

Synchronous Flowering and Monocarpy Suggest Plietesimal Life History for Neotropical *Stenostephanus chiapensis* (Acanthaceae)

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A plietesimal life history has long been noted for certain species among unrelated families of flowering plants including Poaceae, Arecaceae, Scrophulariaceae, Fabaceae, Apocynaceae, and Acanthaceae (e.g., Fuller 1925; van Steenis 1942; Janzen 1976; Young and Augspurger 1991). Bremekamp (1944:20) used the term plietesimal in reference to perennial monocarpic plants “of the kind most often met with in the Strobilantheae” (a subtribe of Acanthaceae containing *Strobilanthes* and allied genera) that usually grow gregariously, flower simultaneously following an interval of several years, set seed, and die. A similar life history is especially well known and documented among certain bamboos (see Janzen 1976). In plietesials, the seed crop typically germinates simultaneously shortly following the mass death of the parental plants and initiates a new cycle with the same periodicity (e.g., van Steenis 1978). Other commonly used expressions that apply to part or all of the plietesimal life history include: gregarious flowering, mast seeding, and supra-annual synchronized semelparity (semelparity = monocarpy).

Species in at least five genera of Old World Acanthaceae have been reported as plietesials: *Acanthopale* C.B. Clarke (Bergsdorf 2006), *Aechmanthera* Nees (Biswas 1975; Garbyal 2000), *Stenosiphonium* Nees (Carine 1997; Carine and Scotland 2000), *Strobilanthes* Blume (e.g., van Steenis 1942, 1985; Wood 1994), *Mimulopsis* Schweinf. (Dale and Greenway 1961; Tweedie 1965), and *Isoglossa* Oerst. (Tweedie 1965; van Steenis 1978). *Strobilanthes* is the largest genus among these with estimates of 300–500 species. Although more species of *Strobilanthes* have been reported as plietesials than in any other genus of Acanthaceae, the total number of plietesimal species of *Strobilanthes* remains unknown. Bremekamp (1944) greatly overestimated their number (cf. Wood 1994). Several species of the genus are reasonably well documented as plietesimal (i.e., *S. accrescens* J.R.I. Wood, *S. asymmetrica* J.R.I. Wood & J.R. Benn., *S. callosa* Nees, *S. cernua* Blume, *S. dian-dra* (Nees) Alston, *S. divaricata* (Nees) T. Anders., *S. echinata* Nees, *S. extensa* (Nees) Nees, *S. helicta* T. Anders., *S. ixiocephala* Benth., *S. kunthiana* (Nees) T. Anders., *S. maculata* (Wall.) Nees, *S. pulcherrima* T. Anders., *S. sexennis* Nees, *S. thomsonii* T. Anders., and *S. wallichii* Nees (Janzen 1976; Wood 1994, 1998; Bennett and Hansen 2000; Wood et al. 2003), and anecdotal or indirect evidence suggests that numerous others are likely plietesimal as well (e.g., Trimen 1895; van Steenis 1942; Scotland 1998; Garbyal 2000; Carine et al. 2000).

Bremekamp (1944) noted considerable variation in life history for *Strobilanthes*. Wood (1994) provided an insightful summary of mass-flowering and the various forms of this phenomenon known in the genus. Most known plietesimal *Strobilanthes* take between 10 and 15 years (usually 12; although reports of 5 to 9 year cycles also have been made, e.g., van Steenis 1972) to flower gregariously, set seed, and die. The flowering periodicity in all individuals is rarely 100%, with the result that flowering of rare individuals in non-mass-flowering years is not uncommon. In some species, mass flowering occurs over a wide area on a species-specific cycle; in other species, pop-

ulations in different regions follow their own cycles. Some species flower gregariously in certain years but do not die following the mass flowering, and are therefore not plietesial. At least one species exhibits different flowering patterns in different portions of its range. The perennial *Strobilanthes wallichii* flowers annually in the eastern Himalayan portion of its range and plietesially in the western Himalayan portion (Wood 1994). Literature reports of life history for some taxa are ambiguous. For example, Robinson (1935) noted a 12 year plietesial cycle for *S. consanguineus* C.B. Clarke whereas Bowden (1950) indicated that this species flowers every year. Such discrepancies likely result either from misidentifications of or life history variations within taxa.

Like *Strobilanthes*, both *Aechmanthera* and *Stenosiphonium* pertain to tribe Ruellieae subtribe Strobilanthinae; indeed, representatives of both of the latter genera are nested among species of *Strobilanthes* s.l. in phylogenetic analyses (Moylan et al. 2004), which suggests that they may not be distinct from it. Bremekamp (1944) accepted two (although he suggested that there were probably three) species of *Aechmanthera*. Biswas (1975) indicated that *A. gossypina* (Nees) Nees flowers gregariously every 12 years and sporadically nearly every year. Garbyal (2000) noted that this species occurs in India above 1000 m, flowers at 12 year intervals, and dies following fruiting. Garbyal (2000) also indicated that the subsequent generation does not appear above ground for the next two years, but is evident above ground from the third year onwards. As currently treated, *Stenosiphonium* consists of three species restricted to southern India and Sri Lanka (Carine and Scotland 2000). At least one species, *S. wightii* Bremek., is plietesial with a 13 year cycle. There is considerable evidence that the other two species, *S. cordifolium* (Vahl) Alston and *S. setosum* T. Anders., are likely plietesial as well (Bowden 1950; Carine and Scotland 2000).

Mimulopsis consists of about 20 species from tropical Africa and Madagascar. Although the genus belongs to Ruellieae, it has yet to be placed in a subtribe by phylogenetic analyses, but it would not appear to pertain to Strobilanthinae as that subtribe is delimited (e.g., Moylan et al. 2004). Tweedie (1965) noted a 9 year interval of mass flowering at high elevations (over 2000 m) in eastern Africa for *M. solmsii* Schweinf. followed by death of the plants and subsequent germination and establishment of seeds. Very rare occurrences of flowering of individuals between mass flowerings, as commonly noted for *Strobilanthes*, were also recorded. Tweedie (1965) also indicated probable similar life history traits for two other east African species (*M. cf. glandulosa* (Lindau) Bullock and *M. arborescens* C.B. Clarke). Dale and Greenway (1961) indicated that *M. glandulosa* flowers on a three to four year cycle.

Like *Mimulopsis*, *Acanthopale* remains unplaced in Ruellieae, but does not pertain to Strobilanthinae (Moylan et al. 2004). The genus consists of at least six species from tropical Africa. Bergsdorf (2006) noted that *A. pubescens* (Lindau ex Engl.) C.B. Clarke, a species of moist montane forests at 1655 to 2790 meters elevation, has a mass flowering one or more times per decade followed by synchronous die-off of the entire population. The mass flowering lasts for about four weeks and capsules are apparent about four to six weeks following fertilization.

Isoglossa pertains to tribe Justiceae subtribe Isoglossinae, and consists of about 50 species occurring in Africa, Arabia, and Madagascar (Kiel et al. 2006). Van Steenis (1978) noted that *I. ciliata* (Nees) Lindau was purported to flower every 10 years and that *I. woodii* was purported to flower with intervals of about seven years. Tweedie (1965) noted probable gregarious flowering for other species of the genus that occur at high elevations (over 2000 m) in eastern Africa.

None of these genera from the Old World occur naturally in the New World, and a plietesial life history has not been reported for any native species of Acanthaceae from the Western Hemisphere. Wood (1988) noted that species of Colombian *Stenostephanus* Nees (as *Habracanthus* Nees) flower only at irregular intervals and for a short time. In correspondence and discussions Wood suggested to me that some species of *Stenostephanus* might be plietesial. His hypothesis was

based on the following observations to which I have appended other pertinent information and references:

1. *Stenostephanus* (at least in Colombia) is difficult to find, and plants that are located tend to be sterile or only sparsely flowering. Wood (*in litt.*) noted that for several Colombian species he observed, he “could find one or two rather miserable flowering shoots in large sterile colonies.” Similar observations have been made for plietesial species of *Strobilanthes* and *Mimulopsis* (see above) for which in non-flowering years a thorough search may locate the odd plant in flower.

2. Both *Stenostephanus* and *Strobilanthes* occupy similar habitats. *Stenostephanus* usually occurs at relatively high elevations (above 1,000 m) in regions of cloud forest, where plants tend to occur along streams, near springs, or in wet ground (Wood 1988; Daniel 1999). Many species of *Strobilanthes* occur in similar regions of southern Asia (e.g., van Steenis 1942; Wood 1994).

3. Plietesial flowering is known in African *Isoglossa*. *Isoglossa* has pollen similar to that of *Stenostephanus* (*cf.* Hansen 1985; Daniel 1999) and often occupies habitats in Africa (*cf.* Clarke 1900; Tweedie 1965) similar to those of *Stenostephanus* in America and *Strobilanthes* in Asia. Recent studies of generic relationships based on molecular sequence data (McDade et al. 2000; Kiel et al. 2006) have confirmed a close phylogenetic relationship between *Isoglossa* and *Stenostephanus*; both belong to the Isoglossinae clade of Justiceae.

I was intrigued by Wood’s hypothesis and by the fact that plants of a Mexican *Stenostephanus* growing in San Francisco (see below) had flourished vegetatively, but had not flowered for several years following their germination. Over the past 28 years I have grown more than 150 species of Acanthaceae representing all of the major lineages of the family. All of them (even large, woody genera such as *Louteridium* S. Wats.) have flowered within a year of germination. Failure of healthy plants of *Stenostephanus chiapensis* T.F. Daniel to flower seemed uncharacteristic of acanthaceous plants. As a result, I indicated (Daniel 1999) that the possibility of gregarious flowering should be considered for this species.

In 1991, Dennis Breedlove collected herbarium specimens (*Breedlove & Burns 72688 at CAS*) and seeds of *S. chiapensis* in southeastern Chiapas, Mexico. The seeds were subsequently germinated in a greenhouse in San Francisco, and plants were transferred to out-of-doors locations in the San Francisco Botanical Garden (then Strybing Arboretum) and to my home garden in another part of the city. By 1993, all plants had reached 1 m in height and were thriving in the cloud forest-like climate of San Francisco. Plants at both locations received supplemental watering during the region’s dry season (May–November). By 1997, the plant in my garden (*Daniel s.n.*, CAS 975153) had grown to 2.5 meters in height while three plants at the Botanical Garden had grown to between 1 and 2.5 meters. None of the individuals had flowered. When I relocated to a different part of San Francisco in 1999, I took a stem cutting from the plant in my garden and rooted it in the very sandy soil of the garden at my new residence. Over the next few years, this plant became established, but did not grow particularly well; it attained a height of only four decimeters. It was likely less healthy due to less favorable growing conditions (e.g., sandy soil, gopher activity, crowding). In March of 2003, all three plants (grown in two separate beds) at the San Francisco Botanical Garden came into flower for the first time (*Daniel s.n.*, CAS 1032071), as did the small plant grown from a cutting in my garden. All plants flowered continuously from March 2003 through May 2004. Abundant flowering (with 25 or more flowers present on the large plants in the San Francisco Botanical Garden) occurred in April–June 2003, followed by a waning of flowering in July–November (by late October, only a few sporadic flowers were produced). A major resurgence of flowering began in December 2003 with the onset of San Francisco’s winter rains. In June 2004, leaves dropped from all plants, stems began to turn brown and wither, and few new flowers were produced on plants at the San Francisco Botanical Garden. The small plant in my garden died completely in June 2004.

By the end of July, all three plants at the Botanical Garden were also dead (Fig. 1). There was neither regrowth from the base of these plants nor evidence of seedlings in the immediate vicinity during the next 18 months.

It is significant that a rooted cutting taken from a large plant and planted at a different site flowered at the same time as other individuals from the same seed source. Indeed, Janzen (1976) noted that transplants of *Strobilanthes* flowered in time with the populations from which they had been removed.

Observations of fresh flowers allows for a more complete characterization of floral coloration in *S. chiapensis* than previously available based on herbarium specimens (e.g., Daniel 1999). The corolla (Fig. 1) is bi-colored with the ventral portion of the tube and throat yellow; the lateral and dorsal portions of the tube red; the lateral portions of the throat alternating red, yellow, and red; the dorsal portion of the throat either prominently yellow or mostly red with yellow toward the upper lip; and the limb (i.e., upper lip) yellow outlined with red around the margin. The staminal filaments, anthers, and style are also red.

During the period that plants had flowers, some capsules were observed to be present on all plants. These had resulted from either autogamy or pollination by local floral visitors (none of which were observed; hummingbirds and bees were common in both gardens). Several flowers were artificially self-pollinated, which resulted in capsule formation. Thus, like most other Acanthaceae tested (Daniel 1993 and unpublished data) *S. chiapensis* is self-compatible.

The following conclusions can be made based on these observations of cultivated plants (grown from seed from a single population) of *S. chiapensis*: 1) plants have delayed (12 years herein) flowering, 2) flowering is synchronous, 3) the flowering period persists for 14–16 months, 4) plants are self-compatible (although fertility of resulting seeds was not determined), and 5) plants are monocarpic. These observations appear to provide some evidence for Wood's hypothesis that some species of *Stenostephanus* are likely plietesial. Because only a single interval of 12 years was observed (from germination to flowering), additional studies are needed to further establish the existence and interval of plietesial flowering in this and other species of *Stenostephanus*.

During my studies of Mexican and Central American *Stenostephanus* in both the field and herbarium, it became apparent that some species were collected often (e.g., *S. haematodes* (Schltdl.) T.F. Daniel, *S. silvaticus* (Nees) T.F. Daniel) whereas others were not (e.g., *S. chiapensis*, *S. tacanensis* (Acosta & R. Fernández) T.F. Daniel). Based on specimens from Costa Rica in several herbaria (CAS, F, GH, MO, NY, US), *S. silvaticus* has been collected with flowers and/or fruits in 1895, 1898–99, 1922–24, 1926, 1931, 1933, 1936–38, 1940, 1947, 1960, 1969, 1970–72, 1974–78, 1982–90, and 1992. Such a pattern suggests annual flowering of the species in Costa Rica. The six known collections of *Stenostephanus chiapensis* have been collected in Chiapas during 1896, 1972–73, and 1990–91. Because the flowering period persists for up to 16 months in cultivated plants of *S. chiapensis*, the 1972–73 and 1990–91 seasons can be assumed to represent single flowering episodes with an interval of about 17 years. Such variation (12 vs. 17 year intervals) suggests that if plants of *S. chiapensis* are indeed plietesial, the intervals between mass-flowering might be irregular. Alternatively, some of the potential pitfalls (e.g., regional variations in flowering cycles and collection of rare, asynchronously flowering individuals) in using herbarium specimens to determine plietesial flowering and/or the duration of cycles were discussed by Bennett & Hansen (2000) and Carine and Scotland (2000).

The distribution of *Stenostephanus* is restricted to the New World. Although it is related to the Old World genus *Isoglossa*, which as noted above contains plietesial taxa, it appears more closely related to another paleotropical genus, *Brachystephanus* (Kiel et al. 2006). As in *Stenostephanus*, most species of *Brachystephanus* Nees (including *Oreacanthus* Benth.) are montane endemics that



FIGURE 1. (a) Flower of *Stenostephanus chiapensis* (corolla = 21 mm from base to tip of upper lip). (b) Dead plant of *S. chiapensis* (foreground) in August 2004 at the San Francisco Botanical Garden (plant height = 1.8 m).

are known from few collections (*vide* D. Champluvier, unpublished monograph on *Brachystephanus*). Plietesimal life histories should be sought among species of this and other genera of Isoglossinae. Irrespective of its presence elsewhere among Isoglossinae, a plietesimal life history occurs in various lineages of Acanthaceae, and apparently in both Old World and New World rep-

representatives of the family. Thus, this life history pattern would appear to have evolved multiple times among Acanthaceae.

Although there is considerable literature on plietesial taxa (see Janzen 1976), various aspects (e.g., adaptive significance, genetic and physiological bases) of this life history pattern are not well understood. In his review and discussion focusing on plietesial bamboos (but also including information on *Strobilanthes*), Janzen (1976) provided insightful hypotheses on the possible evolutionary origins of such plants. He attributed the ecological circumstance that would favor such a life history to satiation of seed predators, resulting in excess seeds during the primary portion of seedling distribution that would grow into the next generation of plants. Young and Augspurger (1991) briefly summarized some of the poorly understood genetic and physiological bases of semelparous plants, as well as theoretical models addressing the differential evolution of semelparous (monocarpic) vs. iteroparous (polycarpic) plants. Janzen (1976) concluded that timing of reproduction in plietesials is set by an internal physiological calendar rather than by external weather cues. As noted above, the perennial species *Strobilanthes wallichii* flowers annually in the eastern Himalayan portion of its range and plietesially in the western Himalayan portion. Wood (1994) speculated that such variation in life history of a species and the occasional flowering of some individuals of plietesial species in non-mass-flowering years suggest that life history in *Strobilanthes* results from some complex interrelationship between genetics and environment.

Irrespective of the factors that result in the origins or maintenance of plietesial taxa, this life history pattern is of considerable significance taxonomically and ecologically. Wood (1994) noted that plants of several plietesial species that flowered asynchronously were less vigorous (e.g., with smaller vegetative and floral organs), as if under some environmental stress. Character variation in such circumstances is without taxonomic basis and needs to be recognized as such. Additionally, because plietesial taxa may be rarely collected through time, this life history pattern may cause inaccurate assessments of the conservation status of those taxa (e.g., *Stenosiphonium wightii*, see Carine and Scotland 2000:112; *Strobilanthes accrescens*, see Wood 1994:196).

Some of the topics that remain to be adequately studied among plietesial Acanthaceae include: 1) identification of plietesial taxa, 2) determination of the length(s) of their life cycles, 3) the geographic extent over which a taxon (or populations of a taxon) exhibits plietesial characteristics, 4) the genetic and/or environmental cues that result in plietesial characteristics, and 5) the ecological implications of this life history pattern (especially with respect to floral visitors, frugivores, herbivores, animals that otherwise use or exploit the plants, and other plants in the communities in which these species occur; cf. Bremekamp 1944:21).

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