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Asynchrony in a Wild Population of *Ficus sycomorus* L.

A phenological study of the riparian forest in the Kuiseb River Canyon, South West Africa/Namibia, has shown that individuals of the *Ficus sycomorus* L. population were asynchronous with respect to syconia (fig) production. Within the fig population, any stage in the reproductive cycle could be found throughout the year. In contrast, the other tree species present (*Acacia albida* Del., *A. erioloba* Meyer, and *Euclea pseudebenus* E. Meyer ex A. DC). flowered and fruited synchronously, exhibiting discrete seasonal cycles.[1] Galil and Eisikowitch[2-4] have explored many of the co-evolutionary aspects of *F. sycomorus*, its pollinator *Ceratosolen arabicus* Mayr, and several inquilines associated with the syconia, but have not specifically examined asynchrony in natural populations of this species. Hill,[5] Morrison,[6] and Newton and Lomo[7] have studied sexual phenology in other *Ficus* species and have recorded or implied some degree of asynchrony. Other authors[8,9] allude to this phenomenon in general discussions of the co-evolution of *Ficus* and its pollinators but provide no supporting evidence. Janzen[10] discussed this topic in some detail in a recent review. Here we present data which verifies the asynchronous flowering pattern in *F. sycomorus*, and give details of some of the interactions between the fig and fig wasp in a wild population.

The Kuiseb is a seasonally dry river with its origins in the central highlands of SWA/Namibia. Where the river crosses the Namib Desert it has incised a deep, narrow canyon 115 km long.[11] From the canyon to the Namib Research Institute at Gobabeb (23°34′S, 15°03′E) the river has a wide, alluvial floodplain that supports a riparian forest dominated by *Acacia erioloba* and *A. albida*.[12] Higher up the river, especially in the confines of the narrow canyon, are found isolated and irregularly spaced trees of *F. sycomorus* and *F. cordata* Thunb. (Table 1). The Kuiseb flows most years after seasonal rains in the highlands (mean annual precipitation 367 mm, in contrast to 17 mm at Gobabeb[13]). After floods, the river bed dries for most of its length, but subterranean water is available about 4 m below the surface.

From September 1976 to December 1978, *F. sycomorus* (33 of 40 trees) and *F. cordata* (14 of 20 trees) were censused monthly along a 60 km stretch of the river from Gobabeb eastwards (Fig. 1, Table 1). With few exceptions, these numbers represent the entire population of both species for this area. The phenophase (green fruit, ripe

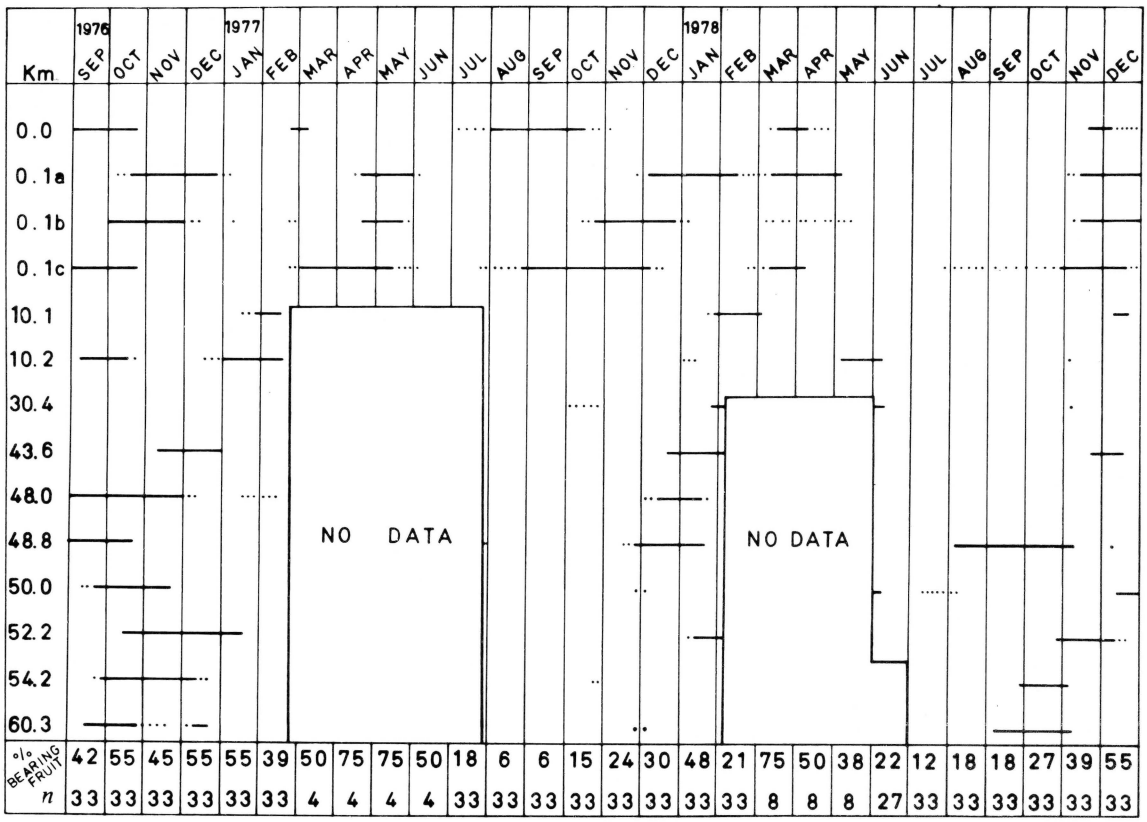

Fig. 1. Phenology of ripe syconium production in 14 individuals of *Ficus sycomorus* from September 1976 to December 1978. Trees were selected from a total sample of 33 to illustrate maximum variation (asynchrony) in seasonal phenology. Distance from Gobabeb is noted in the left-hand column for each individual. Tree 0.1 *a-c* represents an immense, three-trunked *Ficus*. Because of consistent phenological differences among trunks, these are treated as separate trees. The percentage of trees bearing fruit in each monthly sample (*n*) is given at the bottom of the figure. Dotted lines indicate the presence of a few (less than 10% of the potential crop) unripe figs, while solid lines represent the full crop.

fruit, fallen fruit, new leaf, leaf fall) of each marked tree in the census tract was recorded. Seasonal floods and large water-pools in the narrow canyon prevented a month by month analysis (see Fig. 1). Complete data were thus collected only at Gobabeb, for four *F. sycomorus*.

Unripe syconia were found every month, and ripe syconia were found every month except September 1978 (a result of predation attributed to Chacma baboons[14]). The Kuiseb River population of *F. sycomorus* is thus asynchronous, with syconia available for pollination all year long. Even though all but eight trees in both *Ficus* populations (total number of trees = 142) were defoliated by lepidopterous larvae, *Naroma varipes* (Walker), in the winter of 1977, this did not subsequently affect the asynchronous pattern of leaf drop or syconia production in either species. Some seasonality is indicated only by reduced production in austral winter months (July – September). Although not discussed here, pronounced asynchrony was also noted in the *F. cordata* population.

Table 1. Distribution and number of *Ficus sycomorus* and *F. cordata* along 120 km of the Kuiseb River.

Distance upriver from Gobabeb (km)	*F. sycomorus*	*F. cordata*
0 – 10	8	0
10 – 20	3	0
20 – 30	0	0
30 – 40	4	0
40 – 50	17	8
50 – 60	8	12
60 – 70	2	33
70 – 80	3	11
80 – 90	1	4
90 – 100	5	10
100 – 110	1	6
110 – 120	5	1
Total	57	85

From Gobabeb to 65 km upriver (measured on a Land-Rover odometer) the mean distance between each *E. sycomorus* tree was 1.9 ± 3.8 km (range = 0.1 – 19.8 km, n = 39); and for *F. cordata*, the mean distance was 1.5 ± 1.4 km (range = 0.1 – 4.9 km, n = 32). Only trees of 2 m high or taller were counted.

For seven weeks (14 November – 30 December 1978) syconia from a large, three-trunked tree (0.1 *a-c* in Fig. 1) were examined for wasp activity. The pollinator, *Ceratosolen arabicus*, and two major inquilines, *Sycophaga sycomori* (L.) and *Apocrypta longitarsus* (Mayr), were censused every three days. The presence of the diurnal inquilines on or near the figs was recorded at hourly intervals throughout the day (Table 2). Three fluorescent lights at Gobabeb, 500 m from the tree, were checked nightly for the presence of the pollinator.

Ceratosolen arabicus and *S. sycomori* oviposit inside the syconia after crawling through the bracts. To monitor oviposition by these species, 20 syconia were dissected at four-day intervals. *Apocrypta longitarsus* oviposits through the wall of the syconium from the outside, and oviposition could thus be readily monitored during census-taking. Species composition was determined from a sample reared from 300 ripening figs. To confirm pollinator status, 30 ripe figs were opened and the number of seeds compared with the presence of pollinators and inquilines.

Five species of wasps were reared from *F. sycomorus* at Gobabeb.[15] *S. sycomori* was found in 73% of the fig sample (n = 300), followed by *A. longitarsus* (57%), *C. arabicus* (43%), *Parakoebelea gigas* (Mayr), (27%) and *Eukoebelea sycomori* Wiebes (3%). *Ceratosolen galili* Wiebes and *Idnares gracile* Wiebes, recovered from *F. sycomorus* in East Africa,[16] were not found.

Table 2. Activity of *Sycophaga sycomori* and *Apocrypta longitarsus* on *Ficus sycomorus*.

	Mean number of wasps per census*	
	S. sycomori	*A. longitarsus*
November 15	16.9	1.2
November 18	6.7	9.2
November 21	30.4	4.4
November 25	0.0	0.5
November 29	0.0	0.5

*Five-minute censuses conducted at hourly intervals, with 10 – 12 censuses per day.

The seven-week census period revealed the following developmental pattern for *Sycophaga* and *Ceratosolen*: *a*) penetration of the ostiolar bracts began between 7 – 14 November and had ceased by 22 November; *b*) all wasps from the parent generation died within the syconia by 29 November; and *c*) their offspring emerged both before and after fruit fall, from 11 – 30 December (minimum generation time 20 days, maximum 53 days). In 80 figs dissected between 14 – 25 November there were several hundred *Sycophaga* but only 10 *Ceratosolen*. There were never more than two pollinators per fig. Numerous *S. sycomori* were active on the trees from 14 – 21 November (Table 2). *Ceratosolen arabicus*, however, was found only on 21 November, suggesting a very short activity period for this species. Moreover, the timing of this flight suggests that it did not originate from the trees at Gobabeb. The nearest tree bearing ripe fruit was 5 km away. Other evidence of long-distance dispersal in Agaonidae is reviewed by Ramirez.[8]

From a sample of 30 ripe figs, 17 (57%) contained inquilines only; and 19 seeds were recovered, but none of these germinated. In contrast, the remaining 13 figs contained both pollinators and inquilines. From them an average of 255 ± 122 seeds per fig were recovered, half of which germinated. Thus, it appears that *C. arabicus* is the sole pollinator of *F. sycomorus* in the Kuiseb, as it is in East Africa.[3]

In the Kuiseb River, *F. sycomorus* produces axillary figs. Although usually synonymous with typical *sycomorus*, this form is sometimes separated as a distinct species, *F. gnaphalocarpa* (Miq.) A. Rich.[17] Since each *Ficus* species generally has its own specific pollinator,[8,18] and because the pollinator of this '*gnaphalocarpa*' form is the same as that of the typical *sycomorus* studied in Kenya,[3] synonymy[17] is verified.

Populations of most tree species have discrete reproductive cycles. The genus *Ficus* is an exception. In our investigations, asynchronous fruiting periods of individual fig trees were most readily explained by reference to the symbiotic nature of *Ficus* pollination. In *F. sycomorus*,[2] as in many other fig species,[8] all syconia in a tree develop at the same time. The developmental stage during which ostiolar bracts are loosened sufficiently for penetration by pollinators lasts only four days in a six to seven week cycle.[2] Agaonids emerge near the end of this cycle and begin searching for syconia capable of being penetrated. Asynchrony within a population ensures a continuing supply of pollinators and syconia at the proper developmental stage. This is especially critical, since the pollinators are apparently relatively short-lived. Because all the syconia of *F. sycomorus* ripen simultaneously, the advantages of cross-pollination cannot be overlooked. Thus, asynchrony in the reproductive cycle of this species is a population attribute, representing part of a co-evolved pollination system.

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