ECOTROPICA

SEASONALITY IN AN EVERGREEN TROPICAL MOUNTAIN RAINFOREST IN SOUTHERN ECUADOR

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Abstract. More than 400 individuals of 12 tree species growing in an evergreen tropical mountain rainforest in the eastern cordillera of southern Ecuador were examined over a period of 3 to 4 years with respect to flowering and fruiting as phenological events. In spite of the perhumid climate, a high degree of synchronization of flowering and fructification was observed at the intra- and interspecific levels. Except one species that flowered more or less continuously, two groups of trees could be distinguished, of which one flowered during the less humid months (starting September/October) while the second initiated flowering towards the end of that phase and flowered during the heavy rains. Fructification also showed synchronization, but, due to species-specific time-spans of seed maturation was less pronounced than flowering. Concomitantly with the phenological recordings, climate was monitored in detail at both the regional and the local scale. In contrast to seasonal tropical lowland forests, no unambiguous relationship between flowering and fructification and seasonal changes in the amounts of precipitation could be found, but changes in cloudiness, and especially in the ratio of direct to diffuse global radiation, coincided with the induction of flowering of both groups. Superimposed on the periodical synchronization by the light regime were episodic events. Periods of unusual cold or dryness affected incidence of flowering, fruit maturation, and the production of germinable seeds. Knowledge of the biology and timing of reproduction is a prerequisite for the establishment of tree nurseries to produce saplings of indigenous trees for reforestation purposes. *Accepted 14 August 2006.*

Key words: *climatic irregularities*, *cloudiness*, *flowering*, *fruiting*, *phenology*, *tropical mountain forest*.

INTRODUCTION

The phenology of tropical rainforest trees, as shedding and flushing of leaves, periodicity of flowering and fruiting, and growth rhythms is increasingly attracting interest. Aspects which have been addressed from the viewpoint of basic plant science are the coexistence of arhythmic and rhythmic events (Ha-

mann, 2004, Sakai *et al.* 1999), the occurrence of annual and supra-annual cycles, the triggers of such phenomena, and their consequences for the ecosystem in question. In particular the phenomenon of intra- and interspecific synchronization of phenological events, especially of flowering and fruiting, has prompted various suggestive explanations: Climatic triggers as proximate factors (Daubenmire 1972, Shukla & Ramakrishnan 1982), or evolutionary adaptations to the low population densities at which

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individuals of a tree species grow in a highly biodiverse tropical rainforest as ultimate factors. As climatic seasonality is not very pronounced in the humid tropics, evolutionary factors, such as competition for pollinators and seed-dispersers, or the timing of leaf flushing with respect to the development of herbivores, have received much attention (Aide 1988, Ims 1990, Poulin *et al.* 1999, Lobo *et al.* 2005,). Seasonality of flowering, and in particular of fruiting, is also of high interest for collectors of fruits and seeds (De Steven & Wright 2002) for the propagation of indigenous tree species in tree nurseries.

With regard to climate as the triggering factor of phenological cycles, a thorough physiological or ecological understanding is still lacking, although changes from drier to more humid conditions and vice versa have been suggested as obvious proximate factors (Frankie *et al.* 1974, Worbes 1999). Due to the usually gradual transition from an evergreen to a semi-evergreen and a deciduous tropical forest, humidity as a climatic trigger of synchronized events may have been overestimated in the case of perhumid tropical forests, which nevertheless receive an uneven distribution of rain over the year.

Various other components of the climate have also been associated with synchronization and seasonality in the perhumid tropics. Wright *et al.* (1999) attributed seasonality of plant reproduction in the moist forests of Panama to a shortage of assimilates during the rainy season when PAR is low, and Hamann (2004) showed that nearly all canopy tree species in a submontane rainforest (Philippines) flowered during the peak of solar irradiance. Higher doses of UV-B affect flowering (Caldwell 1968, Caldwell *et al.* 1998, Tevini 1999) and inhibit germination of pollen grains on the stigma (Flint & Caldwell 1984). Numata *et al.* (2003) concluded that flowering of tropical canopy trees is triggered by prolonged drought, high solar radiation, and unusually low temperatures. They presumed that a drop in nocturnal air temperatures during cloudless nights is the most plausible cue for a supra-annual synchronization of flowering. On the other hand, slight changes in the daily photoperiod, in particular shifts of sunrise and sunset, have been suggested as triggers of synchronous flowering by Borchert *et al.* (2005).

Synchronization of reproductive events can result in annual (intra- and inter-specific), supra-annual, or irregular flowering and fruiting (intra-specific). Usually, the proportion of tropical trees and shrubs that shows continuous reproduction seems to be small

(Opler *et al.* 1980, Wright *et al.* 1999). In a comprehensive 4-year study of the phenology of flowering and fruiting in a Philippine submontane rainforest, 34 tree species were found reproducing once per year, 13 continuously, 3 supra-annually, and 7 irregularly (Hamann 2004). In a lowland dipterocarp forest in Malaysia, Sakai *et al.* (1999) found 35% of 257 species flowering only during mass flowering (episodically), 19% flowering supra-annually, 13% annually, and only 5% sub-annually or more or less continuously.

Most studies of tropical reproduction phenology have been performed in the lowland rainforests (Frankie *et al.* 1974, Croat 1975, Opler *et al.* 1980, Newstrom *et al.* 1994, Hamann & Curio 1999, Sakai *et al.* 1999, Schöngart *el al.* 2002, Hamann 2004), but to the best of our knowledge there is only one study of phenological aspects of a perhumid tropical mountain rainforest. Koptur *et al.* (1988) have investigated the phenology of bushes and treelets in Costa Rica in an altitudinal range between 1300 and 1650 m a.s.l. Mountain forests differ from lowland forests not only in the climatic effects of higher elevations but also in their light climate. Inclination of the slopes allows a higher proportion of the radiation to penetrate the canopy and to create an improved light climate in the understory. When considering changes of the light climate in the aseasonal tropics, direct and diffuse global radiation must be differentiated. As the ratio of diffuse to direct global radiation increases under a cloudy sky the light climate of shade trees improves, whereas that of canopy trees deteriorates (Endler 1993). However, many of these observations still require confirmation (Sakai 2002), as the link between climate and reproductive cycles can still be modified by other factors. Phenological cycles may become affected by future global climate change. Unfortunately, the knowledge about climate change in Ecuador is rather poor, especially for the Andean region. The IPCC report suggests an increase in annual air temperature for Ecuador, especially so since 1976. Corresponding data for annual precipitation have not yet been published. Folland & Karl (2001) and Bendix (2004b) could not detect a clear trend in precipitation between 1960 and 2000 in the eastern escarpment of the Ecuadorian Andes, while a positive trend in the air temperature was recognizable. Longer-term cloud observations are likewise not available. However, Beniston *et al.* (1997) stated that the altitude of the 0°C level has risen over South America since 1975 due to an increase of the surface tem-
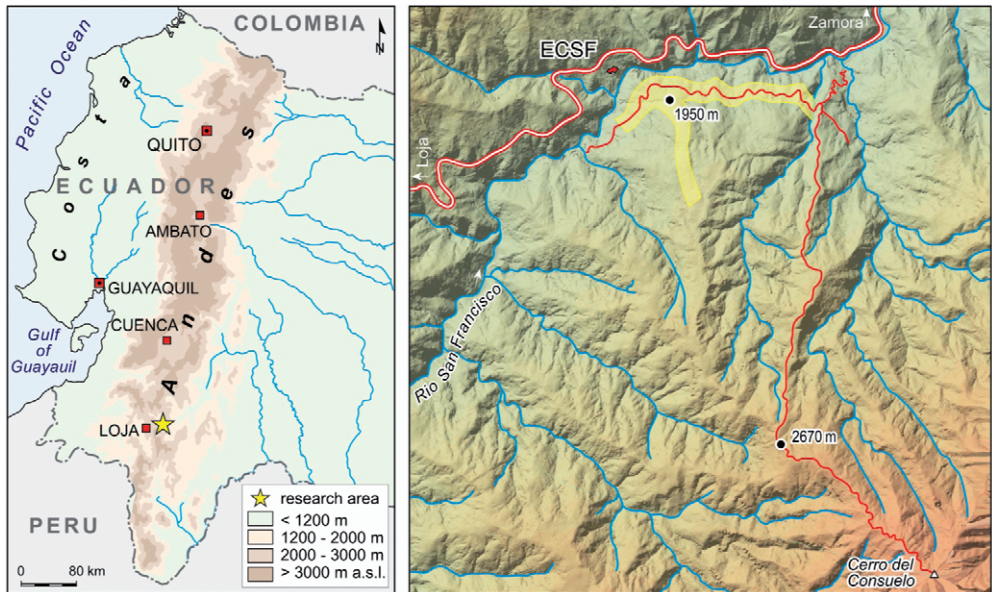
FIG. 1. Position of the study area in southern Ecuador (left) and the topographical GIS-generated overview of the upper Rio San Francisco valley (right). ECSF, Estacion Científica San Francisco (Research station). The research area is marked in yellow; ●, locations of the weather stations; Δ, location of the weather radar.

perature of the Pacific. This could explain the observed warming, and is most likely the main reason for the retreat of the glaciers, in particular in the eastern cordillera of the Ecuadorian Andes (e.g., Cáceres *et al.* 2000, Bendix *et al.* 2004, Jordan *et al.* 2005). Such a change in the thermal stratification of the atmosphere could lead to a lift of the condensation level and hence a reduction in cloudiness.

The present paper examines the hypothesis that in the tropical mountain rainforest of southern Ecuador, cloudiness is the master trigger of periodic phenological events in plant life which are, however, modulated by climatic irregularities.

RESEARCH AREA

The research area (3°58′30′′S, 79°4′25′′W, 1800 m to 2300 m a.s.l.), called "Reserva Biológica San Francisco", borders on the Podocarpus National Park in the eastern cordillera of the South Ecuadorian Andes (Fig. 1). Geographical details of the region in the upper valley of the Rio San Francisco between the provincial capitals Loja and Zamora have been presented by Beck & Müller-Hohenstein (2001). The nat-

ural vegetation of the deeply incised valley is an evergreen forest covering the slopes from the valley bottom up to the tree line between 2700 and 3000 m a.s.l. On the south-facing slopes this forest has been widely cleared for farming purposes, while it appears more or less intact on the slopes facing north. However, aerial photographs show clearings in the lower part of the forest in the middle of the twentieth century and pollen of cereals has been detected in soil samples taken at an altitude of 2400 m (Behling, pers. comm.). Thus at least some parts of the present forest must be considered as secondary forest.

THE CLIMATE

An overview of the climate of the southern part of Ecuador has been presented by Richter (2003) and Bendix *et al.* (2004b, 2006). The research area has a tropical perhumid climate with a steep gradient in the annual precipitation from around 2200 mm at 1850 m a.s.l. up to more than 5300 mm at 2660 m a.s.l. (Fig. 2). A very pronounced rainy period from April to July alternates with a less wet period from September to March. Most of the precipitation results
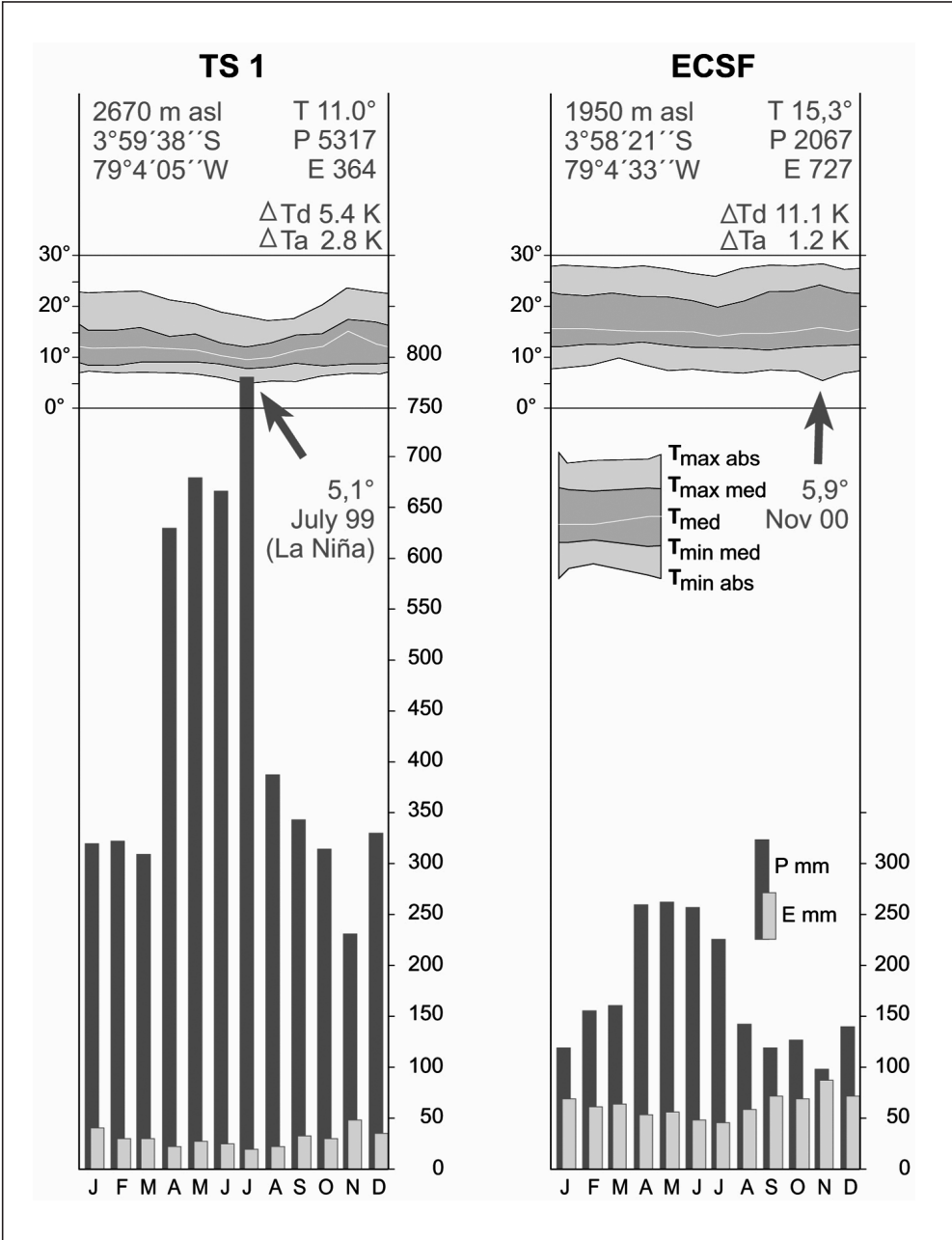
FIG. 2. Climate diagrams of the two weather stations indicated in Fig. 1 (observation period: 1998–2002); T, air temperatures at 2 m above ground (extremes, mean amplitudes, monthly averages); P, monthly and annual sums of precipitation (mm) respectively; E, monthly and annual sums of potential evaporation (mm); ΔTd, average oscillation range of daily air temperature; ΔTa, annual fluctuation range of monthly temperature means.

from humid trade winds passing the Amazon Pre-Andes, and which are pressed against the eastern escarpment of the cordillera. While these advective easterly airstreams dominate the climate between April and mid-October, westerly air flows may cause short periods of sunny days from November to March. However, this period also is humid due to convective processes, partly accompanied by thunderstorms. It should be stressed that cloudiness is high throughout the year (Bendix *et al.* 2004a, 2006). Between 5% (at 1950 m a.s.l.) and 10% (at 2660 m a.s.l.) of atmospheric water input to the ecosystem results from horizontal precipitation driven by high wind speed and collected by deposition onto the forests. The main weather shed is the Cordillera Oriental de los Andes, which separates the moist area around the Rio San Francisco valley from the relatively dry inter-Andean basin. With respect to the temperature regime, the research area partly belongs to the *tierra templada* and partly to the *tierra fria*, with mean annual air temperatures between 19° and 13°C respectively (Richter 2003).

THE EVERGREEN MOUNTAIN RAIN-FOREST

A botanical survey and structural analysis of the forest, designated as "Bosque siempreverde montano lluvioso" (Balslev & Øllgaard, 2003), has been presented by Bussmann (2001), Homeier *et al.* (2002), Homeier (2004), and Müller-Hohenstein *et al.* (2004). Today, the evergreen virgin forest extends from 1950 m a.s.l. up to the tree line. The study area (Fig. 1), however, is partly covered by the above mentioned secondary forest which can be recognized i) by a high proportion of pioneer tree species, ii) by a high frequency of those species in the tree stratum, and iii) by an even canopy in about 15–25 m height, depending on the microsite. Furthermore, this forest is rich in lianas but relatively poor in vascular epiphytes, a feature that is also indicative of its young age. Due to a small-scale pattern of site conditions a mosaic of floristically distinct forest types is encountered. Based on tree species patterns, Homeier *et al.* (2002) described five major forest types for the Reserva Biológica San Francisco, which differ also in their altitudinal ranges and forest structures.

In total, 230 species of trees have been identified in the forest of the Reserva Biológica San Francisco so far, and Lauraceae, Melastomataceae and Rubiaceae are represented above average in the species list (Bussmann 2001, Homeier 2004). Most of the dominating tree species are evergreen, but the highly diverse tree spectrum also contains a few deciduous species, namely *Tabebuia chrysantha*, *Cedrela montana*, and at least one species of *Ficus*.

MATERIALS AND METHODS

Climate. Meteorological data from the research area have been collected via automatic weather stations (Thies Klima, Göttingen) since late 1997, including observations of wind, soil/air temperature, humidity, rainfall (tipping-bucket rain gauge), and of solar irradiance (pyranometer CM3).

Because of the high spatial-temporal dynamics of clouds, fog, and precipitation in the research area, these meteorological elements cannot be properly recorded by point measurements with standard automatic stations, and so additional observation systems were established. Cloudiness was investigated by means of NOAA-AVHRR satellite data (see Bendix *et al.* 2003). A special cloud detection system was developed that provides information about cloudiness both day and night (Bendix *et al.* 2004b). In addition to the standard meteorological stations, six square grid collectors (1 m²) were installed in a vertical position to measure horizontal precipitation and cloud/fog water, mimicking the combing effect of the vegetation.

Phenology. A selection of 12 tree species was made for this study using information from local people about useful trees of the region (Leischner & Bussmann 2002). In addition to the use by the local population, most of the selected species are strongly propagating pioneer species which may also be considered as promising candidates for reforestation purposes. Table 1 shows the investigated tree species and numbers of regularly observed individuals. For identification and nomenclature we used the Flora of Ecuador (Harling & Andersson 1973–2003) and the Herbarium Reinaldo Espinosa (Universidad Nacional de Loja). Images of the investigated species have been entered in the data base www.visualplants.de (Homeier *et al.* 2004).

Individuals with a DBH greater than 10 cm were randomly selected on different microsites (including ravines and ridges) for the study. To minimize scattering of the data, individuals which differed considerably in size (and most probably in age), or were overly attacked by pests or otherwise suffering from a stressful microhabitat, were not included in the survey. None of the examined individuals died during

TABLE 1. Investigated species and number of regularly inspected individuals in the Reserva Biológica San Francisco in southern Ecuador. Investigation period of most species was from August 2000 until April 2003. Number of trees whose monitoring started already in July 1999 is given in parentheses (+XX). *Graffenrieda*, *Pudiaea*, and *Viburnum*, were inspected every four weeks during the whole study period while the other species were examined biweekly.

Tree species	Number of examined individuals
Cedrela montana Moritz ex Turcz. (Meliaceae)	16
Clethra revoluta (Ruiz & Pav.) Spreng. (Clethracae)	38 (+22)
Heliocarpus americanus L. (Tiliaceae)s	25 (+21)
Inga spec. (Caesalpiniaceae)	8
Isertia laevis (Triana) B.M. Boom (Rubiaceae)	30 (+23)
Myrica pubescens Humb. & Bonpl. ex Willd. (Myricaceae)	12
Piptocoma discolor (Kunth) Pruski (Asteraceae)	27 (+25)
Tabebuia chrysantha (Jacq.) G. Nicholson (Bignoniaceae)	23 (+21)
Vismia tomentosa Ruiz & Pav. (Clusiaceae)	21 (+16)
Graffenrieda emarginata (Ruiz & Pav.) Triana	29
Purdiaea nutans Planchon (Cyrillaceae)	22
Viburnum obtectum H.Vargas (ined.) (Caprifoliaceae)	18

the observation period. The trees were labeled with aluminum tags and their phenological state was routinely examined every two weeks (every four weeks for *Graffenrieda*, *Purdiaea*, and *Viburnum*). The percentage of flowering and fruiting individuals in each species sample was noted. Flowering includes floral bud initiation, anthesis, and floral persistence (Rathcke & Lacey 1985). However, when observing broadleaved trees whose crowns reach heights of 15 m and more, only the blossoming phase could be clearly distinguished. Since the transition from flowering to fruiting is floating, fructification was recorded only when fruits were visible. No quantitative assessment was made of the extent of flowering or fruiting of the individual trees.

Germination of the seeds was examined by placing them on wet filter paper, wet sand, and unsterilized moist commercial soil in the light and the dark, and the germination rates were determined over a period of 6 months. *Cedrela montana*, *Tabebuia chrysantha*, and *Inga* cf. *acreana* are fast-germinating species, while *Isertia leavis*, *Piptocoma discolor*, *Vismia tomentosa*, and *Clethra revoluta* required almost quarter of a year for the seedlings to emerge. *Piptocoma*, *Myrica*, and *Isertia laevis* germinated satisfactorily only after pretreatment of the seeds. In this case soaked seeds were either heated at different temperatures in

water or steeped for various time-spans in HCl (5 or 12 %), H_2SO_4 (5, 8, or 12 %), or H_2O_2 (5 or 20 %). Germination protocols of the individual species have been elaborated and will be presented in detail elsewhere. Only maximum germination rates are shown here.

Data processing. Climate data means are based on high-resolution data sets (5-minute cycles). Rainfall data (Fig. 2) have been corrected for horizontal precipitation. Rates of potential evaporation were calculated using the Penman formula. Phenological data were collected from a minimum of 8 and a maximum of 60 individuals for each species as shown in Tab. 1. Mean values are shown in Figs. 6 and 7, but S.D. of the phenological observations was omitted from the figures for the sake of clarity.

To analyze possible relations between irradiance or precipitation and flowering of the trees, overlapping time-series of meteorological and phenological data were used. Data of irradiance and precipitation of the ECSF meteorological station were aggregated to monthly means to meet the shape of the phenological time-series. A moving correlation analysis with twelve monthly time steps was conducted between flowering frequency and precipitation on the one hand, and flowering frequency and solar irradiance on the other. The maximum correlation coefficient was used to de-

scribe the relation between both the meteorological element and flowering frequency, while the time lag until the maximum correlation is reached indicates the delay between the meteorological stimulus and the phenological response.

RESULTS

Climate.

Diagrams of 2 stations are presented (Fig. 2) to characterize the distinct synoptic regimes at the lower and middle parts of the mountain rainforest. Air temperature (average, maximum and minimum), rainfall, and wind speed and direction impressively demonstrate the extreme climatic gradient from 1950 to 2620 m a.s.l. Hourly means for four consecutive years from the central weather station in the research area (ECSF) are presented in detail to provide a basis for a possible relation between phenology and climate (Fig. 3).

The mountain crest (Cerro del Consuelo) is subjected to quasi-permanent strong easterlies, giving rise
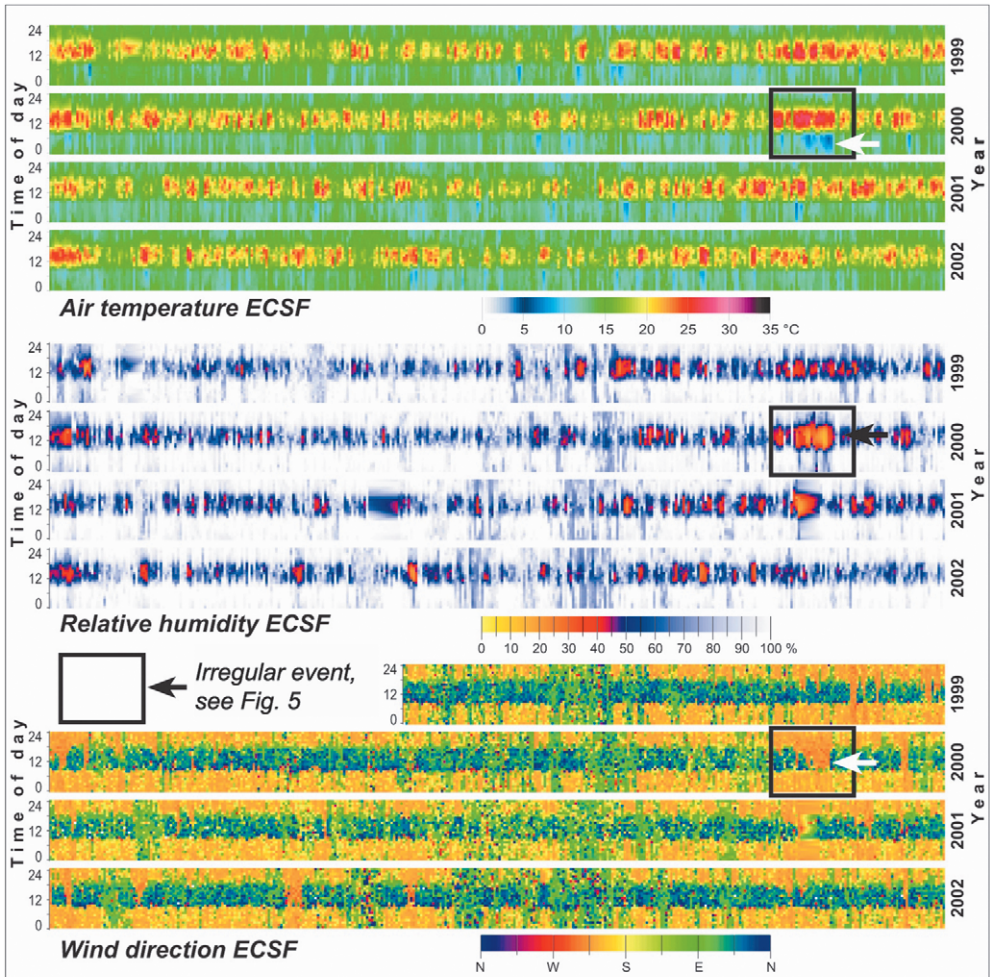

FIG 3. Recordings of wind direction, air temperature, and relative humidity at the research area from January 1999 until December 2002. The highly resolved data are shown by color codes for easier differentiation between diurnal, intra- and inter-annual variations. An irregular prolonged cloudless phase is marked by a box (details of this event in Fig. 5).
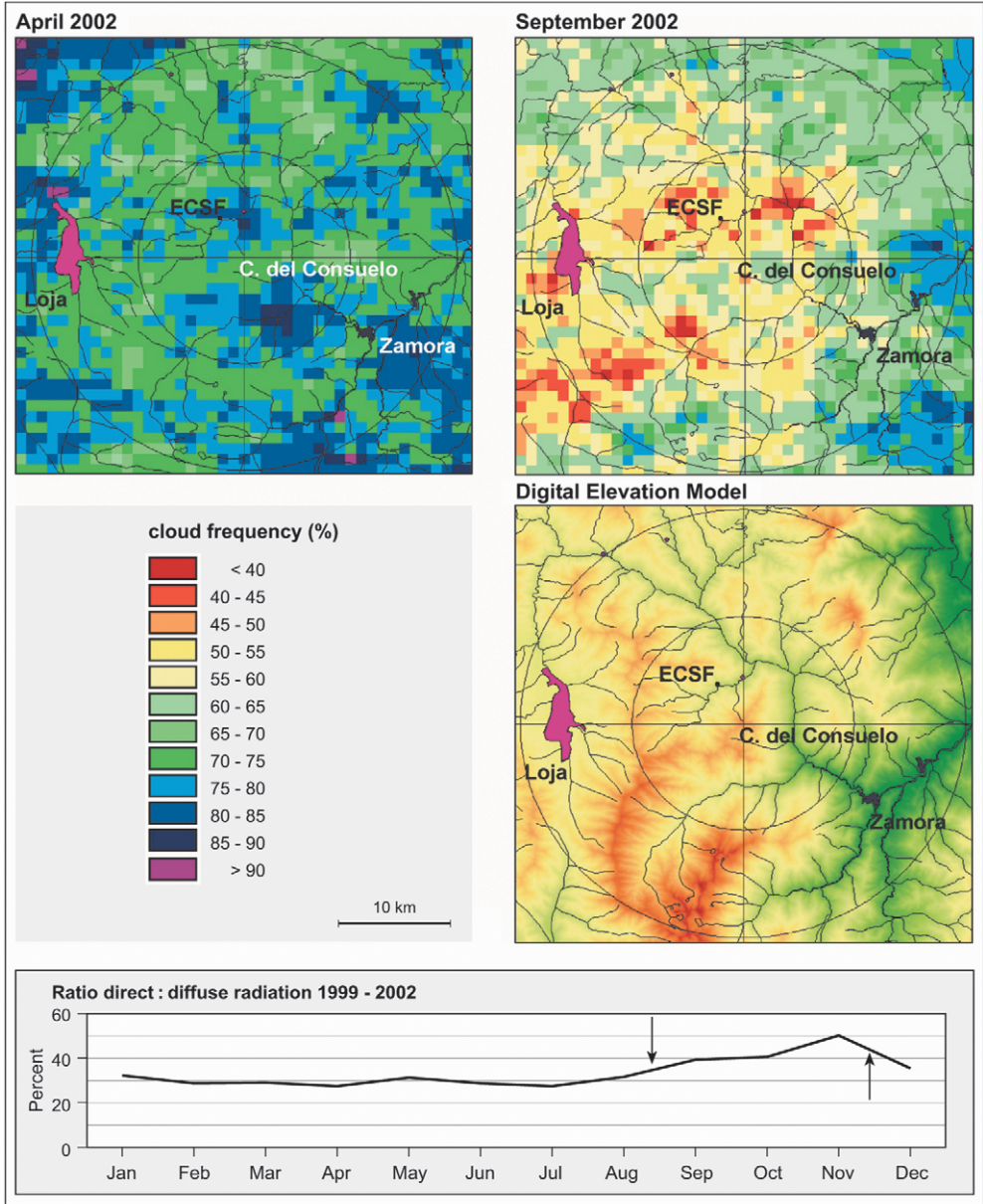
FIG. 4. NOAA-AVHRR-derived relative cloud frequency for April and September 2002 and the digital elevation model of the area covered by the radar. Bottom: mean annual (1999–2001) changes of the light climate at ECSF, as represented by the ratio of direct:diffuse radiation.

to an "upper Andean forest" or *Páramo* vegetation (Cleef *et al.* 2003). In contrast, the bottom of the San Francisco valley is influenced by the diurnal regime of a mountain-valley breeze system. Radar data analysis revealed that precipitation on the research area is affected both at a mesoscale and at the local level.

Especially the predawn rains frequently result from mesoscale instabilities over the East Andean foothills, spreading with the easterlies to the Rio San Francisco Valley. Consequently, morning rainfall is rather uniform from the crest of the mountain to the valley bottom. The afternoon/evening peak of precipitation originates predominantly from local convection and is characterized by a sharp maximum above 2300 m a.s.l.. Below this line, rain droplets evaporate in the atmosphere due to the higher air temperature near the valley bottom.

For an assessment of climatological elements as proximate factors synchronizing seasonal plant-life phenomena, cloudiness was examined as one integrative parameter representing several cues which could possibly trigger recurrent events. The maps of cloud frequency (Fig. 4) show completely different situations for a month typical of the rainy period (April 2002) and another characteristic of the less humid period (September 2002). Compared to mean values, April 2002 exhibited cloudiness frequencies ranging from 70–85 % in the research area and a high amount of rainfall (Fig. 2). In September 2002 cloud frequency decreased to about 40–50 %, concomitant with an approximately 2.5-fold decrease in monthly precipitation.

Seasonality of climate can be focused on two major periods that can be clearly delineated (Fig. 2): The overly humid period from April to July, with lower maximum temperatures but only slightly depressed nocturnal minima, and the less humid period from August to February/March. Due to its widest monthly temperature amplitude, November seems to be the most critical month with respect to low temperature (minimum temperature 5.9 °C).

Associated with cloudiness, but more directly related to plant life, is that part of the global radiation that triggers developmental steps such as induction of flowering or leaf senescence. Although we do not have data on the spectral composition of the light climate, a clear seasonal change in the proportions of direct and diffuse radiation was observed during August and November (Fig. 4). These changes coincided roughly with changes in the precipitation regime from August to November, but not for the rest of the year.

Superimposed on the annual courses of temperature, precipitation, and irradiation are irregularities originating from special meteorological constellations, e.g., northwesterly winds during the southern summer
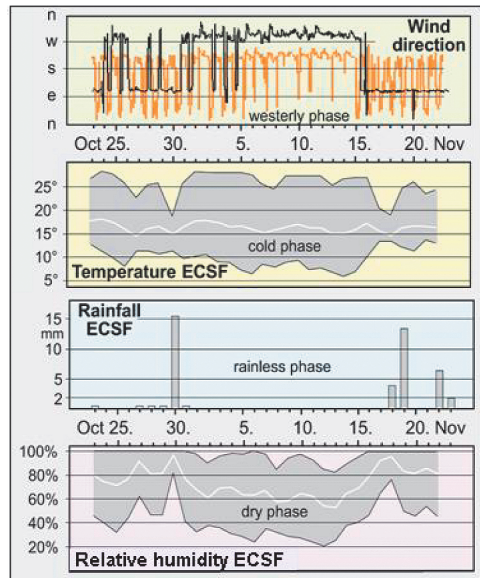

FIG. 5. Climatic irregularities (wind direction, rainfall, minimum and maximum temperatures, and relative humidity) during the prolonged cloudless period between late October and mid-November 2000, highlighted by boxes in Fig. 3. Note that the temporary westerlies, monitored above the treeline (3400 m, black line) even extend down into the valley bottom (ECSF, red line).

months accompanied by a clear sky, i.e., high day and unusually low night temperatures. A good example is the rainless period between October 30th and November 17th, 2000 (Fig. 5) when nocturnal temperatures dropped to 6 °C and even below (boxes in Figs. 3 and 5).

Other climate anomalies are connected with El Niño and La Niña. However, El Niño, which mainly affects the coastal parts of Ecuador and northwestern Peru (Bendix 2000, Block & Richter 2000), had only little impact on the study area. Rainfall was similar to non-EN periods and warming did not exceed +2 K for minimum temperatures and monthly means. La Niña (e.g., Nov 1999–Feb 2000) was characterized by reduced rainfall (60 % of the normal) in the study area, with the highest deficit in November.

Seasonality of flowering
Annual cycles. The records of flowering of the examined 404 individuals of 12 tree species (see Tab. 1)
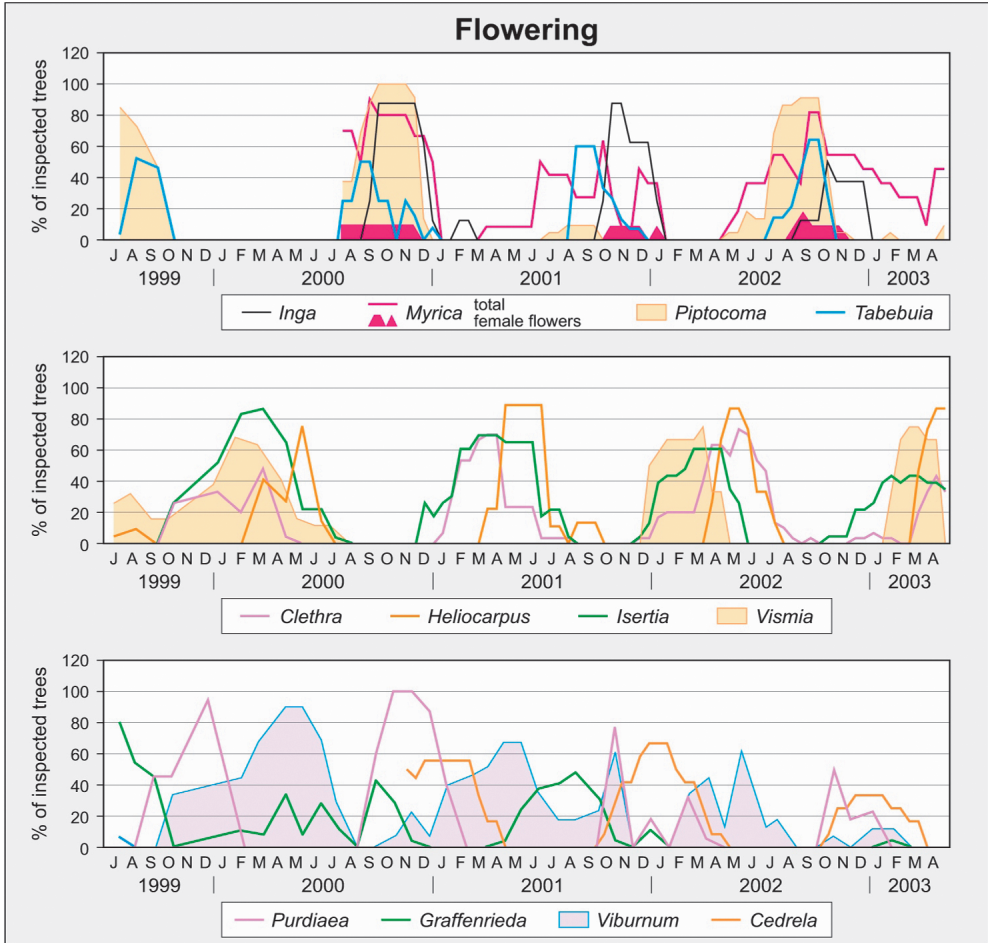
FIG. 6. Periods of flowering of 12 tree species of the evergreen mountain forest in the Rio San Francisco valley. Flowering was quantified as percent of flowering trees of the respective species sample (for sample size see Table 1).

showed two principal patterns (Fig. 6). One group of trees, consisting of *Piptocoma*, *Tabebuia*, *Myrica*, *Cedrela*, *Purdiaea* and *Inga*, flowered during the less humid period of the year, i.e., between August and February, while *Clethra*, *Heliocarpus*, *Isertia*, *Viburnum*, and *Vismia* flowered during the wettest season (March to July). The flowering periods of the majority of species were clearly discernible and confined to 3–4 months (sometimes with smaller extra peaks, e.g., for *Clethra* or *Inga*, indicating late or early flowering of individuals growing at the upper or lower boundaries

of the research area). One exception were male individuals of *Myrica*, of which flowers were seen for 10 months of the year (but also with a clear maximum during the less humid period), while female individuals usually flowered less than 1 month (Fig. 6). Another exception was *Graffenrieda emarginata*, of which pronounced periodicity of flowering could not be observed. However, this species extends over a wide altitudinal range and therefore the collected data may not be sufficient to reveal intraspecific synchronization. Interestingly, flowering of the majority of the wet

season species (*Clethra*, *Isertia*, *Vismia*, and *Viburnum*) started already in December or even earlier, when the monthly rainfall was still low. This observation suggests a climatic factor other than precipitation that triggers flowering of that group of plants.

The maximum proportion of flowering individuals of the examined species differed considerably. Of *Heliocarpus*, about 90% of individuals flowered at the same time, and of *Piptocoma* the peak of simultaneously flowering trees even exceeded 90% (except in 2001, as discussed below). *Vismia*, *Myrica*, *Clethra*, *Isertia*, and *Inga* were further species with reasonably

high rates of flowering (between 35 and 90%). On the other hand, relatively low percentages of flowering individuals were recorded for *Cedrela* and *Tabebuia*, two of the obligatory deciduous species in the forest.

Seasonality of fructification

Due to the differing species-specific time-spans required for seed-set and fruit ripening, the annual phases of fruiting were wider and in most cases not as clearly defined as for flowering. Nevertheless, again two separated groups of trees can be differentiated with respect to fructification (Fig. 7). *Piptocoma*, *Tabe-*
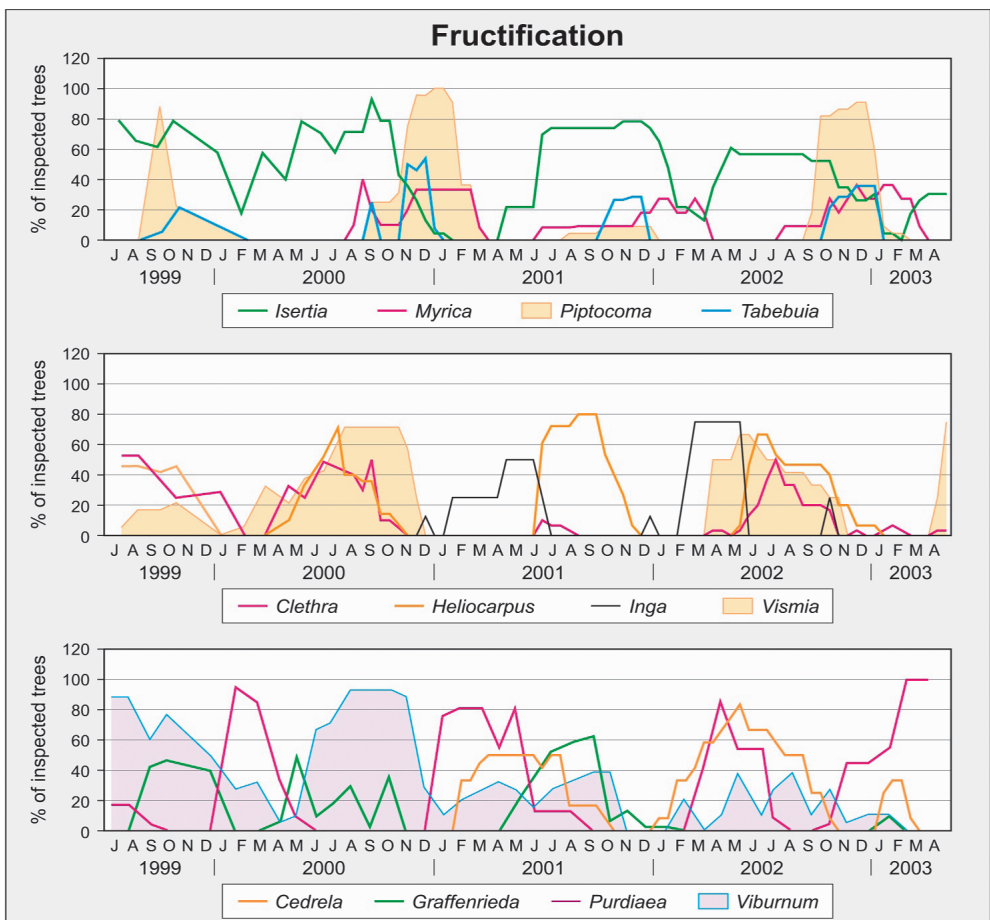

FIG. 7. Periods of fructification of 12 tree species of the evergreen mountain forest in the Rio San Francisco valley. Fructification was quantified as percent of fruiting trees of the respective species sample (for sample size see Table 1).

buia, and *Myrica* were found still fruiting during the less humid season, i.e, in November, December, and January. The second group of trees consists of *Cedrela*, *Clethra*, *Heliocarpus*, *Inga*, and *Vismia*, which exhibited maximum fruiting predominantly during the wet season. Fruiting trees of *Isertia* were present all year round, however, with a pronounced minimum in February/March (in February 2001 fruiting trees were not found). While *Vismia* showed a long fruiting period of 8 months in 2002 (though no flowers and fruits in 2001), other species like *Heliocarpus*, *Tabebuia*, or *Piptocoma* had comparatively narrow time-windows for fructification (3–4 months).

Episodic events

While the rhythms of flowering (and fructification) of the individual species were generally maintained over the 3–4 years of observation, the extent of flowering of some species varied substantially from year to year. This was especially true for *Vismia*, of which flowering individuals were not observed in 2001, while in the following years it flowered by more than 70%. The reaction of *Piptocoma* was similar; only a few individuals flowered in 2001 (9%) while in 2000 100% and in 2002 90% of the individuals were found in blossom. Fruiting was consequently affected in the same way (Figs. 6 and 7). These two species showed an evident reaction to the irregularity mentioned above (Fig. 5).

Other examples of phenological irregularity were *Cedrela*, *Clethra*, and *Inga* which flowered to a high percentage in 2000 and 2001, but much less so in 2002 and 2003. Flowering of *Purdiaea* and *Viburnum* declined consistently from the year 2000 onwards (Fig. 6).

Viability of seeds

Germination rates of the seeds varied greatly from species to species, but also for the same species from year to year. Highest rates of germination were achieved with freshly collected seeds as shown in Table 2. The only exception was *Inga acreana*, whose germination rate could be increased from 62 to 90% by seasoning for 2 months. Of *Piptocoma* germinable seeds were obtained only in 2001 and of *Vismia* only in 2000 and 2001. In the case of *Piptocoma*, microscopic inspection of the seeds suggested incomplete embryos. Except *Cedrela* and *Inga acreana*, germinative capability of the seeds of all investigated species decreased within a few weeks of storage. An ecologically important consequence of the short viability of the seeds is their frequent absence in the soil seed-bank.

TABLE 2. Maximum germination rates achieved immediately after harvesting of the seeds. Whenever possible, seed from more than 1 tree were combined in a sample. A sample consisted at least of 50 seeds.

Species	Maximum germination rate (%)	Year of seed collection
Cedrela montana	100	2002
Myrica pubescens	76	2002
Isertia leavis	97	2001
Heliocarpus americanus	36	2001
Piptocoma discolor	60	2002
Inga acreana	72	2002
Inga spec. *1*	96	2002
Clethra revoluta	100	2002
Vismia tomentosa	100	2001
Tabebuia chrysantha	100	2001

DISCUSSION

Patterns of seasonal events reveal annual periodicity in the tropical mountain rainforest of South Ecuador. In tropical lowland and submontane moist forests, overlaying a region-specific fraction of continuously or episodically reproducing trees, a variable percentage exhibits annual periodicity that requires synchronization and proper placement of reproductive events in the course of the year. Synchronization of phenological events like flowering or leaf-shedding has been reported from several more or less moist lowland forests of the paleo- and neotropics (Daubenmire 1972, Frankie *et al.* 1974, Shukla & Ramakrishnan 1982, Mikich & Silva 2001, Sakai 2002, Hamann 2004). Most cases have been related to patterns of changing humidity (e.g., Opler *et al.* 1976, Reich & Borchert 1982, Borchert 1983) or to evolutionary traits, like the competition for pollinators or seed dispersers (Poulin *et al.* 1999, Lobo *et al.* 2003). More recently, seasonal changes in light intensity (Wright & Van Schaik 1994), or in the length of the photoperiod (Zipparro 2004, Borchert *et al.* 2005), have also been proposed as triggering periodic events in the humid tropics.

Factors synchronizing flowering. In the perhumid tropical mountain rainforest reported in this communication only one tree species (*Graffenrieda emarginata*) out of 12 examined did not show rhythmic flowering,

while all others exhibited more or less distinct species-specific peaks of flowering and fruiting. Given an altitudinal range of several hundred meters, synchronization of the reproductive cycle in that region emphasizes the question of how it is achieved (proximate factors) and which biological traits (ultimate factors) might be involved in it (Ims 1990, Herrera *et al.* 1998). With regard to the proximate factors of synchronization, flowering will be preferentially considered here because, i) it takes place once a year, ii) it is the first step in reproduction, iii) it is commonly briefer than fruit production and ripening, and iv) it can be observed with higher accuracy.

As shown in Fig. 2, the area where the phenological data were collected received a monthly precipitation of 120–220 mm during the driest and 320–720 mm during the wettest months, and evaporation was consistently lower than precipitation. The climate can thus be characterized as perhumid with an overly rainy period of 4 months (April to July). Thick humus layers (Schrumpf *et al.* 2001) as well as an effective interflow from the wetter upper parts of the mountain may provide sufficient soil moisture for the few rainless phases. Seasonal deficiency of moisture is thus very unlikely as a proximate synchronizing factor of tree reproduction. Rather than a change in water supply, cloudiness appears as a potential cue that could be related to synchronization of seasonal events in the investigated mountain forest. Cloudiness involves several meteorological factors: radiation, rainfall, and air temperature, and may also have an impact on the activity of phytophagous insects (Wright & Van Schaik 1994). Available-time series of cloudiness are not as complete as the phenological observations and the records of rainfall and radiation. Nevertheless, rainfall requires clouds and a certain relation between cloud frequency and rainfall has been established for the study area (Bendix 2004b). Moreover, even non-raining clouds significantly alter incoming solar radiation at the ground level. This means that irradiance

is a good proxy for cloud frequency. The relationship between clouds, rainfall, and irradiance is reflected in the relatively low, but negative correlation coefficient between solar radiation and precipitation of –0.55 for the observation period at the ECSF meteorological station.

Table 3 shows moving correlation coefficients between incoming radiation, precipitation, and flowering percentages of the examined tree species. The time lag reveals clearly that the influence of irradiance and precipitation on flowering is counterphased. For most species, irradiance is more closely correlated to flowering activity than rainfall, with the exception of *Clethra* and *Vismia*. However, flowering of the majority of the wet-season species (*Clethra*, *Isertia*, *Vismia*, and *Viburnum*) started already in December or even earlier, when rainfall was still low. Hence this observation and correlation analysis suggests that cloudiness and irradiance are more likely triggers of flowering than precipitation.

Floral control by the daily photoperiod and light quality is a well-known phenomenon of plant life (e.g., Simpson & Dean 2002, Boss *et al.* 2004), and this has also been proposed for the tropics (Rivera & Borchert 2001, Zipparro 2004). However, apart from direct control by the length of the photoperiod, substantially reduced solar irradiance and light intensities during the wettest months can greatly reduce photosynthetic biomass production (Graham *et al.* 2003) and thus trigger the conversion of resting buds into flower buds (Borchert 1983). Borchert *et al.* (2005) have analyzed the significance of even small changes in the daily photoperiod for phenological synchronization in the tropics and have come to the conclusion that seasonal shifts in sunrise or sunset time induce the breaking of bud dormancy, rather than the only slightly changing day length. They showed bimodally synchronized flowering of 7 Neotropical tree species growing at a similar geographical latitude (3.8°S) as the RBSF. One group flowered between

TABLE 3. Time-lag (months) and correlation coefficient (r) for the highest correlation between flowering of the investigated species and precipitation and solar irradiance respectively. The data of the time period between July 1999 and January 2003 were used. Substantially higher r is underlined.

	Cedrela	Clethra	Graffen-rieda	Helio-carpus	Isertia	Pipto-coma	Purdi-aea	Tabe-buia	Vibur-num	Vismia
Irradiance	10; 0.63	6; 0.60	10; <u>0.46</u>	6; <u>0.71</u>	4; 0.56	11; <u>0.56</u>	1; <u>0.59</u>	10; <u>0.73</u>	6; <u>0.61</u>	3; <u>0.53</u>
Precipit.	4; 0.65	11; <u>0.69</u>	2; 0.40	11; 0.65	11; <u>0.69</u>	4; 0.41	5; 0.54	3; 0.56	12; 0.53	9; 0.38

December and March, after the winter solstice, the other from August to September, after the summer solstice. Flowering periods of the interspecific groups reported here for the RBSF differ significantly from those reported by Borchert *et al.* (2005), rendering the theory of changing sunrise und sunset time inapplicable. The almost regular morning rains mentioned earlier obscure the time of sunrise, and of course at least during the heavy rains the time of sunset is likewise indiscernible. We propose that in the mountain forest of the perhumid eastern cordillera of southern Ecuador the shading effect of clouds (decreased photosynthesis), combined with a change in the spectral composition of the solar radiation (direct versus scattered irradiation) could explain synchronization of flowering. As shown in Fig. 4, the ratio of direct (sunshine) to diffuse (clouds) radiation changes significantly in favor of the direct radiation during August until mid–November, when it drops drastically due to the increase of cloudiness until February. Initiation of flowering in both groups coincided more or less with these changes, taking into account that the time required for the development of flowers from buds is species-specific and therefore the onset of blossoming of the individual species may differ by some weeks. Fig. 2 also shows annual oscillations of the monthly minima and maxima of the air temperature, resulting in an increase of the daily temperature range during the less humid, and a decrease during the overly wet months. From studies with the laboratory model plant *Arabidopsis*, a modifying effect of temperature on the control of flowering by light quality has been suggested (Blázquez *et al.* 2003). Appreciating the completely different situation of a laboratory model plant and trees in a tropical forest, an additional effect of the varying daily temperatures on the induction of flowering by the light climate cannot be ruled out.

Controversial reactions of certain species to synchronizing factors. Having identified possible synchronizing factors, the question arises of why some trees react positively and others negatively to the seasonal changes in light climate and temperature. In principle this is the question of long-day and short-day plants whose floral control is by the phytochrome system, but with different sensitivities to the levels of the photoactive molecule species. In that context, the ultimate factors resulting from the meteorological conditions during the flowering period gain in importance. Annual oscillation of photosynthetic active radiation has also

been shown for a tropical lowland forest in Barro Colorado Island, which more or less coincides with flowering and leaf flushing of deciduous tree species (Wright & Van Schaik 1994). Pollination, fruit ripening, and fruit or seed dispersal greatly depend on the meteorological conditions during the flowering period. Most of the investigated species produce conspicuous flowers that are pollinated by specialized animals (bats, insects, birds, Dziedzioch *et al.* 2003, Wolff *et al.* 2003) which need to interact with their host plants even during the months of maximal rainfall. Flowering of *Myrica*, as the only obligatory wind-pollinated species, is well positioned in the less humid period of the year. In general, the phases of fructification from fruit set until fruit maturation are longer than those of flowering, and environmental events may become more critical with respect to seed development. Viability of the seeds is short: seeds of most of the investigated species are viable for less than 6 months and therefore adjustment of the time required for seed maturation and germination to the environmental conditions is crucial. This applies in particular to those species with a comparatively short fructification period, like *Tabebuia* and *Piptocoma*. Since the reported data are observations from which certain interpretations were deduced, these conclusions would become more stringent by experimental proof. However, this is difficult with the issues of flowering and fruiting of trees in a natural tropical forest, where the number of individuals of each species is low. Once nurseries have been established that can also cultivate trees for seed production then the individual variations in timing and correlations with specific meteorological events can be based on more detailed and statistically elaborated data sets.

Aseasonal climatic events cause irregularities of flowering, fructification, and seed ripening. Mass or general flowering of woody plants is an aperiodical phenomenon of the tropics but is also known from temperate forests (Herrera *et al.* 1998). In a Malaysian lowland forest the most abundant life form is represented by trees flowering only in aperiodic mast years (Sakai *et al.* 1999), and in a submontane Philippine rainforest about one-sixth of the tree species were episodic reproducers (Hamann 2004). During the 4 years of monitoring phenological events in the Ecuadorian mountain rainforest, mass flowering was not recorded. Rather the contrary, namely lack of flowering and/or production of germinable seeds in one or two years was the case, e.g., for *Vismia* and *Piptocoma*. In 2001

Vismia did not flower at all and *Piptocoma* flowered only to an almost negligible extent (Fig. 6). Consequently there were no fruits of *Vismia* in 2001 and only few fruits of *Piptocoma* (Fig. 7), which, however, did not germinate. Interestingly, also the ample fructification of *Piptocoma* late in the year 2000 did not produce germinable seeds. As shown in Fig. 3 (white arrow) and Fig. 5, in that year an extraordinarily long period of cold was recorded between October 31 and November 13, following a short breakdown of the easterly air flow between October 24 and 26. An air stream from the north-west overflowing the easterlies temporarily even interrupted the diurnal mountain-valley breeze system (white arrow in Fig. 3: wind direction ECSF). During that two-week episode the study site did not receive any rainfall, and sunny weather caused the relative humidity to drop to 20% (Fig. 5). Simultaneously, nocturnal temperatures repeatedly dropped to about 6°C. Whether the exceptional nocturnal minimum temperatures or drought or both factors affected flowering and seed development of *Vismia* and *Piptocoma* is still an open question. However, since the exceptional La Niña dry period at the turn of the year 1999–2000 did not affect plant performance in a comparable way, cold is suggested as having affected flower induction and seed production rather than a two-week period without precipitation. This interpretation is corroborated by taking the upper limit of the areas of *Piptocoma* and *Vismia* into consideration. Both are typical representatives of the lower, i.e., warmer montane forest, not growing higher than 2100 m (*Piptocoma*) and 2300 m a.s.l. (*Vismia*), and thus may be indeed sensitive to unusually low temperatures.

Conclusion. In the tropical evergreen mountain rainforest of southern Ecuador, periodical flowering and fruiting of trees appears to be mainly triggered by cloudiness and its influence on light climate and temperature. These periodical events are, however, overlaid by episodic climatic incidents, mainly low temperatures, which affect reproduction. Investigating the biology of reproduction, favorable seasons have been identified for the collection of seeds as a basis for establishing nurseries for useful indigenous trees.

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