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Flowering Phenology and Diversity in Tropical Bignoniaceae

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ABSTRACT

Central American Bignoniaceae show five distinct patterns of flowering phenology. Four of these phenological types characterize different bee-pollinated species. Only the generalized "cornucopia" strategy is employed by temperate Bignoniaceae. In the tropics this strategy is also prevalent and is often associated with a seasonal sequence of flowering by related species. The more specialized phenological strategies employed by many tropical species of Bignoniaceae are viewed as making possible differential and essentially contemporaneous attraction of similar pollinators from the same limited pollinator resource. The high diversity of tropical Bignoniaceae appears to be facilitated by use of a variety of phenological strategies by the different species. It is suggested that such mechanisms may be an important factor in maintaining increased tropical diversity in other groups of plants.

DIFFERENCES in flowering phenology among Central American Bignoniaceae illustrate an overlooked mechanism for maintenance of high species diversity in tropical plant communities. The ecological importance of these differences in phenology is in making possible effective and often contemporaneous sharing by numerous plant species of a limited pollinator resource. Evolutionary diversification of floral morphology in the Bignoniaceae has, of course, given rise to genera employing most of the potential pollen vectors available in a tropical community (Gentry 1972, 1973). But although bats (in *Parmentiera*, *Crescentia*, *Dendrosicus*), hummingbirds (in *Martinella*), hawkmoths (in *Tanaecium*), and butterflies and small bees (in *Tynnanthus* and *Arrabidaea florida*) are the principal pollinators of some Bignoniaceae, the majority of the 76 species occurring naturally in Costa Rica and Panama are pollinated by large and medium-sized bees, especially female euglossines. In some bee-pollinated species additional morphologic specializations further restrict potential pollen vectors as in *Amphilophium* where pseudocleistogamous flowers which never open spontaneously can be entered only by the strongest members of the apifauna (*Megachile*, large anthophorids, presumably xylocopids). However, most bee-pollinated species of Bignoniaceae secure their requisite pollinators by different strategies of flower production rather than morphologic differentiation.

SEASONALITY

One well-known mechanism of phenological diversification is seasonality of flower production. Thus many plants, both tropical and temperate, produce flowers at a characteristic time of year. As illustrated by temperate plants this situation typically involves a period of flowering lasting from two weeks to a

month with all individuals of a species blooming during the same general time span and flowering triggered by exposure to cold or changing day length or both (Evans 1971). In tropical areas (and some dry temperate regions) flowering time of such species may be dependent on seasonal changes in precipitation (Alvim 1960), but the pattern of flower production is basically the same. In both temperate and tropical areas closely related species may flower at different times of year making seasonality not only an effective isolating mechanism but also a means of diversification through time with respect to a pollinator resource. In the Bignoniaceae a good example of this type of differentiation is supplied by *Arrabidaea* with *A. candidans* (L. Rich.) DC. flowering in early and mid dry season, *A. corallina* (Jacq.) Sandw. and *A. mollissima* (HBK.) Bur. & Schum. in mid dry season, *A. patellifera* (Schlect.) Sandw. in early wet season, *A. chica* (H.&B.) Verl. in early to mid wet season, *A. pubescens* (L.) A. Gentry in mid wet season, and *A. florida* DC. in mid to late wet season in Panama and Costa Rica. Each of the six more or less sympatric species of *Arrabidaea* occurring in the central part of the Canal Zone has its flowering peak in a different month (fig. 1).

PHENOLOGICAL TYPES

Differences in types of phenology on the other hand make possible contemporaneous use of the same limited pollinator resource. The Bignoniaceae of Panama and Costa Rica can be divided into five groups on the basis of flowering phenology (Gentry 1972, 1973). The Type 1 (fig. 2A) pattern is associated with bat pollination and will not be considered here. The other four patterns are all associated, at least in part, with bee pollination. The Type 3 (fig. 2 C, D) or "cornucopia" pattern appears the most widespread

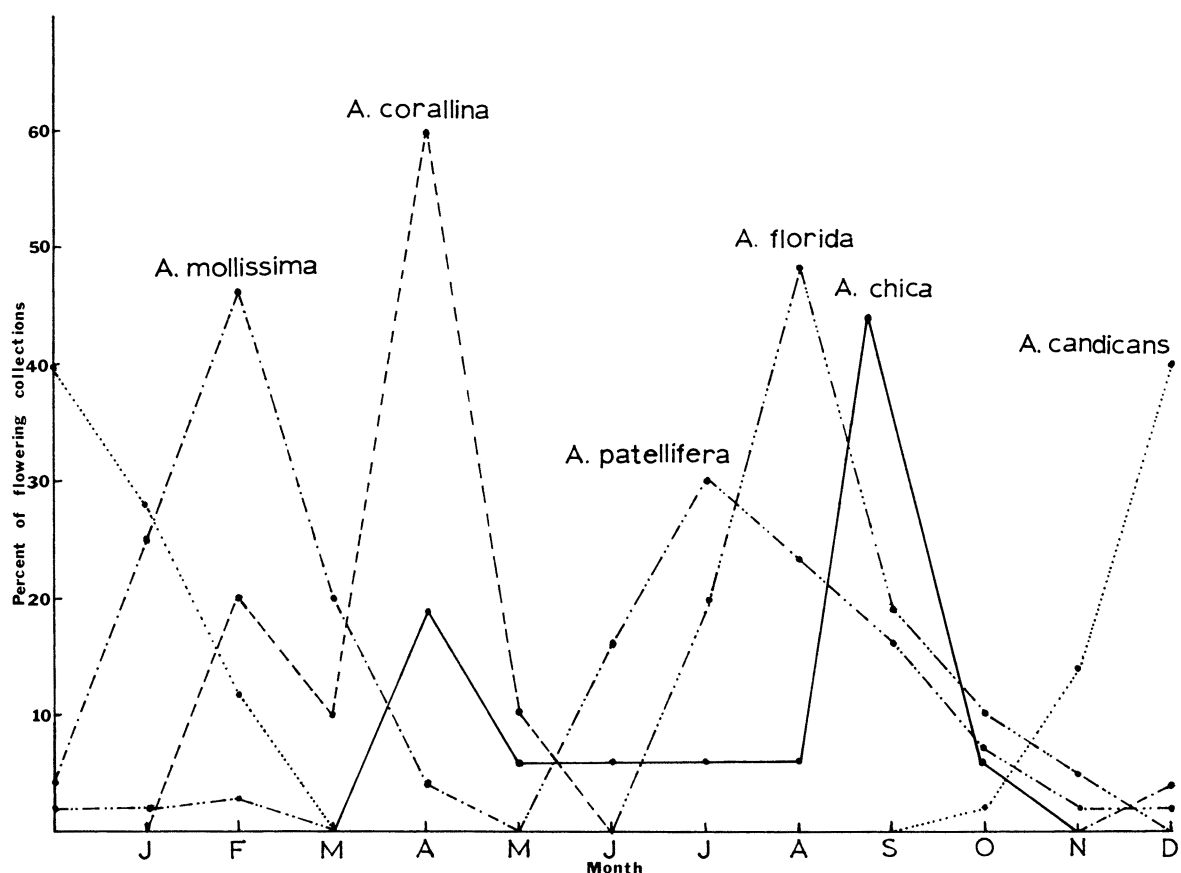


FIGURE 1. Seasonality of flowering in common species of *Arrabidaea*. Cumulative data for herbarium specimens from Costa Rica and Panama. (For a given year or locality the peaks are much sharper.)

and most generalized. Plants with this pattern produce a large number of flowers over a time span of several weeks and attract a rather diverse spectrum of potential pollinators including such bees as *Eulaema polychroma*, *Eulaema* spp., *Euglossa variabilis*, *E. viridissima*, *E. tridentata*, *E. bursigera*, *E. townsendi*, *Euglossa* spp., *Exarete* sp., *Apis mellifera*, and several anthophorids as well as nectar-robbing xylocopids and pollen-robbing halictids and trigonids. This is the pattern shown by temperate Bignoniaceae (e.g., *Catalpa* and *Campsis* (fig. 3)) and by the hawkmoth-, bee/butterfly-, and hummingbird-pollinated species of Central American Bignoniaceae, as well as by many bee-pollinated species. It is the only phenological type associated with seasonal differentiation of related species of Bignoniaceae (cf. *Arrabidaea* above). The great majority of temperate plant species appear to belong to this phenological type. The other three pheno-

logical patterns displayed by the Bignoniaceae are peculiarly tropical. I have designated as Type 2 (fig. 2B) or "steady state" the pattern whereby a plant produces a few flowers a day over an extended period of time (usually a month or more). These species depend for pollination on the fixed foraging patterns of many tropical bees, designated "trapliners" by Janzen (1971), which, having learned the location of a particular flowering plant, visit it each day as part of a standard sequence. Although some of the same bee species which visit "steady state" plants also include "cornucopia" plants on their daily foraging routes, the lesser expenditure of reproductive energy by the former makes possible longer individual flowering periods and, for the species as a whole (individual plants lacking seasonality), flowering throughout the year. Once incorporated on a trapline such a plant enjoys a higher frequency of pollinator visits per unit of energy expended and

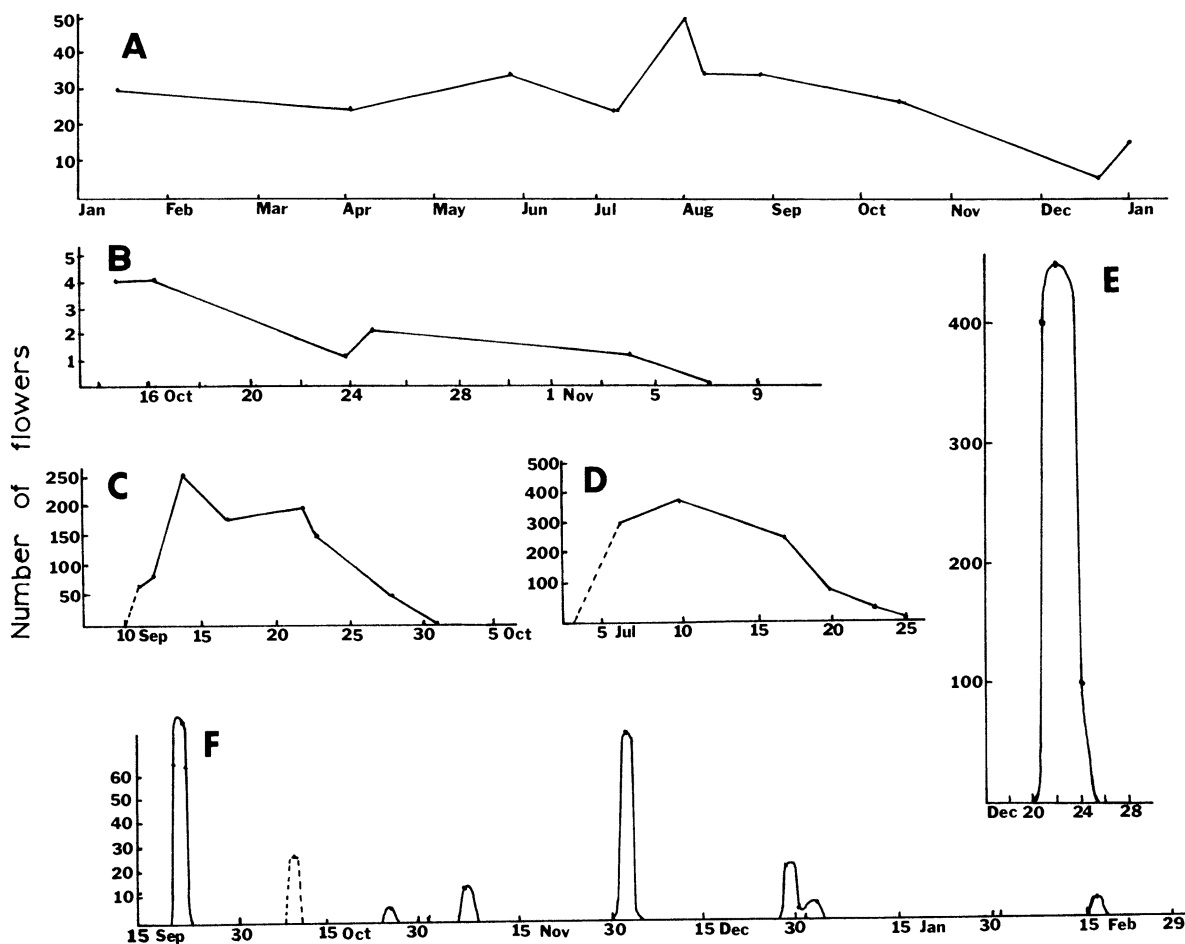


FIGURE 2. Representative patterns of flowering phenology. All from plants observed in the Canal Zone. Figure 2A. Type 1 (bat flower), *Crescentia cujete* L. Figure 2B. Type 2 ("steady state"), *Stizophyllum riparium* (HBK.) Sandw. Figure 2C. Type 3 ("cornucopia"), *Arrabidaea florida* DC. Figure 2D. Type 3 ("cornucopia"), *Arrabidaea patellifera* (Schlect.) Sandw. Figure 2E. Type 4 ("big bang"), *Tabebuia ochracea* ssp. *neochrysantha* (A. Gentry) A. Gentry. Figure 2F. Type 5 ("multiple bang"), *Phryganocydia corymbosa* (Vent.) Bur. ex K. Schum.

a greater likelihood of cross pollination. A second phenological specialization of bee-pollinated species of Bignoniaceae, also elucidated by Janzen (1967), is the kind of mass flowering which I have designated as the Type 4 (fig. 2E) or "big bang" strategy. This strategy depends, in contrast to Type 2 or "steady state," on opportunistic behavior of potential pollinators which may abandon their regular foraging patterns to take advantage of a conspicuous and munificent, if fleeting, source of nectar. In the Bignoniaceae, "big bang" flowering occurs only in the dry season and is associated with an amazingly precise synchronization of flowering periods of different individual plants so that the flowering season

of a species may be only a few days each year (see Gentry 1972 and 1973 for documentation and further discussion).

The third specialization in phenology of bee-pollinated species, the Type 5 (fig. 2F) or "multiple bang" strategy, has not previously been reported. Again it is peculiarly a tropical phenomenon, and makes use of many of the same pollinators, mostly female euglossines, as the previous types. "Multiple bang" flowerers, all vines, have numerous short flowering periods of two or three days scattered throughout the year. Synchronization of different individuals is very pronounced as in the "big bang" species. Flowers of most species exhibiting this type of

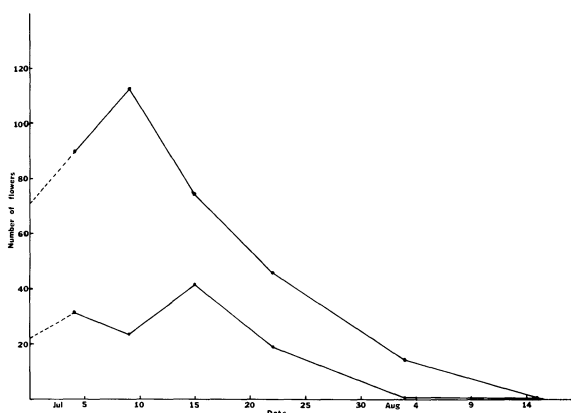


FIGURE 3. Phenology of *Campsis radicans* (L.) Seem., a temperate species with "cornucopia" flowering. Two representative plants growing at Babler State Park, Missouri.

phenology lack a nectariferous disk and apparently depend on mimicry of nectar-producing, mass flowering species, including other Bignoniaceae, to attract pollinators. These plants are thus dependent for pollination on exploratory visits by nectar-seeking bees investigating apparent new nectar sources. Repeated but separated short bursts of flowering allow maximum exposure to naive prospective pollinators of new flowers to be investigated. Conspicuous visual and olfactory stimuli aid in attracting first-time visitors. The plant saves the energy that would have been expended on nectar production and is guaranteed a very high percentage of cross pollination, should pollination be effected at all, since bees invariably enter only one or two flowers on a visit to such an unrewarding plant.

As might be expected, relatively few visitors are attracted by these plants. I have observed only a single visit by a potential pollinator (*Euplusia*?) to *Cydista aequinoctialis* (L.) Miers, none to *C. diversifolia* (HBK.) Miers or *C. heterophylla* Siebert, and two to *Phryganocydia corymbosa* (Vent.) Bur. ex K. Shum. (both by *Euglossa* sp.) in many hours of observation of each. Small pollen-collecting halictids and trigonids are sometimes visitors but do not make contact with the receptive surface of the stigma and apparently do not effect pollination. Paul Opler (personal communication) has observed a single visit to a flower of *Cydista diversifolia* by a *Euglossa* which had been foraging on an adjacent flowering vine of nectar-producing but morphologically similar *Arrabidaea patellifera*. In approximately eight hours of observation of the same two vines I saw hundreds of visitors to "cornucopia" *A. patellifera* but not a single one to the far more conspicuous "multiple bang" *C. diversifolia*. Hausmann

(1968, unpublished OTS field study report) saw only cantharid beetles enter the flowers of *C. diversifolia* in 10 hours of observation and concluded, presumably in frustration, that these were the probable pollen vector although they were found to be carrying no pollen. This conclusion is most unlikely to be correct in view of floral morphology and other knowledge of Bignoniaceae pollination. Ganders (personal communication) observed *C. diversifolia* in the same area for approximately 15 hours without noting a single pollinator, though likewise remarking constant pollinator activity at flowers of *A. patellifera*.

DISCUSSION

Competition for pollinators is apparently the selective pressure which has resulted in the diverse phenological patterns of the bee-pollinated tropical Bignoniaceae. Significant competition for pollinators and its apparent effect on flowering times has been documented in a temperate community of flowering plants (Mosquin 1971). Although competition for pollinators between tropical plants has not been so conclusively proven, it seems evident that this phenomenon also exists in tropical communities (Frankie, Baker, and Opler 1973). Circumstantial support of this idea comes from the observation that diversity of the apifauna in most tropical regions is surprisingly low in comparison with rich temperate areas and with respect to patterns of diversity in other groups of organisms (Michener 1954, A. Moldenke, personal communication).

Female euglossine bees constitute the most important group of pollinators for the majority of species with phenology of Types 2, 3, 4, and 5. While temporal separation of flowering periods through seasonality is effective for "cornucopia" species, it is possible for species with different flowering types to bloom at the same time and still differentially attract the same group of pollinators. Thus a female *Euglossa* might normally follow a daily trapline containing plants of a few "steady state" species of Bignoniaceae as well as plants of other families. She might also incorporate some "cornucopia" plants on her regular trapline for the few weeks they are in bloom. Upon occasion she would investigate potential new nectar sources including Type 5 "multiple bang" species of Bignoniaceae and, especially during the moisture stress of the dry season, might opportunistically abandon her regular route for a few days to take advantage of an abundant Type 4 "big bang" nectar source. Thus several different flowering strategies can be effective at any given time as a result of the different behavioral patterns in even a very limited group of pollinators. That such differential

use of a community's pollinator resource would minimize direct competition between species employing different phenological strategies is obvious. The reasons for the failure of the more specialized strategies to develop in temperate regions are less evident. The limited warm season available for flowering each year, compressing the blooming periods of all species in a temperate plant community, might result in such a surfeit of available flowers that an occasional burst of flowering (as in Type 4 or 5) would be lost in the profusion of alternate nectar sources. Alternatively the much-vaunted unpredictability of temperate climates might limit the effectiveness of strategies dependent on ultraprecise synchronization between individual plants. Type 2 "steady state" patterns likewise would not be favored in competition with the many species producing more conspicuous and abundant flowers during the limited temperate blooming season. A difference in

longevity and foraging behavior of temperate bee species would also make a "steady state" strategy less effective.

In any event different phenological strategies clearly play an important role in making possible effective competition by many related species of tropical Bignoniaceae for the services of the same pollinators. The role of differences in flowering phenology in other groups should be further investigated to evaluate the overall importance of such mechanisms in maintaining high diversity in tropical plants.

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Errata: Volume 5, Number 3

Clewell's Table 5 (page 181) All numbers are percentages except 'Total number of taxa.'

Index. Stone Benjamin C. *Citrus halimii*: New Species. Volume 5, not Volume 3.
Tryon, Rolla. Fern floras of Oceanic Islands. Volume 2, not Volume 3.