

Seasonal changes in light availability determine the inverse leafing phenology of *Jacquinia nervosa* (Theophrastaceae), a neotropical dry forest understory shrub

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ABSTRACT. The leafing phenology of tropical plants has been primarily associated with seasonal changes in the availability of water and light. In Tropical Dry Forests most plants are deciduous during the dry season and flush new leaves at the onset of the rains. In contrast to this pattern, a small group of species present an inverse strategy of leaf production, being deciduous during the wet season and flushing new leaves during the dry season. In Costa Rica, the only species with such behavior is the phreatophytic understory shrub *Jacquinia nervosa* (Theophrastaceae). In this study, we determined how seasonal changes in light availability (photon flux density, PFD) influence the leafing and reproductive phenology of this species. We monitored leaf production, leaf survival and leaf life span in 36 adult plants (1.2-5.5 m in height) during 16 months (April 2000 through October 2001) in Santa Rosa National Park. Leaf censuses, as well as flower and fruit counts (when available), were done every two weeks. Changes in PFD were monitored using canopy photos to measure the direct and indirect radiation reaching each plant from December 2000 to February 2001. We also analyzed how leaf structure matched dry season conditions by inspecting changes in leaf specific mass, leaf expansion rates, and internal leaf anatomy. During 2000 and 2001 leaf flushing started in mid October (late wet season). Leaf fall occurred gradually during the first three months of the wet season (May through July). Both

leaf flushing and leaf fall showed high synchronicity among individuals, and were directly related to temporal changes in light availability. Maximum leaf flushing coincided with peaks in direct radiation at the end of the dry season (April). Leaf fall increased with decreasing light levels during May and July 2001 (early to mid wet season). Leaf expansion was completed in 20.5 days (S.D. = 5.7, N = 150). Leaf specific mass varied little relative to PFD levels. Analysis of leaf anatomy showed that *J. nervosa* is a typical evergreen sclerophyllous species, with esclerenchimatous hypodermis, and a multilayered palisade mesophyll. The close relationship between light availability, leaf flushing and leaf fall, a leaf structure capable of tolerating drought conditions, and high biomass allocation to roots in seedlings (and very likely in adult plants) suggest that *J. nervosa* modifies its physiological functioning to benefit from higher light levels prevalent during the dry season. Low light conditions dominating the understory during the wet season are likely to induce high respiration demands that make it expensive to maintain leaves when the understory is shaded. The inverse leafing phenology allows *Jacquinia* to cope with sharp seasonal fluctuations in light while maximizing carbon gain.

KEY WORDS: *Jacquinia nervosa*; Tropical Dry Forest; inverse phenology; light limitation, Santa Rosa National Park.

INTRODUCTION

Proximate causes influencing plant phenology have been largely associated with climatic seasonality (Frankie *et al.* 1974, Hegarty 1990, Reich 1995, Williams-Linera & Meave 2002), especially water availability (Borchert 1983, 1994, 1995, Reich 1995). In tropical forests broad weather patterns are determined by the seasonal movements of the Intertropical Convergence Zone, which influences the distribution of precipitation, cloud cover, wind, temperature, and light regimes (van Shaik *et al.* 1993, Wright 1996). Of these factors, light shows the highest spatial and temporal variation (Chazdon 1986, 1987, Chazdon & Pearcy 1991, Turnbull 1991), imposing a significant selective pressure on patterns of resource allocation (Avalos *et al.* 2003). Fluctuations in cloud cover, daylength, sun position, self-shading and shading by neighboring trees, limit light interception, and thus, the primary productivity of tropical forests (Hutchison & Matt 1977, Wright 1996, Wright *et al.* 1999). Clark & Clark (1994) and Wright (1996) have demonstrated clear links between plant growth and peaks in radiation, suggesting that limited light availability is an important selective factor on the phenology of tropical plants.

In neotropical dry forests the majority of canopy trees are deciduous during the dry season (Janzen 1967, Frankie *et al.* 1974). However, some species present an inverse leafing phenology. These species produce and maintain all leaves during the dry season, and abscise them at the onset of the rains when the canopy begins to close (Janzen 1970, Sobrado 1986, Reich 1995, Wright 1996, Roupsard *et al.* 1999). *Jacquinia nervosa* –formerly *J. pungens*- (Janzen 1970, 1983, Daubenmire 1972, Bullock & Solís-Magallanes 1990) and *Faidherbia albida* (Roupsard *et al.* 1999) belong to this category. An inverse leafing phenology is prevalent in phreatophytic species (Janzen 1970, Holbrook *et al.* 1995) where the depth of the root system facilitates access to underground water sources reducing water stress during the dry season (Dawson & Pate 1996, Roupsard *et al.* 1999).

In this study, we determined the extent to which seasonal changes in light availability influence the leafing phenology of *J. nervosa*, which produces leaves during the dry season when the majority of canopy species are deciduous, to benefit from increased understory light levels. Our objectives were: 1) to quantify

the effect of light on the leafing and reproductive phenology of this understory shrub; 2) to measure the extent of synchrony of leaf, flower and fruit production; and 3) to analyze the effect of plant size on leaf, flower and fruit production. We predicted that: 1) plants receiving more light will produce new leaves, flowers and fruits earlier than more shaded plants; 2) plants growing under more open conditions will retain leaves longer than more shaded individuals; 3) the different phenophases will take place sooner and be expressed with stronger intensity in larger individuals, which have more access to light, water and nutrients. Understanding how light affects the phenological behavior of *J. nervosa* will increase our knowledge on the strength of proximate causes influencing the phenology of tropical plants.

METHODS

STUDY SITE. This study was carried-out over 16 months (April/July 2000, and November 2000 to October 2001), along the “Indio Pelado” trail in Santa Rosa National Park, Guanacaste, Costa Rica. Santa Rosa is located between the Gulf of Papagayo and the Interamerican Highway (10°44'13” to 11°00'37” N, and 85°34'48” to 85°58'51” W) at 290 m in elevation. The upper plateau maintains tropical premontane forests, whereas the coastal lowlands present a large extension of Tropical Dry Forests (Tosi 1969). Annual mean rainfall is 1,423 mm, September and October being the wettest months. Average annual temperature is 25.7 °C, and average relative humidity is 81% (Santa Rosa National Park Climatic Records). The dry season extends from late November through April. During the dry season, most of the canopy trees (nearly 70%) are deciduous (Hartshorn 1983).

The “Indio Pelado” trail is dominated by secondary forests with a complex plant community composed primarily by seedlings and saplings of canopy species and understory shrubs (i.e., *Cochlospermum vitifolium*, *Semialarium mexicanum*, *Jacquinia nervosa*), trees of 10-20 m in height (i.e., *Spondias mombin*, *Bursera simaruba*), and a few old trees 20-35 m remanent of the original forests (i.e.,

Pachira quinata, *Manilkara chicle*, *Hymenaea courbaril* and *Pseudobombax septenatum*).

STUDY SPECIES. The genus *Jacquinia* (Theophrastaceae) consists of 34 species of xerophytic shrubs and small trees distributed in dry areas of the Antilles, Central America, and the northern coast of South America (Ståhl 1995, Ståhl 1998). The genus' diversity center is located in the Antilles (20 species). Eleven species occur in Central America (Ståhl 1989, 1995), and of these, only *J. nervosa* (formerly *J. pungens*) has an inverted leafing phenology.

Jacquinia nervosa C. Presl (hereafter referred to as *Jacquinia*) is an understory shrub abundant in deciduous and semideciduous forests throughout the pacific coast of Mesoamerica, from southern Jalisco, Mexico, to northwestern Costa Rica (Ståhl 1989). In Santa Rosa National Park, *Jacquinia* reaches a density of 0.1-60 adults per Ha (Janzen 1970). This species is found in mature and secondary forests, forest edges and pastures. Adult plants range from 1.5-6 m in height (individuals above 5 m are rare), with a basal diameter of 1.5-20 cm (pers. obs.). Leaves are coriaceous, simple, alternate, with the apex modified as a spine. Small orange flowers are produced in terminal cymes and are very likely pollinated by bees, as deduced from flower morphology and scent chemistry (Knudsen & Ståhl 1994). In *Jacquinia*, the root system does not present superficial lateral roots. Instead, the pivotal root reaches considerable depth (down to 8 m, Janzen 1970, 1983, Oberbauer 1985). *Jacquinia nervosa* is the only species in the family with an inverse leafing phenology (B. Ståhl, pers. com.). Fruit production takes place during the dry season (February-March), one month after anthesis. Fruit expansion extends to the onset of the rains (May). Ripe fruits are orange, and contain up to 10 seeds covered by a sweet, fleshy aril. Fruits are maintained in the plant for over two years. Although dispersal agents are not known with certainty, rodents can easily crack the fruit and eat the aril, helping to disperse the seeds (Janzen 1970). We marked 80 individuals > 2 cm of stem diameter 20 cm above the ground, chosen at random, and distributed in three size categories: a) 1-2 m, b) 2-3 m, and

c) 3-5 m. Of these individuals, we randomly chose 36 plants of a variety of heights, on which all measurements were concentrated.

ASSESSMENT OF VARIATION IN THE LIGHT ENVIRONMENT. Hemispheric canopy photos 0,5 m above the crown were taken in December 2000 and February, May and July 2001 under overcast sky conditions using a Nikon Coolpix 950 digital camera model FC-E8 adapted to a fish-eye lens of 7.5 mm. Digital images were analyzed using the software Hemiview (Delta-T Devices Ltd.) We analyzed the specific site distribution of direct and diffuse radiation (site factors) using the expected radiation values per site. We obtained the direct site factor to evaluate the fraction of direct radiation reaching each plant relative to the total amount of light available at the top of the canopy. We calculated the indirect site factor (diffuse factor, or radiation filtered by the canopy) reaching the plant crown relative to the radiation reaching an open site. Using these indices, combined with PFD data obtained from the Santa Rosa National Park weather station, we calculated values of direct and indirect radiation reaching each plant according to the canopy conditions and light intensities prevalent at each sampling date.

MEASUREMENT OF LEAF PHENOLOGY AND LEAF STRUCTURE. Leaf production and life span were measured following bi-weekly censuses done from November 2000 to August 2001. In every plant, we randomly selected 20 external branches and marked them with plastic tags to obtain 200 leaves per plant (5-15 leaves per branch). In addition, we tracked leaf production and life span in 20 seedlings grown from seeds collected at the study site. We obtained a sample of 5 leaves taken from each of 30 different adult plants and measured leaf length and width, and then measured actual leaf area with a Li-Cor Li-3100 leaf area meter. We used a regression to calculate leaf area in the field using leaf length and width as predictor variables ($r^2=0.97$, $n = 125$, $p = 0.001$). Estimates of leaf area were done weekly at the beginning of the dry season (between December 2000 and February 2001) using 20 marked leaves from each plant. To determine leaf specific mass (LSM) 10 leaves from each plant were taken every two weeks from

December 2000 to June 2001. Using the above-mentioned regression we calculated leaf area, and then put the leaves in an oven at 60 °C for three days to obtain dry weight. Finally, we determined LSM by calculating the fraction of dry weight over area in g/cm². Leaf internal anatomy was studied in 40 leaves coming from 20 plants selected at random in April and May 2001. In this case, we measured the distribution of tissues within each leaf, as well as leaf thickness, by obtaining cross sections observed under the microscope.

LEAF, FLOWER AND FRUIT SYNCHRONY. Synchrony in leaf, flower and fruit production was calculated following Augspurger (1983) using the formula: $X_i = \sum_{j=1}^n e_{ij} / (n-1) f_i$, where X_i is average synchrony in module production at the population level, e_{ij} is the number of days in which plants i and j produced a particular module, f_i is the life span of the module in plant i ; and n is the sample size. The index varies between 1 (100% of synchrony) and 0 (total asynchrony).

BIOMASS ALLOCATION IN SEEDLINGS. To analyze biomass allocation to roots and above ground parts, we carefully dug out 15 seedlings of 4-15 cm in height and measured root and stem length. The proportion of biomass distributed to roots, stems, petioles, and leaves was determined from dry weights of this material stored and dried in an oven at 60°C for two days until constant weight.

STATISTICAL ANALYSES. To determine the effect of radiation and plant size on leaf, flower and fruit production over time, we applied general mixed linear models (GMLM) for repeated measures (SAS 1994) considering that deviations from normality and heterogeneity of variances of the response variables did not allow the use of MANOVA or repeated measures ANOVA. GMLM do not assume normal distributions or homogeneous variances, but rather inspect different probabilistic distributions to calculate the residual error (Breslow & Clayton 1993). The models calculate a response variable Y from a linear function of a group of values y_1, y_2, \dots, y_p obtained from the original response variables Y_1, Y_2, \dots, Y_p . The response is known as the linking function ($g_{(\mu)}$):

$$g_{(\mu)} = \beta_0 + \sum \beta_i x_i$$

According to Breslow & Clayton (1993), the regression coefficients, β_i , compare the effect of each factor a_i on the dependent variable Y with a base factor chosen at random, whose effect, by definition, is zero. When $\beta_i > 0$ the base factor increases the value of Y , if $\beta_i < 0$ the base factor decreases the value of Y , and when $\beta_i = 0$ there is no effect on Y . In this case, the effects of indirect and direct radiation and plant size on leaf, flower and fruit production were analyzed through GMLM using a logarithmic linking function, since the data and the error showed a negative binomial distribution ($X^2 = 74.5$, d.f. = 224, $p = 0.34$). We obtained the following model:

$$g_{(\mu)} = \log(p) = \mu + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + e,$$

where p is leaf, flower or fruit production assuming a repeated measures model, x_1 is the effect of direct radiation, x_2 is the effect of indirect radiation, and x_3 is plant size. Finally, e is the residual error according to the negative binomial distribution. The degree of significance of each component is calculated using a X^2 test. To control type I error we applied a sequential Bonferroni correction following Rice (1988).

RESULTS

EFFECT OF LIGHT AND PLANT SIZE ON PHENOLOGY. Direct light significantly influenced leaf production, flower bud production and number of flowers. Diffuse light and plant size did not have a significant effect on plant phenology (Table 1). Leaf production was significantly affected by the temporal variation in direct light (Fig 1A). The number of new leaves per plant was directly related to direct light throughout the study period ($r^2 = 0.37$, $n = 27$, $p = 0.0006$). Direct light reached a peak high in February during the middle of the dry season, and started to decrease with the onset of the rains as the canopy began to close. Leaf numbers closely tracked direct light at the start of the dry season, but decreased significantly with decreasing light and increasing canopy cover, although decreasing leaf numbers

lagged two weeks behind the reduction in direct light (Fig. 1A). In addition, peaks in leaf flushing, flower and fruit production in February 2001 coincided with a peak in direct light lasting two months (Fig. 1B, 2A) during which these phenophases were concentrated. The increase in direct light and temperature (Fig. 2) coincided with the onset of leaf flushing and the production of flower buds (Fig. 1B). This temporal relationship was reflected in a significant interaction between direct light and time vs. leaf production (Table 1). Leaf production increased in November (beginning of the dry season) and reached a peak during the first week of February (middle of the dry season, Fig. 3). Leaf fall began at the end of May (onset of the rainy season) and increased continuously during the following months. All plants were deciduous by August (mid rainy season). Average life span was 8.15 months (S.D. = 1.33, n = 120), which includes the time from leaf bud production to leaf fall. This value could be overestimated, since most senescent leaves reached a light yellow coloration but remained a substantial time in the plant before falling off. The synchronicity of leaf production was considerably high (mean = 0.88, S.D. = 0.06, n = 36). Leaf production coincided with flower bud production in the majority of plants (Fig. 3). Anthesis started by mid January and reached a peak during the first week of February (Fig. 1B). The synchronicity of flower (mean = 0.38, S.D. = 0.26, n = 36) and fruit production (mean = 0.18, S.D. = 0.18, n = 36) was relatively low. Only direct light had a significant effect on number of flowers during the study period. Neither, direct light, nor indirect light or plant size had a significant effect on the number of fruits (Table 1).

RATE OF LEAF EXPANSION. Leaf expansion was completed in 20.5 days (S.D. = 5.7, n = 150, Fig. 4) reaching 5.28 cm² (S.D. = 3.32, n = 155) at the end of the wet season. Leaf area in fully expanded leaves was not related to the initial light environment in which expansion took place ($r^2 = 0.031$, n = 18, P = 0.57).

LEAF SPECIFIC MASS (LSM). This parameter showed a steady increase throughout the study period (Fig. 5). It continued to increase with the advancing dry season, reaching 103 gm⁻² (D.S. = 33.77, n = 215) at the end of May, then

decreased during the following months. The decrease in LSM was associated with loss of photosynthetic pigments, and increase in the yellow tone of the leaf before abscission.

LEAF ANATOMY. Mature leaves of *Jacquinia* showed typical xerophytic characteristics, such as a hypodermis composed of longitudinal layers of sclerenchyma surrounding the central vascular bundles. The palisade mesophyll was made of 2-3 layers of elongated parenchyma cells with abundant chloroplasts. The spongy mesophyll was formed by cells of variable size and shape with little chloroplasts and abundant intercellular spaces.

BIOMASS ALLOCATION IN SEEDLINGS. In contrast to adult plants, seedlings were evergreen. Leaves were maintained throughout 2001 (n = 20 seedlings). Germination took place in the field during the middle of the rainy season (July-August). In seedlings, average root length was 31.6 cm (S.D. = 11.7, n = 15), whereas average stem length was 8.48 cm (S.D. = 3.14, n = 15, Table 2). In all observed seedlings, root biomass was up to seven times larger than stem biomass, despite of the significant effect of between-plant variation (Table 1). Root to shoot ratios were 2.53 (S.D. = 0.93, n = 14).

DISCUSSION

EFFECT OF LIGHT ON PLANT PHENOLOGY. Many investigations in weakly-seasonal tropical forests have demonstrated that the vegetative and reproductive phenology of canopy trees is concentrated during periods of high radiation (Janzen 1967, Wright 1992, Wright & van Schaik 1994, Grace *et al.* 1995). This tendency has been observed for diameter increases in the evergreen forests of Suriname (Schultz 1960), in the flowering of canopy trees of peninsular Malaysia (van Schaik 1986), in diameter growth and flower and fruit production of canopy trees at La Selva (Raich *et al.* 1991, Clark & Clark 1994), in leaf (Barone 1998) and flower production on Barro Colorado Island, Panama (Croat 1969, 1975), and in seed

production of canopy trees in Borneo (Wycherley 1973). Hladik (1978) mentions that 95% of lianas and trees in a Gabonese forest concentrate leaf and flower production during the sunniest months of the dry season. This phenological pattern is also prevalent in several species of the dry forest regarding reproductive synchronization (Janzen 1967, Borchert 1983, 1995).

In *Jacquinia*, leaf and flower production was closely related to increased levels of direct light. Janzen (1970) observed leaf production from late November to early December coinciding with canopy aperture and increased light intensity. Leaf fall started a few weeks after the first rains and was completed in July. In this study, leaf flushing started in late October, with a relatively high degree of synchrony (0.88). The variation observed was influenced by the level of canopy aperture (Fig. 1A), as well as by endogen factors such as the level of resource accumulation and overall physiological status. In contrast to leaf production, flower and fruit production had low values of synchrony. It is likely that plants, independently of their size, will invest in reproduction accordingly to their access to light resources (significant effect of direct light on leaf, flower buds and flower production, Table 1). It is probable that leaf and flower bud production were the result of storage since both started at the same time coinciding with canopy aperture (Fig. 1, 3) and reached a peak relatively fast. Flower initiation was not determined by achieving a peak in leaf area, although it is possible that concentrating leaf area during the dry season favors the rapid nutrient accumulation that will balance the expenses of growth and reproduction of the following year. Although increased light affected flower bud production and number of flowers, to fully explain these differences it is necessary to study the reproductive ecology of *Jacquinia*, which still is poorly understood. The number of flowers that are fertilized is dependent on the behavior of pollinators, but this aspect, along with the dispersal ecology of the species, is not well known.

In addition to the increase in PFD observed in October 2001, we recorded a slight increase in mean air temperature (from $23,68^{\circ}\text{C} \pm 0,47$ in September to $24,44^{\circ}\text{C} \pm 0,7$ in October), which could have affected initial leaf flushing. Slight changes in air temperature affect solute transport in the phloem (Johnson &

Thorley 1985), as well as the initiation of bud aperture and leaf expansion (Reddy *et al.* 1993). Although in several tropical dry forest species early leaf flushing coincides with peaks in air temperature (i.e., *Tabebuia rosea*, Gómez & Fournier 1996, and *Enterolobium cyclocarpum*, Rojas 2001) we do not consider this to be the case in *Jacquinia*, due to the magnitude of the differences (Fig. 2B) and the timing of peaks in air temperature (where highest values were observed in April at the end of the dry season -Fig. 2B- whereas the peak in leaf production was observed in February, Fig. 3).

In weakly-seasonal forests, leaf phenology is directly influenced by seasonal changes in light availability (Wright & van Schaik 1994, Wright 1996, Barone 1998). Angulo-Sandoval & Aide (2000) showed that in the Luquillo forest of Puerto Rico, leaf flushing was related to an increase in light conditions, but not precipitation. For evergreen as well as for species with inverse leaf phenology in seasonal forests, water is not such a critical limiting factor, since in both cases, a deep root system capable of reaching the water table provides the necessary water to balance the transpirational costs associated with maintaining leaves during the dry season (Wright 1992, Dawson & Pate 1996, Sandford & Cuevas 1996, Roupsard *et al.* 1999). During the dry season deciduous species use water from the deepest soil layers and have a reduced water deficit (Jackson *et al.* 1995). A well developed root system favors leaf production during the season of higher light availability (Sandford & Cuevas 1996, Roupsard *et al.* 1999). In addition, increased above- and belowground growth during the dry season can be mediated through increased arbuscular mycorrhizal infection activated by the last rains of the wet season (Allen *et al.* 1998).

In adults of *Jacquinia* the root system can reach 8 m in depth (Janzen 1970), allowing water access throughout the entire growing season. In another species with inverse phenology, *Faidherbia albida*, Dupuy & Dreyfus (1992) found roots reaching 30 m in depth. Roupsard *et al.* (1999) showed that the phreatophytic character of this species allows it to tolerate the dry season without being exposed to severe water stress in comparison with deciduous species. Consistent with this pattern, seedlings of *Jacquinia* showed high biomass allocation to roots. Here, the

length of the root system was seven times that of the stem, with a root:shoot ratio of 2.53. High root to shoot ratios are indicative of habitat specialization, being predominant in species adapted to dry habitats. It is likely that seedlings in the understory of the dry forests experience prolonged drought during the dry season. Under these conditions, small seedlings benefit more from higher root allocation, which favors access to deeper, more humid soil profiles. Higher root allocation enhances root storage, which is important to support new growth during favorable periods (Condon *et al.* 1992). It is possible that *Jacquinia* switches from evergreen to deciduous when it is more advantageous to grow in pulses rather than maintaining a carbon balance close to zero, which is the situation that young plants experience being evergreen during the wet season, or while withstanding the dry season with little water. It is likely that young plants will switch as soon as the level of resource access (reflected in a large root area) is sufficient to allow growth increases (increased leaf area and sexual reproduction) during the time where competition for light decreases, but access to water becomes important.

In addition to root allocation, specific climatic factors, such as dew deposition, can influence stomatal function, affecting the extent to which high photosynthesis rates can be maintained under conditions of potential water stress. In the dry forest of Chamela, Mexico, Barradas & Glez-Medellín (1999) observed that early morning dew, concentrated on leaf surfaces of the understory heliophytes *Jacquinia* and *Coccoloba liebmanni*, reduced transpiration rates during the morning, allowing the exploitation of higher light levels and higher growth rates during the dry season by increasing the number of days with low transpirational demands.

Jacquinia was specialized to exploit the higher light levels prevalent in the understory during the dry season. This specialization was reflected in the tight coupling between the leafing phenology and increased light levels, the development of a deep root system, the biomass allocation pattern of seedlings, and the leaf structural characteristics. In most sun-adapted species, high metabolic rates represent high respiratory costs relative to shade adapted species (Bazzaz & Carlson 1982, Pearcy *et al.* 1987, Mulkey *et al.* 1993, Chazdon *et al.*

1996, Zotz & Winter 1996). High metabolic rates are incompatible with prolonged shade (Givnish 1988, Rice & Bazzaz 1989, Chazdon *et al.* 1996). Due to the potential high respiratory demands and the reduced light levels *Jacquinia* loses all its foliage during the wet season. It is likely that with higher light availability during the wet season *Jacquinia* could maintain an evergreen habit. In the Sonoran Desert, *Jacquinia* is evergreen, but shows inverse phenology in the deciduous forests of Veracruz (A. Búrquez, *pers. com.*), which has a seasonality similar to Santa Rosa.

The evolution of inverse phenology should involve sufficient genetic variation for drought tolerance, in addition to selective factors that make periods of increased light predictable within the context of the life history strategies of the plant. There must be environmental cues that can be perceived at the population level and will adjust plant phenology to periods in which light is highly limited, or readily available. Changes in soil water content (Borchert 1994) and the increase in direct light during the wet-to-dry season transition could act as an environmental signal for understory plants to modify their leaf phenology (Wright & van Shaik 1994).

LEAF EXPANSION AND LSM. In this study, *Jacquinia* showed rapid and highly synchronic leaf expansion, but low LSM. Rapid leaf expansion (< 1 month) is common in tropical species (Coley & Kursar 1996) and has been related to a reduction in the period of exposure of young leaves to herbivores (Coley & Kursar 1996, Barone & Coley 2002). Parallel to the increase in leaf area, LSM increased with increasing biomass associated to a higher proportion of vascular and supporting tissues, and a high carbon:nitrogen ratio (Sobrado & Medina 1980, Medina 1984). All these factors combine to increase leaf resistance to physical damages and damage by herbivores (Castro-Díez *et al.* 2000, Barone & Coley 2002). An increase in LSM can be associated with high radiation levels, as it is the case in species exploiting light gaps and the top of the canopy (Fetcher *et al.* 1983, Mulkey & Wright 1996, Baruch *et al.* 2000). Here, developing thicker leaves increase water flux while maintaining high water use efficiency (Nobel 1991). The

reduction in LSM, and the decoloration of leaves observed at the end of the dry season is very likely associated with an internal process of nutrient reallocation. In *Jacquinia*, reabsorbed nutrients are probably stored in stem and branch parenchyma. According to Janzen & Wilson (1974) two thirds of total carbohydrates (as well as nitrogen and phosphorus) stored at the end of the dry season are consumed gradually throughout the wet season due to maintenance respiration (from May to November) and to new leaf and branch production (from November to December) during the growing period.

CONCLUSIONS

We found a tight coupling between the level of canopy openness, increased direct light and leaf production in *Jacquinia*, which were independent of plant size. Increased light levels also affected the production of flower buds and the number of flowers. *Jacquinia* is adapted to exploit the higher light levels prevalent in the understory during the dry season. This specialization was reflected in the tight relationship between leaf phenology and increased light, the development of a deep root system, the biomass allocation pattern of seedlings, and the xerophytic structure of the leaves. More research needs to be done on the reproductive ecology of *Jacquinia*; still the primary pollinators and seed dispersers of this species have not yet been identified. Understanding the influence of pollinators and dispersers on the timing of reproductive events will complete the picture on the proximate and ultimate factors that control the evolution of an inverse leafing phenology in this dry forest understory shrub.

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Table 1. Significance of regression coefficients (± 1 S.E.) calculated through the Lineal Generalized Mixed Models (LGMM) to determine the relation between light availability and leaf, flower and fruit production in 36 adults of *J. nervosa*, Santa Rosa National Park, Costa Rica.

Modules	Factor	β	S.E.	χ^2	d.f.
Leaves	Direct light	0.0013	0.0001	19.23 ***	1
	Direct light *date	0.028	0.007	24.8 **	8
	Indirect light	-0.0001	0.0027	0.002 N.S.	1
	Size	0.0007	0.0009	0.65 N.S.	1
Flower buds	Direct light	0.011	0.0004	14.50 **	1
	Indirect light	-0.0262	0.0125	1.65 N.S.	1
	Size	0.0035	0.0038	0.75 N.S.	1
Flowers	Direct light	0.0086	0.0015	10.03 **	1
	Indirect light	-0.0594	0.0132	3.15 N.S.	1
	Size	-0.0028	0.0026	0.62 N.S.	1
Fruits	Direct light	-0.0015	0.0004	3.52 N.S.	1
	Indirect light	0.0183	0.0075	4.62 N.S.	1
	Size	0.0081	0.0030	2.07 N.S.	1

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, N.S. non significant

Table 2. Variation in mean length (± 1 S.E.) and dry weight allocation to roots, shoots and leaves (mean ± 1 S.E.) in seedlings of *Jacquinia* (n = 15) in Santa Rosa National Park.

Module	Biomass (g)	Length (cm)
Roots	1.46 (0.75)	31.6 (3.4)
Shoots	0.19 (0.05)	8.5 (0.9)
Leaves	0.23 (0.05)	3.6 (0.2)

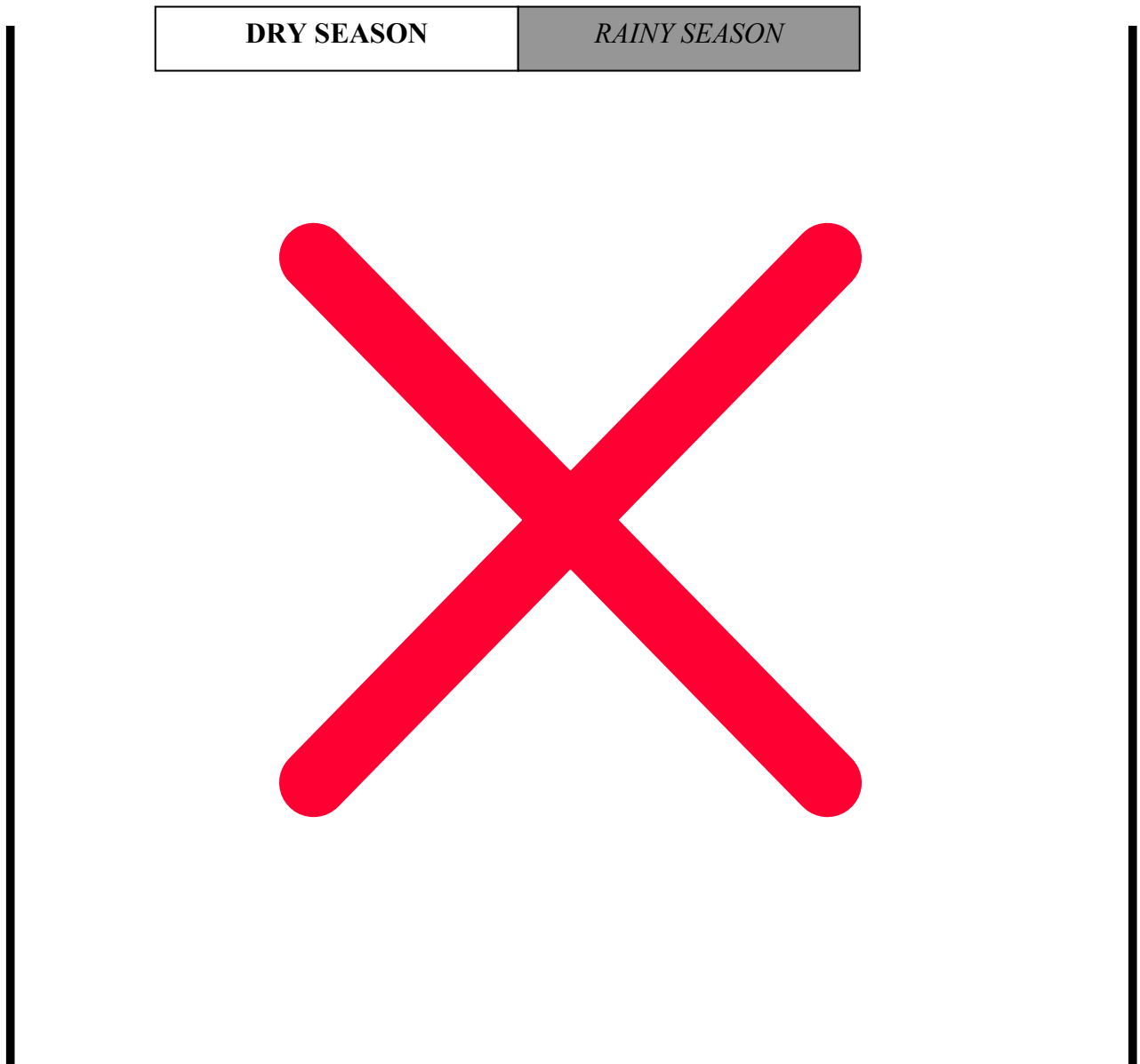


Fig. 1. Seasonal variation in the availability of direct light and its relationship with: **(A)** leaf production; **(B)** flower and immature fruit production in *Jacquinia*. Values are means (± 1 S.E.) of module censuses of 36 reproductive plants.

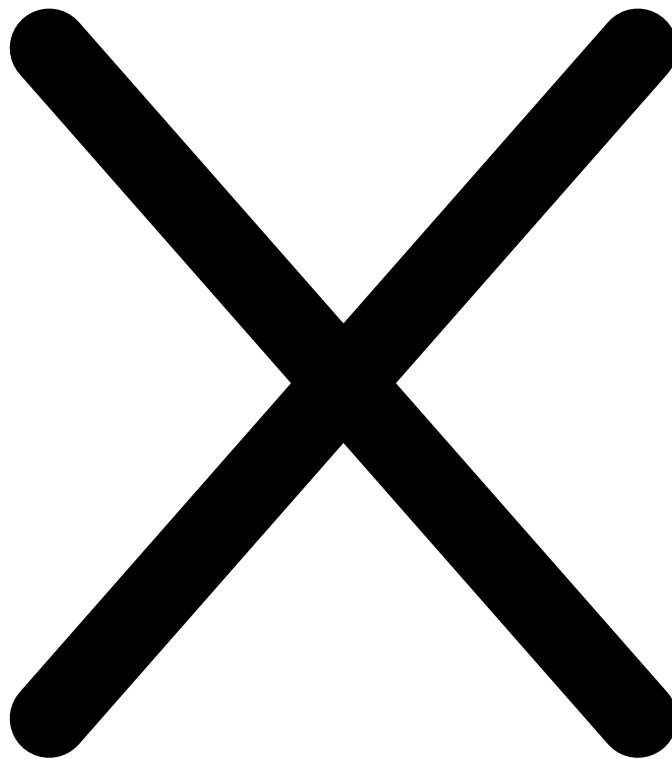
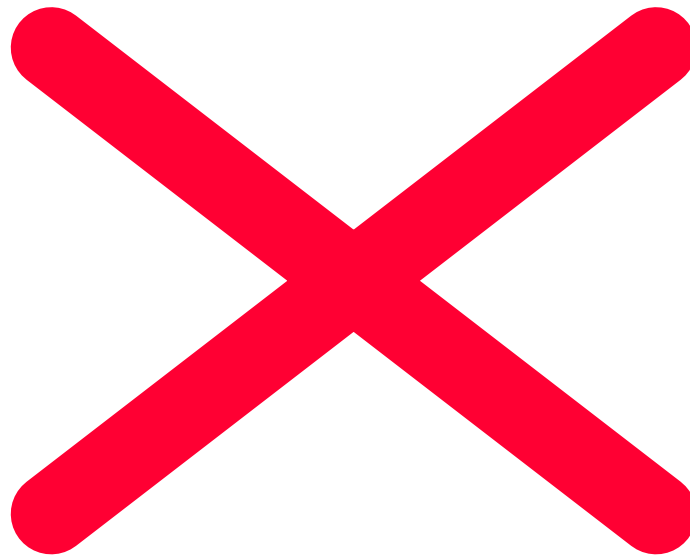
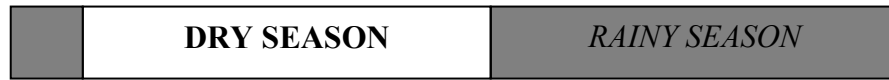


Fig. 2. (A) Changes in mean monthly direct and indirect –or diffuse- radiation (± 1 S.E.) and (B) Mean air temperature (± 1 S.E.) from September 2000 to July 2001 in Santa Rosa National Park.



ELLUVIOS

Fig. 3. Changes in mean number of leaves and flower buds (± 1 S.E.) in *Jacquinia* from October 2000 to August 2001).



Fig. 4. Temporal changes in the rate of leaf expansion in 25 adult plant of *Jacquinia*. Values are means (± 1 S.E.) of five marked leaves per plant.

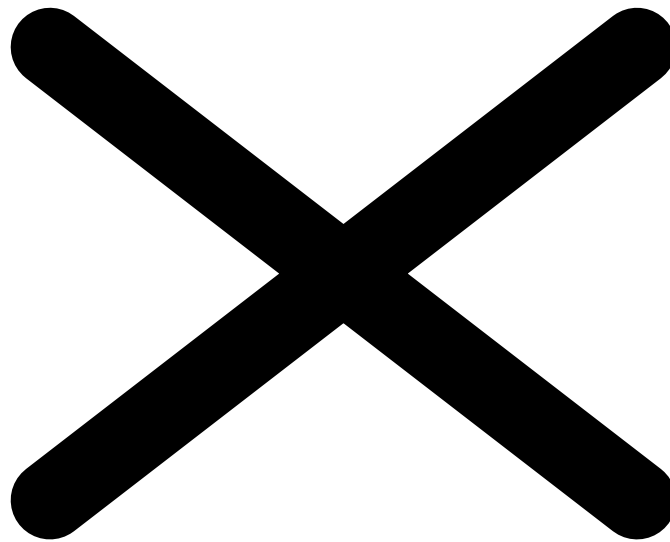


Fig. 5. Seasonal changes in mean LSM. Values are means (± 1 SE) of four leaves from each of 25 adult plants of *Jacquinia*.



Fig. 6. Relationship between total leaf production in mature plants of *Jacquinia* (n = 22) and seasonal variation in direct light during the dry season (January and February) and the start of rainy season (May and June) of 2001.

