Theobroma cacao--Herbivory in Monoculture and in Diverse Vegetation

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Introduction

Studies have indicated that herbivores maintain higher densities in monocultures than in more diverse vegetation. At La Selva, the proximity of active and abandoned plantations of cacao provides an opportunity to test whether levels of herbivory are indeed higher in monocultures. Plantations of Theobroma cacao (Sterculiaceae) within La Selva proper have been invaded by second growth since 1968; there are now understory species growing among the cacao trees and the trees themselves have become covered by epiphytes. Adjacent to La Selva is an active cacao plantation (owned by Dr. Robert Hunter), in which the ground is kept clear of understory plants and the trees are kept free of epiphytes. In this herbivory levels were compared for Theobroma trees in the two locations.

Methods

Fifteen leaves were collected from each of six trees in each site. The leaves were collected so as to sample each tree around its entire circumference, selecting the third green leaf from the end of each branch sampled in order to obtain leaves of approximately the same age.

An "ideal" version of each leaf collected was traced onto paper. There "ideal" tracings represented the complete leaf, i.e., the leaf without any herbivore damage. All the traced patterns and all the leaves were put through a leaf area meter, and the surface area of each leaf was compared with that of its "ideal" tracing, giving an estimate of herbivore damage to that leaf.

Sweep sampling for insects was done at each site, both idiosyncratically and systematically (one set of twenty sweeps in each site), in the hope of getting some idea of insect density and of the types of insects present in each site.

Results

The results of this study were diametrically opposed to the more-herbivory-in-monocultures theory (Isn't science wonderful? It's days like this that make it all worthwhile.) The mean percent leaf loss to herbivory in the active plantation was 6.89, while in the abandoned plantation it was 10.20 (Fig. 1). With between-tree variance assumed to be equal in the monoculture and the diverse culture, data were pooled and a two-tailed t-test was done, after performing an arcsin transformation of the data. This test showed a difference between the means after transformation for the monoculture (13.85%) and the diverse culture (16.94%) which was significant at the $p < 0.01$ level.

Of the insects found in the sweep samples, the most likely herbivores were weevils, which were found in both sites. One researcher actually observed a weevil eating cacao (the big thrill of the day, I assure you). The twenty sweeps in the monoculture turned up more insects than the twenty sweeps in the abandoned plantation, though the sample size was too small for any statistical analysis (see also discussion).

Discussion

Certain complicating factors and possible methodological weaknesses should be pointed out (disarming honesty). For one thing, cultivation practices in the active plantation could affect herbivore densities; this study was conducted without any information on these practices. The sampling method was somewhat biased; for practical reasons, the leaves sampled tended to be leaves on the lower branches of the trees. Observations suggest that there may be important differences between the cacao trees in the two locations. Though both plantations are the same age, the trees in the monoculture were smaller in circumference ($\bar{x}$ = 15.73 cm, as measured at the height of Allan's waist) than the trees in the abandoned plantation ($\bar{x}$ = 22.23 cm, as measured at the height of Allan's waist). This raises the possibility that tree size may affect herbivory levels, as well as the question of why the cultivated trees should be smaller than the abandoned trees--but that's another story.

The greater number of insects obtained with twenty sweeps in the monoculture should be viewed as a somewhat suspect result since it was much easier to sweep in the monoculture. Much more thorough and systematic sampling would need to be done before any conclusions could be made about insect/herbivore density in the monoculture and the more diverse culture.

The question of why herbivory levels should be higher in the diverse culture than in the monoculture can be approached from several angles. In those other studies in which the opposite result was obtained, the general theory suggested was that specialist herbivores were more likely to move into monocultures and decimate them; if these specialists try to move into more diverse areas, they may well hit the "wrong" plant and do no damage. It is possible that generalist herbivores are responsible for some or all of the damage found in our diverse culture of cacao, and it is tempting to suggest that the presence of these generalists might be tied to some specific aspect of the abandoned plantation, e.g., the presence of the epiphytes. If the epiphytes attract generalists, then the trees in the monoculture, which are kept free of epiphytes, may escape these ferocious herbivores. The sort of systematic insect sampling discussed above would indicate, it is to be hoped, whether the same species of insects are eating the cacao in both sites.

Other possible factors are cacao tree density (which was not measured in this study) and tree size (discussed above), which could affect herbivory levels even if the same species of insects are responsible for the herbivory in the two sites. Increased cacao density might be expected to increase herbivory, regardless of diversity of culture. Tree size could be a determinant of herbivory levels and/or partially determined by herbivory levels (though the bigger trees were found where herbivory was higher, making the former seem more likely than the latter).

In conclusion, to understand more completely what is going on in these two sites with respect to herbivory on cacao, several sorts of data are necessary. The plantations themselves should be more carefully examined and cacao density and tree size should be considered, as well as cultivation practices. Careful insect sampling and observation are necessary to see who is eating all those leaves. The issue of monocultures as opposed to diverse culture is of economic importance as well as of theoretical interest. From the theoretical point of view, it touches on questions of specialization and coevolution. The two types of cacao plantations at La Selva offer an excellent opportunity to pursue this question.

We all enjoy a chocolate bar
From off the grocery shelf
But truly dedicated bugs
Will eat the plant itself.

Fig. 1. This is a stem and leaf diagram showing the percent of each leaf lost to herbivory. The upper diagram is for the active plantation and the lower for the abandoned plantation. To read this diagram, the number on the far left of any given row is read as the first digit for all the other numbers in the row. Thus, the top row in either diagram covers herbivore damage from 00% through 04%. Each "4" in the row represents one leaf which had lost 4% of its area to herbivory. The number above the exclamation point is the mode, and the underlined number is the median.

Active Plantation

0 00000111111111111112222222333333334444444444
!
0 5555555555556666777778888899 9

1 0001

1 678

2 34

2 5678

3 0123

3

4

4

$\overline{X} = 6.89$

Abandoned Plantation

0 0001111112223334444

0 55555556666666667777777888899 9
!
1 000111222222233

1 556668889999

2 0001224

2 58

3

3 9

4 2

4

$\overline{X} = 10.2$