Effects of Selective Defoliation by Tent Caterpillar on Red Maple

General Ecology- Spring 1995
Ami Grace
Kim Baranek
Melea Hungerford
Keren Barfi

The Effect of Selective Defoliation by the Tent Caterpillar, on Growth of the Red Maple

Abstract

Species in a community cope differently with natural disturbances. For some, disturbance is harmful. For others disturbance may be beneficial. Red maple is an example of a species that took advantage of the effects of disturbance caused by the tent caterpillar in 1989. This beneficial response was assessed by examining red maple's annual rings. Through a series of statistical tests we were able to investigate red maple's growth response in defoliated versus the non-defoliated sites. Also, we tested whether genotype and/or microsite played a significant role in determining the growth response. Finally, tests were run to see if any long-term effects from the defoliation occurred -- specifically, whether there was an effect on subsequent years.

In comparing defoliated versus non-defoliated, the results showed no significant difference in the 1989 relative growth response between these two sites, but a trend was seen. Moreover, there was also no significant clump or dbh effect on the growth response. The effect on subsequent years showed that defoliation was beneficial to the red maple's long-term growth. Finally, we also found trees that increased their growth in 1989, continued to increase their growth in subsequent years.

Introduction

Disturbances are a natural part of every ecosystem. Some disturbances are quite dramatic, such as forest fires and other natural disasters, but even small parasitoid and herbivore outbreaks can cause major disturbance to an area. In many cases, disturbance may affect different organisms differently; if so, formerly unavailable resources may become available to less affected species. Resource availability, resource utilization, growing conditions and many other factors influence ecosystem function; disturbances have the powerful capability of altering any or all of these factors.

Defoliation by forest herbivores is a common forest disturbance, affecting all trees in the forest either directly or indirectly. Loss of leaves dramatically decreases photosynthetic rate, and therefore sharply reduces the amount of photosynthate a tree produces. Since transpiration occurs in leaves, defoliation also reduces the amount of water a tree uses. Because soil nutrients are absorbed by roots and distributed throughout the tree in dissolved form, nutrient uptake would also be affected. The effects of defoliation may differ among tree species, due to their specific physiological needs and abilities, and to differences in their attractiveness to the herbivore.

Areas subjected to selective defoliation by herbivores are unique because they allow a comparative study of the effect of this type of disturbance on different tree species. Since light is crucial to tree growth, the shading of neighboring trees in the forest canopy should profoundly affect the growth of a single tree (Horn, 1971). It is plausible that growth of non-defoliated trees in a defoliated area may be affected by increased light, water, and nutrients. Alternatively, increased light intensity may exceed the light saturation point of a tree and therefore hinder growth.

In June of 1989, an outbreak of the forest tent caterpillar, *Malacosoma disstria*, defoliated large sections of forest around the University of Michigan Biological Station (UMBS) near Pellston, Michigan. Although *M. disstria* attacked most tree species, they demonstrated selective defoliation by completely avoiding red maple, *Acer rubrum*.. Consequently, red maples in defoliated areas were exposed to increased sunlight and increased nutrients as *M. disstria* converted the leaves of other species into frass. As explained above, the red maples may also have had increased access to nutrients and water because of reduced competition of all other defoliated tree species. Since red maple is an opportunistic species, it can adapt to changes in growing conditions. Also, red maples most often grow in the understory as clumps, which are often genetically identical clones.(Wilson, 1984)

The effect of past disturbances may be studied by dendrochronological analysis, the study of tree rings. A tree ring is defined as, "a sheath of cells appearing as one of a series of concentric rings in the cross-section of a woody stem."(Allaby, 1992) Each ring is usually a result of a single year's growth starting in spring and ending in late summer. Xylem, which transports water, makes up the wood region. Xylem vessels produced during the spring, when water is plentiful, have larger diameters than those produced in the summer. The contrast between the summer xylem of one year and the spring xylem of the next year makes annual rings visible. The entire band of xylem formed in one growing season makes up one annual ring (Kimball, 1965). By comparing the relative width of the red maple's 1989 growth ring between defoliated and non-defoliated areas, we can investigate this species' response to selective defoliation by *M. disstria* . Moreover, by examining at least two trees per clump, we can also determine whether response to defoliation is affected by genetic and/ or microsite factors.

The purpose of this study is to determine the effect of selective defoliation on growth of red maple. The specific questions we address are:

1) Did selective defoliation by *M. disstria* in 1989 result in increased or decreased growth of red maple in 1989?

2) Did selective defoliation by *M. disstria* in 1989 affect growth of red maple in subsequent years?

3) Did 1989 growth response due to selective defoliation by *M. disstria* , correlate with the growth response of 1990-91?

Materials and Methods

Site and Data Collection

In order to determine the effect of selective defoliation by the forest tent caterpillar on red maple, the width of tree rings was used to compare growth between an area that had been defoliated in 1989 and adjacent non-defoliated areas. Both areas were located off Greenstar Trail, on UMBS property, Cheboygan County, Michigan. Within each area, every clump of red maples was identified, flagged and assigned a number. The diameter at breast height (dbh) of each tree was measured using a dbh tape.

In order to determine the effect of selective defoliation, core samples were taken from red maples in both the defoliated and non-defoliated sites. Only trees with a dbh of six centimeters or more were sampled. From each clump, the two largest trees were cored. Clumps were systematically chosen to provide the largest range of dbh values. Sampled clumps in the non-defoliated area were at least 50 meters from the defoliated site and samples were taken from all sides of the defoliated area. The clumps from the non-defoliated area were randomly selected with the only requirement being a minimum dbh of six centimeters.

Red maple samples were extracted with a tree corer, placed immediately into straws and brought back to the lab for analysis. The samples were glued to trays, sanded and shaved in order to accentuate the growth rings (neither wood stain nor phenoglucinol dye were effective in increasing ring visibility). A dissecting microscope was used to measure the width of growth rings for the years: 1) 1986-1988 2) 1989 3) 1990-1991.

<u>Statistical Analysis</u>

An analysis of variance test, ANOVA, was used to determine whether clumps within each site differed significantly in 1989 relative growth. Dbh was used as a covariate to determine whether trees of different sizes responded differently to defoliation. By itself, the absolute width of the 1989 ring does not indicate response to defoliation for two reasons, microsite and genotype. First, in a typical year, growth may be greater in the non-defoliated site, if for instance, nutrient availability is greater in the non-defoliated site. If so, trees in the defoliated site may exhibit increased 1989 growth yet still produce rings smaller than those of trees in the non-defoliated site. Comparison of the absolute width of the 1989 ring is misleading because it would suggest that defoliation had an adverse effect on growth. Secondly, trees within each site may differ genetically such that certain genotypes may grow faster than others. If trees in the defoliated site grew faster due to genotype, looking at only absolute growth for 1989 would again lead to a misleading conclusion. This is because although trees in the defoliated areas had smaller growth rings in comparison to those of non-defoliated trees, they might have growth rings which are bigger relative to their own growth in previous years. However, both these complications are corrected for if 1989 growth is expressed relative to 1986-1988 average growth. Thus the variable 1989 relative growth response was used in order to correct for factors that cannot be standardized (i.e. microsite/ genotype). The test was run separately for the defoliated site which had a sample size of forty-four and the non-defoliated site which had a sample size of forty-eight.

In order to determine whether selective defoliation resulted in increased or decreased growth of red maples in 1989, the 1989 relative growth response was compared between defoliated and non-defoliated sites by ANOVA. Since neither clump nor dbh had a significant effect on growth response (See Results), site was the only factor used.

In order to determine whether defoliation had an effect on growth in subsequent years, three ANOVA tests were run. Though dbh and clump were found to have no significant effect on 1989 relative growth response, it could not be assumed that they would not exert a significant effect on 1990-1991 relative growth response. For this reason, the tests were first run within defoliated and non-defoliated sites separately with variables (ratios) that corrected for these other factors. Once it was it was found that neither clump nor dbh had a significant effect, a test was run with the compiled data from both sites, with a sample size of ninety-two. The dependent variable was 1990-91 relative growth response, this being the ratio of the 1990-1991 average growth to the 1986-1988 average growth.

In order to determine whether trees showed a consistent relative growth response to defoliation in 1989 and in subsequent years, a regression test was run using 1990-91 relative growth response and 1989 relative growth response as the two variables. This test indicated whether trees which had a high or low response in 1989 showed the same response in subsequent years, or if trees responded differently.

Results

Effect of clump and dbh on within-site responses to defoliation.

ANOVA revealed no significant effect of clump ($F= 1.032$, $p= 0.47$) or dbh ($F= 0.093$, $p= 0.76$) on 1989 relative growth response within the defoliated site.[Figure 1a] Similarly, in the non-defoliated site, neither clump ($F= 1.35$, $p= 0.25$) nor dbh ($F= 3.092$, $p= 0.095$) had a significant effect on the 1989 relative growth response.[Figure 1b] In sum, clump and dbh had no significant effect on 1989 relative growth response in either the defoliated or non-defoliated site. By examining the p-value, significance can be determined. If a p-value is less than 0.05, then the difference is significant and the null hypothesis can be rejected with 95% confidence. If the p-value range is between 0.05 and 0.10, confidence in rejecting or accepting the null hypothesis is lower than desired. Therefore, p-values that are greater than 0.05 but less than 0.10 do not allow the null hypothesis to be rejected, but it shows a trend in the collected data that should be addressed. Similarly, p-values that are less than 0.05, but greater than 0.03 allows the null hypothesis to be rejected, but since the value is not extremely lower than the cut off of 0.05, the null cannot be rejected with as much confidence.

Effect of selective defoliation on growth of red maple in 1989.

ANOVA revealed that 1989 relative growth response did not differ significantly between the defoliated and non-defoliated sites. However, the 1989 relative growth response was nearly significantly greater in the defoliated site ($F= 3.31$, $p= 0.072$, mean 1989 relative growth for defoliated= 1.106, mean 1989 relative growth for non-defoliated= 0.94). Relative to the average 1986-1988 ring, the 1989 ring was 15% larger in the defoliated site, but 5.5% smaller in the non-defoliated site.[Figure 2]

Effect of selective defoliation in 1989 of red maple's growth in subsequent years.

ANOVA revealed that there was no significant clump ($F=0.51$, $p= 0.93$) or dbh ($F= 0.055$, $p= 0.82$) effect for the 1990-91 relative growth response within the defoliated site.[Figure 3a] Moreover, the ANOVA also revealed no significant clump ($F= 1.90652$, $p= 0.07446$) or dbh ($F= 0.78$, $p= 0.39$) effect on the 1990-91 relative growth response within the non-defoliated site.[Figure 3b] Therefore, an ANOVA comparing the 1990-91 relative growth response can be compared between the two sites since we have already corrected for these factors (i.e. dbh and clump).

ANOVA revealed that the 1990-91 relative growth response was significantly different between the defoliated and non-defoliated sites ($F= 11.26$, $p= 0.0012$). [Figure 3c] Moreover, by examining the means of 1990-91 relative growth response within these two sites, it showed that the defoliated site had, on average, a higher 1990-91 relative growth response than the non-defoliated site (mean for 1990-91 defoliated= 1.29, mean for 1990-91 non-defoliated=0.99).

Growth of red maple was 29% greater in the defoliated than in the non-defoliated site. Therefore, from this data, it can be noted that defoliation was beneficial to the subsequent growth of the red maple.

Regressional growth response to defoliation

By doing a correlation/regression, which used 1989 relative growth response compared to 1990-91 relative growth response, we were able to assess whether individual red maples showed a consistent growth response to defoliation. For instance, whether those with high relative growth response in 1989 continued to show a high relative growth response in subsequent years (i.e. 1990-1991). At the same time, this test showed whether those individuals that showed relatively low relative growth response in 1989 continued to show low relative growth response in subsequent years. The plot showed that there is no correlation between 1989 relative growth response and response of subsequent years.

Figure 1a -- Defoliated site

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Clump	2.38	22	0.11	1.032	0.47
DBH	0.0097	1	0.0097	0.093	0.76
Error	2.10	20	0.10		

Figure 1b -- Non-defoliated site

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Clump	2.54	27	0.094	1.35	0.25
DBH	0.22	1	0.22	3.09	0.095
Error	1.33	19	0.70		

Figure 2

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Site	0.31	1	0.31	3.31	0.072
Error	8.36	90	0.093		

	Least Square Mean	SE	N
Site 1 (defol.)	1.06	0.046	44
Site 2 (non-defol.)	0.95	0.044	48

Figure 3a -- Defoliated site

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Clump	3.99	22	0.18	0.51	0.93
DBH	0.019	1	0.019	0.055	0.82
Error	7.05	20	0.35		

Figure 3b -- Non-defoliated site

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Clump	3.03	27	0.11	1.91	0.074
DBH	0.046	1	0.046	0.78	0.39
Error	1.12	19	0.59		

Figure 3c -- Comparison of sites

Source	Sum of Squares	DF	Mean-Square	F-Ratio	P-Value
Site	1.91	1	1.91	11.26	0.0012
Error	15.29	90	0.17		

	Least Square Mean	NE	N
Site 1	1.29	0.062	44
Site 2	1.00	0.059	48

Discussion

The results of this study suggest that red maple benefited from defoliation of other tree species by the tent caterpillar in 1989. Compared to non-defoliated sites, relative growth response (the ratio correcting for factors which cannot be standardized such as genotype and microsite) in defoliated sites increased nearly significantly in 1989 and significantly in 1990-1991. Lack of significant response in 1989 may reflect the fact that defoliation occurred in the latter part of red maple's most intense growth period. By late June, when defoliation occurred, the majority of the 1989 growth ring had already formed. Therefore, response to this disturbance may be less apparent in 1989 than in subsequent years. 1989 growth may have already been established because there is greater cambial activity in the spring than in the summer causing larger diameters in latewood than earlywood (Young & Giese, 1982). In fact, in measuring 1990 relative growth response, a significant response was seen. This further supports the notion that though red maples reaped benefits in 1989 from defoliation, and the result mainly manifested itself in later years. This is an interesting find, because it demonstrates red maple's ability to adapt to changing growing conditions.

In assessing the effect of defoliation on growth in subsequent years, it is also interesting to consider how an individual tree responded to defoliation in the short-term in comparison to long-term. We would expect to see that those trees which showed high response in 1989 would continue to show high response in subsequent years. However, our results showed that in fact there was no correlation between growth response in 1989 and response in subsequent years. By looking at the amount of variation in growth response, we can begin to speculate about the absence of a correlation. We would expect to see a greater amount of variation in 1989 since this is when the disturbance occurred. In contrast to our expectation, 1989's variation was surprisingly less than that of 1990-91. This may be explained by the timing of the defoliation. Defoliation occurred in the latter part of the 1989 growing season, after the majority of the 1989 growth ring had been formed. Thus, growth response due to defoliation would be more evident in subsequent years, which accounts for the greater variation in 1990-91.

Because trees from the same clump are often of the same genotype (Wilson, 1984), and certainly share similar microsites, it was expected that response to defoliation would be more similar within than between clumps. However, we did not find this to be the case. In either the defoliated or non-defoliated sites, the lack of difference among clumps suggests that the difference between sites also is not due to microsite or genetic variation. Therefore, any difference in relative growth response can better be attributed to defoliation.

Our results also suggest that trees of all ages responded similarly to defoliation. We found this result surprising. Trees of larger dbh are older, taller and closer to the canopy, making them less limited by light. Therefore, we expected them to show less of a response to increased light exposure. This was not the case, the younger red maples in fact did not show a much greater response than older ones. This could be due to the placement of the younger red maples. For instance, if there was a red maple of small dbh amongst a clump of older, canopy red maples it would not benefit as much from defoliation because it would continue to be shaded. However, if a young red maple of equal dbh was not surrounded by overshading canopy trees, its light exposure would increase dramatically. Therefore, two trees of equal dbh can be affected differently.

We advise caution, however, in embracing these conclusions for several reasons. First, we may not have accurately measured red maple growth rings. Red maples are diffusely porous, making growth rings difficult to distinguish (Wilson, p.86). The ray cells of red maples are very distinct and may decrease visibility of growth rings (Wilson, p. 90). Second, a larger sample size of both defoliated and non-defoliated red maples would add to the credibility of our conclusions. We suggest that future studies use better instruments for coring the trees and more effective methods in distinguishing growth rings. Factors such as slope position and relative abundance of species near the red maples could have been tested to discover any additional effects on relative red maple growth. Sampling more than two trees from each clump could have given a better indication of the effect of genotype on relative red maple growth. In addition, we suggest future studies consider factors, such as slope position of red maples and relative abundance of nearby species, that could have affected red maple growth.

Since our study did not completely resolve all the questions related to this topic, other studies should be done in order to better understand forest disturbance. In contrast to our study, perhaps an experiment examining the growth response of those trees which were subject to defoliation could be done as well. We would expect that these species would show a relative growth response opposite to that of the red maple, showing a decrease in relative growth response in 1989 and subsequent years. Also, another interesting study would be one which could isolate the specific secondary compound which makes the red maple resilient to defoliation. Beyond tree growth response, it is important to realize that disturbance affects many aspects of forest ecology. Our study focused specifically on tree growth response, but many other factors could be studied as well, such as soil composition, light intensity, and water and nutrient uptake.

From our data, it is evident that the red maple is an opportunistic species that has the ability to take advantage of defoliation of surrounding species. Red maple is the only northern hardwood tree that is avoided by the tent caterpillar (Martineau, 1984). Reasons for this selected defoliation against the red maple are unknown, however, possible explanations include an evolved secondary compound or deterent. Most likely, in this case, red maple possessed a deterent that prevented the tent caterpillar from feeding on it because the caterpillars avoided the red maples entirely (Karowe, 1995). Most insects demonstrate selective defoliation such as this because they specialize in detoxifying a limited number of plant secondary compounds. Consequently, natural selection in plants may favor an evolved chemical response to herbivory. The case of the red maple may be an example of a recently evolved response to defoliation. In this study, it is evident that defoliation is beneficial to red maple and harmful to its neighboring species. This study is an example of how disturbance can be both beneficial and detrimental even in a single community.

Literature Cited

Allaby, Michael. The Concise Oxford Dictionary of Botany. Oxford University Press: Oxford, England. 1992, p. 159.

Horn, Henry S. Adaptive Geometry of Trees. Princeton University Press: Princeton, New Jersey. 1984, pp. 51-97.

Kimball, John W. Biology. Addison- Wesley Publishing Company: Reading, Massachusetts. 1965, pp. 220-5.

Karowe, David. Personal Communication

Martineau, R. Insects Harmful to Forest Trees. Multiscience Publication: Canada, 1984, pp. 210.

Wilson, Brayton F. The Growing Tree. University of Massachusetts Press: Amherst, Massachusetts. 1984, pp. 10-20, 55-67.

Young, Raymond A. Introduction to Forest Science- Second Edition. John Wiley and Sons Inc.: New York. 1990, p. 75.

Figure 2. Effect of Amino Acid Concentration on Preference by Honeybees