

Phenology of *Plumeria alba* and its Herbivores in a Tropical Dry Forest

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ABSTRACT

Understanding phenology in plant populations requires distinction between proximate mechanisms and ultimate (evolutionary) causation. Leaf production and abscission, flower production, and herbivory were monitored for 2 yr in a population of the stem succulent tree, *Plumeria alba* L. in the Guánica State Forest in southwest Puerto Rico. Dependence of phenological events on abiotic (rainfall and day length) and biotic factors (herbivore abundance/damage) was quantified to discern potential relationships. Leaf flush and flowering were not associated with periods of highest rainfall as might be expected in a dry tropical forest. Rather, these events were highly correlated with day length. We observed that most leaf flush began in March and April, which was several months before the wettest period of the year (August to November). This result is consistent with other studies that show that leaf flush in *Plumeria* is under photoperiodic control and that the plants initiate growth and reproduction when cloudiness is low and seasonal light availability is greatest. Herbivore damage by caterpillars of the sphinx moth *Pseudosphinx tetrio* is restricted primarily to the wettest season, consistent with the hypothesis that early leaf flush and reproduction has been selected to avoid herbivory. It is not clear whether photoperiodic control of leaf flush and reproduction serves to maximize seasonal light availability, minimize the impact of herbivores, or both. However, it is clear that peak rainfall is not likely to have been the sole selective factor determining leaf flush and flowering in *P. alba*.

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

Key words: Apocynaceae; Guánica; herbivory; photoperiod; plant-insect interaction; *Pseudosphinx tetrio*; Puerto Rico; Sphingidae.

ECOLOGISTS HAVE OFTEN CITED ABIOTIC FACTORS as the principal cause of phenological timing in tropical plants (Hopkins 1970, Frankie *et al.* 1974, Opler *et al.* 1980, van Schaik *et al.* 1993). Monthly precipitation varies greatly in many tropical forests (Lugo *et al.* 1978, Opler *et al.* 1980, Aide 1988, Williams *et al.* 1997) and this may serve as an important evolutionary factor shaping when plants flush new leaves and flower. Van Schaik *et al.* (1993) and Wright and van Schaik (1994) emphasize the importance of seasonal light availability, driven by changes in cloud cover (Graham *et al.* 2003), as a determinant of primary production and the phenologies of tropical plant communities. In their review of tropical plant phenologies, van Schaik *et al.* (1993) suggest that reproduction and leaf flush in tropical plant communities should follow the progression of the zenithal sun. As a result, phenological events should be timed to occur when day length is increasing and sun angle is at a maximum. A weak correlation of community-wide peaks in leafing and flowering with latitude (van Schaik *et al.* 1993) supports their idea.

Consideration of the organisms that tropical plants interact with has led to many biotic explanations for phenological patterns observed in the tropics (*e.g.*, frugivorous birds and the timing of

fruit availability, pollinators and the timing of flowering, and herbivores and the timing of leaf flush; Snow 1965, Janzen 1967, Aide 1991). For example, flowering and leafing in many seasonally dry forest trees coincide with the dry season (*e.g.*, Frankie *et al.* 1974, Mori & Kallunki 1976, Rathcke & Lacey 1985), not with the onset of the wet season. Plants may flower before the period of greatest rainfall so that seeds are available to germinate during the wet season (Garwood 1983). Leaf flush in advance of the wet season has also been interpreted as a phenological response of dry forest trees to avoid or reduce herbivory on young leaves (Aide 1988, Aide 1992, Coley & Barone 1996). The timing of flower production often correlates with pollinator abundance (Janzen 1967, Frankie *et al.* 1974, Ackerman 1983, *cf.*, Zimmerman *et al.* 1989). Janzen (1967) observed that many dry forest plants flower during the dry season when their pollinators, mainly bees, are most abundant. However, insect abundance in general, including herbivores, correlates positively with rain events (Wolda 1988). Thus, it is unclear in tropical forests whether climate determines insect abundance and insects determine when plants flush leaves (Aide 1992, Coley & Barone 1996) and reproduce (Janzen 1967), or whether climate determines plant phenology (van Schaik *et al.* 1993, Wright & van Schaik 1994) and insects merely track their food resources.

In this study, we explore the abiotic and biotic factors affecting phenological timing in the tropical dry forest tree, *Plumeria alba*, growing in southwestern Puerto Rico. *Plumeria alba* is a conspicuous

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component of many tropical dry forests in the Caribbean and is well known for its specialized herbivore, the larvae of *P. tetrio* (Santiago Blay 1985). Here, we describe the leaf flush and flowering phenology of *P. alba* in comparison to the phenology of *P. tetrio* and one other common herbivorous insect. We then evaluate the importance of seasonal rainfall and potential solar radiation (as determined by sun angle and day length) versus seasonal variation in herbivory as evolutionary factors in the phenological timing of *P. alba*.

METHODS

STUDY AREA AND CLIMATE.—The study site was located in subtropical dry forest (Ewel & Whitmore 1973) in the Guánica State Forest and Biosphere Reserve (GSF; 17°58' N, 66°55' W). The forest borders the southwest coast of Puerto Rico in the rain shadow of the Central Cordilleras. Annual rainfall averages less than 800 mm (Department of Natural Resources 1976). The driest months of the year are December to March, a period of intermediate rainfall occurs between April and July, and the wettest months are typically August to November (Fig. 1a). Light availability is greatest from February

to August when the rain-free period coincides with maximal day length and the greatest angle of incidence of the sun (Fig. 1b). *Plumeria alba* is one of the dominant tree species (in terms of basal area and number of stems) in the scrub forest (Lugo *et al.* 1978, Farnsworth 1993), one of four forest types within the GSF (Lugo *et al.* 1978). The scrub forest is the most exposed and driest forest type in the area comprising approximately 15 percent or 599.7 ha of the 4016 ha GSF (Lugo *et al.* 1978, Farnsworth 1993), and it is located in close proximity to the coast on exposed limestone webbed together with veins of reddish-brown, stony-clay, loam soils (Department of Natural Resources 1976; U.S.D.A. Soil Conservation Service 1979).

STUDY SPECIES.—*Plumeria alba* L. (Apocynaceae) is common in the scrub forest habitat found on many islands in the Caribbean, including Puerto Rico (Acevedo Rodriguez 1996). *Plumeria alba* trees are small, 3–7 m in height, with thick stems that produce abundant, white, milky latex from leaves, stems, inflorescences, and flowers. Leaves are up to 30 cm long, 1.2–4 cm wide, alternate, and aggregated at branch tips.

Many insects interact with *P. alba*. We studied the most frequently encountered herbivores, *P. tetrio* larvae (Sphingidae), and three taxa of Homoptera, including two Pseudococcidae (*Paracoccus marginatus* and *Puto* spp.) and one unidentified Margaroididae. Of the homopterans, the most common (S. A. Sloan, pers. obs.) was the recently introduced *P. marginatus* (Miller *et al.* 1999). During the study, a bark beetle, *Microborus laetus* (Wood 1961), was observed to cause dieback of branches and main stem, leading to the death of some plants.

Plumeria is the preferred host plant for the larvae of the hawkmoth, *P. tetrio* L. (Sphingidae). The common names of *P. alba* and *P. tetrio*, “the wormy tree” (Acevedo Rodriguez 1996) and “the *Plumeria* caterpillar” (Martorell 1945), respectively, exemplify this specialized plant–insect interaction. *Pseudosphinx tetrio* has a distribution that ranges throughout the tropics and subtropics of the Americas (Martorell 1945).

Female *P. tetrio* lay clutches of up to 150 eggs on the surface of leaves or branches of *P. alba* (Sloan 2003). Santiago Blay (1985) describes the timing of *P. tetrio* life stages in greater detail. Larvae of *P. tetrio* often completely defoliate *P. alba* trees and have been observed eating inflorescences and damaging the terminal meristems of branches (Sloan 2003).

Homopterans attack the leaves, inflorescences, flowers, fruit, and sometimes the stems of *P. alba*. They tend to form localized infestations on the plant’s surface. Given the difficulty in quantifying homopteran damage, only relatively heavy infestations were noted. The minimum criterion for designating densities of homopterans as “heavy infestations” was that homopterans covered at least 50 percent of a leaf or inflorescence.

PHENOLOGY.—To sample the *P. alba* population, four transects were established parallel to the coastline (three east to west and one southeast to northwest). After haphazardly choosing and tagging one tree near a transect, we used its two nearest neighbors as the next two trees to be tagged. We continued using the nearest neighbors

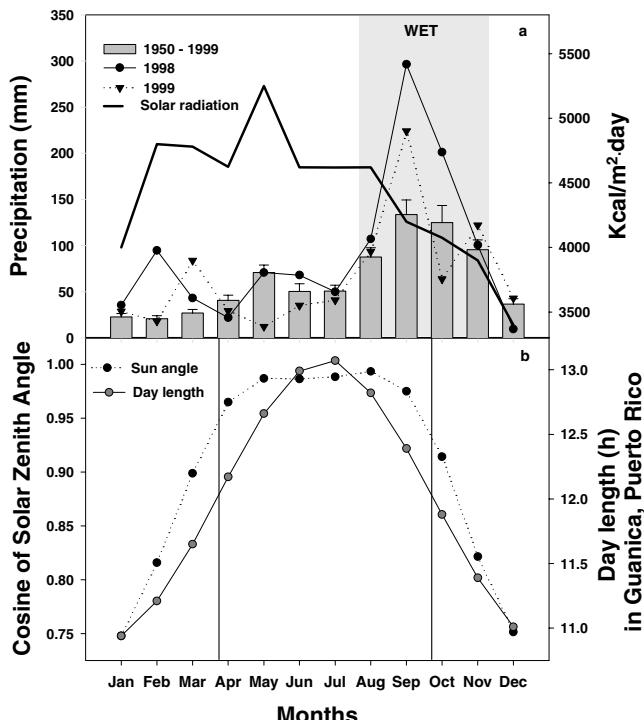


FIGURE 1. (a) Mean monthly precipitation from 1950–1999 (± 1 SE; bars) compared to precipitation for 1998 and 1999 (thin solid and dotted line, respectively; NOAA 2001). Incident solar radiation Jan–May 1976; Jun–Dec 1975 to the GSF (Guánica State Forest and Biosphere Reserve; thick bold solid line; modified from Lugo *et al.* 1978). Single shaded vertical bar delineates the wet season. (b) Cosine of the solar zenith angle at noon (solar angle; dotted line) and day length in the Guánica dry forest (solid line; latitude = 17°58' N). Vertical lines approximate the vernal and autumnal equinox (NOAA 2002).

of tagged trees until 20 trees were tagged, thus forming a “plot.” If the nearest neighbors of a tagged tree were previously tagged then a third neighbor was used. If there were no additional neighbors within 10 meters of tagged trees then the plot would remain with fewer than 20 trees. Therefore plot size varied according to the local density of *P. alba* trees in an area and the number of trees per plot remained somewhat constant. At least 200 m separated the two closest transect areas. Groups of four plots were located on or within 20 m of each transect. Three hundred seventeen *P. alba* trees were tagged in 16 plots of ~20 trees as part of a related demographic study presented elsewhere. The minimum and maximum distances between neighboring plots within a transect were 50 m and 150 m, respectively.

Ten *P. alba* trees were randomly selected in each plot and were censused monthly for 24 mo between March 1998 and March 2000. Thirty-three censused trees that died during the study were eliminated, leaving 127 trees represented in the analyses. Each month, all new leaves were marked with a different color of indelible ink denoting a new leaf cohort. The number of new leaves, evidence of herbivory, presence and stage of *P. tetrio* (eggs and larvae), and the presence and severity of homopteran infestations were noted during each census. During the flowering season, the number of inflorescences, open flowers, flower scars, and flower buds were also noted. Pearson correlations were used to compare the relationship among these phenological variables with day length and monthly precipitation.

WATERING EXPERIMENT.—A separate watering experiment was conducted to test the effect of water availability on herbivory and phenophase timing in adult *P. alba* trees. In September 1998, near the easternmost plot, 16 *P. alba* trees with at least one inflorescence each were chosen haphazardly for inclusion in this study and randomly assigned one of two treatments: (1) watered, where a bucket with a gravity-fed hose that trickled water beneath the soil surface was placed at the base of each tree. In addition to natural precipitation that fell during the study period, these trees received 19 liter of water (equivalent to 19 mm of rainfall assuming these 19 liter wet a 1 m² area) per tree per month for 13 mo; and (2) “control,” where trees received no additional water. Watered trees received their first treatment 16 October 1998. Trees were censused monthly for evidence of herbivory by *P. tetrio*. The trees used in the watering experiment were not the same trees used in phenological censuses.

RESULTS

RAINFALL AND POTENTIAL SOLAR RADIATION.—Annual rainfall in Guánica is highly variable, and over the past 49 yr (1950–1999, without 1976) the extremes in annual precipitation have ranged from 299 mm to 1469 mm, mean 762 mm. During the 2 yr of this study, annual precipitation was well within the historical range, with 1035 mm falling in 1998 and 812 mm in 1999 (Fig. 1a; National Oceanographic Atmospheric Administration 2001). Long-term precipitation data, collected by the National Climate Data Center at Ensenada, Puerto Rico, show that year-to-year variation

in monthly precipitation can vary by an order of magnitude. However, in general, greater than 50 percent of the annual precipitation occurs between August and November.

In the GSF, the solar zenith, an indirect measure of potential solar radiation, is greatest from late-March to mid-September, between the vernal and autumnal equinoxes (Fig. 1b; National Oceanographic Atmospheric Administration 2002). During the winter solstice there is 25 percent less potential light intensity at noon than during the summer solstice (Fig. 1b). At the latitude of the GSF, day length changes roughly 2 h over the course of a year (Fig. 1b).

LEAF PRODUCTION.—The annual peak in leaf flush (Fig. 2a) occurred 2 to 4 mo prior to the peak in precipitation (September; Fig. 1a). Most *P. alba* trees began flushing new leaves in March and acquired their maximum number of leaves by July. More than half of *P. alba* trees in this study retained at least some leaves year-round (Fig. 2b). However, of those trees with leaves during the driest period (December–February), more than 80 percent had fewer than

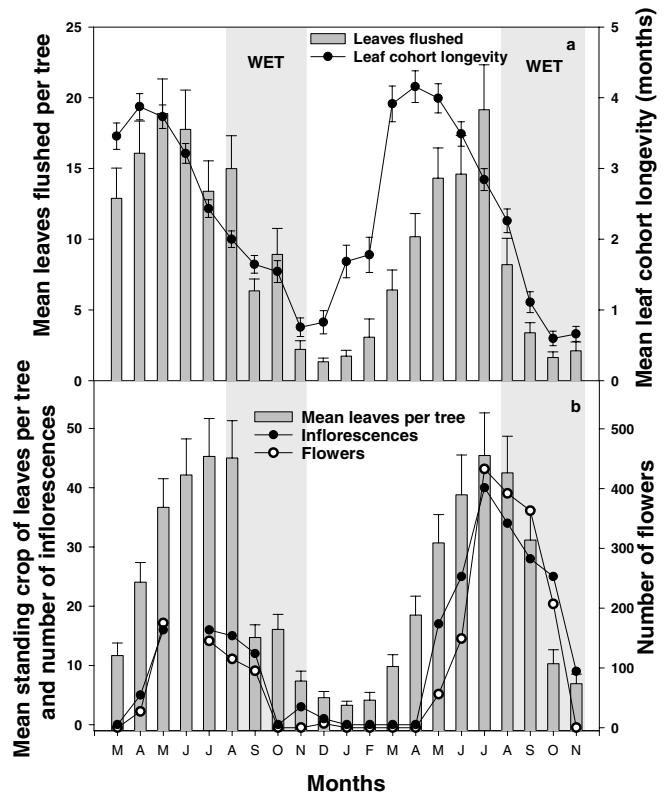


FIGURE 2. (a) Mean monthly number of leaves (± 1 SE; bars) flushed per tree from March 1998 until November 1999 compared to mean cohort longevity (± 1 SE; filled circles) in months from the time of leaf flush. (b) Mean standing crop of leaves (± 1 SE; bars) per *P. alba* tree, total number of inflorescences (filled circles; left axis), and total number of flowers (open circles; right axis). Fourteen trees flowered and one fruit matured in 1998 and 17 trees flowered and 24 fruit matured in 1999. Shaded vertical bars delineate the wet seasons in both panels (a) and (b).

10 leaves, mean \pm 1 SE (5.73 ± 0.81 and 4.35 ± 0.55 , 1998 and 1999, respectively; Fig. 2b).

Though the quantity of leaves flushed varied monthly (Fig. 2a), *P. alba* flushed leaves throughout the year. The duration of a leaf cohort depended on the month in which leaves were flushed (Fig. 2a). That is, leaves flushing toward the end of the wet season (December) had shorter potential longevity. Maximum and minimum average leaf cohort longevity was 4 and less than 1 mo, respectively. On average, 52 percent of leaves in marked cohorts did not survive beyond 2 mo regardless of the month the cohort flushed (Fig. 2a).

FLOWERING.—Inflorescence production in *P. alba* began at the end of the dry season (Fig. 2b), about the same time leaves expanded. Flower production began in March/April and continued until September/October (Fig. 2b). The peak in flower and inflorescence production occurred simultaneously in May or June 1998 and July 1999. During the 1999 flowering season, twice as many inflorescences and flowers were produced as during the 1998 flowering season (Fig. 2b), but the timing of flowering was similar between years.

PATTERNS OF HERBIVORY.—Eighty-seven percent of the censused *P. alba* trees either exhibited herbivore damage by *P. tetrio* larvae, or *P. tetrio* larvae or eggs were observed on the trees at least once during the 24 mo of this study. No difference was observed between the proportion of trees attacked in 1998 (70%) and 1999 (69%). We observed a 42 percent probability of trees that were attacked in 1998 being attacked again in 1999. In addition, we observed a lag time of at least 4 mo between the peaks of leaf flush and *P. tetrio* attacks (Figs. 2a and 3).

During the watering experiment in the dry season, *P. tetrio*, or evidence of their damage, were observed more frequently on watered than control treatment trees (Fig. 4). As many as six of the eight watered trees had leaf damage or supported *P. tetrio* eggs or

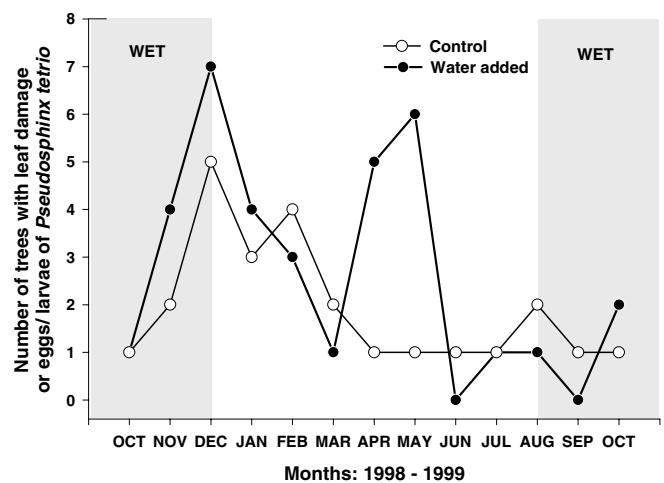


FIGURE 4. The number of *Plumeria alba* trees with at least one life-cycle stage of the specialist herbivore, *Pseudosphinx tetrio*, per month from October 1998 until October 1999 following a watering experiment. Shaded vertical bars delineate the wet seasons.

larvae during the exceptionally dry months of April and May 1999, significantly more frequent than unwatered trees (one of seven; Fisher Exact Test, $P = 0.0203$).

Paracoccus marginatus, *Puto* sp. and at least one species in the Margaroididae as well as other homopterans feed on the sap of *P. alba* leaves. The peak in the percentage of *P. alba* trees with homopterans occurred when the standing crop of leaves was greatest (June to August). At peak infestation, up to 80 percent of *P. alba* trees had homopterans on their leaves (Fig. 3). Leaves of *P. alba* experiencing heavy infestations were frequently contorted and misshapen and did not expand fully.

PHENOLOGICAL CORRELATIONS.—The monthly standing crop of leaves and the number of leaves turned were positively correlated with day length (Table 1). Neither variable exhibited a strong

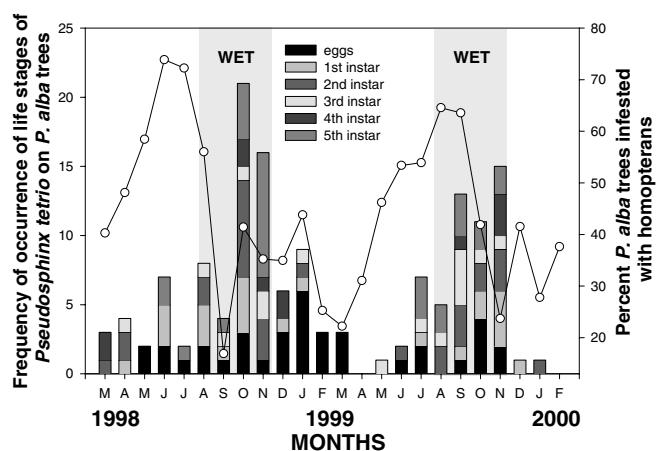


FIGURE 3. Phenology of *Pseudosphinx tetrio* eggs and larval instars (stacked bar graph; left axis) as measured by the frequency of occurrence on *P. alba* trees in the Guánica State Forest, Puerto Rico, and percent of *P. alba* trees infested with homopterans (open circles; right axis) from March 1998 to February 2000.

TABLE 1. Monthly correlations of attributes of *Plumeria alba* with the abiotic variables, day length (on the first day of each month) and precipitation (NOAA 2002). Sample sizes were $N = 24$ except for abscised leaves ($N = 23$).

Variables	Day length (h) r	Monthly precipitation (mm) r
Standing crop of leaves	0.9461	0.0157
Leaves flushed	0.7852	-0.1749
Leaves abscised or eaten	0.3844	0.7212
Inflorescences	0.7028	0.1888
Number of trees with <i>Pseudosphinx tetrio</i>	-0.0267	0.4993
Number of trees with severe homopteran infestations	0.8565	-0.0916

correlation with monthly precipitation. Monthly leaf abscission was positively correlated with monthly rainfall, but not day length. Number of inflorescences found on *P. alba* was correlated with day length, but not monthly precipitation. The number of *P. alba* trees with *P. tetrio* larvae of all instars was significantly associated with monthly precipitation, while the proportion of trees severely infected with homopterans was positively correlated with day length, but not monthly precipitation.

DISCUSSION

Van Schaik *et al.* (1993) and others have emphasized the importance of proximate versus ultimate factors in explaining the phenological behavior of tropical trees. With regard to proximate factors, it is likely that the timing of leafing and flowering in *P. alba* is determined by photoperiod. Murashige (1966) and Lawton and Akpan (1968) experimentally manipulated both day and night length for *Plumeria acuminata* and demonstrated a positive growth and leafing response to interrupted night length. Like many temperate plants (Thomas & Vince-Prue 1997), photoperiod determines phenology in *P. acuminata* in the mode of a “long-day plant.” Similar experiments have not been performed on *P. alba*, but the onset of leaf flush after the spring equinox suggests a similar physiological mechanism. The selective factors favoring initiation of growth and reproduction at this time of the year remain undetermined.

RAINFALL.—The onset of leaf flushing and flowering in *P. alba* is not timed to seasonal rains. Seasonal rainfall in Puerto Rico is more influenced by late summer tropical winds which travel across the Atlantic Ocean from Africa and less influenced by the intertropical convergence zone, which determines seasonal rainfall patterns in much of the tropics (van Schaik *et al.* 1993). Thus, the onset of rains does not closely follow the zenithal sun in Puerto Rico as it does elsewhere in the tropics. Leaf flush and flowering in *P. alba* occurs 3 to 4 mo in advance of September and October, the only months when plants in the GSF do not experience soil water deficits (Lugo *et al.* 1978). *Plumeria* species, like other stem succulent trees, probably store at least some of the water used to flush leaves during the dry season in the main stem and branches (Borchert and Rivera 2001). Plants may also take advantage of infrequent rain storms during the long dry season. If rainfall were, however, an ultimate factor determining phenology, we would expect a much closer concordance of leaf flush, flowering, and the onset of the wettest season. Even if *P. alba* flushes in anticipation of the rainy season (*sensu* Rockwood 1973), once the wet season begins many of the leaves on *P. alba* would be old and plants would begin to lose their leaves (either by dehiscence or due to herbivory) and therefore would be less able to take advantage of the lack of soil water deficits. Thus, our data do not support the hypothesis that phenological events are timed to be associated with maximal water availability.

LIGHT AVAILABILITY.—Our ability to fully test the light limitation hypothesis for phenological timing (van Schaik *et al.* 1993, Wright & van Schaik 1994) is limited by a lack of data on the seasonal vari-

ation in photosynthetic active radiation (PAR). Instead, we infer changes in seasonal light availability from changes in sun angle and day length, which suggest a maximum between the solar equinoxes (March–September). In the open habitat of the scrub forest in which *P. alba* occurs (Lugo *et al.* 1978), the only factor that might additionally limit daily PAR is cloudiness (Graham *et al.* 2003), which is likely to be correlated with rainfall (*e.g.*, Wright & van Schaik 1994). If true, then peak irradiances in GSF must occur between April and August; a 1-yr sample of solar radiation data (Fig. 1a) provided by Lugo *et al.* (1978) confirms this impression. This period coincides with the period of maximal leaf flush and flowering. These correlations may suggest that changes in photoperiod may ultimately ensure that leaf flush occurs when seasonal irradiance is maximal. The nearly perfect correlation between leaf standing crop and day length is most striking in this regard.

Nevertheless, a complete test of the validity of the light limitation hypothesis for explaining the phenology of *P. alba* rests on a number of issues. Of these, the degree to which daily PAR can limit photosynthesis, especially after several months of seasonal drought, is probably the most important unknown abiotic element. A detailed study of the photosynthetic capacity of *P. alba* in response to rainfall variation during April–August would be critical to a comprehensive test of the light-limitation hypothesis.

HERBIVORY.—In *P. alba*, correlations of herbivory with leafing and flowering corroborate the hypothesis that *P. alba* leaf production occurs when the probability of herbivory is low. Herbivory by *P. tetrio* occurs predominantly during the wet season, when leaf production is in decline, suggesting these plants have evolved phenological escape from herbivory. This conclusion is supported by the watering experiment. In control plants, little evidence of attack by larvae of *P. tetrio* was evident during December–July. In watered plants, however, levels of herbivore attack during the driest 2 mo (April and May 1999; Figs. 1 and 4) were similar to those recorded in both treatments during the wettest months (Fig. 4). During the watering experiment, there was no observed treatment effect on leaf quantity (Sloan 2003) and leaf quality was not monitored, so it is unclear what characteristics of leaves the additional water changed. The patterns of herbivore attack, nonetheless, suggest that *P. alba* avoids herbivory by *P. tetrio* by flushing leaves away from the wettest months of the year.

The aposematic coloration of *P. tetrio* suggests that it is able to detoxify and sequester secondary compounds that make it unpalatable to predators, similar to monarch and *Heliconius* butterflies (Gilbert 1980, Coppin & Cobb 1983, Crawley 1983). In the case of *Heliconius*, its host, *Passiflora*, uses a variety of alternative defenses (extrafloral nectaries that attract ants, wasps, and parasitoids, hooked trichomes, false eggs) to defend against herbivory (Gilbert 1980). Phenological escape, as we suggest for *P. alba*, is an alternative for a host plant whose specialized herbivores have overcome their chemical defenses.

Dry season leaf flush did not allow *P. alba* to avoid attack by homopterans. Mealybug infestation closely follows the phenology of the plants, suggesting dry season conditions are not limiting to this herbivore. Leaves infested with homopterans abscised before leaves

without homopterans (S. A. Sloan, pers. obs. unpublished data). The most common homopteran found on *P. alba*, *P. marginatus* (S. A. Sloan, pers. obs.), was introduced to Puerto Rico in the late 1990s (Miller *et al.* 1999), indicating that the interaction between these two species is recent.

CONCLUSIONS

Our study reaffirms the need to separate proximate and ultimate selective factors in the study of phenology. While it is clear that leaf flush and flowering in *P. alba* are not timed to take advantage of peak rainfall in the GSF, the precise selective factors which shaped the phenology of *P. alba* are not fully resolved by our observations. For instance, the importance of water availability, as a selective factor determining phenology may be indirect. Further resolution of these issues will require detailed study of the photosynthetic capacity of plants during the critical period of April–August when plants exhibit maximal phenological activity but during which rainfall is intermediate and variable. Finally, experimental studies of photoperiodic control of leafing and flowering are required to determine if day length is the proximate mechanism controlling phenology in *P. alba* as shown in the congener *P. acuminata* (Murashinge 1966, Lawton & Akpan 1968).

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LITERATURE CITED

- ACEVEDO RODRIGUEZ, P. 1996. Flora of St. John U.S. Virgin Islands. New York Botanical Garden, Bronx, New York, New York.
- ACKERMAN, J. D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biol. J. Linn. Soc. 20: 301–314.
- AIDE, T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. Nature 336: 574–575.
- AIDE, T. M. 1991. Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. Oecologia 88: 511–514.
- AIDE, T. M. 1992. Dry season leaf production: An escape from herbivory. Biotropica 24: 532–537.
- BORCHERT, R. 1992. Computer simulation of tree growth periodicity and climatic hydroperiodicity in tropical forests. Biotropica 24: 385–395.
- BORCHERT, R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75: 1437–1449.
- BORCHERT, R., AND G. RIVERA. 2001. Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees. Tree Physiol. 21: 213–221.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27: 305–335.
- COPPEN, J. W., AND A. L. COBB. 1983. The occurrence of iridoids in *Plumeria* and *Allamanda*. Phytochemistry 22: 125–128.
- CRAWLEY, M. J. 1983. Herbivory. The dynamics of animal-plant interactions. Blackwell Scientific Publications, Oxford, UK.
- DEPARTMENT OF NATURAL RESOURCES. 1976. Master plan for the commonwealth forests of Puerto Rico. Office of education and publication at the Department of Natural Resources, San Juan, Puerto Rico, pp. 52–57.
- EWEL, J. J., AND J. L. WHITMORE. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. Forest Service Research Paper, Institute of Tropical Forestry, Puerto Rico.
- FARNSWORTH, E. J. 1993. Ecology of semi-evergreen plant assemblages in the Guánica dry forest, Puerto Rico. Caribb. J. Sci. 29: 106–123.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 62: 881–919.
- GARWOOD, N. C. 1983. Seed germination in a seasonal tropical forest in Panamá: A community study. Ecol. Monogr. 53: 159–181.
- GILBERT, L. E. 1980. Ecological consequences of a coevolved mutualism between butterflies and plants. In L. E. Gilbert and P. H. Raven (Eds.). Coevolution of animals and plants: Symposium V, First International Congress of Systematic and Evolutionary Biology, Boulder, Colorado, August, 1973. University of Texas Press, Austin, Texas. pp. 210–240 [papers].
- GRAHAM, E. A., S. S. MULKEY, K. KITAJIMA, N. G. PHILLIPS, AND S. J. WRIGHT. 2003. Cloud cover limits CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. Proc. Natl. Acad. Sci. USA 100: 572–576.
- HOPKINS, B. 1970. Vegetation of the Olokemeji Forest Reserve, Nigeria VI. The plants on the forest site with special reference to their seasonal growth. J. Ecol. 58: 765–793.
- JANZEN, D. H. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620–637.
- LAWTON, J. R. S., AND E. E. J. AKPAN. 1968. Periodicity in *Plumeria*. Nature 218: 384–386.
- LUGO, A. E., J. A. GONZALEZ LIBOY, B. CINTRON, AND K. DUGGER. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10: 278–291.
- MARTORELL, L. F. 1945. A survey of the forest insects of Puerto Rico part I. J. Agric. Univ. P. R. 29: 278–281.
- MILLER, D. R., D. J. WILLIAMS, AND A. B. HARMON. 1999. Notes on a new mealybug (hemiptera: Coccoidea: Pseudococcidae) pest in Florida and the Caribbean: The papaya mealybug, *Paracoccus marginatus* Williams and Granara de Willink. Insecta Mundi 13: 179–181.
- MORI, S. A., AND J. A. KALLUNKI. 1976. Phenology and floral biology of *Gustavia superba* (Lecythidaceae) in central Panama. Biotropica 8: 184–192.
- MURASHINGE, T. 1966. The deciduous behavior of a tropical plant, *Plumeria acuminata*. Physiologia Plantarum 19: 348–355.
- NATIONAL OCEANOGRAPHIC ATMOSPHERIC ADMINISTRATION. 2001. National climate data center. Climate data Ensenada, Puerto Rico station. <http://www.ncdc.noaa.gov>. Cited 10 September 2001.
- NATIONAL OCEANOGRAPHIC ATMOSPHERIC ADMINISTRATION. 2002. Surface radiation research branch. <http://www.srrb.noaa.gov>. Cited 18 October 2002.

- OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 68: 167–188.
- RATHCKE, B., AND E. P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.* 16: 179–214.
- ROCKWOOD, L. L. 1973. The effect of defoliation on seed production of six Costa Rican tree species. *Ecology* 54: 1363–1369.
- SANTIAGO BLAY, J. A. 1985. Notes on *Pseudosphinx tetrio* (L.) (Sphingidae) in Puerto Rico. *J. Lepidopterian Soc.* 39: 208–214.
- SLOAN, S. A. 2003. The effect of water availability and herbivory on the demography of a dry forest tree *Plumeria alba* (Apocynaceae). Dissertation. University of Puerto Rico, Rio Piedras, Puerto Rico.
- SNOW, D. W. 1965. A possible selective factor in the evolution of fruiting seasons in a tropical forest. *Oikos* 15: 274–281.
- THOMAS, B., AND D. VINCE-PRUE. 1997. Photoperiodism in plants. Academic Press, San Diego, California.
- U.S.D.A. SOIL CONSERVATION SERVICE. 1979. Soil survey of Ponce area of southern Puerto Rico, p. 80. United States Department of Agriculture, San Juan, Puerto Rico.
- VAN SCHAIK, C. P., J. W. TERBORGH, AND S. J. WRIGHT. 1993. The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353–366.
- WILLIAMS, R. J., B. A. MYERS, W. J. MULLER, G. A. DUFF, AND D. EAMUS. 1997. Leaf phenology of woody species in a north Australian tropical savanna. *Ecology* 78: 2542–2558.
- WOLDA, H. 1988. Insect seasonality: Why? *Annu. Rev. Ecol. Syst.* 19: 1–18.
- WOOD, S. L. 1961. New species of bark beetles. *Great Basin Nat.* 21: 100–103.
- WRIGHT, S. J., AND C. P. VAN SCHAIK. 1994. Light and the phenology of tropical trees. *Am. Nat.* 143: 192–199.
- ZIMMERMAN, J. K., D. W. ROUBIK, AND J. D. ACKERMAN. 1989. Asynchronous phenologies of a neotropical orchid and its euglossine bee pollinator. *Ecology* 70: 1192–1195.