, Beard *et al.* 2005). Recent major disturbance events were hurricane Hugo in 1989, a major drought in 1994, and hurricane Georges in 1996. Forest resilience is, however, remarkably high for some ecosystem process as 5 yrs after Hugo, litterfall was 80 percent of the prehurricane values (Scatena *et al.* 1993), forest floor carbon and nutrients standing stocks returned to prehurricane values 2–10 mo after hurricane Georges (Ostertag *et al.* 2003), and litterfall inputs returned to long-term mean rates within 1 mo after droughts (Beard *et al.* 2005).

Multiannual mean monthly temperature (1975–2004) is 20.6–25.8°C, with an annual mean of 23.0°C (SD = 1.9; Luquillo Long Term Ecological Research–LTER climate data: http://luq.lternet.edu/data/). Multiannual mean annual rainfall is 3592.3 mm (SD = 829.0; LTER climate data: http://luq.lternet.edu/data/). Rainfall regime is weakly seasonal, with a mild and short dry season occurring between December and March (most commonly in March). Between 1975 and 2004, only 5 yr experienced a month with < 60 mm and 14 yr (*i.e.*, 50%) experienced a month with < 100 mm. The wettest periods are April–May and September–November. For the year of study, rainfall in March was 66.8 mm and rainfall peaks occurred in April and November (Fig. S1). Solar radiation and photosynthetic photon flux density (PPFD) (two climatic variables directly related to photosynthetic activity and primary productivity) present a bimodal pattern in the Caribbean, with peaks occurring during April–May and August–September (Fig. S2). Soils are a complex of well and poorly drained ultisols and oxisols (Soil Survey Staff 1995) with a clay and silty clay loam texture (Vogt *et al.* 1996). Dominant tree species are: *Dacryodes excelsa* Vahl, *Buchenavia tet-*

raphylla (Vahl) Eichl., *Homalium racemosum* Jacq., *Guarea guidonia* (L.) Sleumer, *Sloanea berteriana* Choisy, and *Prestoea montana* (Graham) Nicholson (Thompson *et al.* 2002).

LITTERFALL COLLECTION.—Sampling design used corresponds to a larger study within the LUQ-LTER program and included three blocks each containing four plots of 20 × 20 m. Distance between blocks was *ca* 150 m and plots within blocks were *ca* 10 m apart. Within each plot, we installed three baskets of 3 m² at 1.3 m from ground level. Material collected in the baskets from each plot was combined into a single sample, to total 12 samples per collection date. The total area covered by the 36 baskets was 110.4 m². Litter was collected every 2 weeks from November 2002 to November 2003 and sorted into the following categories: leaves (including petioles only when attached to leaves), reproductive parts (flowers, fruits, and seeds), fine wood (< 5 mm diameter), coarse wood (> 5 mm diameter), and miscellaneous (insects fragments, dead animals, faeces, dust, and any unidentified material). Leaves were sorted to species level following the nomenclature and species description of Little *et al.* (1974) for trees and Acevedo-Rodríguez and Woodbury (1985) for vines. Samples were air-dried to constant weight and then weighed. After weighing, species leaf litter from each date was combined and stored for subsequent chemical analysis. Leaf litter from this study is being used in a decomposition experiment. For that reason, samples were not oven-dried. A correction factor for the water content of air-dried samples was applied to the final values to obtain litterfall on an oven-dried weight basis (65°C for at least 48 h).

DATA ANALYSIS.—Litter production rates (g/m²/d) for each litter category and each plant species were obtained by adding the weights from all plots within a block and later dividing by the pooled area and number of days between collections. The 32 most abundant species were selected as those having > 10 kg/ha/yr of leaf litterfall. Litterfall data, initially as absolute rates, were converted to percentages of the annual litterfall for each block and then averaged. This accounted for the differences in the absolute amounts of litterfall between blocks and species.

Temporal patterns of litterfall were analyzed with a one-way ANOVA using the general linear model (GLM) procedure, in which month was the fixed factor, block was the random factor (when enough plots were included as replicates), and litterfall for main categories and for the 32 selected species was the dependent variables. When the effect of month was significant, differences among specific months were established by the Least-Square Difference (LSD) Post hoc test that uses a *t*-test to perform pairwise comparisons between group means (SPSS 2001). A peak was considered significant if it differed from the values for adjacent months and could span from one to several months; namely, peaks could be sharp or wide. According to the number of significant peaks, the species were further classified as nonmodal (no apparent peaks in litterfall), unimodal (one peak), bimodal (two peaks), or multimodal (> two peaks).

Correlations using the Pearson coefficient were carried out between selected species leaffall relative rates and the following climatic

variables: total and maximum rainfall (mm); number of dry days; PPFD (moles/m^2/day), which represents the portion of photosynthetic active radiation—PAR intercepted by plants (Grant & Slusser 2004); solar radiation (kjoules/m^2/day) which, in addition to PAR, includes UV-A (320–400 nm) and UV-B (280–320 nm) radiation (Grant & Slusser 2004); day length; maximum and minimum temperature; temperature range; mean and maximum wind speed; and minimum relative humidity. These data were obtained from the LUQ-LTER web page and calculated for the specific sampled periods (*i.e.*, 15 d periods). Correlations between leaffall and climatic variables for the period previous to the collection of litterfall (*i.e.*, 15–30 d before) were also performed to establish if phenological patterns were delayed in relation to specific climatic conditions. To improve the statistical power of the analysis, all correlations were done for every sampling period rather than for monthly time steps.

It should be noted that many climatic variables are cross-correlated (*e.g.*, PPFD, solar radiation, day length, and temperature; or number of dry days, total and maximum rainfall), however, we have chosen to include them all to explore if some may be more responsive to changes in the littterfall.

All tests were performed with SPSS (2002) and significance was established for *P* values < 0.05.

RESULTS

TOTAL LITTERFALL AND LEAFFALL.—Total litterfall during the collecting year was 7.5 mg/ha. Leaves accounted for 65.4 percent of total litterfall, while wood represented about 15.5 percent, and reproductive parts (flowers, fruits, and seeds) 13 percent (Table 1). Sixty-two tree species and 12 woody vines (or lianas) were present in the leaffall, among which the 32 most abundant species accounted for 92.3 percent of annual leaffall (Table 2). The periods with major leaffall were April–June and August–September (Fig. 1). These peaks were the result of the overlapping of leaffall peaks for individual species, especially trees, since lianas contributed just a small percentage to the total leaffall (Table 1).

PHENOLOGICAL PATTERNS.—Nineteen of the 32 species analyzed presented statistically significant phenological patterns (Table 2). Additionally, two more species (*Coccoloba swartzii* and *Eugenia stahlii*) presented strong peaks of leaffall but the significance of these peaks could not be determined since they were present only in one plot. Sixteen species were unimodal, having one significant peak of leaffall (Fig. 2). *Buchenavia tetraphylla*, *C. swartzii*, *E. stahlii*, *Heteropteris laurifolia*, *H. racemosum*, and *Tabebuia heterophylla* peaked in April and May (Fig. 2A) and were responsible for the April–May peak observed for total leaffall. *Cyrilla racemiflora*, *Micropholis garciniifolia*, and *Tetragastris balsamifera* peaked in June and July, while *Schelegelia brachyantha* peaked in March (Fig. 2B); *Inga fagifolia* and *Manilkara bidentata* peaked in August and September, while *Byrsonima spicata* and *Laetia procera* had peaks in May–June and April–July, respectively (Fig. 2C). Finally, *Casearia arborea* and *Marcgravia sintenisii* presented wide peaks between March and October (Fig. 2D).

TABLE 1. *Absolute and relative amounts of litterfall per category.*

Category	Annual litterfall (kg/ha/year)[a]	% Annual litterfall
Leaves	4910.5	65.4
Trees	4585.9	93.4[b]
Woody vines (lianas)	246.4	5.1[b]
Herbaceous (herbs, ferns, vines)	78.2	1.6[b]
Total wood	1160.8	15.5
Fine wood (≤5 cm diameter)	512.5	6.8
Coarse wood (≥5 cm diameter)	566.6	7.6
Flowers, fruits and seeds	973.9	13.0
Miscellaneous	458.1	6.12
Total litterfall	7504.3	100

[a]Oven-dried weight corrected from air-dried values.

[b]Proportion of total leaffall.

Three species were bimodal, having two significant peaks of leaffall: *D. excelsa*, *Guarea guidonea*, and *Matayba dominguensis* (Fig. 3). Together, these three species represent 30 percent of the total annual leaffall, since *D. excelsa* is the most abundant species in this forest. *Dacryodes excelsa* leaffall caused the June and September peaks observed for the total leaffall (*cf.* Figs. 1 and 3). Two species: *Drypetes glauca* and *Rourea surinamensis*, were multimodal, having three or more significant leaffall peaks (Fig. S3). The remaining 11 species were nonmodal. However, only two species of understory trees—*Croton poecilanthus* and *Hirtella rugosa*—were constantly nonmodal among all plots. All the other species appeared as nonmodal due to a high spatial variation (*i.e.*, asynchrony) in their phenological patterns. For these species, both the specific timing and the number of leaffall peaks differed among plots. Although we do not have means to test the statistical significance of those peaks, their presence indicates that other factors rather than climate can be influencing the phenology of these species.

CORRELATIONS WITH CLIMATIC VARIABLES.—Total litterfall was positively correlated with rainfall for the 2 weeks previous to litterfall collection, as well as with PPFD, solar radiation, day length, and maximum temperature (Table S1). The same pattern of correlations was observed for total leaffall and trees leaffall (Table S1). Total and coarse wood fall were correlated with maximum rainfall for the same period during which litterfall was collected, while fine wood fall was correlated with maximum temperature (Table S1) and leaffall from some species (*D. excelsa* $r = 0.57$, *M. garciniifolia* $r = 0.56$, *Hippocratea volubilis* $r = 0.50$, *T. balsamifera* $r = 0.44$, *Pinzona coriacea* $r = 0.40$, *D. glauca* $r = 0.44$, and *M. sintenisii* $r = 0.41$). Correlation between specific leaffall and fine wood is due to the fine wood including little branches, twigs, and petioles.

Two reproductive peaks were found, one in early January and a second in mid-August. Reproductive parts litter was correlated with PPFD for the preceding 2 weeks, mean and minimum temperature, and relative humidity for the same period (Table S1).

TABLE 2. *Annual leaffall, relative contribution to total leaffall, and effect of month on leaffall for the 32 most abundant species.*

Species	Growth form[a]	Annual leaffall (kg/ha/year)	% Annual leaffall	Effect of month on leaffall P[b]	Effect of month on leaffall N[c]
Dacryodes excelsa Vahl	T	1264.4	25.6	< 0.001	3
Manilkara bidentata (A. DC.) Chev.	T	587.3	11.9	< 0.001	3
Prestoea montana (Graham) G. Nicholson	P	396.5	8.1	0.14	3
Buchenavia tetraphylla (Aubl.) R. Howard	T	301.4	6.2	< 0.001	3
Homalium racemosum Jacq.	T	262.4	5.3	< 0.001	3
Rourea surinamensis Miq.	L	131.4	2.7	< 0.001	3
Sloanea berteriana Choisy ex DC.	T	128.3	2.6	0.67	3
Guarea guidonia (L.) Sleumer	T	111.3	2.3	< 0.001	3
Tetragastris balsamifera (Sw.) Kuntze	T	111.0	2.2	< 0.001	3
Cyrilla racemiflora Griseb.	L	103.9	2.1	< 0.001	3
Schlegelia brachyantha L. Swamp	T	103.2	2.1	< 0.001	3
Marcgravia sintenisii Urban.	L	95.8	2.0	< 0.001	3
Matayba domingensis (DC.) Radlk.	T	94.3	1.9	< 0.001	3
Alchorneopsis floribunda (Benth.) Müll. Arg.	T	90.1	1.8	0.48	3
Tabebuia heterophylla (DC.) Britton.	T	85.4	1.8	< 0.001	3
Inga fagifolia (L.) Willd.	T	82.2	1.7	0.01	3
Ficus citrifolia Mill.	T	73.3	1.5	0.19	3
Cecropia schreberiana Miq.	T	71.7	1.5	0.44	3
Croton poecilanthus Urban	T	67.2	1.4	0.26	2
Byrsonima spicata (Cav.) DC	T	64.8	1.3	< 0.001	2
Hirtella rugosa Pers.	T	53.1	1.1	0.63	3
Laetia procera (Poepp.) Eichler.	T	51.6	1.0	0.003	3
Drypetes glauca Vahl	T	36.2	0.7	0.004	3
Eugenia stahlii (Kiaersk.) Krug et Urb.	T	29.5	0.6		1
Casearia arborea (Rich.) Urb.	T	28.2	0.6	0.03	3
Micropholis garciniifolia Pierre	T	22.4	0.5	0.03	3
Pinzona coriacea Mart. & Zucc.	L	20.5	0.4	0.66	2
Sapium laurocerasus Desf.	T	17.3	0.4	0.37	2
Coccoloba swartzii Jacq.	T	17.2	0.4		1
Heteropteris laurifolia (L.)Juss.	L	13.6	0.3	0.002	3
Schefflera morototoni (Aubl.)	T	12.8	0.3	0.50	2
Ormosia krugii Urban	T	11.2	0.2	0.06	2
Cumulative percentage			92.3		

[a]P = Palm, T = Tree, L = Liana (woody vine).

[b]Significant P values mean the species shows some kind of leaffall phenological pattern.

[c]N refers to either plots or blocks according to the spatial distribution of each species (for $N = 1$ no P value could be obtained).

Among the 32 species analyzed, 22 were correlated either with PPFD, solar radiation, day length, or temperature; eight were correlated with rainfall (six of them for the preceding two weeks); seven species were correlated with wind speed; and only two species were not correlated with any of the climatic variables considered (Table S2). For unimodal species peaking in April (*B. tetraphylla*, *H. laurifolia*, *H. racemosum*, *T. heterophylla*) we found significant correlations for a specific set of climatic variables (Table S2), meaning that the concurrence of particular weather conditions during the preceding 2 weeks (*e.g.*, high rainfall, low temperatures, strong winds, and a wide range of variation between maximum and minimum temperature) could trigger leaf shed for these species. The other unimodal species were correlated mainly with solar radiation, PPDF, day length, and temperature, although some were also correlated with rainfall and wind (Table S2). Bimodal species were correlated with temperature; while multimodal species were correlated with PPDF, solar radiation, temperature, and wind (Table S2).

DISCUSSION

PATTERNS OF TOTAL LEAFFALL.—Total litterfall and leaffall amounts are toward the lower end of the range reported for other tropical and subtropical forests (*cf.* Leigh 1999), and are quite reasonable
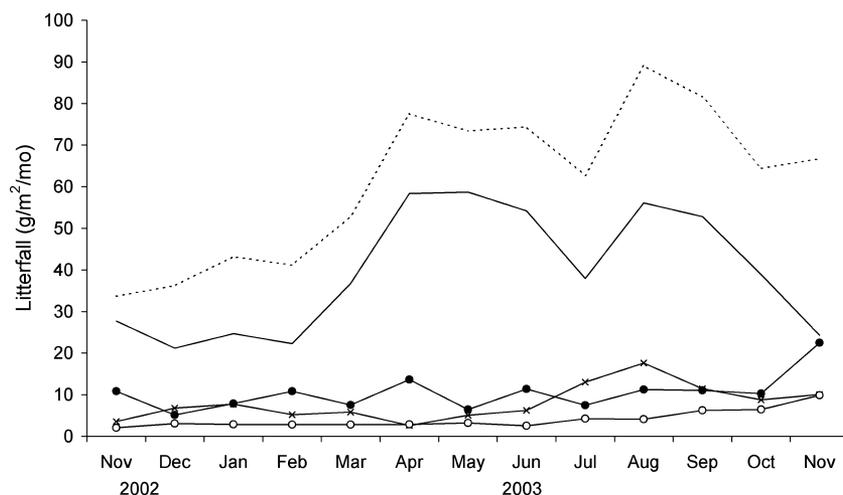
FIGURE 1. Monthly rates of total litterfall (dashed line), leaffall (solid line), reproductive parts (crosses), wood (closed circles), and miscellaneous components (open circles).

for the study area (*cf.* Estrada-Pinto 1970, Lodge *et al.* 1991, Lugo 1992, Zou *et al.* 1995, Lawrence 1996); thus, we will restrict the following discussion to litterfall phenological patterns.

Major peaks of leaffall for the study site have been consistently observed in May–June and August–September (Weigert 1970, Lawrence 1996 and references therein, Vogt *et al.* 1996).

Additionally, data gathered from El Verde and Bisley Experimental Forests (also within the Luquillo mountains area) show a slight bimodal pattern with major peaks in May–June and September–November (Luquillo LTER data bases: lterdb95, lterdb98, and lterdb111). However, it is often difficult to detect phenological patterns at the community level because leaffall is not
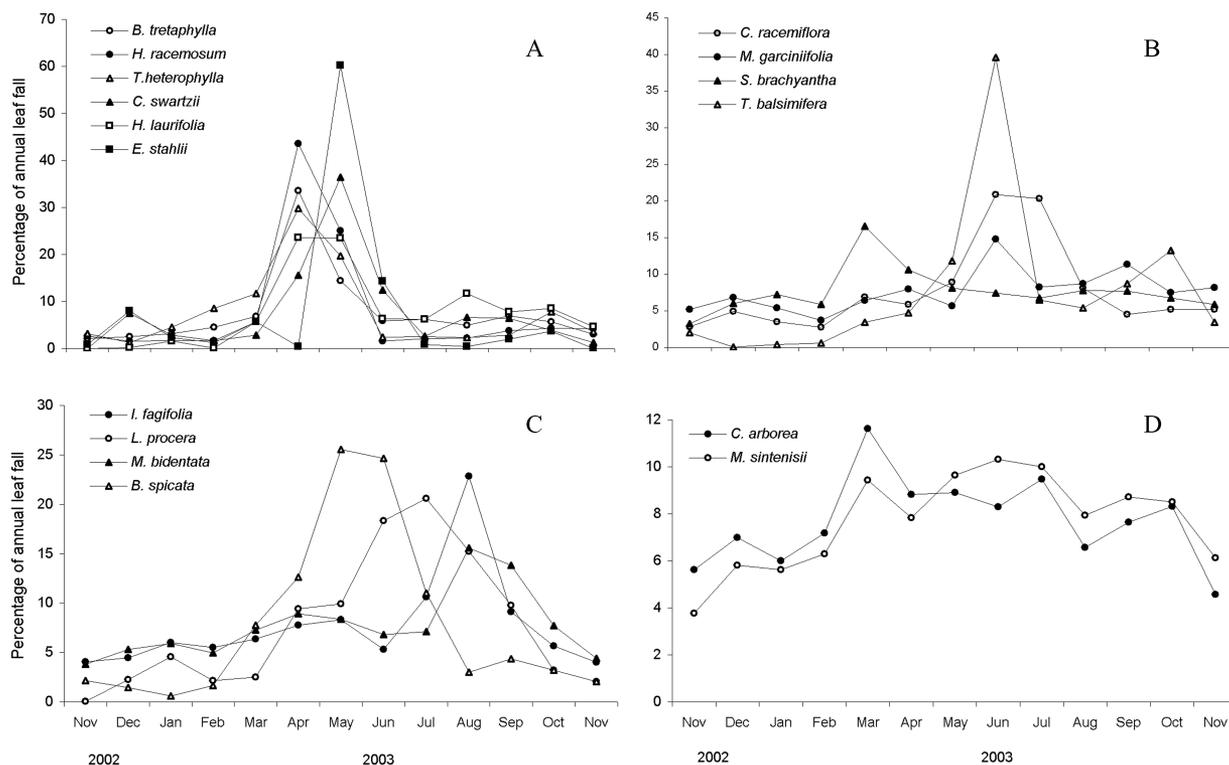

FIGURE 2. Leaffall patterns for unimodal species: (A) Species peaking in April and May; (B) species peaking between March and July; (C) species with wide peaks distributed along the year; and (D) species presenting one peak spanning from March to October. Leaffall is represented as percentage of the annual leaffall for each species.
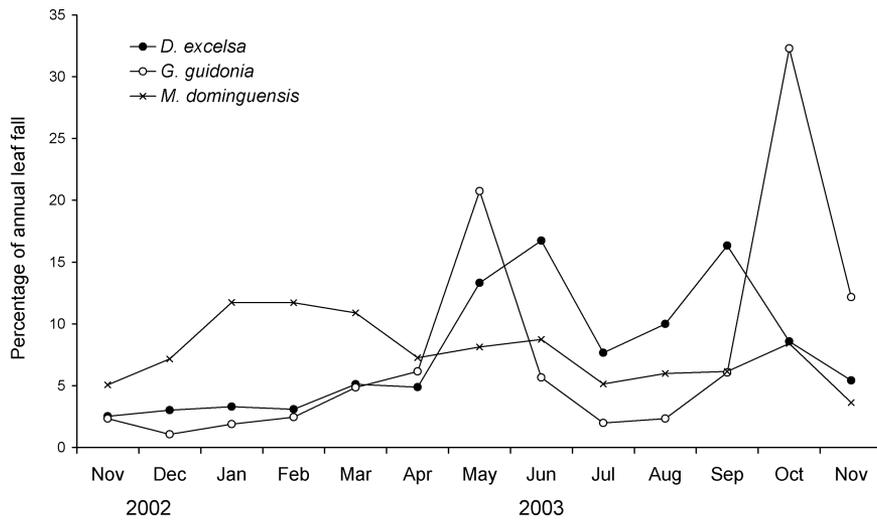
FIGURE 3. Leaffall pattern for bimodal species; represented as percentage of the annual leaffall for each species.

usually sorted by individual species. Our data show that total leaffall is the result of the overlapping of leaffall peaks for individual or groups of species. When we reanalyzed a subset of leaffall data from El Verde that were sorted by the five more abundant species in the standing vegetation—*D. excelsa*, *M. bidentata*, *C. schreberiana*, *S. berteriana*, and *B. tetraphylla*—between September 2000 and June 2001 (raw data obtained from Luquillo LTER: http://luq.lternet.edu/data/); we found that, in addition to the May and September peaks, there was another peak in December 2000, caused by *C. schreberiana*. Thus, the whole community shows a less seasonal leaffall pattern than species do individually.

The aforementioned bimodal pattern of leaf shed has been traditionally linked to rainfall (*e.g.*, Weigert 1970, Lawrence 1996). Nevertheless, it is well known that phenological events such as

leaffall and flowering in the tropics are related to the sun's annual cycle, specifically changes in the angle of incidence of the sun upon the earth (Longman & Jenik 1974, Larcher 1995). At latitudes $< 23°$ there are two periods when the incidence angle of the sun upon the earth is perpendicular (*i.e.*, equinoxes) and consequently, the insolation received is higher than at other times during the year. Periods of maximum irradiation for the latitude of Puerto Rico (18° North) are April–May and August–September (Odum *et al.* 1970; *cf.* Fig. S2), the two periods when leaffall was found to be the highest. Furthermore, most of the 32 species analyzed in this study had significant peaks in May and September (Fig. 4) and their leaffall peaks were correlated with climatic variables associated with light availability such as PPFD, solar radiation, day length, and temperature (*cf.* Table S2). On the contrary, the
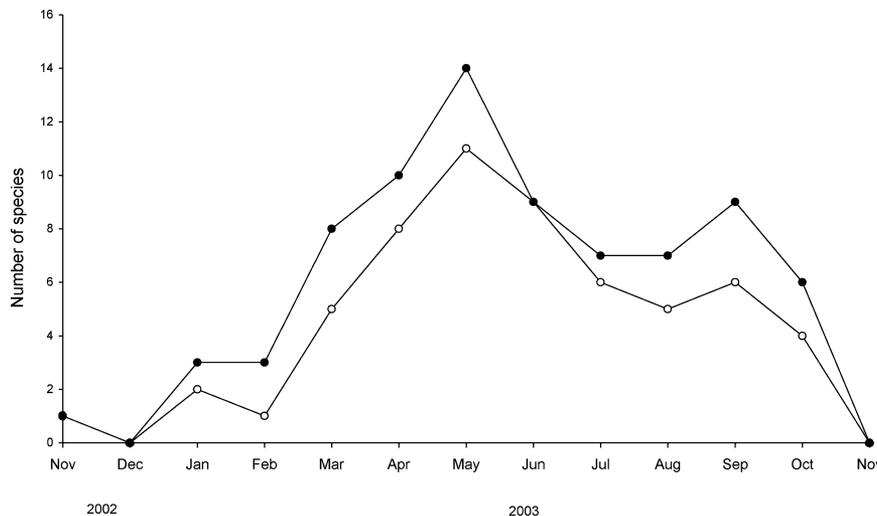

FIGURE 4. Number of species having leaffall peaks per month. Closed circles: all leaffall peaks, including those that could not be tested statistically due to lack of replicates but that were observed in specific blocks. Open circles: statistically significant peaks.

period between November and February—corresponding to summer in the southern hemisphere, when the sun is in its farthest southern position—is characterized by 25 percent less insolation, lower mean temperatures, lower humidity, and higher frequency of clear days (Odum *et al.* 1970), and coincides with a period of lower litterfall and low number of species showing leaffall peaks (Fig. 4).

The relation between equinoxes and leaf production was established decades ago (*e.g.*, Longman & Jenik 1974 and references therein). When water availability is not a limiting factor (as in the forest studied), one of the factors considered most closely related to phenological patterns is irradiance (Wright 1996). Our data support the idea of a causal relationship between solar radiation and leaffall rather than the traditional link between rainfall and leaffall. During periods of maximum solar radiation, leaf production is enhanced and as a consequence, higher leaffall rates can be observed (Longman & Jenik 1974, van Schaik *et al.* 1993, Larcher 1995). Models of gross and net primary productivity (NPP) in Luquillo Mountains support this explanation (Wang *et al.* 2003). According to these models, solar radiation is the major control of primary productivity at regional scales. NPP is maximal in April, when the combination of solar radiation, temperature, and rainfall is optimal for plant growth (Wang *et al.* 2003). A second peak of NPP occurs in the rainy season, between September and October. This peak is lower probably due to cloudiness (which is presumably higher during the rainy season, implying lower solar radiation and consequently lower NPP). Therefore, we suggest that there is higher leaffall in May as a result of higher photosynthetic activity in April and not as a response to changes in rainfall as has been previously hypothesized. Furthermore, models of leaf phenology, emergence, and senescence (*e.g.*, Kikuzawa 1995, Reich 1995) suggest that, during high irradiance periods, increased photosynthetic rates would decrease leaf longevity and consequently increase leaf shedding, which may be observed as higher leaffall during periods of intense primary production. Moreover, several studies on leaf-shed phenology in tropical and subtropical wet forests around the world report bimodal patterns of leaffall with a consistent first peak around February–May and a second less well-defined peak in September–November (*e.g.*, Medway 1972, Frankie *et al.* 1974, Kunkel-Westphal & Kunkel 1979, Putz & Windsor 1987, Lowman 1988, Burghouts 1993). Some of these studies found no relationship between rainfall and leaffall (Frankie *et al.* 1974, Putz & Windsor 1987, Lowman 1988, Hegarty 1990), while in others, such a link is mentioned, but it is hard to establish a causal relation since the dry season is also the period of major solar radiation in most of these forests. Another phenological study in an Atlantic rain forest in Brazil (Morellato *et al.* 2000), under a weakly seasonal climatic regime also found a positive correlation between leaf-flush and leaffall, and temperature and day length, suggesting that leaf-flush and leaffall occurred when photosynthetic activity was the highest. Experimental approaches have also failed to establish a causal relationship between rainfall and leaffall (*e.g.*, Wieder & Wright 1995). Although we found a correlation between leaffall and rainfall (especially for species peaking in April), leaffall peaks occurred during the following 2 weeks after the rainfall peak in early April and are unlikely to be a response to low water availability. Moreover, positive correlations with rain-

fall occurred mainly for species peaking in April, but not for those peaking in August or November, when the other rainfall peaks occurred (*cf.* Fig. S1); therefore, we cannot affirm that rainfall was a trigger for leaf shed.

Finally, the spatial variability in leaffall pattern for some species such as *A. floribunda*, *F. citrifolia*, *O. krugii*, and *S. laurocerasus*, indicate that climate is not the only factor triggering leaf shed. Internal hormonal rhythms, intrapopulation variability, and microclimate differences could lie behind this variation.

PATTERNS OF SPECIES-SPECIFIC LEAFFALL.—We classified the species according to their leaffall phenology, however it is interesting to note that neither the growth form (trees vs. lianas), or the relative vertical position in the forest (canopy, subcanopy, or understory), or any other ecological feature of the species (*e.g.*, pioneers vs. shade tolerant, or climbing mechanisms for lianas) could be associated with the patterns of leaf shed. For instance, the five species of lianas included in this study (*H. laurifolia*, *M. sintenisii*, *R. surinamensis*, *S. brachyanta*, and *P. coriacea*) presented different leaf shed patterns: *H. laurifolia*, *S. brachyanta*, and *M. sintenisii* were unimodal but differed in the timing and width of leaffall peaks; while *R. surinamensis* was multimodal. Moreover, although these species have very different climbing strategies (*H. laurifolia* is a stem twiner, *M. sintenisii* and *S. brachyanta* use adventitious roots, while *R. surinamensis* uses modified branches as tendrils [Acevedo-Rodríguez 2003]), leaffall for all of them was related to solar radiation and/or PPFD. Thus, it seems that, disregarding the life history, most lianas face similar constraints related primarily to light availability. Our results did not support the common idea that lianas have year-round growth due to open access to the forest canopy that could surpass the sunlight limitation that restrains growth in other species (*e.g.*, Putz & Mooney 1991, Schnitzer & Bongers 2002). On the contrary, lianas seem to be subject to the same constraints and triggering factors affecting trees.

Concerning other groups of species with similar ecological features such as canopy trees, despite showing a variety of phenological patterns: from unimodal (*e.g.*, *M. bidentata*), bimodal (*e.g.*, *D. excelsa*) to nonmodal (*e.g.*, *S. berteriana*), almost all the species were correlated with either PPFD, solar radiation, or temperature (all being variables related to light availability), indicating that leaf-shed dynamics could be driven by similar processes. Frankie *et al.* (1974) and Opler *et al.* (1980) mentioned that the majority of species in wet forests in Costa Rica, which had marked peaks of leaffall were canopy or subcanopy trees, while understory trees in general did not present marked leaffall peaks. Van Schaik *et al.* (1993) mentioned that understory plants are not exposed to seasonal changes in solar radiation, and so are not expected to present a phenological pattern of leaf production associated with irradiance. This would also explain the lack of modality for *C. poecilanthus*, and *H. rugosa*, two understory trees found in this study.

Previous studies done in the same or similar forests as our study, as well as available data sets from Luquillo LTER (lterdb95, 98, and 111 data bases) support our findings concerning *B. tetraphylla*, *C. arborea*, *C. racemiflora*, *G. guidonia*, *P. montana*, *S. berteriana*, and *T. heterophylla*. For *B. tetraphylla*, a major leaffall

peak around April–May coinciding with the first rainfall peak of the year can be found both in Luquillo LTER data sets and previous literature (Estrada-Pinto 1970s, Lawrence 1996, Francis *et al.* 2000). At La Selva in Costa Rica, Frankie *et al.* (1974) observed a leaffall peak in April–May for *C. arborea*, while Lawrence (1996) reported a broadly seasonal pattern, in agreement with our findings. Drew (1998) reported a leaffall pattern for *C. racemiflora* with peaks between April and June, with leaf production beginning in April and increasing until a major peak in June, as we found. Lawrence (1996) also reported a bimodal pattern with peaks in April–May and October-November for *G. guidonia*. For *P. montana*, Lugo *et al.* (2000) reported a rather constant growth of 4 leaves/yr, which would concur with the nonmodal pattern found in this study. For *S. berteriana*, Luquillo LTER data also show an irregular pattern. Finally, for *T. heterophylla*, Estrada-Pinto (1970) mentioned a marked leaffall peak synchronized with *B. tetraphylla*, while Lugo (1992) observed a consistent peak of leaffall in May for a secondary forests dominated by *T. heterophylla*. Contrastingly, for other species, our results differed markedly from previous observations, *e.g.*, for *D. excelsa* we found a bimodal pattern with peaks in May–June and September (*cf.* Fig. 3), contrasting with unimodal patterns found in Luquillo LTER data (lterdb 111; single peak in May 2001) and the literature (Lawrence 1996; single peak in July 1981). For *C. schreberiana*, Lawrence (1996) reported a bimodal pattern, while we found a nonmodal one. Finally, for *M. bidentata,* Lawrence (1996) reported a multimodal pattern with leaffall peaks occurring in March, June–July, and October, while from Luquillo LTER data (lterdb 111), only one peak was recorded in June 2001. According to our data, *M. bidentata* presented a unimodal pattern, although there is a slight (nonsignificant) second peak in March–May (*cf.* Fig. 2C), which occurred only in one of the blocks. Since our data represent relative means for the three blocks, this second peak was underscored. These discrepancies between leaffall patterns for individual species found in different studies show that for some species phenological patterns vary considerably between years.

Summarizing, this study, unlike others, links species' phenological patterns with patterns at the community level, showing that patterns of leaffall in a forest stand are the result of the overlapping individual species phenology. Our data support the statement that leaffall in tropical forests can be seasonal even though climate seems constant or aseasonal. Moreover, leaf-shed seasonality can be better explained by changes in solar incidence than by rainfall seasonality. However, our findings also highlight the importance of interannual variation and asynchrony of leaffall events, suggesting that leaffall events are the result of a complex interaction between environmental and physiological factors. Additionally, we have presented patterns of leaffall phenology for several species, including some lianas for which—to our knowledge—no reports have been previously made.

ACKNOWLEDGMENTS

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

TABLE S1. *Correlation coefficients between litterfall categories and climatic variables for the same and the previous (Prev.) 2 weeks period during which litterfall was collected.*

TABLE S2. *Correlation coefficients between species leaffall and climatic variables for the same and the previous (Prev.) 2 weeks periods during which litterfall was collected.*

Figure S1. Monthly rainfall for the year of study (2003) and multiannual mean between 1975 and 2004 (LTER climate data: http://luq.lternet.edu/data/). Error bars refer to SD of the multiannual mean.

Figure S2. Multiannual monthly maximum for Photosynthetic Photon Flux Density (PPFD; 2001–2004 average; closed circles) and solar radiation (2003–2004 average; open circles) at El Verde subtropical wet forest in Puerto Rico. Graphed from El Verde Field Station meteorological data available at LUQ-LTER web site. Hourly data were summed up to get daily totals from which maximum values per month were taken.

Figure S3. Leaffall pattern for multimodal species. * Denote significant peaks.

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