Impact of Defoliation by the Colorado Potato Beetle on Potato Yields

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ABSTRACT

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Potato plots were partially defoliated by populations of *Leptinotarsa decemlineata* (Say) to learn how insect defoliation affected potato yields. The experiment was repeated 7 times at 2-wk intervals throughout the season to determine how plant sensitivity to defoliation changed with plant development. The percent yield reduction of defoliated rows was regressed on percent defoliation for each time period. Yields were little affected by defoliation except during the middle 4-6 wk of the season when yields were reduced up to 64% by total defoliation. The most critical period of plant development corresponds to the emergence and oviposition of summer adult Colorado potato beetles. Levels of defoliation and yield reduction were not correlated during the last month of the season, and the value of continuing weekly insecticide treatments during this time is called into question.

The premise that leaf removal by animals reduces plant productivity is based on the assumption that the photosynthetic area removed by herbivores directly reduces plant growth. Unfortunately, the relationships between leaf removal and plant growth are not nearly as simple and straightforward as the aforementioned statement might imply. The ratio of seed yield to leaf area reduction is usually less than unity (e.g., Turnipseed 1973), and defoliation of annual crops apparently must exceed a threshold, usually between 5 and 30%, before primary productivity is impaired (Mattson and Addy 1975). It is also known that the sensitivity of plant species changes as some function of plant development, but few studies have tried to relate these plant changes to the abundance patterns of their natural defoliators to determine their direct impact on plant growth and reproduction.

Making these determinations directly presents many technical problems in terms of obtaining enough herbivores and manipulating them to cause the desired levels of defoliation at the desired times. Thus, in most investigations, mechanical defoliation has been substituted for herbivorous defoliation. However, herbivores can be less debilitating than mechanical defoliators for several reasons. Most herbivores, for example, selectively feed on plant tissues, some of which may be less "valuable" than others, whereas mechanical defoliation tends to be nonselective (Jameson 1963). Natural defoliation may even have positive effects on plants as well, for example, by stimulating the rate of photosynthesis in remaining leaves (Maggis 1964) or by causing the production of more new foliage than was removed (Harris 1974, Dyer and Bokhari 1976). Since these factors could introduce errors in mathematical models predicting plant yield losses due to insects, data for such models must be obtained by defoliating plants naturally by insects.

Potatoes, one of the more important agricultural crops in Connecticut, can be completely defoliated by the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). The beetle is multivoltine in Connecticut, but because adults oviposit repeatedly for several weeks, all life stages are usually present throughout most of the growing season. Uncontrolled populations may defoliate and kill plants before tuber initiation. Little more is known about the effect of insect defoliation on potato production, although several studies have shown the impact of mechanical defoliation that simulate hail damage on yields (Beresford 1967, Murphy and Goven 1962, Snyder and Michelson 1959, Sparks et al. 1957, Takatori, et al. 1952). They generally show yields being little affected by defoliation late in the season, after tubers have nearly reached full size, and also early in the season as well.

To quantify the impact of Colorado potato beetle feeding on potato yields, I manipulated beetle densities on several potato plots, allowed them to feed for 2 wk, measured the amount of foliage remaining, and related the degree of defoliation to the degree of yield reduction. To determine if the sensitivity of potato changed with seasonal development, these experiments were repeated at 2-wk intervals throughout the season. Linear regression analysis was used to determine the effect of insect defoliation on yield for each time period, and curvilinear regression analyses were used to determine the changes in plant sensitivity with time. Also, the seasonal abundance pattern of *L. decemlineata* was studied and compared to the plant sensitivity function to determine the most critical times to control insect populations.

**Methods and Materials**

Potatoes (cv 'Katahdin') were planted at the Lockwood Fann, Mt. Cannel, CT, on May 3, 1979. Seed pieces, treated with a fungicide, were planted at 0.3-m intervals in 120 blocks, each consisting of 3 rows spaced at 0.91 m and 3.0 m long. Blocks were separated by a buffer of bare ground 1.83 m on all sides. After obtaining the results of a soil test, the whole field was fertilized at the rate of 830 kg/ha of 10% N,P, and K. Weeds were controlled by a preemergence herbicide applied shortly after planting and by 2 cultivations during the 1st month after emergence. Starting in mid-July all plants were treated with fungicide weekly for prevention of late blight.

Plants began to emerge May 21 and completed, emerging May 31; the number of plants per row was recorded at this time. Adult beetles were first seen on plants May 24. Plants were carefully examined, and all adults and egg masses were removed and saved on a daily basis.
through June 11. Plants became too large to examine carefully after this time, and beetles were controlled for the remainder of the season with insecticides applied weekly. A number of materials was used but formulations of permethrin combined with endosulfan appeared to be most effective.

Eighteen plots were used in the 1st 2 defoliation periods, 12 were used in the 3rd, and 10 were used in each of the others. Four plots were used as undefoliated controls in the 1st 3 periods and 2 were used in the rest.

Cages large enough to contain a whole plot were covered with a coarse nylon mesh (3-mm openings) to minimize light reduction. Beetles collected previously were released on caged plots in varying numbers to cause a range of defoliation levels between 25 and 100% over a 2-wk period. After the initial adult colonization period (after the 1st 2 defoliation periods), the tops of cages became unnecessary (since larvae cannot fly and adults seldom did so) and were removed. With the bottoms of the cages sealed with earth, adults and larvae were effectively retained within cages.

After 2 wk of feeding, insects were removed, a foliage sample was taken, and plots were sprayed to prevent further defoliation. Two fully-expanded, mature leaves were collected from each of 3 plants from each of the 3 rows in each plot. All leaflets, including secondary leaflets, were removed from the petioles, and the total area of these leaflets was determined with a photoelectric leaf area meter. The mean area of leaves sampled from undefoliated rows through the 1st 3 defoliation periods was calculated, and the percent leaf area remaining in samples from defoliated rows was calculated with respect to this value.

Leaf removal for leaf area measurement imposed an additional defoliation of between 2-10%/sampled plant, depending on the defoliation period. The amount was proportionally greatest early, when plants were small. However, only 30% of the plants in each row were sampled; thus, total defoliation due to leaf sampling amounted to no more than 3%/row. Because such defoliations were slight and applied equally to control and insect-defoliated rows, they were ignored. Similarly, the effect of defoliation caused by egg mass removal also was ignored. The amount of leaf area removed was 1-3%/plant, at most, assuming all leaflets were the same size, and such defoliation was at random with respect to insect defoliation treatments. As will be shown subsequently, the amount of defoliation inherent in experimental methods was only a fraction of that imposed by insects and proportionally greatest when plants were least sensitive to defoliation.

There were 7 defoliation periods in all. The 1st began on June 5, when plants were 15-20 cm tall, and the last ended Sept. 12, when virtually all adult beetles had entered diapause. Vines were killed to facilitate harvesting on Sept. 13.

Potatoes were harvested with a 1-row mechanical digger, and the yield of each row was recorded. The 1st 10 rows also were harvested manually after mechanical harvesting to recover any missed tubers. This was discontinued because no additional tubers were unearthed. Where necessary, yields were adjusted upward if less than 10 plants/row emerged. More plots were prepared than were ultimately used, and the yields of rows from these additional undefoliated plots were included in the calculation of the mean yield of undefoliated rows. Yields of undefoliated rows did not differ significantly with position within plots (center vs. edge), with plot position within the whole field, or with the defoliation period during which they served as controls. Thus, yields of all undefoliated rows were pooled to determine the average yield of undefoliated rows. The percent yield of each defoliated row was calculated relative to this.

After performing linear regression analyses between percent yield and percent leaf area remaining for each defoliation period, successive regression coefficients were compared statistically to determine if the sensitivity of plants varied with time. The expected yield reductions resulting from the defoliation levels of 100, 90, 80, and 70% at each time period were then calculated using the parameters obtained from each linear regression analysis. The formula $Y = a + bX$ was used, where $a$ and $b$ are the y-intercept and regression coefficients, and $X$ is the percent leaf area remaining, or 100 minus the percent defoliation desired. The best-fitting 2nd-order least squares regression equation for each defoliation level was then calculated from these expected values. The resulting family of curves was plotted to depict the changes in plant sensitivity to defoliation as a function of seasonal development.

To compare the changes in potato defoliation sensitivity with the seasonal abundance of the plant's major herbivore, a summary of the life history of *L. decemlineata* on insecticide-free potatoes in Connecticut was prepared from data collected in 1978 (Hare, unpublished data). Briefly, all life stages of the Colorado potato beetle were counted weekly on individual potato plants. Weekly relative abundances of adults were calculated by dividing the number of adults counted per week by the season-long total. Relative abundances of larvae were calculated similarly after pooling all instars. Relative abundances of each were plotted, and smooth curves that connected points were fitted by eye. Limited sampling performed in 1979 showed no significant changes in abundance patterns between years.

**Results**

Yields increased linearly with increasing leaf area during the 2nd through 5th defoliation periods, especially in the 4th (Fig. 1, Table I). The y-intercepts (the expected % yield when plants were 100% defoliated) show that yields were reduced 39, 64, and 54% during periods III, IV, and V, respectively, but were little affected by 100% defoliation if it occurred earlier (periods I-II) or later (periods VI-VII). The regression coefficients differed significantly between periods I and II, III and IV, and V and VI, but not between II and III, or IV and V. The last pair (VI and VII) were not tested since neither differed significantly from O.

Fig. 2 shows the curves depicting the sensitivity of plants to defoliation throughout the season. Fig. 3 shows the abundance patterns of larvae and adults of *L. decemlineata*. Comparing Fig. 2 and 3 shows that plants are most sensitive to defoliation when summer generation adults are emerging and beginning to oviposit.
FIG. I. Scatter diagrams showing the relationship between % remaining leaf area (horizontal axes) and % yield (vertical axes) for each defoliation period. The least-squares regression line is included when yields were reduced significantly by defoliation (see Table 1).
Table I.-Regression statistics between % leaf area remaining and yields expressed as % yield of undefoliated rows. Yield of undefoliated rows was 3.71 kg/m² (±0.07 SE, N=117). Mean area of foliage samples from undefoliated rows was 7.27 ±0.20 dm² (N=38).

<table>
<thead>
<tr>
<th>Defoliation period</th>
<th>Number of Rows</th>
<th>Regression Dates</th>
<th>Regression coefficient</th>
<th>V-intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>52</td>
<td>(6/5-6/20)</td>
<td>-0.029</td>
<td>101.11</td>
</tr>
<tr>
<td>II</td>
<td>53</td>
<td>(6/21-7/3)</td>
<td>0.242*</td>
<td>85.91</td>
</tr>
<tr>
<td>III</td>
<td>29</td>
<td>(7/4-7/16)</td>
<td>0.431*</td>
<td>61.33</td>
</tr>
<tr>
<td>IV</td>
<td>30</td>
<td>(7/17-7/30)</td>
<td>1.32**</td>
<td>36.42</td>
</tr>
<tr>
<td>V</td>
<td>30</td>
<td>(7/31-8/13)</td>
<td>1.06**</td>
<td>49.13</td>
</tr>
<tr>
<td>VI</td>
<td>30</td>
<td>(8/14-8/28)</td>
<td>-0.244</td>
<td>99.59</td>
</tr>
<tr>
<td>VII</td>
<td>30</td>
<td>(8/29-9/12)</td>
<td>0.131</td>
<td>83.36</td>
</tr>
</tbody>
</table>

* P < 0.01. ** P < 0.001.

FIG. 2.-Defoliation curves showing changes in plant sensitivity to defoliation with seasonal development. The points on each curve are the % yield reduction caused by the specified % defoliation at each time during the growing season.

FIG. 3.-Generalized seasonal abundance pattern of Colorado potato beetle adults (solid line) and larvae (dashed line).

Discussion

Potato tuber production can be reduced nearly 13 by 100% defoliation by insects near the middle of plant development but is little affected by single periods of insect defoliation earlier or later. The critical period during which potatoes are most severely affected by insect leaf removal corresponds with the emergence and oviposition by summer generation adult potato beetles.

These results generally correspond to patterns of potato sensitivity to hail damage. Up to 100% simulated hail damage reduced yields 37% when plants were 15-20 cm high, 93% at full bloom, and 63% when plants were "full-grown", whereas defoliations estimated to be 20% reduced yields 1, 14, and 9%, at the same periods (Sparks and Woodbury 1959). My yield reductions were not as great but followed the same general trend. The differences in the ways plants are defoliated by insects and hail are likely responsible for the observed differences in magnitude. Hail not only removes leaflets, but also bruises and breaks stems, thus reducing the number of viable axillary buds from which new leaves could be produced. Potato beetles remove all leaflets from a petiole but generally do not damage stems or dormant buds. These insect-defoliated plants may have refoliated faster than the hail-defoliated plants in other studies. The possibility that insects also physiologically induce rapid plant growth (e.g., Reardon et al. 1974, Dyer and Bokhari 1976) cannot be ignored. In any event, insect defoliation seems to be only 65-70% as debilitating as mechanical defoliation.

That potatoes are insensitive to leaf removal late in the season comes as no great surprise since tubers were no doubt nearly full-sized before defoliation occurred (Sparks and Woodbury 1959). The more surprising result that potato is insensitive to insect defoliation early may be a consequence of changes in photosynthetic allocation during plant development. Under specific environmental conditions, plant growth can be limited either by capacity of a plant to produce photosynthate ("source limitations") or to utilize it ("sink limitations"). Plants are more likely to be sink-limited early in their growth but become more source-limited after creating such additional sinks as developing tubers or fruits (Wareing and Patrick 1975). Mechanical defoliation of many plant species demonstrates that defoliation before flower initiation affects yields less than does the same amount during flowering and fruit production (Jameson 1963, Turnipseed 1973, Harriss 1974).

The critical period for insect control on Katahdin potatoes in Connecticut centers on the middle of July when potato beetle summer adults emerge and begin oviposition. However, to conclude that beetle populations require no control at any other time would be erroneous. The density of summer adults would be reduced by earlier control of larvae and also, albeit to a more variable amount, by control of the previous generation. Currently, adequate control is obtained by systemic insecticides at planting and weekly sprays during the remaining 8-10 wk of the season. Within one season, my results strongly suggest that yield improvements due to insecticide applications diminish rapidly. They also call
into question the value at all of the later applications, even though plants may be heavily defoliated by 2nd generation Colorado potato beetle larvae (see Fig. 3).

The tolerance to defoliation of this and other agricultural species, which have been selected for high and uniform yields may not be comparable with "natural" plant species. If these results were extrapolated to natural plant-herbivore associations, then apparently the evolutionary impact of a seasonal period of intense phytophagy is slight. For example, if we postulate 2 potato genotypes differing only in potato beetle susceptibility, then even at the most critical period, the susceptible genotype must be defoliated nearly 55% before the vegetative reproductive biomass, i.e., tuber yield, would be reduced significantly (i.e., 2 SE) below that of the resistant genotype.

There are, of course, some beetles present at times other than their peak abundance and they would impose continuous but mild defoliation. Although young plants certainly have sufficient reserves and potential to compensate for some insect damage, there is obviously some level of repeated damage for which plants could not compensate.

REFERENCES CITED


