Interactive effects of soil fertility and herbivory on *Brassica nigra*

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Soil nutrient availability may affect both the amount of damage that plants receive from herbivores and the ability of plants to recover from herbivory, but these two factors are rarely considered together. In the experiment reported here, I examined how soil fertility influenced both the degree of defoliation and compensation for herbivory for *Brassica nigra* plants damaged by *Pieris rapae* caterpillars. Realistic levels of defoliation were obtained by placing caterpillars on potted host plants early in the life cycle and allowing them to feed until just before pupation on the designated plant. Percent defoliation was more than twice as great at low soil fertility compared to high (48.2% and 21.0%, respectively), even though plants grown at high soil fertility lost a greater absolute amount of leaf area (38.2 cm^2 and 22.1 cm^2, respectively). At both low and high soil fertility, total seed number and mean mass per seed of damaged plants were equivalent to those of undamaged plants. Thus soil fertility did not influence plant compensation in terms of maternal fitness. However, the pathways used to achieve compensation in seed production were different at low and high soil fertility. At low soil fertility, relative leaf growth rates (area added per inital area per day) of damaged plants were drastically reduced over the second week of caterpillar feeding. Damaged plants recovered the leaf area lost to herbivory in the two weeks following insect removal by increasing leaf relative growth rates above the levels seen for undamaged plants, but the replacement of leaf tissue lost to herbivory came at the expense of stem biomass. At high soil fertility, relative leaf growth rates of damaged plants were similar to those of undamaged plants both over the second week of caterpillar feeding and following caterpillar removal, and stem biomass was not affected by herbivory. These results suggest that higher levels of soil nutrients increased the ability of plants to stay ahead of their herbivores as they were being eaten. Because damaged plants at high soil fertility were able to maintain leaf growth rates to a greater extent than damaged plants at low soil fertility, they did not fall as far behind undamaged plants over the period of insect feeding and did not have as much catching up to do after feeding ended to compensate for herbivory.

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The interaction between environmental resource availability and plant responses to herbivore damage is poorly understood. Two general hypotheses that incorporate how resource availability is expected to affect herbivore impacts on plants generate conflicting predictions. The compensatory continuum model of Maschinski and Whitham (1989) holds that plants will be more likely to compensate for herbivore damage as soil nutrient levels increase, because greater nutrient availability will increase plant growth rates and allow plants to

replace tissues lost to herbivores more easily. In contrast, Hilbert et al. (1981) predict that plants are more likely to compensate for damage when they are growing slowly, such as under conditions of stress like low resource availability. Their mathematical model shows that a plant with a low relative growth rate at the time of defoliation needs to increase its relative growth rate only a small amount following grazing to equal the production of an ungrazed plant. When plant relative growth rates are higher, much larger increases in

growth rate following defoliation are necessary for pro- duction of grazed plants to equal that of ungrazed plants, and compensation is less likely. There is empiri- cal evidence in support of both of these hypotheses. Some studies have shown that plants are better able to compensate for damage at higher levels of soil fertility (McNaughton et al. 1983, Coughenour et al. 1985, Verkaar et al. 1986, Benner 1988, Maschinski and Whitham 1989, Chapin and McNaughton 1989, Steinger and Müller-Schärer 1992, Willis et al. 1995), while others show that herbivore impacts are more pronounced at higher soil fertility (McNaughton and Chapin 1985, Banyikwa 1988, Van Auken and Bush 1989, Mihaliak and Lincoln 1989, Stafford 1989, Schmid et al. 1990, Meyer and Root 1993). Thus, higher soil fertility can either ameliorate or exacerbate the effects of herbivory, and the reasons underlying these different outcomes are not clear. The difficulty of distinguishing between two hypotheses that generate mutually exclusive predictions on the basis of the avail- able evidence suggests that the full range of conditions important in determining how resource availability influ- ences herbivore impacts on plants have not been iden- tified (see also Alward and Joern 1993, Hicks and Reader 1995).

In addition to affecting plants' ability to compensate for damage, environmental resource availability may also influence the amount of damage that plants re- ceive. Plants growing under fertile conditions frequently support higher densities of insect herbivores than plants growing under less fertile conditions (Price 1991, War- ing and Cobb 1992, Meyer and Root 1996). Herbivore consumption can also be affected by the fertilizer status of the host plant. For example, a low-nitrogen diet often causes insect herbivores to increase their con- sumption, either by increasing the rate of feeding or extending feeding periods (Slansky and Feeny 1977, Mattson 1980). It is therefore likely that plants grown at different levels of soil fertility will also experience different amounts of damage, but this aspect of the interaction between resource availability and plant re- sponse to herbivory has not been incorporated into the general models discussed above. In addition, it is com- mon in experimental studies examining how soil fertility influences plant compensation for herbivore damage to remove a specified proportion of tissue from plants grown under different fertilization regimes (for exam- ple, Verkaar et al. 1986, Mihaliak and Lincoln 1989, Stafford 1989, Schmid et al. 1990, Mutikainen and Walls 1995). Removing a specified proportion of plant tissue rather than allowing damage levels to vary natu- rally with soil fertility obscures the role that differences in herbivore consumption may play in determining how resource availability affects plant response to herbivory.

In the study reported here, I examined the effects of soil fertility on both the amount of damage sustained by plants and on their ability to recover from her-

bivory. I worked with caterpillars of the European cabbage butterfly (*Pieris rapae*, Pieridae) feeding on black mustard (*Brassica nigra*, Brassicaceae). Realistic levels of herbivory at both low and high soil fertility were generated by placing caterpillars on potted host plants early in the life cycle and allowing them to feed on the designated plant until just before pupation. Thus the caterpillars fed as needed to complete their larval development, and the amount of leaf area lost to herbivory at low and high soil fertility was determined. Plant compensation for herbivory was assessed by mea- suring seed set and seed mass at the end of the growing season. In addition, plant vegetative growth was mea- sured periodically over the growing season, both to determine how plants responded to damage as it was occurring and to see if plant growth changed in ways that would enhance recovery after caterpillar feeding ended.

Methods

Study system

Brassica nigra and *P. rapae* were both introduced into North America from Europe (Glassberg 1993, Weath- erbee 1996). *Brassica nigra* is an annual plant that inhabits open, disturbed areas (Rollins 1993). *Pieris rapae* females usually lay a single egg on host plants in the field (Shapiro 1981), thus caterpillars are commonly found at a density of one per plant. After hatching, the caterpillar goes through five instars before pupation. *Pieris rapae* caterpillars are sluggish and will generally remain on an acceptable host plant as long as there is sufficient food. However, the caterpillars show a behav- ioral change as pupation approaches. The normally placid caterpillar becomes very active and begins to wander. It is therefore relatively easy to determine when the caterpillar has completed feeding and is ready to pupate.

Soil fertility and herbivore damage experiment

Plants were grown individually in 15-cm pots, using field-collected seed from a single maternal parent. Plants were grown in sand amended with dolomitic lime and micronutrients. Two levels of soil fertility were created by adding N:P:K fertilizer to this potting medium, so that the high level received three times as much as the low (concentrations of N, P, K respec- tively, in grams per pot for low: 0.32, 0.14, 0.27, for high: 0.96, 0.42, 0.81). The pots were arranged in random order with respect to the fertilizer treatment outside on a flat roof adjacent to the greenhouse at Williams College, Williamstown, MA, USA.

Caterpillars were placed on half of the plants within each fertilizer level on 20 June 1994, at a density of one per plant. The plants that received caterpillars were selected randomly, and cages were not used. Caterpillars were obtained from a captive colony, and were generally in the second instar when they were first placed on the plants. They fed on the plants until just before pupation. Caterpillars were removed from the plants when they became large fifth instars and started wandering off their host plants to pupate. Plants were censused regularly and caterpillar size was recorded. Missing caterpillars were replaced from the colony if they disappeared prior to becoming large fifth instars. Large fifth instar caterpillars that disappeared were assumed to have wandered off the plant to pupate. Towards the end of the caterpillar feeding period, some plants became heavily defoliated. Caterpillars that disappeared from plants with 75% or more leaf area loss were not replaced, even if they had not yet reached the fifth instar, because the heavy defoliation could have caused the caterpillar to abandon the host plant. The first caterpillars began wandering and were removed on 30 June after 10 d of feeding, and the final caterpillars were removed on 5 July.

The effects of soil fertility and caterpillar feeding on plant leaf area, biomass and allocation were assessed by harvesting plants at pre-determined intervals. There were four whole-plant harvests over the growing season. The first took place when caterpillars were placed on the plants to estimate initial plant size, the second after one week of feeding, the third at the end of the insect feeding period, and the fourth after a two-week recovery period following insect removal. For each of these harvests, plants were removed from the pots and the sand was gently washed from the roots. Plants were then separated into their component parts (roots, stems, leaves, and inflorescence if present) and each plant part was dried and weighed. A subsample of leaves on each plant was used to determine leaf areas prior to drying and weighing, and total leaf area per plant was calculated from the subsample. Leaves were digitized using a CCD camera connected to a computer and areas were measured with an image analysis program (NIHImage). Each of these harvests consisted of 48 plants (12 in each of the four soil fertility–insect damage treatment combinations), except for the initial harvest which included 12 plants (six per soil fertility level).

The amount of leaf area lost to herbivory was estimated for damaged plants at the end of the caterpillar feeding period by filling in the missing portions of damaged leaves to create an image of an undamaged leaf. The area the leaf would have had if undamaged was then estimated with the image analysis program and the amount missing calculated by subtraction. However, approximately 30% of the leaves from damaged plants had so much leaf area missing that the

outline of the leaf could not be reconstructed. In these cases, the area the leaf would have had if undamaged was estimated using a regression relating leaf area to leaf length. It was sometimes possible to estimate the length a leaf would have had if undamaged from the damaged leaves, as *P. rapae* caterpillars avoid the leaf midrib. However, in cases where undamaged leaf length could not be reconstructed, length was estimated from undamaged leaves on the same plant.

The rate at which plants added leaf area was calculated for two intervals: the second week of the insect feeding period, and the two weeks following insect removal. A relative leaf growth rate, or the amount of leaf area added per initial leaf area per day, was used to remove the effects of initial plant size. Since plants grown at high soil fertility had much more leaf area than plants grown at low (see Results), correcting for initial area allowed direct comparison of leaf growth rates for plants grown at high and low soil fertility. Relative leaf growth rates were calculated using the following formula: $(\ln \text{area}_1 - \ln \text{area}_0)/(t_1 - t_0)$ where area_0 = leaf area at the start of the interval, area_1 = leaf area at the end of the interval, and $t_1 - t_0$ = the time period in days (Evans 1972). Initial leaf areas were estimated by regressions that predicted total leaf area from leaf number and the length of the longest leaf for each soil fertility–damage treatment combination separately. Leaf areas at the end of each interval were determined at the harvest, as described above.

An additional set of 48 plants was not harvested as described above but instead was left to flower and set seeds. These plants were checked daily as inflorescences developed and the date that the first flower opened was recorded. Since the plants were grown outside they were accessible to pollinators, and pollinators were often observed visiting the inflorescences. Infructescences were harvested as seeds developed. When the most advanced siliques on a plant were dry, brown, and appeared ready to split open, the entire infructescence was harvested. This method allowed me to collect seeds when they were ripe but before seed dispersal occurred. After harvest, seeds were separated from the infructescence and other structures, dried, and weighed, to determine the total mass of seeds produced by each plant. Seeds were then counted and mean mass per seed was calculated. Nine of the original 48 plants developed flowers but the flowers aborted and seeds did not develop for unknown causes. These plants are excluded from all analyses. There was no bias with respect to the herbivore treatment (five were damaged and four were undamaged) but more high soil fertility than low soil fertility plants were lost (six were lost at high and three at low).

There was little extraneous herbivory over the course of the experiment, except that some plants were colonized by aphids. Aphid colonies were removed by hand during the period that caterpillars were feeding on the

plants. After caterpillar removal, all plants were sprayed once with carbaryl. Other work has shown that carbaryl had no detectable effects on plant growth or reproduction (Simms 1992, Maron 1998). In any case, treatment with carbaryl could not bias results in this experiment since all plants were sprayed.

Data analysis

A three-way analysis of variance that included fertility level, damage treatment and harvest was used for variables that were measured more than once over the growing season (total leaf area, biomass of each plant part, biomass allocation, specific leaf area, and relative leaf growth rate). Harvests are independent because a separate set of plants was used for each harvest. When the analysis indicated that the effect of damage depended on harvest ($p < 0.05$ for interaction terms), each harvest was analyzed separately with a two-way ANOVA that included soil fertility level and damage treatment. A two-way ANOVA was also used for variables that were measured only once over the growing season (total seed number, mean mass per seed, and the number of days to open the first flower). When the interaction between damage and soil fertility was significant ($p < 0.05$), the effect of damage was analyzed for each soil fertility level separately. The amount of leaf area lost to herbivory at the end of the caterpillar feeding period was analyzed with a t-test that compared damaged plants at low and high soil fertility. Leaf areas, vegetative biomass data and mean mass per seed were ln transformed, inflorescence mass and total seed number were ln + 1 transformed, and proportions were arcsine square root transformed for statistical analysis.

Results

Effects on leaf area

Higher levels of soil fertility greatly increased plant leaf area. Undamaged plants grown at high soil fertility had 3–4 times as much leaf area as undamaged plants grown at low soil fertility throughout the growing season (Fig. 1). Damaged plants lost leaf area to herbivory over the two-week insect feeding period. During the first week of feeding, the caterpillars were small and their consumption rates were low. There were no significant differences in total leaf area between damaged and undamaged plants after one week of feeding (Fig. 1), even though light feeding damage was visible on plants with caterpillars. Caterpillar consumption greatly increased in the second week as the caterpillars grew. By the end of the insect feeding period, damaged plants had significantly less leaf area than undamaged plants

at both high and low soil fertility (Fig. 1). However, by two weeks after insect feeding stopped, damaged plants had completely recovered the lost leaf area. Total leaf area of damaged plants was equivalent to that of undamaged plants at both high and low soil fertility (Fig. 1).

Plants grown at high soil fertility lost more leaf area to herbivory than plants grown at low soil fertility. On average, 38.2 cm^2 (s.e. = 5.11) of leaf area was missing from plants grown at high soil fertility at the end of the insect feeding period, compared to 22.1 cm^2 (s.e. = 3.84) for plants grown at low soil fertility, and this difference was significant (t-test on ln transformed data, $p < 0.03$, df = 22). However, a different pattern emerged when percent defoliation was calculated. Although the absolute amount of missing leaf area was greater for plants grown at high soil nutrients, percent defoliation was lower for these plants. Plants at high soil fertility lost only 21.0% of their leaf area (s.e. = 4.25), compared to 48.2% leaf area loss at low soil fertility (s.e. = 5.58), and this difference was significant (t-test on arcsine square root transformed data, $p < 0.01$, df = 22).

Soil fertility affected the rate at which damaged plants added leaf area, both over the insect feeding period and in the two weeks after caterpillars were removed. At high soil fertility, relative leaf growth rates were similar for damaged and undamaged plants over the second week of insect feeding (Fig. 2A). In contrast, at low soil fertility, the relative leaf growth rate of
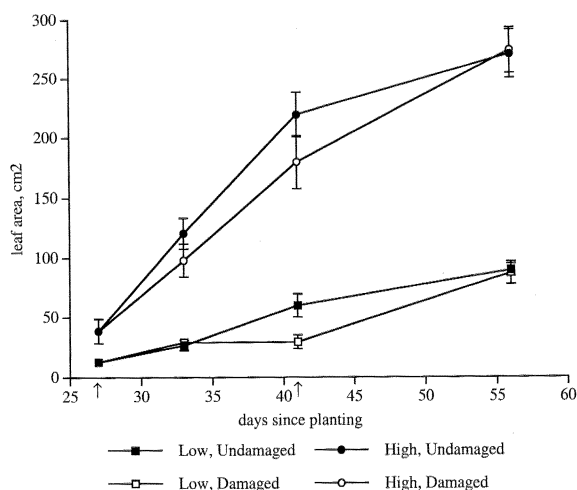

Fig. 1. Effects of soil fertility and herbivore damage on total leaf area. Means and standard errors are shown. First and second arrows along x-axis indicate beginning and end of insect feeding period, respectively. Herbivore damage caused a significant reduction in leaf area only at the end of the insect feeding period, for plants grown at both low and high soil fertility (41 d since planting, two-way ANOVA: soil fertility $p = 0.0001$, damage $p = 0.02$, interaction $p = 0.21$). Fertilizer effects were significant for all harvests ($p < 0.05$). There were no significant interactions between damage and fertilizer level. Data were ln-transformed for analysis.
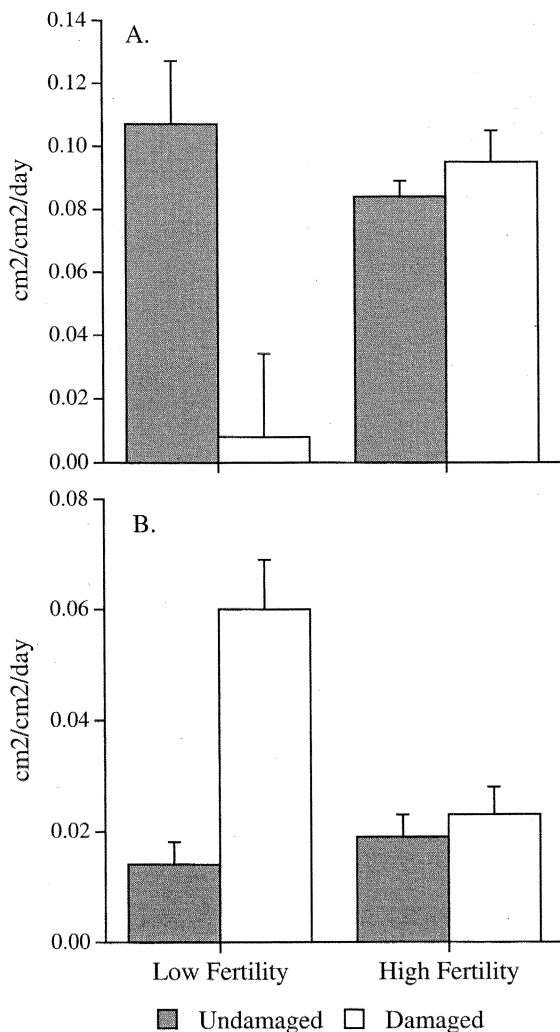
Fig. 2. Effects of soil fertility and herbivore damage on relative leaf growth rate. A. Second week of insect feeding. B. Two weeks following insect feeding. Means and standard errors are shown. Damage affected leaf relative growth rate at low soil fertility but not at high for both intervals (for A, effect of damage at low soil fertility $p = 0.007$, at high soil fertility $p = 0.37$. For B, effect of damage at low soil fertility $p = 0.0002$, at high soil fertility $p = 0.52$).

damage affected only leaf mass and stem mass. The results for leaf mass parallel those already presented for changes in leaf area. Total leaf mass was significantly reduced by damage at both high and low soil fertility at the end of the caterpillar feeding period. By two weeks after feeding stopped, total leaf mass of damaged plants at both high and low soil fertility had recovered to the levels seen for undamaged plants (Fig. 3C). Effects of damage on stem mass did not appear until two weeks after insect removal, and then were seen only for plants grown at low soil fertility. Damaged plants grown at low soil fertility had reduced stem mass compared to undamaged plants, while at high soil fertility stem mass was not significantly affected by damage (Fig. 3B).

Herbivore damage affected how plants allocated biomass to different plant parts at low soil fertility but not at high. At low soil fertility, damaged plants had a lower proportion of their biomass invested in leaves and a higher proportion in roots at the end of the insect feeding period, compared to undamaged plants (Fig. 4A). By two weeks after insect removal, damaged plants grown at low soil fertility had proportionally more biomass invested in leaves and less in stems compared to undamaged plants (Fig. 4B). In contrast, damage did not significantly affect biomass allocation for plants grown at high soil fertility, either at the end of the insect feeding or at two weeks following insect removal (Fig. 4).

Specific leaf area (leaf area/leaf mass) was not affected by herbivory, but was increased at high soil fertility (three-way ANOVA: soil fertility $p = 0.0005$, damage $p = 0.95$, harvest $p = 0.0001$. For all interactions, $p > 0.05$). Specific leaf area of plants grown at high soil fertility was about 10% greater than that of plants grown at low soil fertility (mean ± s.e. was 133.7 ± 3.68 cm²/g at low soil fertility and 146.7 ± 3.11 cm²/g at high soil fertility, averaged across harvests).

Effects on plant reproduction

Total seed production was strongly influenced by soil fertility, but there were no detectable effects of herbivory. Plants grown at high soil fertility produced more than three times as many seeds overall as plants grown at low soil fertility (Fig. 5A). While total seed set of damaged plants was greater than that of undamaged plants at high soil fertility, this difference was not significant, and at low soil fertility seed set of damaged and undamaged plants was similar (Fig. 5A). Mean mass per seed was not affected by either soil fertility or herbivory (Fig 5B). Flowering phenology was advanced at high soil fertility, but was not affected by herbivory (two-way ANOVA: soil fertility $p = 0.002$, damage $p = 0.31$, interaction $p = 0.84$). Plants grown at high soil fertility opened their first flower eight days sooner than plants grown at low soil fertility (number of days from

damaged plants was dramatically reduced compared to undamaged plants (Fig. 2A). In the two weeks following insect removal, there were no significant differences in relative leaf growth rates between damaged and undamaged plants at high levels of soil fertility. However, at low soil fertility, relative leaf growth rates of damaged plants were significantly elevated compared to undamaged plants (Fig. 2B).

Effects on biomass and allocation

Plants grown at high soil fertility were larger than plants grown at low soil fertility (Fig. 3). Caterpillar

planting to first open flower, mean ± s.e.: 58 ± 1.5 for low soil fertility, 50 ± 1.6 for high soil fertility, pooled across damage levels).

Discussion

The results reported here show that soil nutrient availability can affect both the amount of damage that plants experience and the mechanisms by which plants recover from herbivore feeding. It is not sufficient to assume that damage will be constant across environments or proportional to plant size when making predictions about how herbivore impacts will vary with resource availability. In the experiment reported here, plants grown at high soil fertility experienced greater absolute losses of leaf area, but lower percentage reductions, compared to plants grown at low soil fertility. Caterpillars probably consumed more leaf tissue at high soil fertility than at low, but missing leaf area is not an exact measure of caterpillar consumption in this experiment for two reasons. First, plants grown at high soil fertility had higher specific leaf areas than plants grown at low, so a given amount of lost leaf area represented less biomass at high soil fertility compared to low. This difference in specific leaf area was not sufficient to

explain the greater leaf area loss at high soil fertility, as specific leaf area was increased by about 10% at high soil fertility, but leaf area loss increased by approximately 73%. Second, the loss of leaf area includes both direct consumption of leaf tissue and expansion of holes made by feeding caterpillars, since *P. rapae* caterpillars often feed on young leaves (pers. obs.). Differences in the expansion of holes or the extent to which caterpillars fed on young leaves could have also contributed to the difference in the amount of leaf area lost at high and low soil fertility. These considerations show that the interaction between soil nutrient availability and the amount of leaf area loss can be complex, as it depends on herbivore consumption, specific leaf area, the degree to which herbivores feed on young leaves, and leaf expansion rates (see also Coleman and Leonard 1995).

In contrast to the strong influence of soil nutrients on defoliation levels, soil fertility did not affect the ability of damaged plants to match the reproductive output of undamaged plants. Plants grown at both low and high soil fertility fully compensated for herbivore damage in terms of seed production. No significant effects of herbivory were detected for flowering phenology, total seed number, or mean mass per seed. Measures of seed production were used as correlates of lifetime maternal
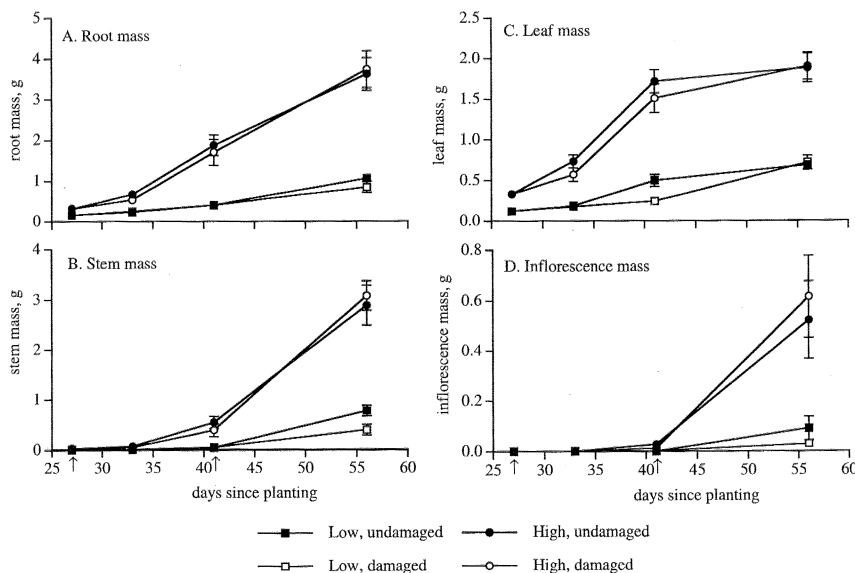

Fig. 3. Effects of soil fertility and herbivore damage on plant biomass. Means and standard errors are shown (standard errors not visible fell within the symbols). First and second arrows along x-axis indicate beginning and end of insect feeding period, respectively. Only leaf mass and stem mass were significantly affected by damage. Herbivore damage caused a significant reduction in leaf mass only at the end of the insect feeding period, for plants grown at both low and high soil fertility (41 d since planting, two-way ANOVA: soil fertility $p = 0.0001$, damage $p = 0.01$, interaction $p = 0.10$). Stem mass was affected by herbivory only at two weeks after the caterpillar feeding period (56 d since planting), when damage reduced stem mass at low soil fertility ($p = 0.01$) but not at high soil fertility ($p = 0.48$). Fertilizer effects were significant for all harvests ($p < 0.01$) except for root mass at 27 d after planting ($p = 0.09$). Data were ln transformed (root, stem, and leaf mass) or ln + 1 transformed (inflorescence mass) for analysis.

A.

B.
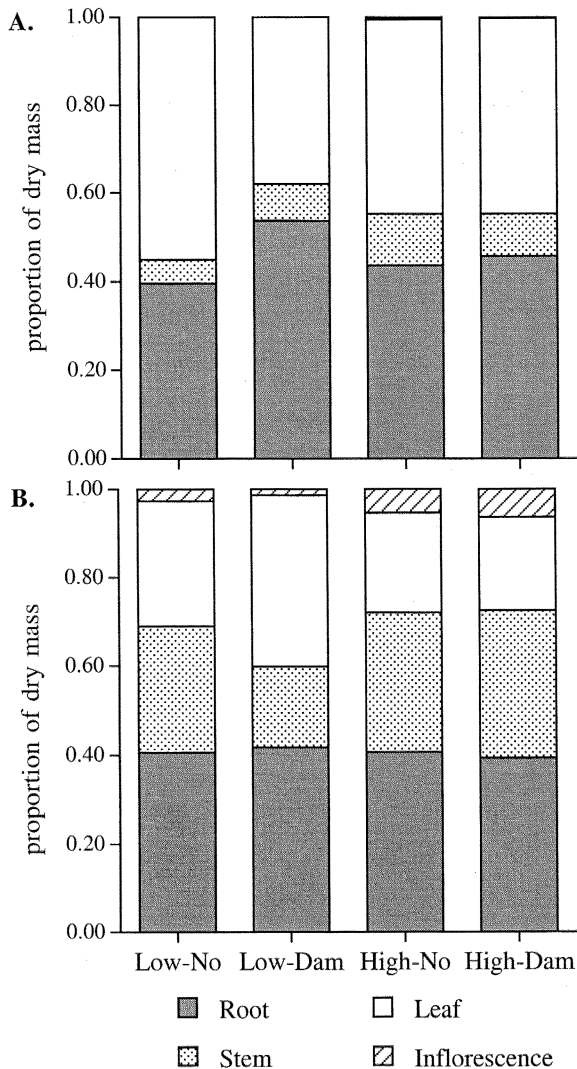
Root	Leaf
Stem	Inflorescence

Fig. 4. Effects of soil fertility and herbivore damage on proportion of biomass allocated to each plant part. A. Biomass allocation at the end of the insect feeding period. B. Biomass allocation two weeks after insect removal. Means are shown. For A, damage increased allocation to roots and decreased allocation to leaves at low soil fertility, but did not significantly affect allocation at high soil fertility (for roots, effect of damage at low soil fertility $p = 0.006$, at high soil fertility $p = 0.44$. For leaves, effect of damage at low soil fertility $p = 0.0005$, at high soil fertility $p = 0.96$). For B, damage increased allocation to leaves and decreased allocation to stems at low soil fertility, but did not significantly affect allocation at high soil fertility (for stems, effect of damage at low soil fertility $p = 0.03$, at high soil fertility $p = 0.60$. For leaves, effect of damage at low soil fertility $p = 0.02$, at high soil fertility $p = 0.68$). Proportions were arcsine square root transformed before analysis.

fitness for this annual plant. Effects of herbivory on male fitness were not measured in this experiment and cannot be ruled out. Herbivore damage has the potential to affect pollen production or floral characters that influence the attractiveness of plants to pollinators (Mutikainen and Delph 1996, Strauss et al. 1996).

However, even with the possibility of effects on male fitness, the results reported here indicate that *B. nigra* had substantial capabilities to compensate for herbivore damage and the degree of compensation in seed production did not depend on soil nutrient availability.

While the end result in terms of maternal fitness was the same regardless of soil fertility, the results reported here show that the pathways used to achieve full compensation in seed production were different for plants grown at low and high soil fertility. At low soil fertility, damaged plants could not keep up with caterpillar feeding as it was occurring. Relative leaf growth rates of damaged plants were severely depressed compared to
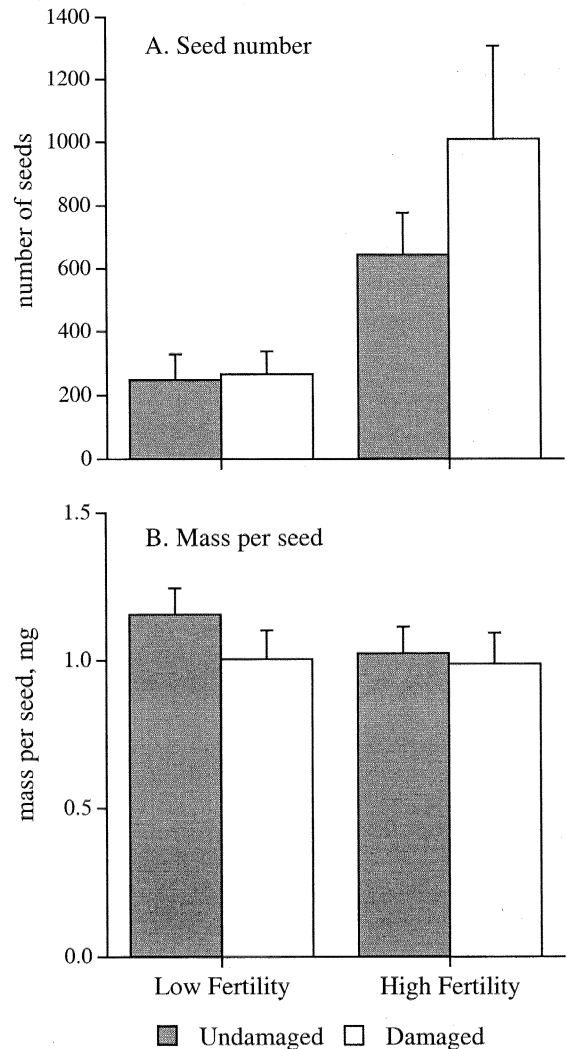

Undamaged	Damaged

Fig. 5. Effects of soil fertility and herbivore damage on plant reproduction. A. total seed number, B. mean mass per seed. Means and standard errors are shown. Results of two-way ANOVA for total seed number: soil fertility $p = 0.003$, damage $p = 0.34$, interaction $p = 0.43$. Results of two-way ANOVA for mean mass per seed: soil fertility $p = 0.42$, damage $p = 0.33$, interaction $p = 0.65$. Statistical analyses performed on ln + 1 transformed data for total seed number and ln transformed data for mean mass per seed.

undamaged plants over the second week of feeding, indicating that damaged plants added very little leaf area over this period. Because of these low leaf growth rates, damaged plants had a lower proportion of biomass invested in leaves at the end of the insect feeding period than undamaged plants. Damaged plants recovered the lost leaf area in the two weeks following insect removal by increasing their relative leaf growth rates above the levels seen for undamaged plants. These leaf growth rates were sufficient to replace the lost leaf area, as total leaf area of damaged plants was equivalent to that of undamaged plants by two weeks after insect removal. However, this recovery of leaf area came at the expense of stem growth; damaged plants had less stem biomass and a lower proportion of their biomass was invested in stems.

In contrast, at high soil fertility damaged plants were able to maintain leaf growth rates to a much greater extent during herbivore feeding. Although damaged plants did suffer reductions in leaf area at the end of the insect feeding period, they did not fall as far behind undamaged plants as did plants grown at low soil fertility. Since they did not lose as great a percentage of leaf area over the caterpillar feeding period as did plants grown at low soil fertility, they did not have as much catching up to do after caterpillar feeding ended to attain leaf areas similar to undamaged plants. Damaged plants at high soil fertility recovered the lost leaf area in the two weeks following insect removal, as did damaged plants at low soil fertility. However, at high soil fertility, this recovery of leaf area did not come at the expense of any other plant part. There were no detectable effects of herbivory on any plant part other than leaves for plants grown at high soil fertility.

These different pathways suggest that plants growing at low soil fertility could experience additional costs of herbivory that would not occur at high soil fertility. Plants in the present experiment were grown singly in pots, so they were not subject to competition. The increase in leaf growth rates after caterpillar removal seen for damaged plants at low soil fertility might have been more difficult to achieve if the plants were competing with other plants. Since damaged plants at high soil fertility did not fall as far behind undamaged plants during the period of insect feeding and did not rely on increased leaf growth rates after damage to recover lost leaf area, it seems likely that they would not be as affected by competition as plants grown at low soil fertility. Therefore growing the plants in a competitive environment might reduce the effectiveness of compensation more at low soil fertility than at high. Similarly, the timing of herbivory might influence the degree of compensation more at low soil fertility than at high. Since plants at high soil fertility were better able to stay ahead of their herbivores as they were being eaten, the availability of a recovery period after damage in which to replace the lost leaf area might be less important. In addition, herbivory caused reduced stem biomass at low soil fertility but not at high. While the lower stem biomass of damaged plants at low soil fertility did not affect maternal fitness in the experiment reported here, it is possible that there could be costs of reduced stem biomass under different conditions.

The results presented here support the compensatory continuum model of Maschinski and Whitham (1989) better than the model developed by Hilbert et al. (1981). Plants grown at high soil fertility were better able to replace resources lost to herbivores through growth. In addition, although plants at both low and high soil fertility compensated fully for herbivory in terms of seed production, there was more potential for costs of herbivory (under conditions other than those used in this experiment) at low soil fertility than at high. However, there is an important distinction between the experiment reported here and the two models. Both models were developed to explain plant responses to grazing, where damage to the plant is more or less instantaneous. A plant loses some proportion of its biomass to an herbivore at a single point in time, and to compensate for damage must increase growth in the period following the grazing event. In contrast, the caterpillar herbivory of this experiment was chronic, extending for about two weeks. When herbivory is chronic and gradual, there is greater potential for plants to adjust to damage as it is occurring. The results reported here show higher levels of soil fertility enhance the ability of plants to stay ahead of their herbivores while they are being eaten, reducing the need for increased growth after herbivory ends to match the performance of undamaged plants.

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