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Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings

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Summary

Responses of forest trees to defoliation by insects such as gypsy moth vary greatly from site to site and from individual to individual. To determine whether some of this variation could be explained by variation in other stress factors, red oak (*Quercus rubra* L.) seedlings were exposed to low and high light, water, mineral nutrient, and defoliation treatments, in a complete factorial design in a greenhouse. Significant interactions were observed among factors for photosynthesis, growth, and mortality, indicating that the response to defoliation was influenced by other stresses. Defoliation increased the photosynthetic capacity per unit leaf area of seedlings grown in the low-water, but not in the high-water, regime. In response to defoliation, growth of seedlings in a low-mineral-nutrient, or low-light, regime was depressed less than that of seedlings grown in a high-mineral-nutrient, or high-light, regime. However, defoliation resulted in a similar percent reduction in biomass in all seedlings in both the high and the low light, water, and mineral nutrient treatments. Defoliation-induced mortality of shaded plants was twice that of plants grown in full sun.

Introduction

Effects of gypsy moth defoliation on eastern deciduous forest trees vary (Campbell and Sloan 1977, Herrick and Gansner 1987, Gansner 1987). Some of this variability is due to differences in tree species composition among stands. Gypsy moth feeds on many hosts, but it exhibits preferences for certain species, such as oak (*Quercus* spp.) (Mosher 1915, Houston and Valentine 1977, Lechowicz and Jobin 1983, Herrick and Gansner 1986). Even in stands of preferred species that are defoliated to a similar extent, there is much variability in the impacts of defoliation. For example, Gottschalk (1990) observed that mortality in gypsy-moth-defoliated stands classified as oak-dominated varied from 5% (not significantly different from undefoliated stands) to more than 80% (Gottschalk 1990). This variation in response to defoliation might be associated with the availabilities of resources. Such factor interactions have been invoked to explain non-linear responses to environmental perturbations such as acid precipitation (e.g., Kohut et al. 1987, McLaughlin et al. 1987) and elevated atmospheric CO_2 (e.g., Strain and Bazzaz 1983).

There is a trend toward reduced herbivory in plants adapted to low-resource environments, e.g., deserts and tundra (Coley et al. 1985, Room et al. 1989). However, within communities, periodic stresses such as drought may promote insect outbreaks through effects on host–plant physiology and insect response (Wargo 1984, Mattson and Haack 1987). Several studies with herbaceous plants have shown

that effects of defoliation depend on resource availabilities (Lee and Bazzaz 1980, Belsky 1986, Verkar et al. 1986, Maschinski and Whitham 1989, but see Fowler and Rausher 1985). Defoliation causes a reduction in root starch content of oaks (Parker and Patton 1975, Wargo 1981) that is dependent on resource availabilities (Parker and Patton 1975, Parker 1978, 1979). Crown condition is also a good predictor of the effects of defoliation (Campbell and Valentine 1972, Campbell and Sloan 1977). However, in most studies of deciduous tree species in which interactions between resource availabilities and defoliation were assessed, resource availabilities were not controlled.

The objective of this study was to determine whether variability in the response of *Quercus rubra* to defoliation by gypsy moth could be explained by variations in other stress factors. *Quercus rubra* seedlings were exposed to a factorial combination of high and low water, mineral nutrient, light, and defoliation treatments and the responses of photosynthesis, growth, and survival were observed.

Materials and methods

Plant materials and experimental design

Acorns from a bulk seed collection were obtained from the Pennsylvania Bureau of Forestry State Tree Nursery. Two or three acorns were planted 3–5 cm deep in each of 448 pots (30 cm deep × 15 cm diameter, Hanson et al. 1987) containing 4 l of turface, an arcillite-clay, plant-growth medium. All pots were watered daily for 3 weeks while germination proceeded. Transplanting and thinning were then carried out to ensure a final density of one tree per pot. Pots were segregated into eight blocks in the greenhouse, with 56 plants per block. Four blocks were covered with 70% neutral black shadecloth. Shaded blocks were alternated with unshaded blocks to minimize any effect of greenhouse position on irradiance. Within blocks, half the plants were watered to saturation twice weekly (low water) and the remaining half were watered to saturation daily (high water). In a factorial manner, half of the plants in each block received 500 ml of 10% Hoagland's solution once weekly (low mineral nutrients) and the other other half received 500 ml of 50% Hoagland's solution once weekly (high mineral nutrients). After two months, half of the plants were manually defoliated by removing all leaf blades with scissors. Thus, there were 16 treatments (light × water × nutrients × defoliation) with a total of 28 trees per treatment (seven trees per treatment block). Refoliation began within 1 to 2 weeks.

Photosynthesis measurements

One month after defoliation, photosynthetic light response curves were made on a single leaf of one or two trees per block in each treatment (n = 4–8 trees per treatment) with a Li-Cor 6200 photosynthesis system. Individual plants had one, two, or three flushes of leaves, and the leaves of defoliated plants differed in age from controls. Therefore it was not possible to control for leaf age or flush because seedlings differed in growth stage. Measurements were made in a growth chamber

at 25 °C equipped with a high-density discharge, mercury-vapor lamp as the light source. Humidity and CO_2 concentration in the chamber were not controlled. Measured leaves were chosen for convenience of access to the cuvette within the growth chamber. Net photosynthetic rates were measured at irradiances of 0, 130, 250, 410, and 1100 μmol m^{-2} s^{-1} after an adjustment period of at least 20 min between measurements to provide estimates of dark respiration, light compensation point, quantum yield, and light saturated net photosynthesis or photosynthetic capacity (photosynthetic rate at 410 or 1100 μmol m^{-2} s^{-1}, whichever was higher). Four-way analyses of variance were carried out for each measure.

Final harvest

After four months, seedlings were harvested and separated into roots, stems, and leaves. Leaf area was determined with a Li-Cor portable area meter (LI-3000), after which all plant parts were dried at 65 °C for at least 48 h and then weighed. A four-way nested analysis of variance was carried out with leaf area, leaf weight, specific leaf weight (leaf weight per unit leaf area), stem weight, root weight, total weight, root/shoot ratio (analysis of root/shoot ratio was performed on arcsine transformed proportions, i.e., root weight/total weight), and leaf area ratio (leaf area per g dry weight) as dependent variables and light, water, mineral nutrients, defoliation, and their interactions as independent variables. Total weight was interpreted as a measure of growth because all trees started as acorns of approximately equal size. In defoliated plants, a part of any effect on growth included the effect of the experimental removal of leaf biomass.

In addition, the effects of two-way interactions among factors (e.g., defoliation × drought) on mortality (number of plants dying in each treatment) were analyzed as two-way contingency tables with a G-test for lack of independence of each pair of factors. Significant differences in mortality between levels of each factor were determined by Student's t-test.

Results

Mortality

Mortality of defoliated plants was 32±7%, which was significantly greater than that of undefoliated plants (1±1%, t-test, $P < 0.001$). Among defoliation treatments, mortality of shaded trees was significantly greater than that of unshaded trees (Figure 1; t-test, $P < 0.05$).

Photosynthesis

Defoliation alone did not have a significant effect on the cardinal points of the photosynthetic light response curve. However, the effects of defoliation on photosynthesis varied with watering regime. Leaf photosynthetic capacity increased in response to defoliation in seedlings subjected to the low-water treatment, but not in seedlings subjected to the high-water treatment (Figure 2; defoliation × water

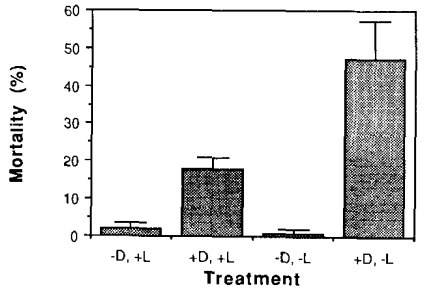

Figure 1. Mortality of red oak seedlings in response to defoliation (D) and light (L). +D = defoliated, −D = not defoliated, +L = unshaded, −L = shaded,.

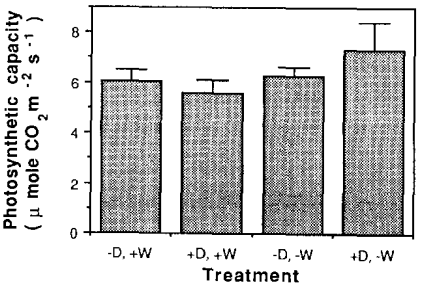

Figure 2. Effect of defoliation on light-saturated net photosynthesis at 25 °C in seedlings subjected to the high-water (+W) or low-water (−W) treatment.

interaction, $P < 0.05$). The photosynthetic response to defoliation depended on irradiance (defoliation × water × light interaction, $P < 0.01$) and mineral nutrient supply (defoliation × water × light × mineral nutrients interaction, $P < 0.05$). There was also a significant three-way interaction (defoliation × water × light interaction, $P < 0.05$) affecting the light compensation point.

Plants grown in high light had typical sun-leaf photosynthetic light curves, whereas plants grown in low light had typical shade-leaf photosynthetic light curves, (Figure 3). As expected, the light compensation point and photosynthetic capacity were significantly higher for plants grown in high light than for plants grown in low light (Figure 3; $P < 0.05$ for both variables). Dark respiration of plants grown in high light was greater than that of plants grown in low light (Figure 3; $P < 0.01$). Two-way interactive effects of mineral nutrient and water availabilities with irradiance were observed for all four photosynthetic characteristics examined (mineral nutrients × light interaction—light compensation point, $P < 0.05$; respiration rate, $P < 0.05$; water × light interaction—quantum yield, $P < 0.05$; light compensation point, $P < 0.05$; photosynthetic capacity, $P < 0.05$).

Growth

Defoliation caused a sharp reduction in root, stem, and leaf weights as well as leaf

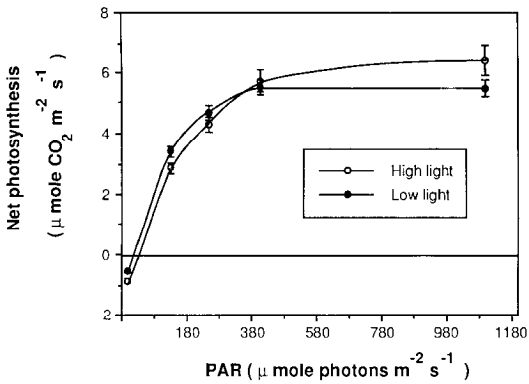

Figure 3. Photosynthetic light response curves of shaded plants and plants grown in full sun.

area ($P < 0.001$ for all four variables) and a shift in biomass distribution. Defoliated plants produced thinner leaves ($P < 0.01$) and had a higher root/shoot ratio ($P < 0.01$) and a lower leaf area ratio ($P < 0.001$) than undefoliated plants. The effects of defoliation were modulated by low-light or low-mineral-nutrient availability (defoliation × mineral nutrient interaction—leaf area, $P < 0.05$; stem weight, $P < 0.001$; root weight, $P < 0.01$; total weight, $P < 0.01$; defoliation × light interaction—stem weight, $P < 0.05$; root weight, $P < 0.01$; total weight, $P < 0.001$). The absolute decrease in biomass caused by defoliation was generally less when resources were low than when resources were high (Figures 4a and 4b), but there was no significant difference in percent reduction in total biomass due to defoliation between seedlings grown with low availabilities of resources and seedlings grown with high availabilities of resources (ANOVA for each factor, $P > 0.05$).

Oak seedling growth was significantly reduced in response to low availabilities of mineral nutrients ($P < 0.01$) or light ($P < 0.001$). When the availability of mineral nutrients was low, seedlings allocated proportionally more biomass to roots ($P < 0.001$). The effect of low mineral nutrient availability was greater at high irradiance than at low irradiance (mineral nutrient × light interaction, $P < 0.01$ for total weight) (Figure 4b). The water treatment had no influence on growth either alone or in combination with the other resources.

Discussion

Effects of defoliation on oak seedling photosynthesis, growth, and survival varied as a function of the availability of resources experienced by the plants as shown by several other studies (Lee and Bazzaz 1980, McNaughton and Chapin 1985, Verkar et al. 1986, Karban et al. 1989, Maschinski and Whitham 1989). Defoliation stimulated photosynthetic capacity in plants subjected to low water availability. This may have been due to decreased leaf expansion during refoliation because lower water potentials would result in thicker leaves (high specific leaf weights were observed) with higher nitrogen concentrations and thus a higher photosynthetic capacity per

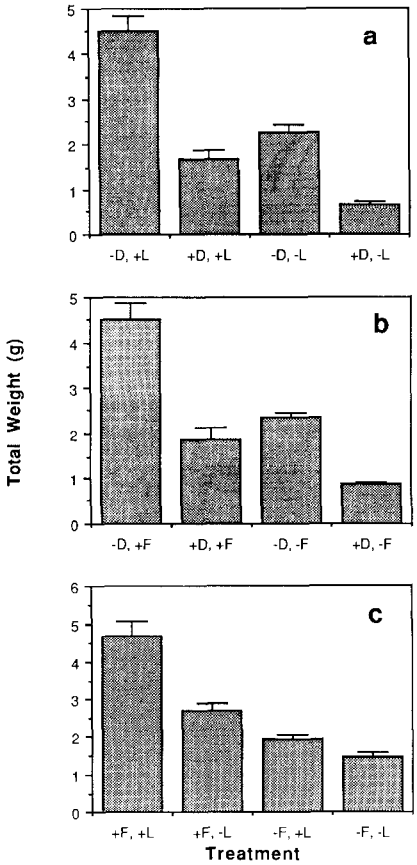

Figure 4. Illustration of two-way interactive effects on total plant weight of greenhouse-grown seedlings. (a) Response to defoliation of shaded (–L) and unshaded (+L) seedlings; (b) response to defoliation at low (–F) and high (+F) mineral nutrient availabilities; and (c) response to fertilizer of shaded (–L) and unshaded (+L) seedlings.

unit leaf area (Field and Mooney 1986). Because red oak seedlings are able to adjust their morphology and physiology in response to mild drought, compensatory photosynthesis may explain why the low-water treatment did not significantly reduce growth. This does not imply that drought is an unimportant variable, because drought in the field could be more severe than that imposed in this study.

In absolute, but not relative terms, the effects of defoliation on growth were modulated by light and mineral nutrients. These results must be viewed with caution, however, because dead plants were not included in the analysis of the growth data. This omission could have resulted in an overestimation of the means for defoliated plants, because, before death, these seedlings probably grew the least.

If mortality is a "threshold" phenomenon, biomass may be a poor indicator of the ultimate impact of an interaction between defoliation and resource availability, because the probability of an individual death will not be a simple linear function of

biomass. The observations that defoliation-induced mortality was twice as high in shaded plants as in plants grown in full sun, whereas defoliation-induced inhibition of growth was less in shaded plants than in plants grown in full sun, suggest that mortality is a threshold phenomenon. The increase in mortality of defoliated seedlings under low-light conditions may be due to a reduction in stored carbon reserves in shaded plants. The photosynthetic light response curves showed only a moderate acclimation to low-light conditions, which might not allow plants in 70% shade to maintain sufficient carbon reserves for refoliation. In the field, the interactive effects of defoliation and light could be greater in subcanopy trees, because irradiance beneath a forest canopy is typically less than 10% of full sun (Jenkins and Chambers 1989).

In the field, trees on drought-prone or low nutrient sites may often be near the threshold of stress causing death. How near they are to that threshold when the additional stress of defoliation is imposed is likely, therefore, to be a major factor determining mortality. At least part of the difficulty in predicting response to defoliation is the inability to assess how stressful a particular environment is for a given trees species. Until a reliable measure of tree stress is available that can be related to mortality, predicting the response to defoliation is likely to remain inaccurate.

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