Long-term suppression of insect herbivores increases the production and growth of *Solidago altissima* rhizomes

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Summary. Although insect herbivores have many well documented effects on plant performance, there are few studies that assess the impact of above-ground herbivory on below-ground plant growth. For a seven year period in which no large-scale herbivore outbreaks occurred, a broad spectrum insecticide was utilized to suppress herbivorous insects in a natural community dominated by *Solidago altissima*. Ramet heights, rhizome lengths, rhizome biomass, and the number of daughter rhizomes all were lower in the control plots than in the insecticide-treated plots. These effects should lead to a decrease in the fitness of genets in the control plots relative to the fitness of genets in the insecticide-treated plots. We also found that ramets in the control plots appear to have compensated for herbivory: the ratio of rhizome length to rhizome biomass was greatest in the control plots, which indicates that clones moved farther per unit biomass in these plots than in the insecticide-treated plots. Clonal growth models show that this shift in allocation patterns greatly reduced the magnitude of treatment differences in long-term clonal displacements.

Previous work has shown, and this study verified, that clonal growth in *S. altissima* is well represented by random-walk and diffusion models. Therefore, we used these models to examine possible treatment differences in rates of clonal expansion. Although rhizome lengths were greater in the insecticide-treated plots, results from the models suggest that our treatments had little impact on the short- and long-term displacement of *S. altissima* ramets from a point of origin. This occurred because *S. altissima* ramets backtrack often, and thus, treatment differences in net displacements are less pronounced than treatment differences in rhizome lengths.

Key words: Plant-insect interactions – Herbivory – Rhizomes – *Solidago altissima*

Insect herbivores have numerous, well documented effects on individual plant performance. For example, her-

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bivory by insects can alter plant metabolic patterns (Mattson 1980), limit plant distributions (Parker and Root 1981; Louda 1982), mediate the outcome of plant competition (Bentley and Whittaker 1978), and reduce the growth, reproduction, and survival of host plant individuals (see reviews in Crawley 1983 and Belsky 1986).

Although many of the effects of insects on plants are well studied, there are relatively few papers that address the impact of above-ground herbivory on below-ground plant growth. For agricultural plants, above-ground herbivory can reduce tuber yields in potatoes (Johnson et al. 1986) and root growth in wheat and barley (Burton 1986; Castro et al. 1988). Similarly, field experiments have demonstrated that defoliation stress (simulated herbivory) can reduce the growth of both roots and rhizomes (Kathju et al. 1985; Schmid et al. 1988; Lubbers and Lechowicz 1989; Mihaliak and Lincoln 1989). In addition, Moran and Whitham's (1990) common garden experiments showed that leaf-galling aphids decreased the root biomass of *Chenopodium album*, an introduced annual. However, we know of no studies conducted in natural communities that document the effects of insect herbivores on below-ground plant growth.

Rhizome size can affect above-ground plant growth and reproductive success (Ashmun and Pitelka 1985; Cain 1990a), and the number of rhizomes produced can affect observed plant densities. Furthermore, in rhizomatous species, the below-ground storage organ provides a mechanism for lateral spread. Patterns of lateral spread can influence the rate at which clones expand (Angevine and Handel 1986), as well as the probability that plant-plant interactions are interspecific, intraspecific, or intraclonal (Lovett Doust 1981; Maddox et al. 1989). Thus, any effects insects have on rhizome growth have the potential to alter plant-plant interactions, and subsequently, to change plant community structure.

In this study we assess the impact insect herbivores have on the below-ground growth of the old-field perennial *Solidago altissima* L. (Asteraceae). For a seven year period in which no large-scale herbivore outbreaks occurred, a broad spectrum insecticide was utilized to suppress insects in a natural community dominated by *S*.

altissima. Our research addressed the following questions: (1) What impact does the long-term suppression of endemic levels of insect herbivores have upon rhizomatous growth in *S. altissima*? (2) Can we use recently developed clonal growth models (Cain 1990b) to quantify the effects of insect suppression on patterns of below-ground growth?

Methods

Our study was conducted at Whipple field, Ithaca, New York (42°25' N, 76°30' W). In central New York, *S. altissima* (tall goldenrod) ramets emerge in March-April from the apical tips of underground rhizomes. Ramets increase in height until August, at which time flower heads begin to form. Rhizome growth is sympodial. Most rhizomes are initiated at the base of the stem, but a few are initiated along the parent-grandparent rhizome axis (Cain 1990b). Rhizome growth begins in early summer and continues throughout the fall. The above-ground portion of ramets die over winter, and their daughter rhizomes remain dormant until the following spring (Bradbury and Hofstra 1976). *S. altissima* has a pseudo-annual (Salisbury 1942) biomass allocation pattern: ramets rarely if ever grow from the same node in successive years, so a particular genetic individual survives from one year to the next only through the production of new rhizomes. Rhizome connections among ramets persist for up to 5–6 years. For more information about the biology of *S. altissima,* see Werner et al. (1980), Hartnett and Bazzaz (1985), and Goldberg (1988).

To assess the impact of insects on a goldenrod community, an insect suppression study was begun in 1982. Thirty 5×4 m. plots were established in an old field dominated by *S. altissima*, with *S. rugosa* and several *Aster* species subdominant. Subcanopy species included *Hieracium pratense Fragaria virginiana Daucus carota Chrysanthemum leucanthemum* and *Rumex acetosella.* Fifteen of the thirty plots were selected at random to receive monthly applications of the broad spectrum insecticide "fenvalerate"; the remaining 15 plots were left as controls. Treatments were maintained for seven years (1982–1988), and herbivore loads were monitored for the duration of this period.

Fenvalerate has no known physiological effects on several crop plants (Jones et al. 1986), and greenhouse trials have shown no effects on *Solidago altissima* (Carson and Root, unpublished data). In addition, the fenvalerate molecule contains minimal nitrogen (Berg 1984). Thus, insecticide application has a negligible contribution to plant nutrition: we calculate that on a yearly basis, we applied less than 0.07 kg N/ha/year, four orders of magnitude less than recommended agricultural rates.

To document the impact of insect herbivores on below-ground growth in *S. altissima*, in mid-October of 1988 we selected 10 insecticide-treated plots and 10 control plots at random from the plots established in 1982. In each of these 20 plots, we randomly selected 4–5 *S. altissima* ramets (for a total of 88 ramets) and examined the rhizomes leading to these ramets. We carefully dissected rhizomes from their substrate *in situ* in order to follow the total length of all rhizomes connected to each of the initially selected ramets. Thus, we unearthed 88 clonal fragments, each of which contained one of the originally selected ramets. Most of these clonal fragments also contained genetically identical sister ramets of the initial ramet. For every ramet and old shoot stub in each clonal fragment, we recorded parental ramet identity, rhizome branching angle, and rhizome length. For the 1988 cohort of ramets only, we also measured plant height and number of daughter rhizomes. In addition, we recorded the net displacement of each ramet and old shoot stub from its point of origin, which was defined as the location of the oldest shoot stub in each chain of connected ramets. Net displacements were utilized to test predictions from clonal growth models (see below).

To record branching angles and rhizome lengths, we approximated *S. altissima* rhizomatous growth as a series of linear displacements (see Fig. 1 in Cain 1990b). This approximation is reasonable due to the highly linear nature of rhizome growth in *S. altissima* (Cain 1990b). Rhizome lengths were measured as the linear distance between ramet locations in successive years. Branching angles between successive ramet locations were measured relative to the direction taken in the previous year of growth. Zero degrees was defined as straight ahead.

Rhizomes initiated in the summer of 1987 (i.e., those rhizomes from which the 1988 cohort of ramets emerged) were dried for five days at 50° C and then weighed to the nearest 0.01 gram. Older rhizomes were not weighed as they frequently were damaged or partially decayed; new rhizomes (those initiated in the summer of 1988) were not weighed because rhizome growth is not complete in October.

Data analysis

We constructed frequency distributions of rhizome lengths and branching angles for both the insecticide-treated and control plots. We used χ^2 contingency analyses to test for between-treatment differences in these frequency distributions, and we utilized t-tests to compare treatment means. Because subsamples within plots may not be independent, within plot values were averaged to obtain one (independent) data point for each of the 20 plots. All t-test comparisons were performed in the original scale of measurement, except rhizome lengths, which were log-transformed to help stabilize the variance.

We tested whether random-walk models (Kareiva and Shigesada, 1983; Marsh and Jones, 1988) could be used to quantify treatment effects on short-term clonal growth patterns. We took this approach because clonal growth in *S. altissima* is highly variable and is well represented by random-walk models (Cain 1990b). In a random walk, branching angles and rhizome lengths are independent of each other and of previous branching angles or rhizome lengths. In order to account for the fact that some branching angles are more probable than others, Cain used what technically is called a correlated random walk. In this paper, we refer to correlated random-walk models simply as random-walk models.

We performed two sets of analyses to test random-walk models. First, we utilized Spearman rank correlations and χ^2 contingency analyses to test the (model) assumption that rhizome lengths and branching angles are independent within and across years. Second, we used results from McCulloch and Cain (1989) to test if observed ramet displacements from a point of origin differed from random-walk predicted displacements. The mean and the variance used in these tests are calculated directly from observed branching angle and rhizome length frequency distributions. See Cain (1990b) for a detailed application of these methods to clonal growth in *S. altissima.*

We also were interested in whether the long-term expansion of clones differed between experimental treatments. Our results (see below) indicated that random-walk models were suitable on a short time scale: therefore, because random-walk models can be approximated by diffusion models when time is long (Okubo 1980), we used diffusion models to examine possible long-term treatment effects.

Results

Insect herbivore abundances were low in 1982–84, so treatment differences in herbivore load were relatively small: the average herbivore load (expressed as the dry weight of insect herbivores per meter of goldenrod stem) was 26 mg/m in the control plots and 10 mg/m in the
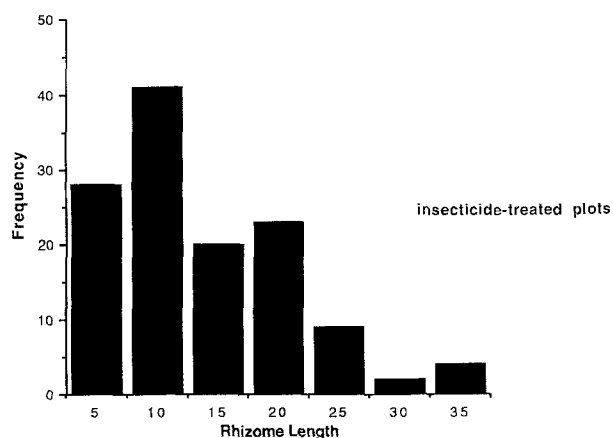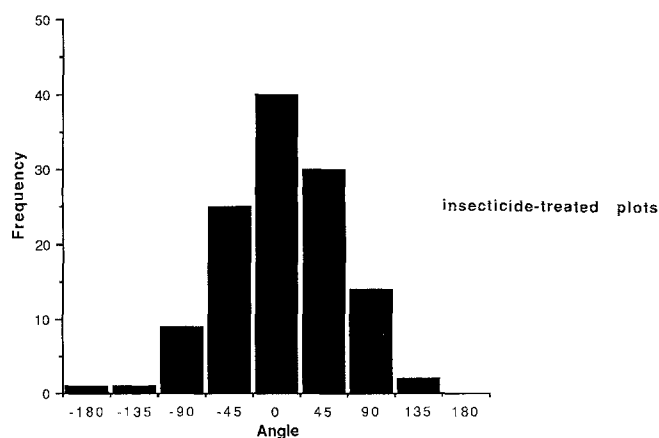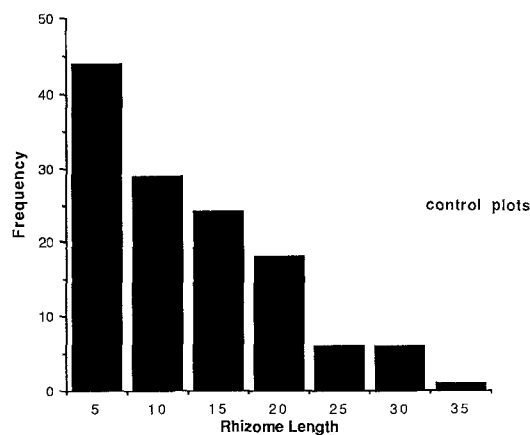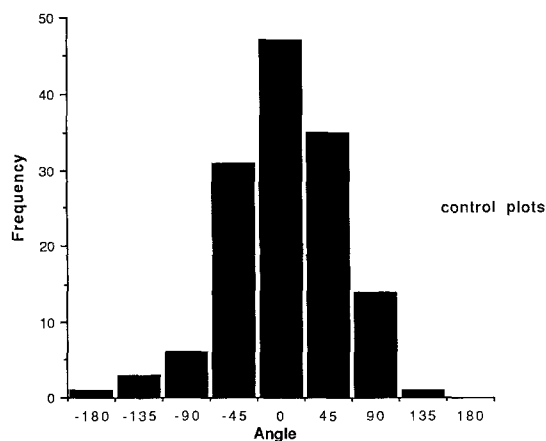
Fig. 1. Frequency distribution of *S. altissima* branching angles in the control and insecticide-treated plots. Values on the x-axis are the class midpoints

Fig. 2. Frequency distribution of *S. altissima* rhizome lengths in the control and insecticide-treated plots. Values on the x-axis are the class midpoints

insecticide-treated plots. For the 1985–87 growing seasons, the average herbivore load was 128 mg/m in the control plots and 14 mg/m in the insecticide-treated plots (Root and Cappuccino, unpublished ms.). Insect abundance data were not collected in 1988, but it is clear that fenvalerate application greatly reduced total herbivore load over the course of this experiment.

We did not directly observe the effect fenvalerate had upon below-ground herbivores. However, due to its low water solubility, fenvalerate rapidly adsorbs to soil particles. This implies that any fenvalerate that reached the ground should bind to the soil shortly after contact. Thus, it is unlikely that fenvalerate had a strong influence on below-ground herbivory. We therefore interpret our results in terms of above-ground herbivory, not below-ground herbivory.

Frequency distributions and treatment means

There was considerable morphological variation for branching angles and rhizome lengths in both the control and insecticide-treated plots (Figs. 1, 2). Although the

frequency distribution of rhizome lengths in the control plots appears to be shifted to the left of the corresponding distribution in the insecticide-treated plots (i.e., there are relatively more short rhizomes in the control plots), these differences were not statistically significant ($\chi_4^2 = 6.7$, $p = 0.15$). There also were no significant differences between the branching angle frequency distributions in our two experimental treatments ($\chi_4^2 = 0.7$, $p = 0.95$).

Mean values for rhizome number, weight, and (log-transformed) length were significantly greater in the insecticide-treated plots than in the control plots (Table 1). Ramet heights also were significantly higher in the insecticide-treated plots than in the control plots. In contrast, the ratio of rhizome length to rhizome biomass was greatest in the control plots (Table 1). There were no significant differences between the mean sine and cosine of branching angles in the two treatments, which indicates there are no treatment effects on the mean angle of rhizome initiation.

The suppression of insect herbivores first produced noticeable changes in the above-ground plant community structure in 1987 and 1988 (Carson and Root, un-

Table 1. Mean values and t-test comparison between the means for the insecticide-treated (spray) and control plots. The variable *rhizome number* refers to the number of daughter rhizomes produced per ramet in the summer of 1988; Θ is the rhizome branching angle; and *ratio* equals rhizome length (cm) divided by rhizome weight (g). Means for rhizome length, $\cos(\Theta)$, and $\sin(\Theta)$ were based on data from all years, while means for the other variables were based on one year's data only (see Methods). The t-test for each variable had 18 degrees freedom

Variable	Mean value		|T|	Prob > |T|
	spray	control		
Rhizome length (cm)	13.5	11.3	2.2	0.04
Rhizome weight (g)	2.3	1.4	3.5	0.003
Rhizome number	4.0	2.7	3.1	0.006
Plant height (cm)	96	71	4.0	0.001
$\cos(\Theta)$	0.62	0.64	0.38	0.71
$\sin(\Theta)$	0.11	0.07	0.44	0.66
Ratio (cm/g)	6.8	9.5	2.5	0.02

published data). Similarly, it is possible that over time the cumulative effects of insect suppression may have increased the magnitude of treatment differences in rhizome lengths. Because we use rhizome length data to project future rates of clonal expansion, it was important for us to estimate any such increase over time in treatment effects on rhizome lengths. Therefore, in addition to the results shown in Table 1, we also compared treatment rhizome lengths for the 1987 and 1988 data only. We found that mean rhizome lengths were greater (|T| = 2.5, p = 0.02) in the insecticide-treated plots (14.9 cm) than in the control plots (12.0 cm). Note that the difference between these treatment means is somewhat larger than the difference obtained when all years were lumped together (cf. Table 1).

Correlation analyses

Combined across treatments, the number of daughter rhizomes produced in the 1988 growing season correlated positively with ramet height (Spearman Rank Correlation: r = 0.46, p = 0.001) and with rhizome biomass in the preceding growing season (Spearman Rank Correlation: r = 0.57, p = 0.0001). All within-treatment correlations also were positive and significantly different from zero (range: r = 0.30 to r = 0.57, $p \leq 0.01$ in all cases).

Branching angles (Spearman Rank Correlation, p > 0.70 in all cases) and rhizome lengths (Spearman Rank Correlation, p > 0.15 in all cases) were not significantly correlated to those of the previous generation. χ^2 contingency analyses also indicated that branching angles (p > 0.65 in all cases) and rhizome lengths (p > 0.05 in all cases) were independent across generations. In addition, branching angles and rhizome lengths were not correlated within generations (p > 0.20 in all cases).

Random-walk and diffusion models of clonal growth

A critical assumption in random-walk models of clonal growth is that branching angles and rhizome lengths are
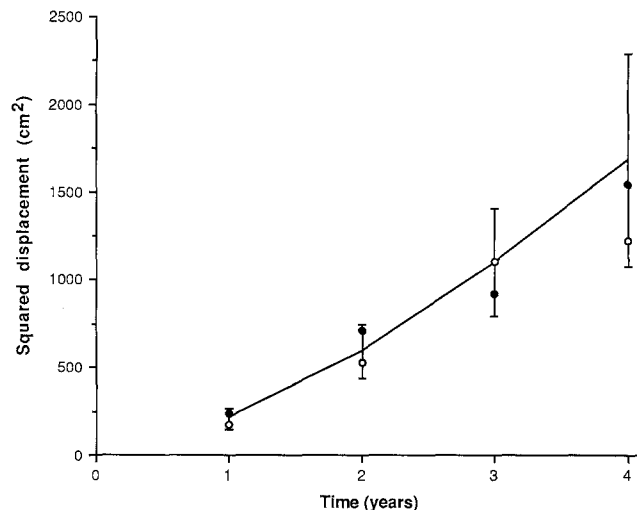

Fig. 3. Relationship between the net squared displacement of *S. altissima* ramets and time. The solid line indicates the random-walk predicted values for ramets in the control plots; $\circ$ indicates observed squared displacements for ramets in the control plots, and $\bullet$ indicates observed squared displacements for ramets in the insecticide-treated plots. The vertical bars represent the 90% confidence intervals about the control plot predicted values

not correlated over time. Results in the previous section and in Cain (1990b) indicate that this assumption is valid for *S. altissima*. Therefore, we utilized random-walk models to predict the short-term expansion of *S. altissima* clones. Random-walk predicted displacements were determined from eqn. 1 in Kareiva and Shigesada (1983).

In the control plots, observed net squared displacements (i.e., the square of the net displacement from a point of origin) did not differ significantly from the values predicted by a random walk (Fig. 3). Thus, we used the random-walk predicted values for the control plots as a baseline against which to compare treatment effects: we found that observed net squared displacements in the insecticide-treated plots did not differ from the control plot predicted values (Fig. 3). This indicates that there was no treatment effect on the short-term rate of expansion of *S. altissima* clones.

Random-walk processes have large variance, and, in some situations, treatment effects can only be distinguished with long-term data (Marsh and Jones, 1988). In *S. altissima* rhizome connections decay after 2–6 years, so we could not directly use field data to consider long-term effects. However, because random walks can be approximated by simple diffusion when time is large (Okubo 1980), we were able to use diffusion models to examine the long-term consequences of our experimental treatments for the expansion of *S. altissima* clones.

The mean (E[r]) and variance for the net displacement of clones that diffuse from a point of origin are (Cain 1991):

$$E[r] = \sqrt{\pi Dt} \qquad \text{Eq. 1}$$
$$\text{var}(r) = (4 - \pi)Dt, \qquad \text{Eq. 2}$$

where t is time (in years) and D is the diffusion constant (a measure of the long-term rate of spread of populations). To use these equations to predict long-term treatment effects, it is first necessary to estimate the diffusion constant for each treatment. Cain (1990b) developed the following estimate:

$$D = \frac{1}{4}\left\{E[l^2] + \frac{2E[l]^2(c - c^2 - s^2)}{(1 - c)^2 + s^2}\right\}, \qquad \text{Eq.3}$$

where the expected rhizome length (E[l]), the expected squared rhizome length (E[l²]), and the expected cosine (c) and sine (s) of the branching angles are calculated directly from empirical distributions of rhizome lengths or branching angles. This estimate for the long-term diffusivity of clones can be applied to any plant species whose vegetative spread can be modeled as a random walk.

Diffusion constants often are estimated with regression techniques (Okubo 1980). However, for situations such as ours in which random-walk models are appropriate and only short-term data are available, the estimate in eqn. 3 is more accurate than the standard regression estimate (Cain 1990b). We therefore used eqn. 3 to calculate the long-term diffusivity of S. altissima clones. We calculated the following four estimates of the diffusion constant: $D_1 = 181$ cm²/yr (control plots, all years), $D_2 = 205$ cm²/yr (insecticide-treated plots, all years), $D_3 = 201$ cm²/yr (control plots, 1987–88 only), and $D_4 = 263$ cm²/yr (insecticide-treated plots, 1987–88 only). Because of the possible delay in the manifestation of treatment effects on rhizome lengths (see above), D_3 and D_4 may more accurately reflect treatment differences in long-term displacements than D_1 and D_2.

If we substitute the values for D_1 and D_2 into eqn. 1, after 50 years of growth clones in the insecticide-treated plots will have moved 11 cm farther on average than clones in the control plots. If we utilize D_3 and D_4 as being more representative of long-term treatment effects, in the first 50 years of growth clones in the insecticide-treated plots on average move 26 cm farther than clones in the control plots. These results suggest that our experimental treatments have a fairly small effect on the long-term expansion of S. altissima clones. Furthermore, any treatment differences in net displacements that do exist might well be swamped out by the variance inherent in a diffusion process: the confidence intervals surrounding the treatment means always overlap (Fig. 4), so if long-term data were collected, there often would be no significant difference between treatment mean net displacements. Similarly, based on the assumption that the diffusion coefficients D_3 and D_4 represent actual treatment effects, diffusion models can be used to show that the probability of detecting treatment differences in long-term displacements is only 9% (Cain 1991).

These calculations assume that treatment diffusion coefficients remain constant over time. However, it is possible that over extended periods of time (10–20 years) our treatments would so alter rhizome lengths that treatment differences in long-term displacements would be
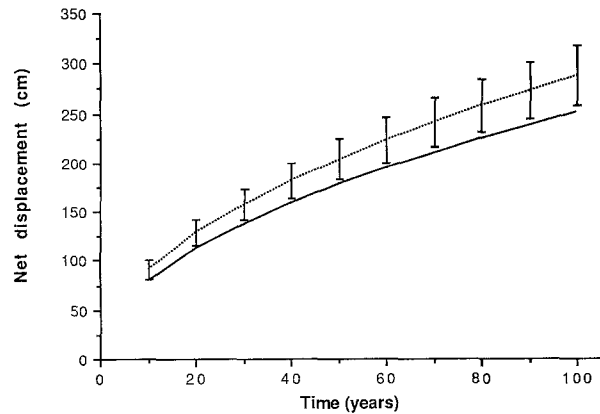

Fig. 4. Net displacements of S. altissima ramets versus time predicted by a diffusion model for the control plots (———) and for the insecticidetreated plots (·····). Diffusion coefficients for the control and insecticide-treated plots were, respectively, $D_3 = 201$ cm²/yr and $D_4 = 263$ cm²/yr. The vertical bars about the dotted line are (year-byyear) t-test 90% confidence intervals. Confidence intervals about the solid line are similar in magnitude; thus, the confidence intervals always overlap

observed. For this to occur, the cumulative effect of our treatments on rhizome lengths would have to be quite large: for example, to have a 70% chance of observing treatment differences in long-term displacements, mean rhizome lengths in the insecticide-treated plots would have to increase from the 15 cm observed in this study to 25 cm (calculated from Eq. 3 in this paper and eqn. 7 in Cain 1991). This would represent an increase in mean rhizome length equal to 1.3 rhizome length standard deviations.

Discussion

In this paper, we show that the long-term suppression of endemic levels of insect herbivores alters below-ground growth in S. altissima. We found that rhizome lengths, rhizome biomass, and the number of daughter rhizomes all were lower in the control plots than in the insecticide-treated plots. We also found that ramet heights were considerably lower in the control plots. Such effects have important consequences for the dynamics of S. altissima ramets: small rhizomes tend to develop into small ramets, and small ramets produce fewer and smaller daughter ramets than do large ramets (Cain 1990a). In addition, small ramets have lower survivorship and fecundity than large ramets (Cain 1990a), and a decrease in the production of daughter rhizomes (this study) should decrease initial above-ground ramet densities.

The effects insect herbivores have upon ramet dynamics may, in turn, alter the dynamics of plant communities. For example, a decrease in both the initial ramet density and the probability of ramet survival should lead to an overall reduction in the density of S. altissima ramets. Since S. altissima tends to dominate large portions of old fields, this suggests that the control plots should be a more open community than the insecticide-treated plots, with greater light levels available to the subcanopy. In

combination, a decrease in *S. altissima* densities and an increase in subcanopy light levels should release subcanopy plants from asymmetrical competition with canopy plants (Carson and Barrett 1988; Carson and Pickett 1990; Goldberg and Miller 1990), leading to an increase in the diversity, density and performance of subcanopy species. For the old-field site used in this study, such changes in plant community structure indeed have been found (Carson and Root, unpublished data).

The impact of insect herbivores on plant fitness is usually assessed in terms of such fitness components as the number or weight of seeds or flowers (Marquis 1984; Crawley 1985). Our study is the first study in a natural community to show that above-ground insect herbivory can decrease below-ground vegetative reproduction. By decreasing the number of rhizomes produced per ramet, herbivory should lead to an overall reduction in the number of ramets per genet. Because each ramet in a genet is capable of producing seeds, this should decrease the fitness of genets in the control plots relative to the fitness of genets in the insecticide-treated plots. Our observation that ramet heights were lower in the control plots also has fitness implications. Ramet size is positively correlated with flower production in *S. altissima* (Cain 1990a), so ramets in the control plots should produce fewer seeds than ramets in the insecticide-treated plots. Thus, insect herbivory appears to exert a powerful, dual effect on *S. altissima* fitness: it lowers both the number of ramets in a genet and the average number of seeds each ramet produces.

Another effect insect herbivores could have on clonal plant species is to decrease their rate of clonal expansion. We found that rhizome lengths were significantly shorter in the control plots than in the insecticide-treated plots: from this it might be tempting to argue that clones spread more slowly in plots not treated with insecticides. However, when we utilized random-walk models to analyze the short-term expansion of clones, we found no significant differences between the control and the insecticide-treated plots. In addition, predicted net displacements (eqn. 1) suggest that treatment effects on the long-term expansion of clones are small. Hence, our experimental treatments altered rhizome lengths but had little effect on rates of clonal expansion.

There are several possible explanations for this result. First, our treatments could have altered another movement parameter, such as branching angles, in a way that counteracted the changes in rhizome lengths. Our data, however, provide no evidence of this (Fig. 1; Table 1). A second explanation hinges on the variable nature of clonal growth processes. It is common for rhizome branching angles to diverge considerably from the preceding year's direction of growth (Cain 1990b). This causes *S. altissima* ramets to backtrack often, which, in turn, causes differences in net displacements to be less pronounced than differences in rhizome lengths. For *S. altissima* such variation in clonal growth patterns was sufficiently high to obscure treatment differences in long-term displacements (Fig. 4). More generally, results from diffusion models indicate that treatment differences in long-term displacements often will not be detected unless

treatment differences in rhizome lengths are large (Cain 1991). These results sound a cautionary note for studies that utilize treatment differences in mean rhizome lengths to infer treatment differences in long-term patterns of clonal growth (Slade and Hutchings 1987a).

The absence of large treatment differences in long-term displacements has an interesting interpretation. Ramets in the control plots appear to have compensated for herbivory: the ratio of rhizome length (cm) to rhizome biomass (g) was 9.5 cm/g in the control plots and 6.8 cm/g in the insecticide-treated plots (Table 1). Thus, clones moved farther per unit biomass in the control plots than in the insecticide-treated plots. To quantify the effect of this change in allocation patterns, we multiplied rhizome length data in the control plots by $\frac{6.8}{9.5} = 0.72$. In effect, this scaled rhizomes in the control plots to have the same average length per unit biomass as rhizomes in the insecticide-treated plots. When rhizome lengths for 1987 and 1988 were adjusted in this way, diffusion coefficients in the control plots dropped from 201 cm²/yr to 104 cm²/yr. This drop caused a corresponding increase in the ability to detect treatment differences in rates of clonal expansion: for example, when rhizome lengths in the control plots were scaled down, the probability of observing long-term treatment differences rose from 0.09 to 0.52 (calculated from eqn. 7 in Cain 1991). Similarly, after adjustment for compensation, mean net displacements after 50 years differ between treatments by 75 cm, instead of 26 cm (see Results). These results suggest that ramet compensation for herbivory greatly reduces the magnitude of treatment differences in the long-term displacement of clones. Similar changes in allocation patterns have been found for other clonal species (Ginzo and Lovell 1973; Hartnett and Bazzaz 1983; Slade and Hutchings 1987b). As pointed out in these and other studies, it may be common for plants to shift allocation patterns in this way when stressed, and perhaps thereby to aid in their escape from adverse conditions.

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