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FLOWERING PHENOLOGY OF *WERAUHIA SINTENISII*, A BROMELIAD FROM THE DWARF MONTANE FOREST IN PUERTO RICO: AN INDICATOR OF CLIMATE CHANGE?

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ABSTRACT. Tropical montane cloud forests are experiencing climatic change that may alter their sensitive biota and ecosystem processes. We studied the relationship between several environmental factors and the flowering phenology of *Werauhia sintenisii,* an epiphytic bromeliad from the dwarf montane cloud forest in Puerto Rico, to infer responsiveness of this species to climate and to suggest how useful its phenology may be in monitoring climatic change. We applied a cross-correlation analysis to the number of open flowers per month to eight different environmental variables for 1999–2000. After determining the lag-time at which the environmental factor was best correlated with the number of open flowers, we performed a stepwise regression with the environmental factor shifted by the number of months indicated by the cross-correlation analysis and the number of open flowers per month. Differences were observed between years in the timing of flowering, which began one month earlier in 2000 than in 1999. The production of flowers was related to the monthly mean minimum temperature three months previous and to the monthly mean daily irradiance two months earlier. Together both variables explained 66% of the variation. The flowering of *W. sintenisii,* which appears to be susceptible to nocturnal temperatures and solar irradiance, may be useful as a biotic indicator of climate change in cloud forests.

Key words: Bromeliaceae, elfin forest, epiphytes, global warming, tropical montane cloud forest

INTRODUCTION

Tropical Montane Cloud Forests (TMCF) occur under narrowly defined environmental conditions and are among the most sensitive and vulnerable of the world's ecosystems to climate change (Lloyd & Giambelluca 1998). TMCF, also called cloud, elfin, or dwarf forests, are generally of small stature and have lower productivity than tropical lowland forests (Tanner et al. 1992). Persistent cloud or fog cover, reduced insolation, low temperatures, low nutrient availability, saturated soils, impeded root respiration, high winds, high humidity, and the presence of phenolic compounds in leaves are some of the hypotheses considered, either individually or together, to explain the lower stature and productivity of the TMCF (reviewed by Bruijnzeel & Proctor 1993). These unique environmental conditions account for the specialized, and often endemic, biota in TMCF. Species restricted to these forests may be very sensitive to a decrease in cloud cover and associated changes in relative humidity and rainfall (Pounds et al. 1999). Because of this sensitivity, TMCF species are excellent candidates for monitoring global climate change (Lugo & Scatena 1992, Benzing 1998, Lloyd & Giambelluca 1998, Nadkarni & Solano 2002). Specifically, TMCF epiphytes may be the best floristic group for use as indicators of changes in atmospheric conditions and for understanding how global atmospheric changes impact tropical forests (Lugo & Scatena 1992, Benzing 1998, Nadkarni & Solano 2002).

Epiphytes experience greater climate stress than associated terrestrial vegetation (Benzing 1998), which makes them more vulnerable to perturbations in climate than non-epiphytes (Lugo & Scatena 1992, Benzing 1998, Nadkarni & Solano 2002). Epiphytes root in the canopy and lack contact with soil. They depend, therefore, on moisture directly from the atmosphere, and usually their carbon and water balance mechanisms are tightly coupled to prevailing climate (Benzing 2000). Flowering phenology can be particularly susceptible to environmental variation. Although phenology has been used as an indicator to track climate change on terrestrial plants (Fitter et al. 1995, Thórhallsdóttir 1998), it has not been used in epiphytic systems.

Flowering phenology in tropical plants often is associated with seasonal patterns in climate or

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the availability of certain animal pollinators (Frankie et al. 1974, Opler et al. 1976, Stiles 1978, Augspurger 1980, Ackerman 1985, Rathscke & Lacey 1985, van Schaik et al. 1993, Wright 1996). Irradiance and rainfall appear to be the main seasonal abiotic variables influencing the phenology of tropical plants (Wright & van Schaik 1994, Wright 1996). Most tropical plants produce leaves and flowers during peaks in irradiance, except when water-stressed (Wright & van Schaik 1994). Few studies have described the flowering phenology of TMCF species (Koptur et al. 1988, Berlin et al. 2000). In TMCF, where climate is relatively aseasonal, flowering peaks are less pronounced and may occur multiple times throughout the year. Significantly more flowering peaks (of different species) occurred, nevertheless, during the warmest and least cloudy months in the TMCF in Costa Rica (Koptur et al. 1988) and Hawaii (Berlin et al. 2000). If global warming can alter temperature and cloud cover in TMCF (Still et al. 1999), then phenological patterns of TMCF plants should be affected.

At Pico del Este, a TMCF in Puerto Rico, environmental conditions have changed during the last 30 years. Monthly mean minimum temperature has increased along with a trend for more days with ≥ 12.7 mm precipitation (FIGURE 1). Daily minimum temperature has increased worldwide (Easterling et al. 1997) three times faster than maximum temperature during the period 1951–1990 (Harvey 1995). The possible consequences of environmental changes on any ecosystem process in Pico del Este are unknown. In this study, we monitored the flowering phenology of *Werauhia sintenisii* (Baker) J.R. Grant, one of the most common epiphytic bromeliads at Pico del Este (Richardson et al. 2000). Two years of environmental and flowering data were compared to detect which environmental factors are likely affecting flowering phenology. We infer the susceptibility of this species to climatic change and suggest how useful its phenology can be for monitoring climatic change in TMCF ecosystems. Additionally, we contrasted our results with qualitative data on flowering phenology taken 35 years ago from a population on Pico del Oeste (Nevling 1971) located ca. 2 km northwest of Pico del Este at 1050 m.

METHODS

Study Site and Species

The study area, Pico del Este, is located in the Luquillo Experimental Forest (LEF) in eastern Puerto Rico (18°16′30 N, 65°45′46 W) at 990 m elevation. Mean annual precipitation is 4200 mm (7% of which is intercepted mist) and mean monthly temperatures range 17–20°C (Walker et al. 1996). The vegetation is a dwarf forest (canopy 2–6 m), classified as an atmospheric association within subtropical lower montane rain forest (Ewel & Whitmore 1973). The most common tree species are *Tabebuia rigida* Urban, *Ocotea spathulata* Mez, and *Calyptranthes krugii* Kiaersk. Together these species account for 80% of total tree density (Howard 1968).

Werauhia sintenisii (syn. *Vriesea sintenisii* (Baker) J.R. Grant) has a Type 4 life form (Benzing 2000) with an impounding phytotelm shoot that grows both epiphytically and terrestrially (FIGURE 2). In Pico del Este, this species is one of the most common epiphytes (FIGURE 2) and accounts for 12.8% of forest net primary productivity (Richardson et al. 2000). Its cistern-like shoot intercepts litter from the canopy and water from precipitation and mist. Intercepted moisture maintains a humid habitat within the funnel-form shoot, which in turn sustains the associated decomposers. Therefore, *W. sintenisii* may be especially vulnerable to any change that dries out this microcosm.

Werauhia sintenisii produces a single inflorescence with 2–14 flowers. One to two flowers open per day, and all flowers in one inflorescence will open during a 1–2-week period. Flowers have a tubular yellow corolla surrounded by bright red bracts, are odorless, and last for only one day. Most plants do not flower every year. Of the plants that reproduced in one year (n = 241), only 6.4% flowered again in the following year (Lasso 2001). In Pico del Este, this species is visited by the Puerto Rican emerald hummingbird (*Chlorostilbon maugaeus*).

Flowering Phenology

We monitored the phenology of tagged individuals (epiphytic and terrestrial) within 12 plots (9 m × 14 m) and along trails connecting the plots, between October 1998 and October 2000. Six of the plots have been fertilized since 1989, every 3 months, with macro- and micronutrients (Walker et al. 1996). Differences between plants growing in fertilized and nonfertilized plots, in the nutrient content of the litterfall accumulated in the tank, and in the foliar nutrient content indicate that fertilization indeed affected the nutrient status of plants (Lasso 2001). We were able to assess, therefore, whether or not nutrient availability affects flowering phenology in this species.

Monthly censuses began in October 1998 and continued until the beginning of May 1999,

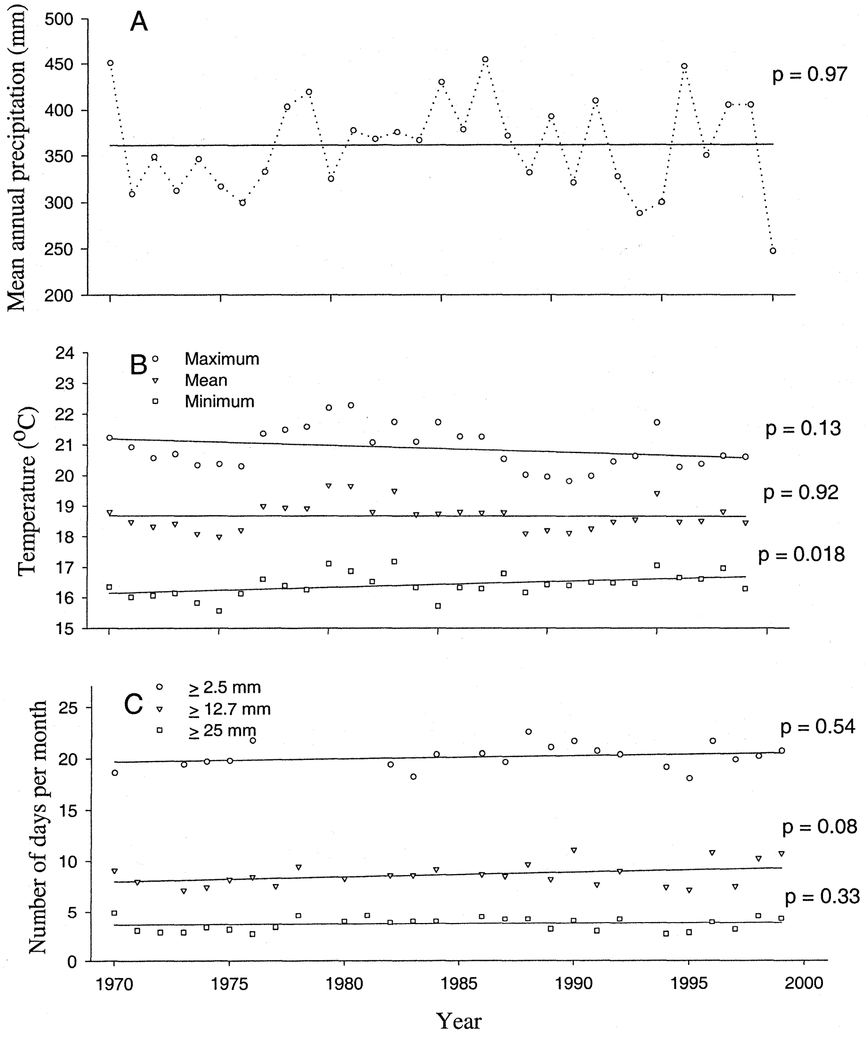

FIGURE 1. Trend in several environmental factors in Pico Del Este, 1970–2000. Environmental factors plotted are **A.** Mean annual precipitation (mm). **B.** Mean annual maximum, mean, and minimum temperature (°C). **C.** Mean annual number of days with equal to or more than 25 mm, 12.7 mm, and 2.5 mm precipitation. Values of p within graphs are the significance levels for the linear regression between time and each environmental factor. Data were obtained from NCDC (2000).

when we shifted to weekly censuses, as inflorescences appeared. During 1999, a total of 299 of the surveyed plants flowered. Flower production (i.e., number of open flowers per week) was followed until December 1999. Monthly censuses were resumed in January 2000 and continued until the end of March, when inflorescences were again evident, and we returned to weekly censuses. During 2000, a total of 242 plants produced flowers in the study area, and the number of open flowers per week was counted until October 2000.

Environmental Data

Temperature and precipitation records were obtained from the National Climatic Data Center (NCDC 2000). These data are from the weather station located in Pico del Este (18°16′04 N, 65°46′00 W) at 1051 m altitude, ca. 890 m from the study plots. Specific data were monthly mean minimum and maximum temperature, monthly mean temperature, total monthly precipitation, and number of days with equal or more than 25.4 mm, 12.7 mm, and 2.5 mm of precipitation.

FIGURE 2. Plants of *Werauhia sintenisii* growing epiphytically and terrestrially at Pico del Este.

TABLE 1. Time at which the number of open flowers/month was best correlated with the environmental factors presented. Time lag and r^2 were obtained from a cross-correlation analysis between the number of open flowers per month and each environmental factor. Variables with an asterisk explained the majority of the variation in flowering phenology in a stepwise regression model ($P < 0.05$), where environmental data were adjusted by number of months (time lag) indicated by the cross-correlation.

Environmental factor	Time lag	r^2
Monthly mean minimum temperature (°C)	3 months before	−0.70*
Monthly mean maximum temperature (°C)	4 months before	−0.69
Monthly mean temperature (°C)	4 months before	−0.69
Total monthly precipitation (mm)	2 months before	−0.62
Number of days with ≥ 25 mm precipitation	2 months before	−0.64
Number of days with ≥ 12.7 mm precipitation	3 months before	−0.68
Number of days with ≥ 2.5 mm precipitation	2 months before	−0.61
Monthly mean of total daily irradiance (μmol m^{-2} s^{-1})	2 months before	0.61*

Records of total daily irradiance for Pico del Este were obtained from the International Institute of Tropical Forestry (W. Silver unpubl. data). We calculated the mean of total daily irradiance for each month, referenced hereafter as the monthly mean of total daily irradiance.

Data Analysis

We used a cross-correlation analysis to determine the lag time at which two time series variables are best correlated (Box & Jenkins 1976). The dependent variable was the number of open flowers per month (using number of flowers per month instead of number of flowers per week, because most of the environmental data obtained were in a per month basis), and the independent variables were the environmental factors mentioned above. Once the lag time was determined for each variable, we adjusted the environmental data by the number of months that gave the highest correlation in the cross-correlation analysis (TABLE 1). To determine which environmental factors best explain the flowering phenology, we used a stepwise regression with the shifted environmental factors as independent variables and the number of open flowers per month as the dependent variable. For this part of the analysis we included all plants censused within the plots and along the trails.

To determine how nutrient availability affected flowering timing, we compared the flowering pattern (number of open flowers per week) of plants growing in fertilized and nonfertilized plots during 1999. Plants censused along the trails were not included.

RESULTS

Flowering Phenology

The timing of flowering of *Werauhia sintenisii* varied between 1999 and 2000 (FIGURE 3). Total flower production was greater during 1999 (1373 vs. 1090). During 1999, flowering started at the beginning of May and ended at the beginning of August; whereas, in 2000, flowering started in the beginning of April and ended at the end of July. Also the timing of the flowering peaks differed between years (FIGURE 3). In 1999 the highest flower production occurred at the end of June; in contrast, during 2000 the first peak of flower production was reached at the end of April, and the second peak in the middle of June.

Plants in fertilized and nonfertilized plots started flowering at the same time (FIGURE 4). Differences in the number of flowers produced (the height of the peaks) are the result of differences in the number of plants censused (nonfertilized plots had more flowering plants than fertilized plots).

Environmental Factors and Flowering Phenology

The number of open flowers per month was best correlated with the monthly mean minimum temperature three months before and the monthly mean of total daily irradiance two months before flower production (T = −3.30, P = 0.004 and T = 2.62, P = 0.02 respectively; FIGURE 5). Together these factors explained 66% of the variation in flower production. None of the other variables analyzed were correlated to flower production (TABLE 1). The positive relationship with solar irradiance two months before and the negative relationship with minimum temperature three months before (TABLE 1) suggest that floral initiation occurred 2–3 months before the flowers opened. These data also suggest that an increase in solar irradiance combined with a decrease in minimum temperature are the environmental cues affecting flowering phenology in this species.

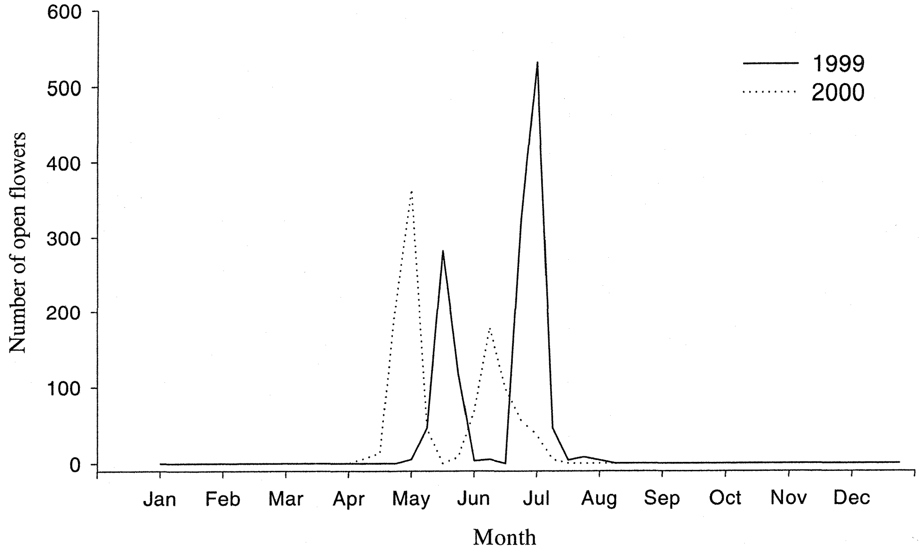

FIGURE 3. Flowering phenological patterns of *Werauhia sintenisii* during 1999–2000 at Pico del Este, based on weekly censuses.

DISCUSSION

Werauhia sintenisii began flowering one month earlier in 2000 in comparison to 1999, apparently in response to two environmental factors that also varied during this interval. The monthly mean minimum temperature three months prior to flowering and the monthly mean of total daily irradiance during the preceding two months proved to be the best predictors of the number of flowers open (FIGURE 5). Although only 6.4% of the plants that reproduced in 1999 also flowered in 2000, those plants shifted their flowering by one month as well, which further suggests that the differences in timing reflected a response to environment, not the effect of polymorphism.

Reports of flowering phenology for *Werauhia sintenisii* (syn. *Vriesea sintenisii*) in LEF, Puerto Rico, have been inconsistent. Nevling (1971) reported *W. sintenisii* flowering in Pico del Oeste for 9 months (February to November), but these

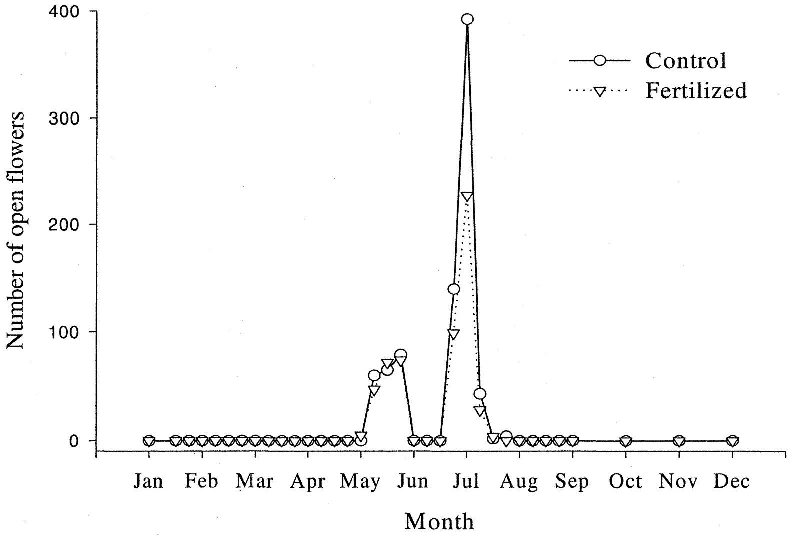

FIGURE 4. Comparison of flowering phonological patterns of fertilized and nonfertilized *Werauhia sintenisii* during 1999 at Pico del Este.

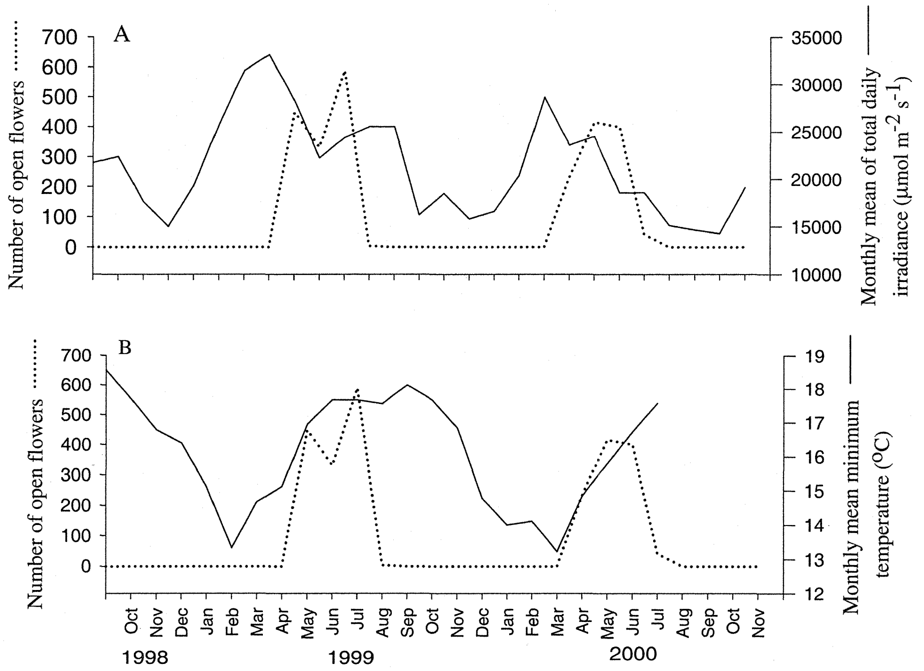

FIGURE 5. Relationship between monthly patterns of flowering and **A.** Monthly mean of total daily irradiance and **B.** Monthly mean minimum temperature. The two peaks in flowering (weekly censuses) observed in FIGURE 3 are collapsed into a single peak for the analyses with monthly climate data.

data are unreliable because the inflorescences are persistent and were scored incorrectly as flowers. Richardson et al. (2000) reported 0% of plants flowering for this species in a 3-year study in Pico del Este, because they were collecting from December to March, during the nonflowering period of this species. Nevling (1971) clearly showed that young inflorescences were present earlier in the year (February) 35 years ago, and today the flowering season takes place between April and July.

One of the environmental variables that increased significantly in the last 30 years in Pico del Este is the mean minimum temperature (FIGURE 1), which accordingly to our analysis is correlated with flower induction. Data for irradiance (the second variable correlated with flower induction) during the last 30 years are lacking for Pico del Este; however, the result of climate simulations for four cloud forests around the globe (Still et al. 1999) and actual change in fog frequency observed from 1973 to 1998 in the Monteverde TMCF in Costa Rica (Pounds et al. 1999) suggest that irradiance also may have changed. How these two variables affect flower induction is not known for this or any other species in TMCF ecosystems. Such knowledge is essential to predict how and where climate change may affect flowering and reproduction.

In TMCF, nutrient supply and light are two of the principal factors that limit photosynthetic productivity (Grubb 1977, Tanner et al. 1990, Walker et al. 1996), which often is linked to reproductive performance. Although nutrient supply affected the reproductive output of this species (Lasso 2001), it did not affect flowering phenology (FIGURE 4). The timing of flowering, however, was correlated with light, which does affect photosynthetic rate and thus carbon gain to invest in reproduction. Lower irradiance limits photosynthesis among a variety of tropical trees (Oberbauer & Strain 1986, Pearcy 1987), and TMCF receive 50–60% of the solar radiation recorded in lowland areas (Cavalier & Mejia 1990). In Pico del Este, four of the most common tree species gained more carbon during sunny (March–April) compared to cloudy periods (October–November, Cordero 1997). Besides light, nocturnal temperatures have the potential to affect the rate of carbon gain. High nocturnal temperatures together with high humidity have resulted in high respiratory losses in some species of epiphytic lichens (Lange et al. 1994). If this phenomenon is common in epiphytic plants of wet forests, an increase in warmer nights might increase the time necessary to accumulate resources to start reproduction, delaying flower production in these plants.

Biotic factors such as pollinator and predator abundance may determine flowering synchrony as well (Auspurger 1980, 1981). Because *Werauhia sintenisii* is autogamous (Lasso 2001), we do not think that the flowering pattern observed is the result of the interaction with pollinators. Lack of information on predator abundance and seasonality, however, prevents us from excluding predators as a selective force in the flowering phenology of this species.

A review of TMCF plant phenology suggests that flower production in this ecosystem may have been selected to coincide with peak irradiance. Both in Hawaii and Costa Rica, most TMCF species bloom between April and August (Koptur et al. 1988, Berlin et al. 2000), corresponding in both cases to the period of greatest solar irradiance. In Pico del Oeste, the flowering peak of most species occurred from May through August, with July having the most species (45) at their flowering peaks (Nevling 1971). Most of the *Vriesea* species, many of which have been reassigned as *Werauhia* (Grant 1995), from montane, lower montane and premontane forests in Central America were collected with flowers between March and August (Utley 1983). Any change in the seasonality of cloud cover thus potentially can have an impact on the flowering phenology of TMCF plants.

TMCF are unique among terrestrial ecosystems in that they are strongly linked to regular cycles of cloud formation. Many features of these forests, from vegetation morphology to nutrient budgets (Bruijnzeel & Proctor 1993), are directly or indirectly related to cloud formation. Modeling results of Still et al. (1999) imply that climate change will probably affect the distribution of cloud forests. Montane forests differ from lowland forests in rainfall, temperature, and exposure (Cavalier & Mejia 1990). If those environmental variables change, then changes in species composition and abundance may occur, as Pounds et al. (1999) reported for frogs, lizards, and birds in the Monteverde cloud forest. Recently Nadkarni and Solano (2002) provided the first experimental evidence that reduced cloud water can affect productivity and longevity of epiphytes. At Pico del Este, higher nocturnal temperatures and more days with higher precipitation (FIGURE 1) and any change in cloud cover may substantially affect plant communities and ecosystem processes.

Interpreting the ecophysiology and phenology of plants in response to future climatic conditions may be complicated further by the fact that carbon dioxide (CO_2) concentrations are predicted to double over the next century (Watson et al. 1990). Elevated CO_2 also may affect flowering phenology by affecting tissue carbohydrate content, which may directly regulate gene expression (Garbutt & Bazzaz 1984). Moreover, in nutrient-poor conditions, elevated CO_2 actually may decrease photosynthetic capacity (Baxter et al. 1997, Harmens et al. 2000).

This study is the first report on how month-to-month data in environmental variables are correlated with flowering production in an epiphytic montane cloud forest plant. Although more yearly data are necessary to confirm the apparent susceptibility of the flowering of this species to environmental conditions, these 2 years of data suggest a linkage. Epiphytic species of montane cloud forests are good indicators of climatic change, as proposed by Lugo and Scatena (1992) and Benzing (1998) and tested and confirmed by Nadkarni and Solano (2002). We hope that our findings will stimulate further interest in flowering phenology of epiphytic plants in these cloud forest ecosystems.

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