# THE EFFECT OF DEFOLIATION ON SEED PRODUCTION OF SIX COSTA RICAN TREE SPECIES[1]

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*Abstract.* The experiments reported here test the hypothesis that increased foliage losses lead to decreased reproduction in plants. Six Costa Rican tree species were defoliated by hand twice during 1970. Subsequent collection of fruit crops during 1971 showed that control totals for fruit number and weight were much larger than totals of defoliated trees in all six species. Over 80% of the experimental defoliated plants produced no fruit whatsoever. Individual controls outproduced their experimental counterparts in 39 of 41 paired cases where reproduction occurred in either. It is concluded that heavy defoliation of wild trees will practically eliminate seed production for the year in which it takes place. These data and other work with crop plants have shown that both growth and reproduction are functions of leaf area. Consequently, heavy defoliation drastically reduces the fitness of a plant. Herbivore consumption of plant parts has probably played an important role in the evolution of both the morphology and chemistry of plants. These data support the view that physical and chemical defenses evolved by plants have played an important role in plant-herbivore co-evolution.

## INTRODUCTION

A discussion of the evolution of chemical defenses in plants usually begins in the following manner: individual plants, through mutation and recombination, produce certain compounds not involved in normal metabolism. Some of these are unpalatable to herbivores, and these plants increase their numbers relative to their conspecifics until this unpalatability becomes characteristic of the species (Ehrlich and Raven 1964, Whittaker and Feeny 1971).

The underlying assumptions are that herbivore consumption of plant parts leads to lowered fitness through (1) increased mortality, (2) decreased growth rate, and (3) lowered seed production. There is ample evidence in the literature to document (1) and (2) (Kulman 1971, Jameson 1963). The relationship between herbivore defoliation and seed production is, however, poorly understood. It is assumed that selection will operate in such a manner that a plant whose herbivore damage or "herbivore load" has been lessened will have more surviving progeny. Janzen (1971), for example, stated that replacement of leaves lost to herbivores would "exhaust some of the reserves stored from previous years for seed production." Yet only a limited amount of data from crop and range grasses (Jameson 1963) and casual observations on trees (Heron 1956, Capek 1962) is available to substantiate this assumption. In a review of insect defoliation of trees

Kulman (1971) cites 174 studies, most of which relate growth loss to quantity of foliage lost to insects; however, he fails to discuss the effects of herbivore defoliation on seed production.

The experiments reported here test the hypothesis that a heavy herbivore load, as represented by hand defoliation of experimental wild trees, will lead to a lowered fruit production. A strong positive correlation between increased herbivore damage and decreased reproduction would strengthen those theories that emphasize an important role for plant chemical defenses in the evolution of plants and their animal herbivores.

## METHODS

The study area was near Cañas, Guanacaste Province, Costa Rica. The precise location differed for each tree species, but all plants were either on a farm 4 km north of Cañas, Finca La Pacifica, or along the Pan American highway between the towns of Cañas and Bagaces (45–80 m elevation). According to Holdridge (1967), the natural vegetation of the area is Tropical Dry, deciduous forest. Most of the forests in this region have been cleared for crops and pastures or selectively cut. The climate is characterized by a long rainy season (May–November) and an equally long dry season (December–April) featuring high winds. Most woody species drop their leaves during the dry season, and many trees flower and fruit at this time (Janzen 1967, Baker and Frankie 1973). Of the six tree species used in this experiment, five bear flower and fruit during the dry season. The sixth, *Crescentia alata*, flowers for

many months during the rainy season; the fruits are mature during the dry season. All experimental trees except *Cochlospermum* were twice hand-defoliated, once during the middle of the rainy season (August 1970) and again in the late rainy season (September–October 1970).

Mature experimental and control trees were selected and paired if they were of similar size and shape, and growing under comparable conditions. For all species 10 pairs were selected, except that only eight pairs of *Crescentia* were used because of the time needed for defoliation. Data from only nine pairs of *Spondias purpurea* are available since a 10th pair was chopped down by local people after treatments had been completed.

Specific details of locations of plants, treatments, etc. are outlined below for each of the six species. More details on the biology of individual species can be found in Allen (1956).

(1) *Acacia farnesiana* (L.) Willd., Mimosaceae, is a common spiny shrub or small tree 1–4 m high that produces bright yellow flowers and indehiscent pods in the dry season. It is found throughout the Central American Pacific lowlands growing in pastures and other open places.

The study site was a lightly used pasture at Finca La Pacifica. Twenty plants 2–3 m tall were picked haphazardly from this area and paired by similar size and shape. The 10 experimental plants were defoliated by hand during August 1970, and had completely refoliated within 2 weeks. In mid-September all of these plants were defoliated a second time, and again refoliation occurred in 2 weeks. Brown, dry pods were collected between January 21 and April 12, 1971.

(2) *Bauhinia ungulata* L., Caesalpinaceae, is a shrub or small tree characteristic of disturbed areas, attaining a maximum height of 5 m. It produces white flowers in the dry season, closely followed by brown pods.

There were two study areas. Pairs 1–6 were located on Hacienda COMELCO (approximately 20 km north of Cañas) near the Pan American highway. Pairs 7–10 were in the same pasture as the *A. farnesiana* study area. All experimental plants were defoliated in mid-August and again in early October 1970. Refoliation was about 75% of the original number of leaves. Mature pods were collected between February 4 and March 2, 1971.

(3) *Cochlospermum vitifolium* (Willd.) Spreng., Cochlospermaceae, is generally found in the Pacific lowlands of Central America, where it is a small to medium-sized tree of 15–20 m maximum height. It is deciduous during the dry season, when it produces large golden-yellow flowers and large fruits.

The study area was a second-growth forest about

20 years of age. Ten pairs of trees of similar size (approximately 8 m) were chosen. Since the trees were so tall and leaves were found only near the tops of the trees, all defoliation was done with a pole pruner. Trees 4 and 7 were so tall that not all leaves could be reached. This set of trees differed from other experimentals in two ways. When defoliating with the pole pruner, I sometimes clipped off whole sets of leaves by cutting the section of the branch that they were attached to. Second, *Cochlospermum* was unsuccessful at refoliating. Therefore only one defoliation was performed, in early August 1970. Fruits were collected with the pole pruner on March 9, 1971.

(4) *Crescentia alata* H.B.K., Bignoneaceae, is a common tree in areas that are periodically flooded during the rainy season in the Pacific lowlands of Nicaragua and Costa Rica. It is a spreading tree of up to 12 m in height and bears its flowers along the trunk (cauliflory). The large green fruits weigh up to a kilogram each.

The study area was along the Pan American highway between Cañas and Bagaces. The first defoliation was finished in early September, but all trees refoliated within a week. However, six of them were then completely defoliated by a chrysomelid beetle (*Oedionychus* sp.). Only trees 1 and 5 had to be hand-defoliated a second time. All trees refoliated a second time except tree 8 and were defoliated a second time by the beetles (third time over all). Control trees were not attacked by the beetles, nor were mature leaves within experimental trees eaten by them. This appears to be because the beetles normally ate only new leaves (Rockwood 1973*a*).

Fruit was collected on three dates: before defoliation, 6 months after defoliation, and 1 year after defoliation.

(5) *Gliricidia sepium* (Jacq.) Steud., Papilionaceae, is planted throughout Central America as a fence-row tree and is common in second growth. It is deciduous and attains a height of 5–15 m. In the dry season it produces dense clusters of pink flowers and linear dehiscent pods.

The study area was a fence row in a pasture at Finca La Pacifica. Ten pairs of similar size (10 m) and shape were chosen. Trees were defoliated during mid-August and again in early October 1970. Leaf replacement was only 50%–75% after both defoliations. Pods were collected March 3–5, 1971.

(6) *Spondias purpurea* L., Anacardiaceae, is another second-growth tree that is commonly used as a living fence post in the Pacific lowlands of Costa Rica. It can attain a height of 15 m. In the dry season it is deciduous and produces small red flowers and red, plumlike fruits.

The study area was in several fence rows between

TABLE 1. Fruit number and weight in defoliated and control plants

| Species Plant no. | Number of fruit | | Weight of fruit | |
|---|---|---|---|---|
| | Control | Experimental | Control | Experimental |
| *Acacia farnesiana* | | | | |
| 1 | 24 | 0 | 41g | 0g |
| 2 | 0 | 4 | 0 | 4 |
| 3 | 33 | 0 | 17 | 0 |
| 4 | 439 | 3 | 416 | 5 |
| 5 | 140 | 0 | 172 | 0 |
| 6 | 192 | 0 | 249 | 0 |
| 7 | 451 | 0 | 669 | 0 |
| 8 | 242 | 0 | 369 | 0 |
| 9 | 33 | 0 | 66 | 0 |
| 10 | 0 | 0 | 0 | 0 |
| Total | 1554 | 7 | 1999 | 9 |
| *Bauhinia ungulata* | | | | |
| 1 | 0 | 0 | 0g | 0g |
| 2 | 0 | 0 | 0 | 0 |
| 3 | 49 | 0 | 76 | 0 |
| 4 | 24 | 0 | 38 | 0 |
| 5 | 34 | 0 | 64 | 0 |
| 6 | 18 | 0 | 29 | 0 |
| 7 | 53 | 1 | 74 | 3 |
| 8 | 13 | 0 | 22 | 0 |
| 9 | 31 | 0 | 75 | 0 |
| 10 | 27 | 15 | 35 | 18 |
| Total | 249 | 16 | 413 | 21 |
| *Cochlospermum vitifolium* | | | | |
| 1 | 5 | 0 | 135g | 0g |
| 2 | 4 | 0 | 110 | 0 |
| 3 | 0 | 0 | 0 | 0 |
| 4 | 9 | 13 | 250 | 355 |
| 5 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 |
| 7 | 6 | 5 | 160 | 130 |
| 8 | 12 | 0 | 310 | 0 |
| 9 | 0 | 0 | 0 | 0 |
| 10 | 2 | 0 | 55 | 0 |
| Total | 38 | 18 | 1020 | 485 |
| *Gliricidia sepium* | | | | |
| 1 | 49 | 0 | 435g | 0g |
| 2 | 23 | 0 | 165 | 0 |
| 3 | 99 | 0 | 810 | 0 |
| 4 | 1626 | 731 | 9935 | 4715 |
| 5 | 358 | 107 | 3605 | 600 |
| 6 | 572 | 0 | 4175 | 0 |
| 7 | 1067 | 2 | 9940 | 10 |
| 8 | 0 | 0 | 0 | 0 |
| 9 | 401 | 20 | 2440 | 128 |
| 10 | 0 | 0 | 0 | 0 |
| Total | 4195 | 860 | 31505 | 5453 |
| *Spondias purpurea* | | | | |
| 1 | 4533 | 0 | 17.8kg | 0kg |
| 2 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 |
| 4 | 6102 | 0 | 27.2kg | 0 |
| 5 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 |
| Total | 10635 | 0 | 45.0 | 0 |

TABLE 1. (*continued*)

| Species Plant no. | Number of fruit | | Weight of fruit | |
|---|---|---|---|---|
| | Control | Experimental | Control | Experimental |
| *Crescentia alata*, before defoliation (late August 1970) | | | | |
| 1 | 171 | 102 | 76.8kg | 58.2kg |
| 2 | 5 | 11 | 2.1 | 3.9 |
| 3 | 111 | 85 | 38.6 | 21.8 |
| 4 | 128 | 132 | 57.1 | 47.9 |
| 5 | 81 | 135 | 22.7 | 27.0 |
| 6 | 32 | 43 | 11.4 | 19.2 |
| 7 | 69 | 104 | 24.0 | 29.4 |
| 8 | 29 | 29 | 8.6 | 10.0 |
| Total | 626 | 641 | 241.3 | 217.4 |
| *Crescentia alata*, 6 months after defoliation (February 1971) | | | | |
| 1 | 83 | 37 | 28.8kg | 17.8kg |
| 2 | 15 | 0 | 5.2 | 0 |
| 3 | 75 | 0 | 21.8 | 0 |
| 4 | 50 | 0 | 20.4 | 0 |
| 5 | 15 | 0 | 2.2 | 0 |
| 6 | 11 | 0 | 1.6 | 0 |
| 7 | 36 | 0 | 12.0 | 0 |
| 8 | 3 | 0 | 1.0 | 0 |
| Total | 288 | 37 | 93.0 | 17.8 |
| *Crescentia alata*, 1 year after defoliation (late August 1971) | | | | |
| 1 | 65 | 21 | 19.1kg | 9.5kg |
| 2 | 2 | 1 | 1.0 | 0.4 |
| 3 | 50 | 22 | 16.6 | 5.0 |
| 4 | 212 | 15 | 90.4 | 5.2 |
| 5 | 5 | 0 | 1.2 | 0 |
| 6 | 20 | 16 | 5.6 | 4.0 |
| 7 | 5 | 0 | 0.8 | 0 |
| 8 | 4 | 0 | 0.8 | 0 |
| Total | 363 | 75 | 135.5 | 24.1 |

Cañas and Finca La Pacifica. All trees were defoliated in August 1970 and again in October. Refoliation of experimental trees was poor, reaching 50% of the original leaf area at best. Fruit was collected between February 10 and April 12, 1971.

Except for *Crescentia* and *Spondias* all fruit crops were weighed to the nearest gram, wet weight. The fruit crops of these two species were so large and heavy that they were weighed to a tenth of a kilogram on a grain scale. Data were analyzed on the University of Michigan Terminal System (MTS) constant program (*t*-tests). The Sign Test was as described in Brownlee (1965).

RESULTS

Results for all tree pairs are presented in Table 1 and summarized for each species in Table 2. In all six species the control totals for fruit number and weight are much larger than for defoliated plants. Of the 57 defoliated plants, 46 (80.7%) produced no fruit. In contrast, only 17 controls (29.8%) failed to produce some fruit. Individual controls produced

TABLE 2. Mean fruit crop number and weight per individual tree

| Species | Sample size | Mean no. of fruit | | Mean weight | |
|---|---|---|---|---|---|
| | | Control | Exp. | Control | Exp. |
| *Acacia farnesiana* | 10 | 155.4 | 0.7 | 199.9g | 9.0g |
| T-test significance | | P < 0.020 | | P < 0.021 | |
| *Bauhinia ungulata* | 10 | 24.9 | 1.6 | 41.3g | 2.1g |
| T-test significance | | P < 0.003 | | P < 0.003 | |
| *Cochlospermum vitifolium* | 10 | 3.8 | 1.8 | 102.0g | 48.5g |
| T-test significance | | P < 0.175 | | P < 0.165 | |
| *Gliricidia sepium* | 10 | 419.5 | 96.0 | 3150.5g | 545.3g |
| T-test significance | | P < 0.024 | | P < 0.029 | |
| *Spondias purpurea* | 9 | 1182.0 | 0.0 | 5.0kg | 0.0kg |
| T-test significance | | P < 0.174 | | P < 0.179 | |
| *Crescentia alata* (before defoliation) | 8 | 78.3 | 80.1 | 30.2kg | 27.2kg |
| T-test significance | | P < 0.890 | | P < 0.443 | |
| *Crescentia alata* (after defoliation) | 8 | 36.0 | 4.6 | 11.6kg | 2.2kg |
| T-test significance | | P < 0.011 | | P < 0.015 | |

more than their experimental counterpart in 39 of 41 cases where reproduction occurred in either. By means of a sign test for these 41 pairs, the hypothesis that controls outproduced defoliated trees is confirmed ($P < .001$). Moreover, even though *Cochlospermum* experimental 4 produced more than its control, all fruits were produced in that section of the tree that was not defoliated because of its height. In fact, the only defoliated *Cochlospermum* to produce fruit were those trees (4 and 7) that were not completely defoliated.

A two-sample *t*-test performed on the data from each species shows that the difference between experimentals and controls is significant except in *Cochlospermum* and in *Spondias*, where only two controls and no experimental trees set fruit.

It appears that *Spondias* may fruit at irregular intervals or every 2nd year. With the exception of the two control trees which did fruit, no other *S. pupurea* in the entire Cañas area was observed to fruit in any significant amount. This phenomenon is known from other tree species in the Tropical Dry forest and may explain why only 2 of 18 trees set fruit.

Fruit crops of *Crescentia alata* were collected before defoliation, 6 months after defoliation, and 1 year after defoliation. Before defoliation the mean fruit production of experimental and control trees was almost identical, 80.1 vs 78.3. After defoliation, the fruit production of experimentals dropped far below that of controls, 4.6 vs 36.0. Six months later still, or a year after the first count was made, experimental trees were still far behind their counterparts but beginning to recover, 9.4 vs 45.5.

## DISCUSSION

Experiments similar to those reported here have been conducted on crop plants. Early studies correlated size of apples and peaches with leaf area (Magness 1929, Weinberger and Cullinan 1932). Significant decreases in wheat yield have been obtained whenever more than one leaf is removed from wheat plants (Davidson 1964, Lucas and Asana 1968). Stickler and Pauli (1961) found that removal of 33%, 50%, 67%, and 100% of the leaves resulted in yield decreases of 23%, 35%, 43%, and 95% in sorghum. In his review of crop and range plant response to harvesting, Jameson (1963) concluded that clipping or grazing by herbivores adversely affects seed production.

Three factors modify the relationship between leaf area removed and reduction in crop yield. First, a certain amount of foliage is dispensable, and there is little reduction in yield until a threshold of leaf area loss is exceeded. For example, Guene and Minnick (1967) found that snap bean yield is not significantly affected until nearly 50% of the leaves have been removed, and Sackston (1959) cut 25% from each leaf in sunflower plants without decreasing yield significantly. Chester (1950) suggested that when a few leaves are lost, those remaining become more efficient and no energy is lost by the plant. This may not be true for plants in natural, competitive situations. Moreover, removal of leaves beyond this threshold proves quite detrimental to reproduction even in crop plants growing under reduced competition.

The second factor which modifies the relationship between leaf area and reproductive yield is the type

TABLE 3. Partial list of plant species for which heavy defoliation has been reported (adapted from Kulman 1971)

| Defoliator | Plant species attacked | Recorded defoliation |
|---|---|---|
| **A. Sawflies** | | |
| Diprion pini | Pinus sylvestris | 85% |
| Neodiprion pratti | Pinus virginiana | 55 |
| Neodiprion nanulus | Pinus resinosa | 100 |
| Neodiprion taedae | Pinus taeda | 75 |
| Diprion hercyniae | Picea mariana and Picea glauca | 50–95 |
| Neodiprion abietis | Abies concolor | 65 |
| Neodiprion lecontei | Pinus taeda and echinata | 75–100 |
| Neodiprion rugifrons | Pinus banksiana | 90 |
| Cephalcia alpina | Larix leptolepis | 20–85 |
| Pristophora erichsonii | Larix laricina | 25–70 |
| **B. Budworms** | | |
| Choristoneura pinus | Pinus resinosa | 70–100 |
| Choristoneura fumiferana | Picea spp. | 100–800 |
| Choristoneura occidentalis | Pseudotsuga menziesii, Abies grandis, and species of Picea | 20–60 |
| **C. Miscellaneous Lepidoptera** | | |
| Lambdina fiscellaria | Tsuga heterophylla, Pseudotsuga menziesii, and others | 80–100 |
| Zieraphera diniana | Picea sp. | 100 |
| Coleophora laricella | Larix decidua | 40 |
| Melanolphia imitata | Tsuga heterophylla | 90 |
| Porthetria dispar | Quercus spp. | 100 |
| Malacosoma disstria | Populus tremuloides | 25–100 |
| Operophtera brumata | Quercus rubra | 100–400 |
| Dasychira pudibunda | Fagus sylvatica | 90 |
| Heterocampa guttivitta | Acer spp. and Ostyra virginiana | 100–300 |
| Aroga websteri | Artemisia spp. | 25–100 |

of leaves removed. Stickler and Pauli (1961) showed that removal of leaves from the upper portion of a plant causes a greater reduction in yield. When Sackston (1959) removed leaves from the upper half of sunflower plants, seed production was reduced 52% as compared to only 14% when he removed leaves from the lower half. The basal leaves are usually older and approaching senescence, whereas the upper leaves are younger and photosynthesizing more rapidly. The lower leaves also receive less sunlight since they are shaded by the upper leaves.

A third factor which must be considered in these crop studies is the timing of defoliation. Begum and Eden (1965) reported that defoliation on one-third and two-thirds of the leaf area before blooming had little effect on soybean yield. Only when the beans were half-grown did all degrees of defoliation result in significant yield reduction. Chester (1950) reports that in many other crops studied the loss in yield is greatest when plants are defoliated at mid-season. Yield losses are progressively less with earlier and later defoliations.

The literature on the effects of defoliation on seed production in wild trees is limited to observation. Heron (1956) reported that cones were not produced in jack pines (Pinus banksiana) during the year following severe defoliations by the budworm, Choristoneura pinus (Lepidoptera), although cones were abundant on trees not defoliated. In Germany,

Capek (1962) has noted that seed production occurred only on spruce trees (Picea sp.) that were not attacked by Zieraphera diniana (Lepidoptera).

Heavy defoliation of wild trees will reduce and practically eliminate seed production for the year in which it takes place. In this study more than 80% of defoliated trees produced no fruit in 1971. Most of the other 11 trees yielding fruit produced them in the portion of the tree which had been impossible to defoliate. Controls outproduced their counterparts in 39 of 41 cases, and the only results not clearly significant were due to technical difficulties. It is clear that twofold defoliation is normally sufficient to eliminate reproduction in these tropical trees; it is not evident at what level more moderate defoliation becomes significant. However, extrapolating from crop studies, I estimate that reproduction will be significantly reduced any time 50% of the tree's total leaf area is lost. This figure may be reduced considerably if only actively photosynthesizing or upper-canopy leaves are considered.

Some workers have doubted that 50%–200% defoliation occurs in nature. The real question is not only whether this defoliation occurs now, but if it has occurred during the evolutionary history of plant species. In contemporary Central America, leaf-cutting ants of the genus Atta are known to defoliate a number of plant species (Weber 1966, Rockwood 1973b). Of the plant species used in this experiment

I have seen leaf-cutters strip 50%–100% of the leaves from *Acacia farnesiana, Cochlospermum vitifolium,* and *Spondias purpurea.* I have observed *Gliricidia sepium* damaged to a lesser degree by leaf-cutters. The beetle *Oedionychus* sp. defoliated several *Crescentia alata* trees used in this experiment, the damage varying from 50%–200% (Rockwood 1974).

Severe defoliations by insects are not limited to the tropics. In the temperate zone, saw flies, phasmatids, bud worms, gypsy moths, and miscellaneous Lepidoptera have been reported to cause 50%–800% damage in a variety of tree species (Table 3) (Kulman 1971).

Since many extant plant species possess defenses of some kind against herbivores and are still subject to severe damage, defoliations of this severity have surely occurred in the evolutionary past of most plant species. For this reason I conclude that herbivore consumption of plant parts has played an important role in the evolution of both the morphology and chemistry of plants.

Since both growth (Kulman 1971, Donald 1961) and reproduction are, to a great extent, functions of leaf area, medium to heavy defoliation (loss of 50%–100% of leaf area) will have important consequences for a plant. Selection for any physical or chemical means to lessen a plant's herbivore load will operate on four levels. (1) A plant with fewer foliage losses will have more intact photosynthetic surface and more energy to devote to growth. It will be able to grow faster and be more successful in intra- and inter-specific competition. (2) Since it will have fewer energy losses and broken tissues, it will likely be more resistant to disease. (3) It will not put out new leaves at an inappropriate time of year, and will therefore be less prone to attack from other herbivores that feed only upon new leaves (Feeny 1970, Rockwood 1974). (4) As was demonstrated in this experiment and in the work with crop plants, it will produce more seed than its conspecifics and more potential progeny.

The hypothesis that increased foliage losses lead to decreased reproduction in plants is valid. Ehrlich and Raven (1964) have emphasized the importance of plant–herbivore interactions in the evolutionary radiation of both insects and terrestrial angiosperms. They have asserted that the evolution of defensive compounds by plants and the resultant adaptation to them by phytophagous insects have been the dominant factors in the evolution of butterflies and other herbivorous groups. Similar statements have been made by Fraenkel (1959), Janzen (1969), Whittaker and Feeny (1971), and others. The data presented here support these views by emphasizing the highly negative effects of heavy defoliation on plant reproduction.

LITERATURE CITED

Allen, P. H. 1956. The rain forests of Golfo Dulce. Univ. Florida Press, Gainesville. 417 p.

Baker, H., and G. Frankie. 1973. Comparative phenological studies of trees in tropical lowland wet and dry forest sites of Costa Rica. J. Ecol. (in press).

Begum, A., and W. G. Eden. 1965. Influence of (insect) defoliation on yield and quality of soybeans. J. Econ. Entomol. **58**: 591–592.

Brownlee, K. A. 1965. Statistical theory and methodology in science and engineering. Wiley and Sons, New York. p. 242–246.

Capek, M. 1962. The effect of defoliation by *Zeiraphera diniana* Guen. on the annual increment of spruce. Schweiz. Z. Forstwes. **113**: 635–642.

Chester, K. S. 1950. Plant disease losses: their appraisal and interpretation. Plant Dis. Rep. Suppl. **193**: 190–362.

Davidson, J. L. 1964. Some effects of leaf area control on the yield of wheat. Aust. J. Agric. Res. **16**: 721–731.

Donald, C. M. 1961. Competition for light in crops and pastures. Symp. Soc. Exp. Biol. **XV**. Mechanisms in biological competition. P. 282–313.

Ehrlich, P. R., and P. H. Raven. 1964. Butterflies and plants: a study in coevolution. Evolution **18**: 568–608.

Feeny, Paul. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**: 565–581.

Fraenkel, G. S. 1959. The raison d'être of secondary plant substances. Science **129**: 1466–1470.

Guene, G. L., and D. R. Minnick. 1967. Snap bean yields following simulated insect defoliation. Proc. Fla. State Hortic. Soc. **80**: 132–134.

Heron, R. J. 1956. Jack pine staminate flower production. Can. Dep. Agric. For. Biol. Div. Rep. **12**(3): 2.

Holdridge, L. R. 1967. Life zone ecology. 2nd ed. Trop. Res. Center, San Jose, Costa Rica. 206 p.

Jameson, D. J. 1963. Responses of individual plants to harvesting. Bot. Rev. **29**: 532–594.

Janzen, D. J. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution **21**: 620–637.

———. 1969. Seed-eaters versus seed size, number, toxicity, and dispersal. Evolution **23**: 1–27.

———. 1971. Seed predation by animals. Ann. Rev. Ecol. and Syst. **2**: 465–492.

Kulman, H. M. 1971. Effects of insect defoliation on growth and mortality of trees. Ann. Rev. Entomol. **16**: 289–324.

Lucas, D., and R. D. Asana. 1968. Effect of defoliation on the growth and yield of wheat. Physiol. Plant. **21**: 1217–1223.

Magness, J. R. 1929. Relation of leaf area to size and quality in apples. Proc. Am. Soc. Hortic. Sci. **25**: 285–288.

Rockwood, L. L. 1973. The effects of seasonality and host plant selection on foraging of two species of leaf-cutting ants (*Atta*) in Guanacaste Province, Costa Rica. Chapter IV. Ph.D. Thesis. Univ. Chicago. 244 p.

————. 1974. Seasonal changes in the susceptibility of *Crescentia alata* leaves to the flea beetle, *Oedionychus* sp. Ecology **55**: (in press).

Sackston, W. E. 1959. Effects of artificial defoliation on sunflowers. Can. J. Plant Sci. **39**: 108–118.

Stickler, F. C., and A. W. Pauli. 1961. Leaf removal in grain sorghum. I. Effects of certain defoliation treatments on yield and components of yield. Agron. J. **53**(2): 99–102.

Weber, N. A. 1966. Fungus-growing ants. Science **153**: 587–604.

Weinberger, J. H., and F. P. Cullinan. 1932. Further studies on the relation between leaf area and size of fruit, chemical composition and fruit bud formation in Elberta peaches. Proc. Am. Soc. Hort. Sci. **29**: 23–27.

Whittaker, R. H., and P. P. Feeny. 1971. Allelochemics: chemical interactions between species. Science **171**: 757–770.