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Within-population Variation in Response of Red Oak Seedlings to Herbivory by Gypsy Moth Larvae

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ABSTRACT.—The potential for an evolutionary response to gypsy moth (*Lymantria dispar* L.) herbivory was investigated in red oak (*Quercus rubra* L.), a preferred host. Seedlings of nine open-pollinated families were grown in a greenhouse and experimentally defoliated by fourth instar larvae in the summer of 1991 to assay for intraspecific variation in resistance to and recovery from herbivory.

Defoliation increased mortality and reduced growth differentially among the nine families. Family differences in plant size before defoliation explained much of the variation in mortality and growth following defoliation. Different allocation patterns among families explained some of the variation in seedling growth. Absolute growth rate of larvae was significantly different among families and higher on individuals with larger leaf area, but resistance to defoliation and larval growth efficiency were not significantly different among families. Since we have not measured the additive genetic variation in seedling traits, the magnitude of the potential evolutionary response cannot be projected from this study, but intraspecific variability in red oak does exist for tolerance and response to defoliation and possibly for resource allocation. Phenotypic selection on traits related to response to defoliation may result in evolutionary change in natural populations of red oak.

INTRODUCTION

Evolution of a character by natural selection depends on the existence of phenotypic variation that causally affects survival and reproduction, and a heritable basis for such variation (Endler, 1986). Selection pressures exerted by defoliating insects may be an important component of the evolution of plant genotypes (Ehrlich and Raven, 1964). This has been supported by convincing fossil evidence (McNaughton, 1983), although traditionally plant-insect interactions may have been underestimated as forces in plant evolution (Ennos, 1983). Insects have acted as selective agents in plant populations by reducing growth, survival and reproduction of their hosts (Morrow and LaMarche, 1978; Rausher and Feeny, 1980; Maddox and Root, 1987; Simms and Rausher, 1989; Marquis, 1990). Because gypsy moth (*Lymantria dispar* L.) herbivory most increases tree mortality in the areas it invades (Baker, 1941; Herrick and Gansner, 1988), it may be powerful as a force influencing the evolution of its hosts. Phenotypic selection on size, growth rate, root nonstructural carbohydrate concentrations and crown condition has been shown to occur in adult red oak populations (Byington, 1992).

The ability of a population to respond to phenotypic selection depends on the existence of genetic variation in relevant traits. Genetic variation among host plants may make them differentially preferable to herbivores or influence the ability of the herbivores to use them effectively. Defensive chemistry, which is at least partly genetically based, presumably evolves

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because it confers resistance to herbivores (Berenbaum *et al.*, 1986). Intraspecific genetic variation in resistance to insect attack has been observed in *Pinus ponderosa* (Edmunds and Alstad, 1978) and *Rhus glabra* (Strauss, 1990). Genetically based resistance to insect herbivory, once attacked, has also been reported (Hatchett and Gallun, 1970; Mitter *et al.*, 1979; Gould, 1979; Moran, 1981; Kinsman, 1982; Lin and Eckenrode, 1984; Marquis, 1984; Service, 1984; Berenbaum *et al.*, 1986; Fritz *et al.*, 1986; Maddox and Root, 1987; Karban, 1988; Simms and Rausher, 1987, 1989; and Marquis, 1990). The ability of certain genotypes to resist insect herbivores may entail a fitness cost that is dependent upon the level of herbivory: a high proportional allocation to resistance to herbivory may be detrimental in periods of low populations of herbivores, but may confer a fitness advantage to the individual during herbivore population outbreaks (Tuomi *et al.*, 1983; Bazzaz *et al.*, 1987; Simms and Rausher, 1987; Fagerstrom, 1989).

When a nonnative herbivore such as the gypsy moth is released, unexpected patterns of selection may arise (Byington, 1992) because the host species did not evolve in the presence of the herbivore. Variation in resistance to defoliation or response to defoliation may nevertheless exist, due to native herbivore pressure. This variation may account for the large variability in mortality in different populations and among individuals within populations of host trees defoliated by the gypsy moth (Quimby, 1986). In the present study, variation for resistance and response to defoliation by gypsy moth was investigated in nine open-pollinated families of red oak seedlings. If variation in resistance to herbivory among families of seedlings exists, populations may be able to respond to phenotypic selection of the sort observed in natural populations (Byington, 1992).

METHODS

In October 1990, immediately after dispersal, acorns were collected from the ground around 14 isolated red oaks (*Quercus rubra* L.) with nonoverlapping canopies, which made sibship virtually certain (Werkerly *et al.*, 1989). The red oaks were all from a localized geographical region at Cooper's Rock State Forest, in northern West Virginia. The area from which the 14 open-pollinated families were collected had not experienced previous gypsy moth defoliation. All collected acorns were visually inspected to remove those which had been partially consumed or significantly damaged by insects, primarily weevils of the genus *Curculio* (Gibson, 1982). After being float-tested in water to determine viability (viable acorns sink; Olson, 1974), the remaining acorns were treated with a mild fungicide, their pericarps were removed and the seed stored by family in plastic bags at 3 C for 6 mo. In May 1991, the acorns were placed in shallow trays and covered with 3–4 cm of sand. The seeds were kept at room temperature under a 14-h photoperiod and watered daily. After 10 days, nine of the open-pollinated families had sufficient numbers of single-flush seedlings to ensure adequate replication within the experimental design, with at least 20 individuals per family. The seedlings in these families were individually transplanted into each of 398 pots (30 cm deep × 15 cm diam, Hanson *et al.*, 1987; McGraw *et al.*, 1990) in Turface, an arcillite-clay, plant-growth medium (Applied Industrial Materials Corporation). The seedlings were then randomly placed in four blocks within a greenhouse on 28 May 1991 and were maintained with regular watering and the application of one-half strength Miracle-Gro weekly. By the end of the experiment, only one family/treatment/block combination had one individual alive, there were no missing cells in the data set, and a mean of >5 reps per block per treatment per family.

Leaf number, leaf area (determined with Li-Cor LI-3000 portable area meter) and height of all seedlings were determined immediately before the defoliation treatment (early July). Seedlings were in varying stages of growth, with most having extended either one or two

flushes of leaves, and a few in the process of extending their second set of leaves. One-half of the seedlings in each family were randomly selected to be defoliated by gypsy moth larvae. Laboratory-reared fourth-instar larvae (New Jersey Standard Strain), that were preconditioned for ca. 48 h on freshly excised red oak foliage (Kleiner, 1991), were weighed and one larva was placed on each seedling which was enclosed within a nylon mesh bag. Larvae were allowed to feed for ca. 72 h on the seedlings, which was not enough time for all leaf area to be removed; thus, any larva could potentially feed for the entire period of the experiment. After this period, larvae were removed, reweighed and the leaf area of the seedling redetermined. Specific leaf weight (weight per unit area) was determined for each seedling by determining the dry weight of a sample of leaf tissue with a known area. Leaf weight removed by larval feeding was calculated by multiplying the change in leaf area by the specific leaf weight.

We wanted to achieve a defoliation level of 100% since partial defoliation in some seedlings would give them a different starting point for recovery. Because artificial defoliation may not adequately mimic herbivory by insects (Capinera and Roltsch, 1980; Haukioja and Neuvonen, 1985; Hartley and Lawton, 1987; Haukioja, 1990), removal of the remaining foliar tissue was accomplished by placing larvae back on the seedlings. After 1 wk the small amount of remaining foliar tissue was removed by scissors, leaving leaf midveins intact, so that the seedlings in the defoliated group would not differ greatly in the timing of defoliation.

One month after the defoliation treatment, seedling stem height, leaf area, leaf number and mortality were again determined. Seedlings were harvested, and the biomass of root, stem and leaf components was determined after 72 h of drying at 60 C. Seedlings were at various growth stages by this time. This harvest time was selected because seedlings that were not going to survive had generally died by this point and seedlings that had recovered had produced at least one flush of new leaves. Seedlings were defined as dead if all of their leaves were completely dried and there was no sign that buds were going to expand to replace them.

Absolute growth rate of larvae (larval AGR) was calculated as larval weight change per unit time. Larval growth efficiency was estimated by determining how well a larva was able to convert the leaf weight removed by feeding to larval mass; *i.e.*, larval growth efficiency = the change in larval weight per unit mass of leaf consumed. The foliage of oaks contains substantial levels of compounds (*e.g.*, hydrolyzable tannins) which slow larval weight gain and reduce fecundity (Schultz and Baldwin, 1982; Rossiter *et al.*, 1988), and would therefore limit positive larval weight change. Higher resistance to defoliation, due to the presence of such compounds, would result in less larval weight gain per gram of leaf material; thus resistance to defoliation was defined as the converse of larval growth efficiency; resistance = 1 − larval growth efficiency (Byington, 1992).

A recovery index was devised to measure the proportion of leaf area produced following defoliation relative to the leaf area present immediately before defoliation; recovery index = (leaf area produced postdefoliation)/(leaf area before defoliation). A high recovery index indicated that a seedling was able to regenerate most of its predefoliation leaf area in the month following defoliation.

Relative leaf area growth rates (RGR_A) and relative leaf number growth rates (DRGR) of the control and defoliated seedlings were determined for 1 mo following defoliation (*see* McGraw and Garbutt, 1990, for methods).

Biomass allocation data and the recovery index was arcsine square-root transformed and compared by ANOVA. Significant differences in mortality (defined as seedlings with no evidence of living buds or leaves, Wright *et al.*, 1989) among families and defoliation treat-

TABLE 1.—Survival of red oak seedlings from different families in defoliation and control treatments in the greenhouse experiment

	Defoliated seedlings			Control seedlings		
Family	Survived	Died	Percent survival	Survived	Died	Percent survival
1	22	0	100	22	0	100
2	35	1	97	36	0	100
3	19	0	100	20	0	100
4	14	0	100	15	0	100
5	23	1	96	25	0	100
6	9	1	90	10	0	100
7	12	3	80	16	0	100
8	20	6	77	26	0	100
9	17	10	63	25	1	96
Totals	171	22	88	195	1	99

ments were detected by contingency table analysis (G-test). Defoliation effects and differences among families were determined with analysis of variance. Family differences in response to defoliation (family × defoliation interaction) were of particular interest. All statistical analyses were carried out using SAS JMP version 3.0 (SAS, 1994). Type III sums of squares were used in the analysis, given the unbalanced nature of the data set. Block was explicitly included in the model to remove effects of within-greenhouse environmental variation.

RESULTS

Survival and growth.—Survival was significantly depressed by defoliation, from 99.5% to 88.6% ($G = 25.2$, $P < 0.0001$). In addition, survival was significantly different among families of defoliated individuals ($G = 34.3$, $P < 0.0001$), ranging from 100% to less than 70% (Table 1). More than half the observed mortality of defoliated seedlings was confined to two families (families 8 and 9), and three families had no mortality at all (families 1, 3 and 4). Seedling survival was consistently high in the control individuals and not significantly different among families. Individuals surviving defoliation gained less leaf area ($F = 741.4$, $P < 0.0001$), produced fewer leaves ($F = 628.2$, $P < 0.0001$), and grew less in height ($F = 177.0$, $P < 0.0001$) than the undefoliated controls over the same 1-mo period following defoliation.

Growth in leaf number and height following defoliation were not significantly different among families. Growth in leaf area, however, was significantly different among families ($F = 2.9$, $P = 0.0042$). Moreover, the growth response to defoliation differed significantly among families (a family × defoliation interaction; $F = 2.5$, $P = 0.0112$). Defoliated seedlings of a family had mean leaf area growth ranging from 6% (family 9) to 42% (family 3) of that in controls (Table 2). Two of the three families with the highest mortality produced less than 20% of the leaf area of the control seedlings within their family following defoliation, but low leaf area recovery was not necessarily predictive of mortality: family 1, which had among the lowest mortality rates, recovered a small fraction of leaf area after defoliation relative to the undefoliated members of its family.

The recovery index was significantly different among families ($F = 2.9$, $P = 0.0046$), although only one family (9), which also had the highest mortality rate, was significantly

TABLE 2.—Growth of red oak seedlings in the greenhouse experiment following defoliation. Means are given followed by standard errors in parentheses

	Leaf area change			RGR_A	
Family	Defoliated	Control	Recovery index	Defoliated	Control
1	59.7	306.4	0.47	0.148	0.020
	(7.9)	(47.2)	(0.05)	(0.005)	(0.002)
2	64.3	274.6	0.43	0.140	0.018
	(8.9)	(35.7)	(0.04)	(0.007)	(0.002)
3	54.5	129.4	0.37	0.137	0.011
	(10.3)	(31.9)	(0.03)	(0.007)	(0.002)
4	82.1	224.1	0.61	0.151	0.021
	(14.2)	(37.6)	(0.09)	(0.009)	(0.003)
5	104.3	358.9	0.53	0.156	0.020
	(16.9)	(44.1)	(0.06)	(0.010)	(0.002)
6	64.4	211.0	0.46	0.142	0.012
	(14.2)	(53.9)	(0.07)	(0.012)	(0.003)
7	50.0	270.7	0.48	0.133	0.019
	(9.0)	(44.9)	(0.05)	(0.009)	(0.003)
8	91.8	213.5	0.48	0.136	0.019
	(38.6)	(30.2)	(0.07)	(0.011)	(0.002)
9	18.7	315.1	0.23	0.096	0.026
	(6.6)	(46.7)	(0.05)	(0.011)	(0.005)

lower than the other families when compared using the *a posteriori* Tukey-Kramer HSD test (Table 2). Two other families with high mortality, 7 and 8, had average recovery indices.

Leaf area at the time of defoliation was significantly different among families ($F = 7.6$, $P < 0.0001$). Predefoliation leaf area appeared to be an important determinant of eventual survival after defoliation: seedlings that died after defoliation had significantly less leaf area than seedlings that survived ($F = 60.0$, $P < 0.0001$). Survival, which was significantly different by family in the defoliated seedlings, was dependent upon the mean family leaf area before defoliation (Fig. 1). A spline fit of survival vs. mean leaf area for each family at the time of defoliation ($r^2 = 0.9300$, spline fit $\lambda = 100{,}000$) suggested that below a threshold size of ca. 250 cm^2, mortality rapidly increased, although 70 individuals (from all families) with less than 250 cm^2 survived, including 38 with less than 200 cm^2. Leaf area produced following defoliation was positively correlated with leaf area at the time of defoliation ($r^2 = 0.1166$, $P < 0.0001$); thus recovery as well as survival was linked with seedling size. Specific leaf weight was significantly different among families ($F = 3.0$, $P = 0.0031$) but was not different between surviving and nonsurviving individuals.

Relative leaf area growth rates (RGR_A) of defoliated seedlings for the 1 mo following defoliation were much higher than the RGR_A for control seedlings for every family (Table 2). This is not surprising since RGR_A is a measure of added leaf area relative to initial leaf area, and the initial (postdefoliation) leaf area of defoliated seedlings was small. Families differed considerably in their mean RGR_A ($F = 3.1$, $P = 0.0030$, Table 2). Defoliated plants in most families produced foliage at ca. eight times the rate observed for control seedlings, but family 9 produced it at only four times the rate, and two others, families 3 and 6, had much greater rate increases relative to controls (Table 2). Relative growth rate in leaf number following defoliation was not different among families.

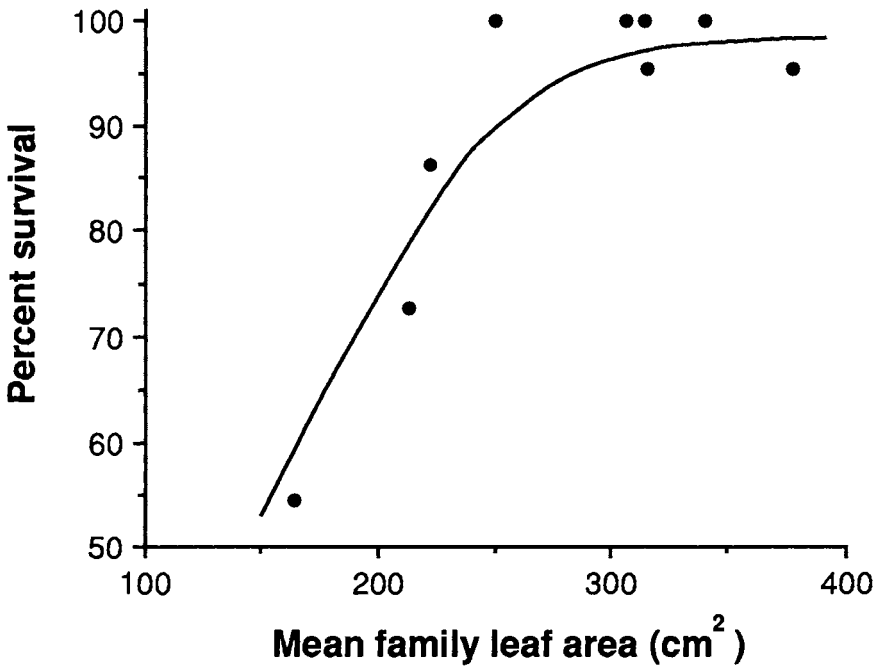

FIG. 1.—Seedling survival vs. mean family leaf area at the time of defoliation. Survival percentage by family was higher in families with larger leaf areas

Biomass allocation.—Total biomass was significantly different among families for plants that were defoliated (Table 3), but not different in controls. Defoliated seedlings had ca. one-fourth of the total biomass of the control seedlings ($F = 389.5$, $P < 0.0001$). Biomass was reduced in all parts of the plant, including roots ($F = 334.1$, $P < 0.0001$), stem ($F = 264.9$, $P < 0.0001$) and leaves ($F = 890.8$, $P < 0.0001$). Among families, significant differences in proportional allocation of defoliated seedlings to stems ($F = 2.2$, $P = 0.0271$) and roots ($F = 2.5$, $P = 0.0129$) occurred (Table 3), but not in allocation to leaves ($F = 1.4$, $P = 0.1929$). Allocation to roots was positively correlated with initial leaf area achieved in controls, albeit with a low percent of variation explained ($r^2 = 0.0324$, $P = 0.0118$). This suggests that family differences in allocation could be related to family differences in leaf area growth. Again using controls, a multivariate response surface model relating mid-season leaf area to all three components of allocation (arcsine square root transformed root, stem, and leaf biomass) explained 14% of the leaf area variation and was statistically significant (whole-model test, $F = 3.2$, $P = 0.0012$).

Biomass allocation patterns of defoliated individuals were significantly different between surviving and nonsurviving individuals. Leaf biomass was 10.4% of total biomass in dead seedlings (leaves were dead but remained on the plant, and so were harvested) and 36% in surviving individuals ($F = 24.1$, $P < 0.0001$). Stem biomass was proportionally lower in surviving seedlings ($F = 14.2$, $P = 0.0002$), 24% vs. 31%. No difference was found in root biomass allocation between survivors and nonsurvivors in defoliated seedlings.

Larval performance and resistance.—Larval growth rate was significantly different among families ($F = 4.4$, $P < 0.0001$). Larval absolute growth rate was a weak positive function of

TABLE 3.—Mean final root:shoot ratio and biomass (standard error in parentheses) produced by defoliated and control red oak seedlings in the nine family greenhouse experiment

	Root:Shoot ratio		Leaf biomass (g)		Root biomass (g)		Stem biomass (g)		Total biomass (g)	
Family	Defoliated	Control	Defoliated	Control	Defoliated	Control	Defoliated	Control	Defoliated	Control
1	1.77	1.13	0.22	2.71	1.65	3.41	0.48	1.17	2.34	7.29
	(0.08)	(0.06)	(0.02)	(0.33)	(0.10)	(0.45)	(0.03)	(0.15)	(0.12)	(0.89)
2	1.59	1.01	0.24	2.67	1.54	3.85	0.54	1.24	2.32	7.76
	(0.04)	(0.05)	(0.03)	(0.21)	(0.10)	(0.40)	(0.03)	(0.12)	(0.15)	(0.68)
3	1.62	0.96	0.21	2.73	1.39	3.66	0.51	1.26	2.11	7.65
	(0.14)	(0.05)	(0.03)	(0.36)	(0.10)	(0.65)	(0.05)	(0.21)	(0.14)	(1.16)
4	1.49	1.05	0.31	2.49	1.36	3.69	0.43	1.17	2.10	7.35
	(0.05)	(0.08)	(0.05)	(0.42)	(0.12)	(0.67)	(0.03)	(0.21)	(0.19)	(1.21)
5	1.41	1.00	0.41	2.95	1.87	5.05	0.72	1.44	3.00	9.44
	(0.04)	(0.05)	(0.09)	(0.26)	(0.15)	(0.56)	(0.06)	(0.18)	(0.27)	(0.94)
6	1.61	1.02	0.23	2.96	1.51	4.65	0.54	1.21	2.45	8.82
	(0.09)	(0.06)	(0.05)	(0.58)	(0.26)	(0.71)	(0.08)	(0.22)	(0.36)	(1.32)
7	1.61	0.94	0.17	3.25	1.06	4.77	0.37	1.39	1.73	9.40
	(0.08)	(0.11)	(0.03)	(0.33)	(0.14)	(0.42)	(0.05)	(0.12)	(0.19)	(0.64)
8	1.39	0.92	0.29	3.18	0.99	4.56	0.37	1.41	1.68	9.15
	(0.05)	(0.05)	(0.12)	(0.22)	(0.14)	(0.47)	(0.04)	(0.13)	(0.29)	(0.70)
9	1.58	1.02	0.11	2.78	0.71	3.53	0.28	1.20	1.19	7.50
	(0.07)	(0.10)	(0.03)	(0.22)	(0.08)	(0.35)	(0.04)	(0.10)	(0.14)	(0.60)

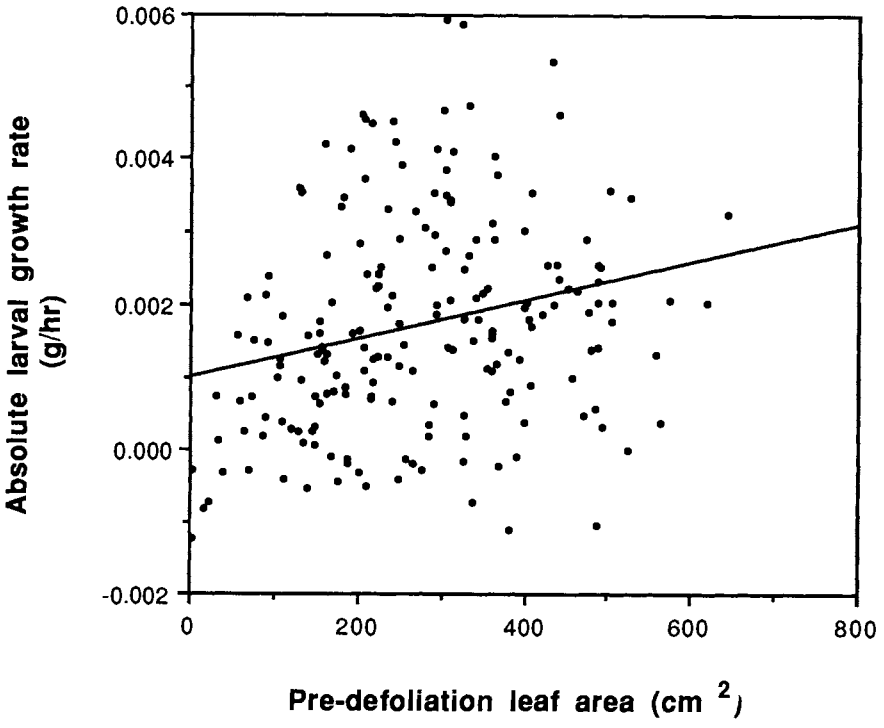

FIG. 2.—Relationship between size prior to defoliation and growth rate of larvae on foliage of red oak seedlings in the greenhouse experiment

seedling leaf area at the time of defoliation (Fig. 2, $r^2 = 0.0611$, $P = 0.0005$), suggesting that genetic or environmental factors that allowed plants to grow large also made them better food for gypsy moth larvae. Supporting this result was the finding that absolute growth rates of larvae were higher on individual seedlings that eventually went on to survive defoliation ($F = 6.5$, $P = 0.0114$).

Larval growth efficiency was not significantly different among families ($F = 0.5$, $P = 0.8248$) or between surviving and nonsurviving individuals ($F = 0.1$, $P = 0.7383$). Resistance to defoliation, being directly related to growth efficiency as its converse, was also not different among families or between survival classes. Resistance to defoliation was positively correlated with specific leaf weight ($r^2 = 0.1020$, $P < 0.0001$).

DISCUSSION

Defoliation caused increased mortality, altered biomass allocation patterns and severely limited growth of surviving seedlings. Defoliation disrupts the normal physiological processes of the seedling, which may result in death. The loss of leaf area to herbivory affects plant growth through the reduction of photosynthetic capacity, disruption of hormone production, and a reduction of transpiration and translocation rates (Kozlowski, 1971; Valentine *et al.*, 1983). The physiological disruption brought about by defoliation, especially the loss of photosynthetic capacity in mid-season, may be especially costly in that energy required to maintain normal metabolic processes and growth must then come from storage.

In small seedlings, storage reserves have not had a chance to build up substantially, therefore storage reserves may be quickly depleted, resulting in death.

Mortality among families of defoliated seedlings was not uniform, with mortality rates ranging from zero to 30%. This is in sharp contrast to the control seedlings, in which mortality was negligible and not different among families. Herbivory resulting in death of seedling genotypes in natural systems is certainly possible, as seedlings have been shown to be attacked by herbivores in sufficiently high numbers to produce mortality (Linit *et al.*, 1986). Experimental studies have shown that differential death at the seedling stage may be an important determinant of genetic diversity (Kalisz, 1986; Stewart and Schoen, 1987).

Mortality differences among families following defoliation suggest that there may be genetic variation among families for the ability to recover from a severe defoliation episode. There are several possible mechanisms that could explain the differential ability of families to recover, including differences in allocation to leaves, roots or stems, differential allocation to storage, or differences in the ability to adjust physiological patterns that allow regrowth of foliage to occur.

Family differences in leaf area at the time of defoliation were a significant factor in mortality. Seedlings that were larger on average survived defoliation at a higher rate than smaller individuals. Plant size has been shown to be important in selection in adult trees brought about by herbivory (Byington, 1992). In this case, size was shown to be important to seedling recovery as well. From our study, we cannot identify all of the sources of early size variation, but family variation in allocation pattern appears to be important. The multivariate model relating root, stem and leaf allocation to early leaf area suggests that a significant portion of the size variation is explained by allocation traits generally. Clearly, developmental and physiological differences among families could also be important (Hanson *et al.*, 1988).

Larval absolute growth rate was significantly different among families, indicating that phenotypic variation among families can be expected to influence the insects as well as the response of plants to the insects. In the field, such effects could result in feedback as the populations reciprocally affect one another. Although results from greenhouse feeding experiments should be interpreted cautiously, consumption of foliage from the larger seedlings promoted faster larval growth, which in the field could result in greater gypsy moth population growth over the long term. Differences among families were not detected in terms of the growth efficiency of larvae or resistance to defoliation, suggesting that once the foliage is consumed it is of similar quality in producing larval growth, regardless of genotype.

The observed variation among families may not be entirely due to additive genetic variation which will produce a response to selection. Variance among groups with different maternal parents may also be due to maternal environmental or maternal genetic effects (Falconer, 1989; Roach and Wulff, 1987). To the extent that the maternal effects are genetic, differential success of the progeny groups may in fact result in evolutionary changes in the red oak population subjected to gypsy moth defoliation. However, those effects which are products of the maternal environment may not result in such change.

Open-pollinated families of red oak varied in survival, early growth (prior to defoliation), allocation, recovery following defoliation and foliage quality. Other studies have demonstrated a significant genetic component to variation in growth characters in adult red oak (Kriebel, 1964; Kriebel *et al.*, 1988), and selection on size and growth characters (Byington, 1992). The present study suggests that if natural populations are exposed to herbivory, such variation will be subject to selection. The ability to recover from total defoliation, and all

the traits related to this ability will likely evolve in red oak as repeated defoliation events impact these populations.

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