

Effect of Defoliation on Fruit-bearing Branches of the Kentucky Coffee Tree, *Gymnocladus dioicus* (Leguminosae)

ABSTRACT: By artificially defoliating fruit-bearing branches of a Kentucky Coffee Bean tree (*Gymnocladus dioicus*), it was shown that seed weight and secondary compound chemistry are not well buffered against foliage damage, a result expected with a tree sufficiently toxic as to be generally free of herbivores.

As part of a study to understand the detailed effects of herbivory on seed production (*e.g.*, Rockwood, 1973), fruit-bearing branches of *Gymnocladus dioicus* (L.) Koch were totally defoliated 3 (1971) and 32 (1970) days after flowering. The results are of general evolutionary interest as *G. dioicus* has foliage sufficiently poisonous that natural defoliation is not a commonplace challenge to its physiology.

METHODS

The experimental plant was a 12-inch dbh adult female *G. dioicus* (10 m tall) in a grove of males of this species in the Morton Arboretum, Lisle (near Chicago), Illinois. In 1970 and 1971, 12 different, healthy-appearing branches were chosen in the top center of the crown and marked with a spot of paint. Each branch chosen was terminated by a healthy female inflorescence with 3-6 immature pods. A flip of the coin was used to determine which branch of each pair was to be defoliated; the petiole of each leaf was cut with a sharp knife about 1 cm above its base (Fig. 1). Great care was taken to do no other harm to the branch. This intensity of leaf removal (7-9 per branch) amounts to less than 0.1% of the leaves on the tree; in each of the years, 90-100 branches bore pods and there were at least 1000 leaf-bearing branches

in the canopy. The tree did not re-foliate the defoliated branches, but the pods and the green stem bearing the leaf bases appeared normal. In 1970, the pods were full length (10-14 cm) but still flat at the time of defoliation (7 July 1970, about 32 days after flowering). In 1971, the pods were 1-3 cm long and old sepals were still hanging on the bases of the shorter ones at the time of defoliation (11 June 1971, about 3 days after the last flowers dropped from the inflorescence). In both years the pods were harvested in late December; by examining scars, I ascertained that no pods had fallen or been removed by animals from the control or experimental branches (over 95% of the 399 and 472 pods on the tree each year were still on the tree at the time of harvest).

RESULTS

Fruits produced from defoliated branches had significantly lighter pods and lighter seeds than those of control branches (Table 1). When the defoliation occurred within a few days of the time that the pods reached full length (1970), there was no pod abortion by the branches. However, there appeared to be a slight reduction in seed number, though the differences between experimental and control were not significant. When defoliation occurred shortly after flower drop (1971), an estimated 75% of the pods



Fig. 1.—A. A healthy sexual branch (control) of *Gymnocladus dioicus* at the time of the 1971 defoliation. B. As in A, but an experimental branch with the leaves clipped off just above their base; the contorted stem is due to repeated production of leafy branch ends over past years. Both branches are from the crown of the tree used in the experiment

were aborted, and there was a significant reduction in number of seeds per pod.

When the seed coats were cut through with a grindstone before planting, 100% of the seeds from the control branches germinated. Of the 75 seeds from the 1970 defoliated branches, 58% of 40 scarified seeds germinated. Only two of the eight seeds from the 1971 defoliated branches germinated.

The seeds differed in chemical composition between experimental and control. Normal *Gymnocladus dioicus* seeds contain about 10% dry weight of the presumably defensive isomers (G_1 and G_2 , two of eight possible stereoisomers) of the uncommon amino acid β -hydroxy- γ -methyl-glutamic acid (Dardenne *et al.*, 1972a, b). These isomers occur at a 9:1 ratio in normal seeds, but in the seeds from the 1970 defoliated branches, the ratio was 1:1 and the concentration was about one-half that in normal seeds (E. A. Bell, pers. comm.).

DISCUSSION

In contrast to wild herbaceous plants, whose seed weights appear to be well buffered against the effects of damage to the parent (Salisbury, 1942; Harper *et al.*, 1970), these experiments show that seed size can be severely lowered by defoliation in the immediate vicinity of the developing fruits of *Gymnocladus dioicus*. It is surprising that the plant did not simply abort the fruits from the damaged branches, or alternately, divert enough resources from the remainder of its large and healthy crown to feed the developing pods.

It is of evolutionary interest to ask why it apparently does not have the behavior (that is, the physiological machinery and cueing systems) to do either of these things. There are two possibilities, neither being mutually exclusive.

(1) The leaves of *Gymnocladus dioicus* have a reputation for being exceptionally free of insect attack and are poisonous (Pammel, 1911; Kingsbury, 1964) and this agrees with my own field data. The foliage of adult plants has a high concentration of β -hydroxy- γ -methyl-glutamic acid and its isomer [however, the ratio of the two isomers ($G_1:G_2 = 1:9$) is the reverse of that in the seeds, E. A. Bell (pers. comm.)]. Dardenne *et al.* (1972a), suspected that these compounds are responsible for freedom from herbivory, and I agree. If the plant is generally free of defoliation, then we would not expect there to have been the evolution of a physiology for coping with the immediate consequences of defoliation.

TABLE 1.—Weight (g) of *Gymnocladus dioicus* seeds and fruits from defoliated and control branches (t-tests of significance)

	Defoliated 7 July 1970 (ca. 32 days after flowering)		Defoliated 11 June 1971 (ca. 3 days after flowering)		+
	exp. (n=22)	control (n=22)	exp. (n=6)	control (n=24)	
\bar{X} pod weight	11.74	14.64***	8.60	12.44***	
SD	2.10	2.27	1.09	2.56	
\bar{X} seed weight	1.46	2.10***	0.82	1.95***	2.09***
SD	0.39	0.38	0.38	0.48	0.22
\bar{X} seeds/pod	3.41	3.73 ^{n.s.}	1.33	2.46*	
SD	0.91	1.24	1.51	1.02	

+ Seed weight recalculated after excluding the six shrunken and inviable seeds in the sample

(2) *Gymnocladus dioicus* is a tree that commonly bears a relatively small crop of toxic seeds each year (in striking contrast to mast-cropping species of trees, trees that produce very large crops of highly edible seeds at intervals of 2-10 years, cf. Janzen, 1971). We may predict from this that it completely exhausts its annual allocation for sexual reproduction each year. This means, then, that fruit development is unlikely to be based on stored resources (as it is in oak, beech, conifers, etc. Cf. Büsgen and Münch, 1929, Chap. 12; Matthews, 1963; and Janzen, 1971) but rather on photosynthates drawn directly from the leaves as the seeds mature. It is surprising that apparently only the photosynthates from the leaves on the fruiting branch support fruit development. Since the majority of the branches are sterile any given year, it seems quite likely that their photosynthate is used entirely for the vegetative welfare of the tree. However, it is possible that the honor of being a sexual branch is rotated among the branches from year to year.

As this defoliation—albeit abnormal in the life of the tree—has produced an alteration of seed size rather than the expected reduction in seed number, it might be worthwhile to note that there are a number of reports in the weed and agricultural biology literature of annual plant seed size and chemical content changing as a result of defoliation (e.g., Harper *et al.*, 1970; Kalton and Eldredge, 1947; Maun and Cavers, 1971; Reed and Stephenson, 1972, 1973). However, the relevance of the more agricultural of these examples to evolutionary biology is always suspect, since so many other selective pressures on the plant have also been altered in the agricultural environment.

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