

DISRUPTION AND RECOVERY OF INTRA-CROWN FRUITING SYNCHRONY IN A *CASSIA GRANDIS* (LEGUMINOSAE) TREE

Daniel H. Janzen

Department of Biology University of Pennsylvania Philadelphia,
Pennsylvania 19104

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ABSTRACT

Five large branches of a *Cassia grandis* tree were deflowered in its flowering year; the consequence was that 10-20 percent of the flowering-fruitlet capacity of the tree's crown was offset by one year from the tree's normal biennial flowering/fruitlet cycle. During the following five years, the sexual cycling of the five experimental branches returned to synchrony with the remainder of the tree. Resynchronization occurred through the process of the 5 branches gradually decreasing their fruit numbers in the tree's non-fruitlet years and gradually increasing their fruit numbers in the tree's fruitlet years. This suggests both independence of sexual behavior by branches and sensitivity of branches to the hormonal cueing of the tree as a whole. In *Cassia grandis*, selection for strong intra-crown sexual synchrony among years is probably based on decreased seed predation by bruchid beetles when the tree lacks a seed crop every other year.

Many wild tropical trees alternate large fruit crops with small ones or none at all, at intervals of two or more years (e.g., Janzen 1978). In some species, the conspecifics are not in supra-annual synchrony within a population, but each individual is strongly synchronized within its crown. Such an individual flowers and fruits during a 6-12 month period and then waits one or more years before again flowering; in such a species, intra-crown asynchrony is usually present only as the occasional small branch that is temporarily out of phase by one year. Examples of such behavior are offered by the Costa Rican deciduous forest legume trees *Lonchocarpus costaricensis*, *Cassia grandis* and *Dalbergia retusa* (Janzen, unpublished field notes). A *C. grandis* tree flowers in the middle third of the dry season (March-April) and matures the fruits from this flowering a year later; a year after this, it again flowers, and again matures the fruit crop a year later. Such a biennial flowering/fruitlet phenology suggests that an individual tree is cued to flower on a particular year not by cues that originate in the external environment, but rather by some

kind of internal cueing system. As new branches are produced in the tree crown, the hormonal system of the extant branches must pull them into intra-crown biennial synchrony. Here I show that the new branchlets on large established branches can also be gradually pulled back into synchrony with the remainder of the tree crown if the large established branches have been experimentally deprived of their flower crop in a flowering year.

The experimental tree was a medium-sized adult *Cassia grandis* (Leguminosae: Caesalpinioideae) with a DBH of 37.3 cm and height of 8 m in January 1983. It grows on a fully insolated site between the machinery yard and a mango orchard on Finca La Pacífica, 7 km north of Cañas, Guanacaste Province, Costa Rica. This tree is a member of a semi-wild population in the deciduous and semi-evergreen forests (and in their derived pastures) of southern Guanacaste Province and northern Puntarenas Province. I chose this species because I am personally very familiar with it (Janzen 1971, 1977, 1981, Janzen and Martin 1982) and I chose this individual for convenience of observation and because I have been watching it since 1965.

On numerous occasions I have observed that when *C. grandis* adult crowns lose patches of flowers or young fruits to crown-damaging agents, or rapidly grow new branches following heavy pruning, there is sometimes 1-year-displaced asynchrony of intra-crown flowering and fruiting at the site of damage; this is followed by gradual recovery of synchrony in the following years. Such disruption of synchrony is common enough that it is commonplace to observe a large *C. grandis* crown with a full mature fruit crop but also a few branches in flower, and or a crown in full flower but bearing a few newly mature fruit (from the previous year's few flowering branches). However, care is required to distinguish the latter case from a flowering crown that contains a few tardily-dehiscent fruits that are still hanging on the tree from the mature fruit crop of the previous year.

The experimental *C. grandis* tree at Finca La Pacífica normally produces 10^5 to 10^6 flowers in March to early April (about the middle of the 5-6 month rain-free dry season) of even-numbered years. It matures a crop of 800 to 1200 large fruits during the dry season of the following year. From 1965 to 1975, this experimental tree matured a large crop of fruits each odd-numbered year. On 10 March, during the heavy flowering of 1976, on five large branches all flowering inflorescences (branchlets 10-20 cm long) were gently snapped off at their bases; the five branches constituted major parts of the tree crown. They occupied between 10 and 20 percent of the crown's leaf-bearing volume. The branches had the following diameters (cm) at a distance of 30 cm from their bases in January 1983: (1) 8.7, (2) 6.9, (3) 9.2, (4) 6.9, (5) 11.4. These branches were fully insolated and they were spread radially and evenly among the compass directions. At the time that the five branches were deflowered, the tree bore approximately 19,500 inflorescences and 449,600 flowers, flower buds and flower scars; 20.2 percent of these flowers, buds and scars were on the deflowered branches. These estimates were obtained by counting all flowers and inflorescences on the deflowered branches, and using these values as estimators

for equal-sized portions of the crown. During the 1975 fruit crop (the year prior to experimental deflowering), the five branches bore 14 percent of the entire crop of 910 mature fruits (Table 1).

I predicted that the five de-flowered branches would flower again in 1977 and bear their usual number of mature fruits in the following year (1978), a flowering year (even-numbered) for the tree as a whole. They did (Table 1). The five experimental branches bore 95 percent of the fruits borne by the entire tree in 1978, in contrast to their usual number of 5 to 15 percent on odd-numbered years. In subsequent heavy-fruited years by the tree as a whole (1979, 1981, 1983), the five branches bore 2, 10, and 13 percent of the tree's crop and regained synchrony with the rest of the crown (Table 1). In the tree's flowering years (1978, 1980, 1982), the five branches decreased their mature fruit crop from 95 to 48 to 3 percent of the fruit crop borne by the tree.

It is evident that a large *C. grandis* branch can be sufficiently independent of the remainder of the crown so as to flower and fruit out of phase if it has been severely perturbed. In this case, I suspect that in late 1976, the branches that had been deflowered in 1976 accumulated exceptional amounts of stored reserves as well as had continuous unused input from new leaf photosynthate. Since they lacked fruits to mature with these resources, the branches produced inflorescences for the 1977 dry season, which in turn bore fruit in the 1978 dry season (while the rest of the tree was in flower). This implies that flowering at biennial intervals is most directly cued by simple resource accumulation. The puzzle is why these five branches did not continue in their new sexual cycle independent of the remainder of the crown. There are potential physiological and evolutionary answers.

The physiology of flower and fruit production involves an interaction between resource levels and flowering/fruited hormones. It is clear that a *C. grandis* branch can generate its own flowering cues with respect to the year of flowering (probably initiated by high levels of stored resources), but the branch is also responsive to the cues generated by the remainder of the tree. While the five branches flowering in 1977 bore a full-sized mature fruit crop in 1978, they also bore a few flowers in 1978 and matured a few fruits in late 1978 in synchrony with the 1979 major fruit crop. Since they only matured a few fruits in late 1978, they had enough reserves for a 1979 flower crop along with the few 1979 mature fruits and enough reserves to have a heavy flower crop in 1980. In short, this suggests that by 1980 the biennial heavy bombardment of the experimental branches with flowering hormones had finally moved those branches into sufficient synchrony with the remainder of the crown that the 1980 and 1982 flower crops and the 1981 and 1983 mature fruit crops were as on the experimental branches prior to deflowering in 1976. As expected, 1984 was a heavy flowering year and 1985 a heavy fruited year for the tree as a whole.

What selective pressures may have been responsible for the evolution of such a system of adjustment within the *C. grandis* crown? Economy of scale is unlikely as a

selection pressure for biennial bearing in *C. grandis*, since it should cost the tree the same to construct half as many equal-sized inflorescences yearly as twice as many every other year. In *C. grandis* the 1-2 fruits set per fruting inflorescence is the same in a large fruit crop as a small one. Pollination considerations are unlikely selective pressures since the five experimental branches bore a normal-sized fruit crop in 1978 even though the tree's 1977 flower crop was only 20 percent of the normal size for an even-numbered year. This suggests that the tree does not have a double-sized flower crop biennially in order to obtain enough pollinations for a normal-sized fruit crop per branch over the entire crown. However, I have no detailed information on the quality of the seeds or fruits on the five branches; they appeared normal and the fruits contained normal numbers of filled seeds. Nor do I have information on whether this apparent lack of pollinator limitation in a small flower crop would occur with *C. grandis* in natural vegetation. It is possible that biennial double-sized fruit crops were more than twice as good as half-sized annual fruit crops in attracting the best disperser coterie; however, the modern habitat naturally occupied by *C. grandis* in Costa Rica lacks wild dispersal agents, and even before the 1600's lacked the Pleistocene seed dispersal agents (Janzen and Martin 1982) that would have been most relevant to testing such a hypothesis.

Finally, biennial bearing prevents the accumulation and survival of a separate and continually present sub-population of bruchid beetle seed predators at each *C. grandis* tree. The beetles are not a trivial aspect of the tree's reproductive biology. Even though the bruchids have to locate each tree's seed crop from afar every other year (by immigration from other trees not in synchrony with the tree in question), pre-dispersal seed predation by *Pygiopachymerus lineola* (Bruchidae) is usually 30 to 50 percent, followed by most of the remaining seeds in the undispersed fruits being killed by *Stator interstitialis* (Bruchidae) (Janzen 1971). If the newly-eclosing bruchids could simply stay from year to year at the tree from whose crop they eclosed, the seed predation percent and rate would likely be much higher than it is. However, testing this hypothesis by examining the intensity of seed predation on the few mature fruits produced in flowering years is not biologically realistic. Both species of bruchids have the behavior of leaving a *C. grandis* tree from whose crop they eclose. They have apparently adapted to the tree's biennial fruiting pattern. On the other hand, a mutant strain of *C. grandis* that fruited annually might quickly acquire over evolutionary time a mutant population of bruchids that did not leave the site after emergence from the fruits. Likewise, its half-sized fruit crops would have a lesser chance of seed predator satiation than would full-sized fruit crops, if there is any bruchid satiation occurring. I favor a seed predator hypothesis in evolutionarily explaining biennial bearing by *C. grandis* because it is the only hypothesis not contradicted by some aspect of *C. grandis* natural history.

Since the *C. grandis* population is made up of biennial bearing individuals that are not in supra-annual synchrony with each other, it would appear to be made up of two genetically distinct populations. However, several processes work against the existence and maintenance of the integrity of two populations. First, as new individuals reach reproductive maturity, they have only a 50 percent chance of

being in supra-annual synchrony with their parents. Second, some trees bear a few flowers in their non-flowering years, flowers that should lead to gene flow between the two potential populations even if no fruit set occurs with these flowers. Third, and I suspect of most importance, entire trees must have their crowns occasionally set back one year by the loss of an entire flower or young fruit crop through environmental stress- or damage-induced flower or fruit abortion. For example, in the exceptionally dry first half of a rainy season in 1971 in southern Guanacaste Province, *C. grandis* in forest and pasture habitats aborted their entire crops of young fruits (as also did other legume trees such as *Hymenaea courbaril*, *Pithecellobium saman* and *Enterolobium cyclocarpum*); while I did not observe the flowering/fruited consequences in subsequent years, those *C. grandis* that flowered in the drought year probably flowered again in the following year and therefore cross-pollinated previously inaccessible individuals in the population. A similar process appears to be occurring with the large legume tree *Andira inermis* in the same habitat. In 1970, 1972, 1974 and 1976 the population flowered and fruited in synchrony over hundreds of square kilometers (Janzen 1978); however, beginning in 1977, numerous individuals were observed in flower in what should have been sterile years, and from 1980-1984, there was almost no population-level supra-annual synchrony in this (usually) biennial bearer. I suspect that some widespread weather event brought the *A. inermis* population into synchrony by eliminating a flower or fruit crop on those individuals that happened to be reproductive on the year of the event. Over subsequent years, new individuals entering the reproductive population and trees that missed two years between crops (owing to local edaphic conditions or poor accumulation of reserves) destroyed the population-wide synchrony.

No matter what mechanisms maintain within-crown reproductive synchrony in various species of biennial-bearing tropical trees, in a healthy and large *C. grandis* tree the mechanisms removed the effects of experimentally-induced asynchrony in a period of five years. The mechanism is probably the same as that which brings newly developing branches into synchrony with the remainder of the crown under normal circumstances.

Resumen

Se eliminaron las flores de cinco ramas grandes de *Cassia grandis* durante un año de floración, la consecuencia fue que el 10-20 por ciento de la capacidad de floración y fructificación no fue del árbol paralela durante un año, al ciclo normal del árbol de producir flores y frutos bianualmente. Durante los siguientes cinco años, el ciclo sexual de las cinco ramas experimentales volvieron a sincronizarse con el resto de la copa del árbol. Esta nueva sincronización se dio por medio del proceso de las cinco ramas que gradualmente disminuyeron el número de frutos producidos en los años sin frutos en el resto del árbol, y gradualmente aumentaron el número de frutos en los años de fructificación del árbol en total. Esto sugiere tanto de año de por medio independencia de las ramas del comportamiento sexual como sensibilidad de las ramas a la cadena hormonal del árbol como un todo.

En *Cassia grandis* es probable que la selección para una firme sincronización de la copa se basa en la reducción de la depredación de las semillas por gorgojos (Bruchidae) cuando el árbol carece de una cosecha de semillas.

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Table 1. Number of mature fruits in the crown of a single *Cassia grandis* tree and on five of its large branches that were deflowered during the 1976 flowering (i.e., the year before a major fruit crop).

	1975	1976	1977	1978	1979	1980	1981	1982	1983	
Total mature fruits on tree	910	11	936	137	785	147	1121	31	1319	
Total mature fruits on branch										
1	36	0	0	29	1	26	31	0	40	
2	15	0	0	28	3	6	12	0	21	
3	21	0	0	15	11	2	21	1	31	
4	20	0	0	24	3	32	8	0	16	
5	34	0	0	24	0	5	44	0	62	
Percent of total mature fruit crop on branches	1-5	14%	0%	0%	95%	2%	48%	10%	3%	13%