Inverse leafing phenology of the dry forest understory shrub *Jacquinia nervosa* (Theophrastaceae)

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**Abstract:** In the dry forest of Santa Rosa National Park, Costa Rica, the understory shrub *Jacquinia nervosa* presents an inverse pattern of phenology that concentrates vegetative growth and reproduction during the dry season. In this study, we tested the “escape from herbivory” hypothesis as a potential explanation for the inverse phenological pattern of *J. nervosa*. We monitored leaf, flower and fruit production in 36 adult plants from October 2000 to August 2001. Leaves of six randomly selected branches per plant were marked and monitored every two weeks to measure the cumulative loss in leaf area. To analyze pre-dispersal seed predation we collected 15 fruits per plant and counted the total number of healthy and damaged seeds, as well as the number and type of seed predators found within the fruits. Leaf, flower, and fruit production occurred during the first part of the dry season (end of November to February). The cumulative herbivory levels were similar to those observed in other tropical dry forest tree species that concentrate leaf production during the wet season, and were concentrated on young leaves, which lost an average of 36.77% of their area (SD=34.35, n=195). Chewing beetles of the genus *Epicauta* (Meloidae) were the most important herbivores. In mature leaves, most of the damage was caused by the beetle *Coptocycla rufonotata* (Chrysomelidae). Fruits took 4 months to develop during the dry season (January - March 2001) but continued increasing in size well into the first 3 months of the wet season (May-July). Average seed number per ripe fruit was 9 (SD=5, n=500). Seed predation in mature fruits was 42% (SD=47, n=122). Most
seeds were damaged by moth larvae of the family Tortricidae. Only 3% of the flowers became fruits. This was influenced by the low level of flower synchrony (0.38±0.26, n=36 plants), but neither leaf synchrony (0.88±0.06, n=36 plants) nor plant size influenced fruit numbers. The significant damaged produced by insect herbivores in young leaves, fruits, and seeds, as well as the low reproductive index observed in J. nervosa, shows that the inverse leafing phenology of this species is not consistent with the “escape hypothesis” since J. nervosa was considerably attacked during the dry season.

Key words: escape hypothesis, Jacquinia nervosa, inverse phenology, insect herbivory, tropical dry forest.

Total word: 5209

Insect herbivores significantly influence plant fitness across ecological and evolutionary scales (Marquis, 1984; Aide, 1988; Cunningham, 1997; Strauss & Armbruster, 1997; Maron, 1998). In tropical forests, leaf damage by herbivores can reach up to 7-20% of total leaf area (Edwards, 1977; Dirzo, 1984; Coley, 1990; Coley & Barone, 1996) although there is considerable variation in levels of damage (Braker & Chazdon, 1993; Dirzo & Domínguez, 1995). Even under moderate damage, herbivory, combined with other stress factors such as competition or water shortages, imposes important limits on plant survival and reproduction (Brown et al., 1987). For instance, moderate levels of leaf herbivory retarded vegetative growth and flowering in the understory shrub Piper arietanum (Marquis, 1988), and damaged individuals of Gutierrezia sarothrae produced up to five times less seeds per branch relative to control plants (Wisdom et al., 1989). However, under certain circumstances, herbivory may have positive effects. Morrison & Reekie (1995) observed increased photosynthetic rates of undamaged leaves that compensated for the leaf area removed in Oenothera biennis. In addition, leaf herbivory could weed out the less resistant individuals in a population (i.e., Maschinski & Whitham 1989).

The expression of a phenological strategy is the outcome of the interaction among ecological (i.e., water availability, and quality and quantity of light) and evolutionary factors (i.e., impact of herbivores, pathogens, and competitors). In tropical dry forests, water stress and decreased water supply have been considered the primary conditions leading to leaf shedding (Borchert, 1983, 1999; Justiniano & Fredericksen, 2000; Borchert et al., 2002; Brodribb & Holbrook, 2003), although light quality and photoperiod may also serve to synchronize leaf flushing and leaf shedding (Rivera et al., 2002). This study examines how effective the “escape hypothesis” is to explain the phenological behavior of J. nervosa. If this hypothesis has the potential to apply to this case, we would expect low levels of leaf, fruit and seed herbivory relative to reported values for other deciduous species within the same habitat. To answer this question we determined: a) the percentage of herbivory in leaves and seeds in comparison to other dry forest species that...
grow and reproduce during the wet season; b) the effect of the magnitude of leaf flushing synchrony and plant size on reproductive success; and c) the type of herbivores associated to leaves, fruits, and seeds. Studying the influence of herbivores on the timing of leaf flushing will help to understand the role of proximate and ultimate factors on the expression of the inverse leafing phenology in this dry forest understory shrub.

**MATERIALS AND METHODS**

**Study site:** This study was carried-out for 12 months (May-July 2000, and November 2000 to August 2001) in 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" - 11°00'37" N and 85°34'48" - 85°58'51" W) at 290m in elevation.

The upper plateau maintains tropical premontane forests, whereas the coastal lowlands present a large extension of Tropical Dry Forests (Tosi, 1969). Average annual rainfall is 1423mm, being September and October the wettest months. Average annual temperature is 25.7°C, and relative humidity is 81% (Santa Rosa National Park Climatic Records). The dry season extends from late November through April. During the dry season, nearly 70% of the canopy trees are deciduous (Hartshorn, 1983). The “Indio Pelado” trail is dominated by secondary forests composed primarily of seedlings and saplings of canopy species and understory shrubs (i.e., *Cochlospermum vitifolium, Semialium mexicanum, Jacquinia nervosa*), trees of 10-20m in height (i.e., *Spondias mombin, Bursera simaruba*), and a few 20-35m old trees remaining from the original forests (i.e., *Pachira quinata, Manilkara chicle, Hymenaea courbari*).

**Study system:** *Jacquinia nervosa* (Theophrastaceae) is an understory shrub abundant in deciduous and semideciduous forests of the Pacific coast of Central America. It ranges from Southern Jalisco, Mexico, to Northeastern Costa Rica (Ståhl, 1989) where a density of 0.1 to 60 adults per ha has been registered (Janzen, 1970b). Adults vary 1.5-6m in height with a diameter at breast height (DBH) of 1.5-20cm.

After dehydrating, seeds and pulp become sweet. The actual pollinators and seed dispersers are not known. Janzen (1970b) suggests that hummingbirds are possible pollinators, but he did not specify a particular species. Gillespie (1999) suggests that it is mammal-dispersed.
Measurement of leaf herbivory: To measure average leaf area lost to herbivores we randomly chose six branches per plant of the above-mentioned individuals, and marked every damaged leaf in all the branches. Leaf loss was quantified through censuses done every 15 days during the study period. To estimate leaf area we collected 200 leaves from different individuals, and measured their length and width. Using these results we calculated a linear regression to predict leaf area based on leaf length and width measurements non-destructively in the field (r² = 0.97, F=36.5, n=125, p=0.001). In addition, we used a plastic transparency with a millimeter grid to quickly estimate the leaf area removed by insects. Based on this, we established seven categories of damage relative to the percentage of leaf area lost to herbivores: 0 (0%), 1 (1-10%), 2 (11-25%), 3 (26-35%), 4 (36-50%), 5 (51-75%) and 6 (76-99%) following Morrow (1984). In addition, we performed bi-weekly observations of the presence and identity of herbivores on 8 external branches in each of 20 J. nervosa mature plants. Observations were done early in the morning (06:00-08:00am) and at night (17:30-19:30pm). We registered and collected the type of herbivores present on the plant with an aspirator and an entomological net. We identified herbivores to species, genus, or family and classify them according with the most important damage they inflicted on the plant (see Table 1).

Measurement of phenological synchrony and reproductive success: We estimated synchrony in leaf, flower and fruit production following Augspurger (1983): 

\[ X_i = \frac{\sum e_{j=i}}{(n-1)\cdot f_i} \]

where e_i represents the days when individuals i and j produced leaves synchronically, f_i represents leaf life span in individual i, n represents sample size, and X_i represents the magnitude of population synchrony. This index ranges from 0 (total asynchrony) to 1 (100% synchrony in the population). Individual reproductive success (E_i) was determined following Fuchs (2000): 

\[ E_i = \frac{f_1}{f_2} \times 100 \]

where f_1 is the number of mature fruits and f_2 is the total number of flowers per plant. Reproductive success at the population level corresponds to the average value of the E_i across all individuals.

We compared herbivory levels among young and mature leaves using a t-test. A Kruskal-Wallis analysis was used to compare temporal changes in herbivore damage among mature leaves produced in different dates, as well as levels of seed predation by date. For comparing synchrony level between leaves, flowers, and fruits we used one factor ANOVA. A multifactorial ANOVA was used to determined how leaf and flower synchrony,
as well as plant size, influenced the level of reproductive success with the following model:

\[ Y = \mu + x_1 + x_2 + x_3 + e \]

where \( Y \) represents reproductive success, \( x_1 \) is leaf synchrony, \( x_2 \) is flower synchrony, \( x_3 \) is plant size, and \( e \) is the residual error. Data were log-transformed to correct for deviations from the normal distribution. All the analyses were done using SYSTAT 9.0 (SYSTAT, 1999).

**RESULTS**

**Phenology**: Leaf, flower and fruit production took place in the first part of the dry season (end November to February). In most plants, leaf flushing occurred simultaneously with the production of flower buds, although the magnitude and temporal trajectories were different (Fig. 1A). Anthesis began in mid January and reached a peak in the first week of February, when the first fruits were also formed. The main fruiting peak occurred in mid February; there was also a slight increase in fruit numbers by the end of February (Fig. 1B). Only 12% of a total of 440 immature fruits developed into mature fruits by March (see peak in fruit production, Fig. 1C). Fruits had an average diameter of 1.80 cm (SD=0.37, n=500), and an average of 9.11 (SD=5.36, n=500) seeds per fruit.

**Synchrony in leaf, flower, and fruit production**: Average synchrony at the population level in leaf, flower and fruit production showed significant differences (\( F_{1,32}=122.7, p<0.001 \)). Leaf production was the most synchronic phenological trait (0.88, SE=0.012), whereas fruit production (0.18, SE=0.03) showed the lowest synchrony followed by flower production (0.39, SE=0.05).

**Remotion of leaf area by herbivores**: Significant differences were found in herbivory levels among young leaves produced at the start of the growing season (late November-early December 2000) and mature leaves (t-test=44.1, d.f.=28, p=0.04). Young leaves lost an average of 36.77% of their leaf area by herbivores of young leaves were chewing insects, especially the beetle Epicauta sp. (Meloidae). Although mature leaves presented different types of insect herbivores, the most important damage was caused by the scraper beetle Coptocycla rufonotata (Chrysomelidae), which removed the leaf mesophyll on both leaf surfaces leaving the vascular system exposed. In addition, 8.22% of the plants had damage caused by larvae of an unidentified hymenopteran leaf miner (Table 1).
**Reproductive success:** This parameter was low showing an average of 3.4%, although variation among plants was high (SD=7.6, n=36). Fruit production was considerably affected by flower synchrony ($F_{3,14}=2.01$, $p=0.027$), but neither by the synchrony of leaf production ($F_{1,3}=1.08$, $p=0.32$) nor by plant size ($F_{1,2}=0.28$, $p=0.76$).

**DISCUSSION**

**Dry season phenology:** The timing of leaf production in tropical plants is associated with favorable periods for growth and carbon fixation. In weakly seasonal forests leaf, flower and fruit production is concentrated in the driest time of the year to take advantage of peaks in light availability (Janzen, 1967; Gentry, 1974; Wright & Cornejo, 1990; van Shaik et al., 1993). .......... The same phenological pattern has been described for *Faidherbia albida* in the dry forests and savannas of West Africa (Wickens, 1969; Roupsard et al., 1999). In this legume, the phreatophytic character facilitates survival during droughts, as well as leaf, flower and fruit production during this very stressful period. Leaves are dropped after the start of the rains possibly due to light reduction and canopy closure, analogous to *J. nervosa*.

**Levels of herbivory:** During the dry season, high radiation, lack of water, and the scarcity of fresh foliage create adverse conditions for the growth and survival of insect herbivores (Janzen, 1967, 1971; Frith & Frith, 1985; Wolda, 1988, 1990; Smythe, 1990). Consequently, plants that flush new leaves and reproduce during the dry season should have a head start relative to plants that flush leaves during the wet season, since they will experience lower herbivory damage (Aide, 1988, 1992; Mopper & Simberloff, 1995). Janzen (1967, 1971, 1981) shows that plants with this behaviour escape in time from their herbivores.

The low fruit output characteristic of many species could the consequence of lack of efficient pollinators (Newstrom et al., 1994; Johnson & Steiner, 2000; Murcia, 2002), fruit abortion induced by herbivores, self-incompatibility, or a combination of all these factors. If there is self-incompatibility (as it seems to be the case in *J. nervosa*) this could result in a selective abortion of seeds and immature fruits (Leopold & Kriedemann, 1975; Richards, 1997).

In summary, the “escape” hypothesis is not congruent with the phenological pattern of *J. nervosa*. .......... Considering the strong seasonality of tropical dry forests, and the heliophyte character of *J. nervosa*, it is more likely that abiotic factors, such as seasonal changes in light availability, light quality and photoperiod could have worked more effectively as selective factors in the evolution of the inverse leafing phenology.

**ACKNOWLEDGMENTS**

We thank Oscar Rocha for his input during fieldwork and on the manuscript, as well as for his logistical support. María Marta Chavarría and Felipe Chavarría provided valuable help.
Analizamos la hipótesis de “escape de la herbivoria” como explicación para la fenología foliar inversa del arbusto de sotobosque del bosque seco Jacquinia nervosa, el cual produce sus hojas durante la estación seca y se mantiene sin ellas durante la estación lluviosa…

Palabras clave: hipótesis de escape, Jacquinia nervosa, fenología inversa, herbivoria de insectos, bosque tropical seco.

REFERENCES


SYSTAT. 1999. SYSTAT version 9.0 for Windows. Chicago: SPSS.
### TABLE 1
List of insect herbivores found in *J. nervosa*

<table>
<thead>
<tr>
<th>Group</th>
<th>Number of Species</th>
<th>Stage</th>
<th>Diet</th>
<th>Damage category</th>
<th>Damage level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acari</td>
<td>1</td>
<td>a, j</td>
<td>ml</td>
<td>sucker</td>
<td>U.D.</td>
</tr>
<tr>
<td>Afidae</td>
<td>2</td>
<td>a, j</td>
<td>jl</td>
<td>sucker</td>
<td>U.D.</td>
</tr>
<tr>
<td>Coptocycla</td>
<td>2</td>
<td>a</td>
<td>ml</td>
<td>scraper</td>
<td>3</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>1</td>
<td>a</td>
<td>ml</td>
<td>sucker</td>
<td>1</td>
</tr>
<tr>
<td>Cicadellidae</td>
<td>4</td>
<td>a, j</td>
<td>ml</td>
<td>sucker</td>
<td>2</td>
</tr>
<tr>
<td>Curculionidae</td>
<td>2</td>
<td>a, j</td>
<td>fr</td>
<td>driller</td>
<td>2</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>1</td>
<td>j</td>
<td>jl, ml</td>
<td>miner</td>
<td>1</td>
</tr>
<tr>
<td>Grillidae</td>
<td>4</td>
<td>a</td>
<td>jl, fl</td>
<td>chewer</td>
<td>2</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>1</td>
<td>j</td>
<td>fr, s</td>
<td>chewer</td>
<td>3</td>
</tr>
<tr>
<td>Epicauta</td>
<td>1</td>
<td>a</td>
<td>jl</td>
<td>chewer</td>
<td>4</td>
</tr>
<tr>
<td>Miridae</td>
<td>1</td>
<td>a</td>
<td>ml</td>
<td>sucker</td>
<td>1</td>
</tr>
<tr>
<td>Pentatomidae</td>
<td>3</td>
<td>a</td>
<td>ml, fr</td>
<td>sucker</td>
<td>1</td>
</tr>
<tr>
<td>Tortrichidae</td>
<td>1</td>
<td>j</td>
<td>fr, s</td>
<td>chewer</td>
<td>5</td>
</tr>
</tbody>
</table>

1. a=adult, j=juvenile.

2. jl=juvenile leaves, ml=mature leaves, fr=fruits, fl=flowers, s=seeds.

3. U.D.=undetermined, 1=light, 2=moderate, 3=moderate to high, 4=high, 5=very high.

Data obtained from periodic observations made on 36 adult plants from November 2000 through June 2001.
FIGURE LEGENDS

Fig. 1. (A) Average number of leaves and flower buds (±1 SE); (B) number of flowers and immature fruits; and (C) ripe fruits in 36 adult individuals of *J. nervosa*, November through August 2001, Santa Rosa National Park, Costa Rica.

Fig. 2. Average percentage of herbivory damage (±1SE) caused by insect herbivores in mature leaves and fruits of 36 adult individuals of *J. nervosa* from December 2001 to July 2001, Santa Rosa National Park, Costa Rica.

After the tables, figure captions are self-contained and parts are labeled in bold upper case, e.g. “(A)”. This section should always be included at the end of the document, and is followed by the figures.
Graphs must be black and white. Each graph is identified with a capital letter (A, B, C.) when needed. Other general tags are also used when required (dry/wet season). Symbols/patterns are simple and readable. Fonts in Helvetica.

**FIGURE 1.**

**FIGURE 2.**
FIGURE 3.

Photographs must be attached as separate JPG or TIFF (100% quality compression) files. They must have a high resolution quality. There is a simple quality check that you can do: enlarge them in your screen. If they still look well, then they will probably be acceptable. Remember that normal figures will be reduced to a width of 6-12cm: label lettering must be easy to read even after that reduction. Color photos have additional charges (Consult the journal).