

DO BALSAM TWIG APHIDS (HOMOPTERA: APHIDIDAE) LOWER TREE SUSCEPTIBILITY TO SPRUCE BUDWORM?

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Abstract

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The balsam twig aphid, *Mindarus abietinus* Koch, infested nearly all trees in a range-wide provenance plantation of balsam fir, *Abies balsamea* (L.) Mill., in Michigan. Infestation levels were highest on eastern and lowest on western seed sources of fir. Large populations of the aphid were correlated with low survival and reduced developmental rates of the spruce budworm, *Choristoneura fumiferana* (Clemens). We propose that chronic, high susceptibility of trees to aphids could reduce concomitant susceptibility to budworm through direct (competition) and indirect (host and community-level) effects.

Résumé

Le puceron *Mindarus abietinus* Koch infestait presque tous les arbres dans une plantation du sapin baumier, *Abies balsamea* (L.) Mill., au Michigan; les arbres étaient de provenance largement répartie dans l'aire de distribution du sapin. Les niveaux d'infestation étaient maximum sur les provenances de l'est, et minimum sur celles de l'ouest. Les populations denses du puceron étaient corrélées avec la baisse de survie et ralentissement du développement de la tordeuse des bourgeons de l'épinette, *Choristoneura fumiferana* (Clemens). Nous proposons que la susceptibilité chronique des arbres au puceron peut réduire la susceptibilité à la tordeuse par des mécanismes directs (compétition) et indirects (au niveau de la communauté).

Introduction

The balsam twig aphid, *Mindarus abietinus* Koch (Homoptera: Aphididae), and the spruce budworm, *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), have similar phenologies and host requirements in eastern North America. Both feed on the newly elongating shoots and foliage of balsam fir, *Abies balsamea* (L.) Mill., and white spruce, *Picea glauca* (Moench) Voss. These insects may compete with one another for food and space especially when their populations are large. For example, when the balsam twig aphid is abundant on balsam, it causes the shoots and the new foliage to become stunted, curled, and coated with waxy secretions, honeydew, and sooty mold fungi. These conditions could cause spruce budworms to avoid feeding on such foliage or at least impair the budworm's normal feeding activities. Furthermore, the balsam twig aphid could trigger a change in plant chemistry (such as the occurrence of juvabione-related compounds) as happens when *Adelges piceae* (Ratzeburg) infests *Abies* (Puritch and Nijholt 1974).

Balsam twig aphid population levels are apparently highest in stands of young fir trees (Martineau 1984). Since the 1930's, 2- to 3-year-long outbreaks have been recorded over large areas every 4–6 years in eastern Canada, especially in the Maritime Provinces (Renault 1983; Martineau 1984). Outbreaks of spruce budworm, however, typically occur in older stands (>40 years). It is unknown why balsam twig aphid and spruce budworm outbreaks usually occur in forests of dissimilar ages.

This study reports on the negative effects of high twig aphid levels on the survival and developmental rates of spruce budworm on balsam fir.

Methods

This study was conducted in 1985, 1986, and 1987 in a 1-ha balsam fir provenance plantation on the Kellogg Experimental Forest of Michigan State University in south-western Michigan. Trees were 21 years old in 1985, spaced at 1.8×2.4 m, and averaged from 9 to 10 m tall.

In 1985 two to five trees (37 total) from each of 13 different seed sources and 40 half-siblings (same mother tree) from lower Michigan were selected at random to measure tree susceptibility to spruce budworm. Four midcrown branches (representing each cardinal direction) from each tree were enclosed in an 85- to 90-cm sleeve cage. We placed a known number (ca. 30) of second-instar budworm larvae in the cage shortly after bud break (approx. 250 degree-days using 2.8°C base and 1 March starting date). After about 50% pupation, all caged branches were cut and returned to the laboratory where we examined each for number of surviving budworm, numbers of predaceous insects (syrphids, chrysopids, coccinellids, etc.), number of new shoots, amount of defoliation, and level of twig aphid infestation based on needle curling and aphid remains per branch (each branch scored as none, light, medium, or heavy). Budworm pupae were placed in vials and monitored twice daily until adult eclosion. Adults were then frozen, oven-dried to constant weight, and weighed. From these data we calculated spruce budworm survival, weights, development time (days), and growth rates (weight gain/development time).

To evaluate the effects of balsam twig aphid abundance on spruce budworm survival (second-instar larvae \rightarrow adult stage), we pooled (over trees and seed sources) bags having similar aphid ranks for both the range-wide provenance and the Michigan half-sibling trees, and then employed Tukey's multiple-range test to compare mean survival rates among the four twig aphid rankings for each group of trees.

In late June, we carefully measured the amount of balsam twig aphid injury on each of the provenance trees by scoring each of 150 shoots (25 per branch, randomly selected from the north and south sides of upper, middle, and lower crown levels) using a scale of 0 to 4: 0, no damage; 1, <10% needles curled; 2, 10–30% needles curled; 3, 30–70% needles curled; and 4, >70% needles curled. The overall tree score was computed as the mean of all measured shoots. We then plotted spruce budworm performance (survival, weight, development time) per tree versus tree aphid score.

In 1986 and 1987, we tested the hypotheses that twig aphid effects on spruce budworm are due to (a) a systemic, whole-tree induced change in foliar quality as the result of heavy aphid feeding on virtually every new shoot and (b) a local effect confined to the individual branch on which spruce budworm were caged with aphids. To execute this test, we used 12 (1987) and 16 (1986) heavily infested trees (Quebec and New Brunswick sources) in completely randomized split-plot experimental design with two main "plot" treatments: half of the trees were drench-sprayed (except for three branches) to decrease aphid levels, and half were unsprayed controls with outbreak levels of balsam twig aphid. The two secondary or "subplot" treatments (spruce budworm growing with abundant balsam twig aphid, and spruce budworm growing with nominal balsam twig aphid) were randomly allocated to each of three midcrown branches on the entire set of trees. We protected three branches with plastic bags on the sprayed trees to obtain branches with abundant twig aphids, and we sprayed three branches using hand-held pressure pump sprayers on the unsprayed trees to obtain branches with nominal balsam twig aphid. Spraying of whole trees and single branches with an aphidicide, pirimor, occurred on 24 April in 1986 and 1987, about 1 week after aphid emergence. Whole-tree drench-spraying was done with a hydraulic tank sprayer. On the next day we enclosed six midcrown branches of each tree with sleeve cages (as before) wherein we placed about 30 second-instar spruce budworm larvae. We analyzed the budworm performance data using an analysis of variance for a

Table 1. Mean percentage survival of spruce budworm on branches that had various levels of aphids on 13 range-wide balsam seed sources and one half-sibling lower Michigan source

Seed source	Percentage budworm survival on four aphid levels:			
	None	Light	Medium	Heavy
Range-wide	30a*	19b	17bc	11c
Michigan	37a	41a	24b	16b

*Row elements having different letters are significantly ($P \leq 0.05$) different from one another using Tukey's range test.

split-plot, completely randomized design. Survival rates were transformed to their arcsin square root equivalents before analysis of variance.

Results and Discussion

Spruce Budworm Survival—1985. Spruce budworm survival per branch clearly decreased as aphid levels increased (Table 1). On the lower Michigan population of half-sibling trees, survival at the lowest aphid level was about 2-fold that at the highest level (37% versus 16%). On the range-wide provenance trees, survival was nearly 3-fold higher at the lowest aphid levels than at the highest (30% versus 11%).

Because aphid levels and shoot damage were substantially different among trees (Fig. 1), we plotted spruce budworm survival per tree (pooling bags per tree) against the mean aphid index per tree based on our independent measure of 150 shoots per tree (Fig. 2). Budworm survival decreased linearly as the aphid index per tree increased ($r = -0.77$,

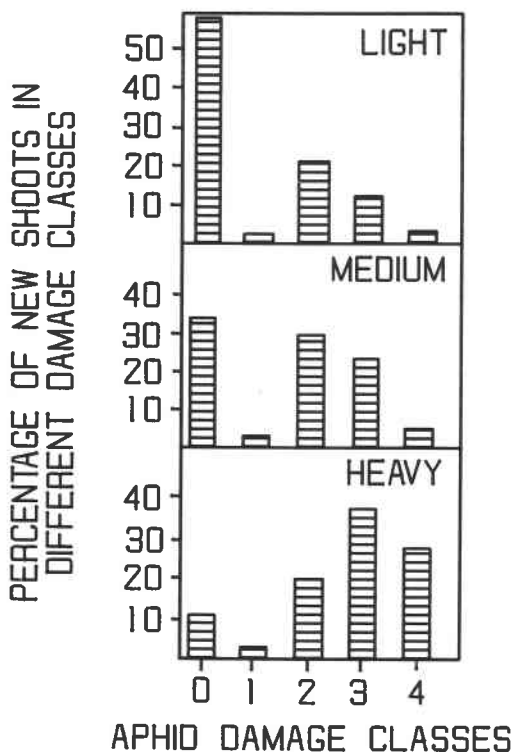


FIG. 1. Frequency distributions of shoots in different aphid damage classes (0, no damage; 1, <10% needles curled; 2, 10–30% needles curled; 3, 30–70% needles curled; 4, >70% needles curled) on lightly ($n = 10$), medium ($n = 11$), and heavily infested ($n = 17$) trees. (See Methods for details.)

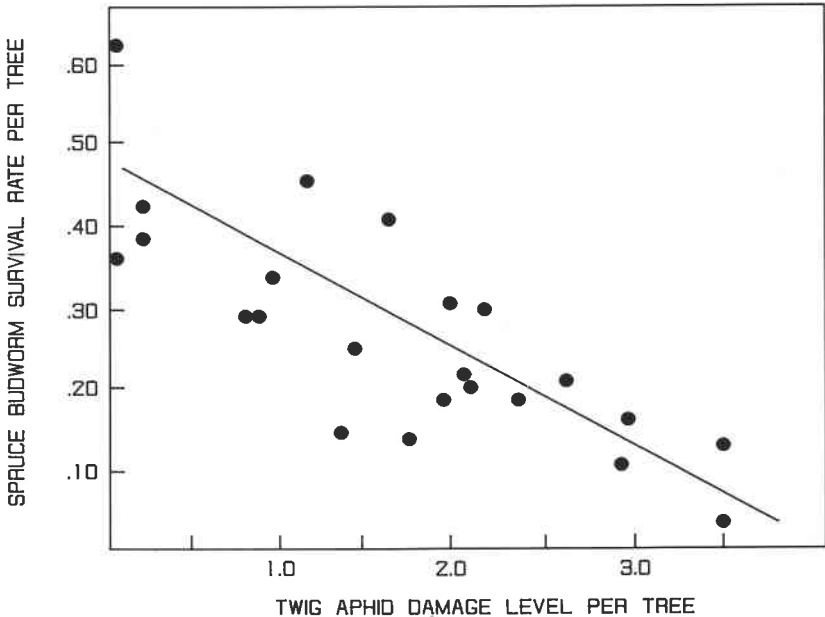


FIG. 2. Survival rate of spruce budworm larvae (cohort of ca. 120) per tree in relation to mean twig aphid damage level per tree. Twig aphid damage was rated as follows: 0, no damage; 1, <10% needles curled; 2, 10–30% needles curled; 3, 30–70% needles curled; 4, >70% needles curled.

$P < 0.001$). Trees with the fewest aphids had survival rates as high as 60%, whereas those with the most aphids had survival rates as low as 5%.

Spruce Budworm Development Time and Growth—1985. To compare male and female spruce budworm development times with aphid damage levels simultaneously, we converted male developmental times (days from second-instar larva to adult) to female-equivalents by multiplying each by the constant 1.03, because females on the average spent 1.03-fold more time growing than did males. Plotting both female and female-equivalent development times per tree against aphid damage index per tree revealed a linear, positive relation ($r = 0.59$, $P < 0.001$) (Fig. 3). Developmental times for trees with the fewest aphids were about 3 days less than those with the most aphids (47 versus 50 days).

Plotting mean female and female equivalent (male weights $\times 1.91$) spruce budworm adult weight per tree against the average aphid rank revealed no apparent relationship ($r = 0.03$, $P = 0.44$). We expected spruce budworm growth to decrease as aphid levels increased because balsam twig aphid caused the new foliage to be thoroughly coated with honeydew and waxy secretions. In the most severe circumstances we have observed spruce budworm larvae nearly immobilized in the heavy honeydew surrounding the new needles. Under such conditions they may be forced to feed on the older, less nutritious, but honeydew-free needles.

Aphid Levels Versus Tree Geographic Source. Twig aphid levels were obviously different among seed sources. DeHayes (1981), who studied a similar provenance plantation of balsam fir in Vermont, concluded that susceptibility to balsam twig aphid was somehow linked to the longitude of the seed source. Trees from the eastern half of the natural range of balsam fir were more susceptible than those from the western half (the natural range extends from New Brunswick and Maine to eastern Alberta). Plotting the average aphid damage index per tree for each seed source against the degrees longitude of that source (Fig. 4) confirmed the results of DeHayes (1981); there was a linear relationship

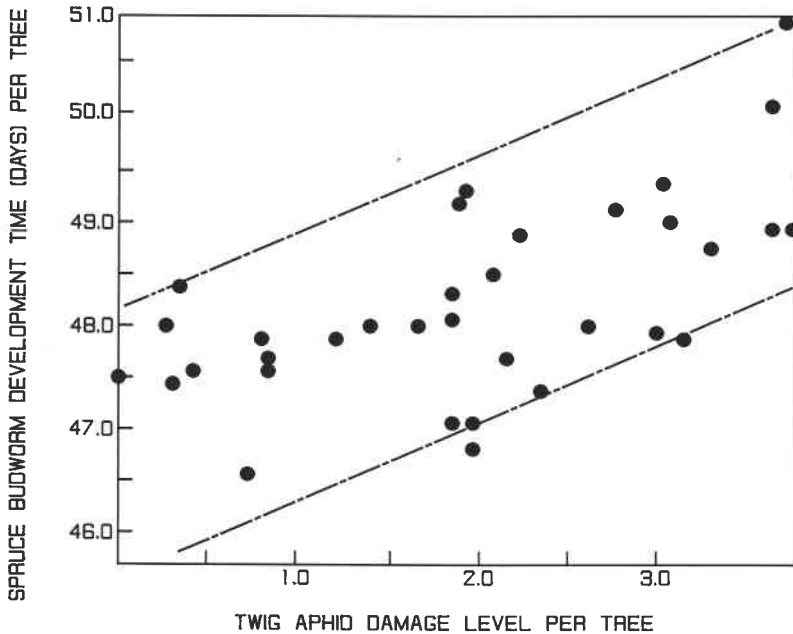


FIG. 3. Mean development time (days) per tree for female and female-equivalent spruce budworm (see Results) in relation to mean twig aphid damage level per tree. Twig aphid damage was rated as follows: 0, no damage; 1, <10% needles curled; 2, 10–30% needles curled; 3, 30–70% needles curled; 4, >70% needles curled.

($r = -0.75$, $P < 0.001$) between aphid susceptibility and longitudinal origin of a seed source, eastern sources being more uniformly susceptible to severe balsam twig aphid damage than western ones.

We cannot explain the differences in susceptibility of balsam fir to balsam twig aphid. Although susceptibility to aphids in some tree species is linked to their phenology of bud break and shoot elongation (Carter and Nichols 1985), DeHayes (1981) concluded that this is not the case for balsam fir. He speculated that variations in foliar and shoot terpenes may explain the differences.

Systemic, Whole-tree Versus Branch-level Aphid Effects on Budworm. Spraying trees was very effective in reducing balsam twig aphid to nominal levels and thereby eliminating most needle and shoot deformation. Nevertheless, in both 1986 and 1987, there were no significant whole-tree aphid effects on spruce budworm survival rates, growth, or developmental rates (Table 2). Heavy infestations of balsam twig aphid on almost every new growing point of 22- to 23-year-old balsam firs did not elicit a systemic change in whole-tree physiology that altered the performance of budworm larvae.

On the contrary, in both years there were significant ($P < 0.05$) branch-level (localized) aphid effects on spruce budworm survival (Table 3). Budworm cohorts growing with low aphid levels (whole-tree treatments pooled) had survival rates 1.5-fold (0.35 versus 0.23), and 1.6-fold (0.19 versus 0.12) higher than those cohorts growing with high aphid levels in 1986 and 1987, respectively. Just as in 1985, there were no significant differences in adult weights for those cohorts growing with low and high aphids. Unlike 1985, however, we found no differences in spruce budworm developmental times (days) or growth rates (milligrams per day) between aphid-nominal and aphid-heavily infested trees and branches. We cannot explain this discrepancy except that there may be tree effects confounded with aphid effects on developmental time in 1985. Lightly and heavily infested

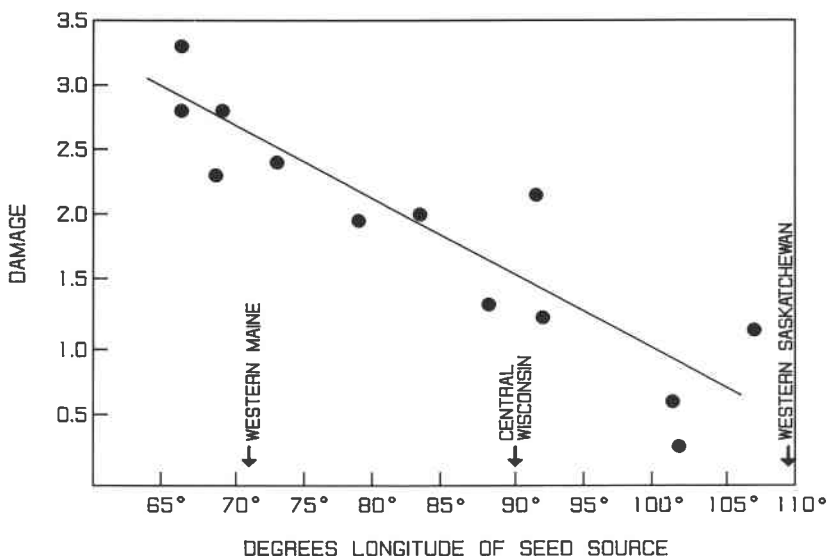


FIG. 4. Mean twig aphid damage level per tree per seed source in relation to the longitudinal (degrees) origin of the seed source in North America. Twig aphid damage was rated as follows: 0, no damage; 1, <10% needles curled; 2, 10–30% needles curled; 3, 30–70% needles curled; 4, >70% needles curled.

Table 2. Mean spruce budworm performance in 1986 and 1987 on trees (main plots) and branches (subplots) with and without heavy balsam twig aphid infestation. Only survival in subplots was significantly different. See Table 3 for analysis of variance

Budworm performance variable	Trees (main plot)		Branches (subplots)	
	Aphid-poor	Aphid-rich	Aphid-poor	Aphid-rich
1986				
Survival (%)	29.8	28.7	34.7a*	22.9b
♂ weight (mg dwt)	11.00	11.49	11.35	11.17
♀ weight (mg)	21.39	23.10	22.72	21.82
♂ dev. time (days)	50.80	49.91	50.66	50.09
♀ dev. time (days)	52.24	51.58	52.15	51.72
♂ growth rate (mg/day)	0.22	0.23	0.22	0.22
♀ growth rate (mg/day)	0.41	0.44	0.43	0.42
1987				
Survival (%)	16.3	16.4	19.0a	12.2b
♂ weight (mg dwt)	11.21	10.79	10.97	11.06
♀ weight (mg)	23.21	24.98	22.87	25.43
♂ dev. time (days)	47.68	48.33	48.03	47.73
♀ dev. time (days)	49.37	48.27	48.97	48.73
♂ growth rate (mg/day)	0.24	0.23	0.23	0.23
♀ growth rate (mg/day)	0.47	0.51	0.47	0.52

*Row elements having different letters are significantly ($P \leq 0.05$) different.

Table 3. Analysis of variance (in split-plot design) of spruce budworm survival rates (arcsin-transformed data) in 1986 and 1987 on aphid-infested balsam firs from Quebec and New Brunswick sources

Source	Degrees of freedom		Mean square		F values	
	1986	1987	1986	1987	1986	1987
Main plot						
Aphids/tree	1	1	0.71	4.81	0.01	0.02
Error	6	10	68.72	270.06	—	—
Subplot						
Aphids/branch	1	1	608.66	571.32	10.49*	6.52*
Aphids/branch × aphids/tree	1	1	131.70	80.10	2.27	0.91
Error	6	10	58.00	87.68	—	—
Bags within trees	30	47	48.42	84.75	—	—

* $P \leq 0.05$.

trees in 1985 were different for reasons other than current levels of aphids. Another related explanation is the unexplored question of lagging, cumulative, long-term inducible changes in tree properties that may cause lightly infested trees to be different from chronically infested trees. Our experiments did not address this issue, only immediate, inducible effects. Chronic, heavy aphid infestations may have a long-term, systemic effect in addition to an immediate one (systemic effect = immediate + long-term components). Hence, the long-term effect may mask the immediate one, if it is cumulative and large relative to the immediate one. We tested only for the immediate effect, because it was immediately feasible, and we expected it to be the dominant systemic effect if there was one. Our rationale was that current, heavy aphid feeding is known to alter normal “source-to-sink” pathways in plants, and that feeding may also elicit an immediate, recognition-type defense or more general defenses through the disruption of local turgor and mineral nutrient balances in plants (Arthur and Hain 1985; Mattson *et al.* 1988; Tuomi *et al.* 1988).

Explaining Branch- and Tree-level Balsam Twig Aphid Effects. The mechanisms by which balsam twig aphids influence spruce budworm survival are not clear. The aphid effects in 1986 and 1987 were apparently largely local ones — those occurring at the branch level. One explanation is that spruce budworm survival is lowered owing strictly to physical competition for food and space between aphids and early-instar spruce budworm. Another is that balsam twig aphids cause an ephemeral change in local (branch-level) foliar chemistry that reduces the success of early-instar budworm larvae in establishing feeding sites. This hypothesis is less likely than the former one because there apparently were no immediate, ephemeral, systemic effects on spruce budworm when whole trees were heavily infested with aphids. On the other hand, there is some support for a chronic, systemic effect hypothesis. For example, lowering twig aphid populations at the branch-level enhanced budworm survival only about 1.5- to 1.6-fold in 1986 and 1987 on chronically infested trees, whereas in 1985 budworm growing on naturally aphid-poor trees had survival rates which were 2- to 10-fold higher than those on chronically, heavily infested trees (Fig. 2). Because both spruce budworm survival ($P < 0.02$) and balsam twig aphid ranks ($P < 0.02$) varied significantly among seed sources, we used a covariance analysis (aphid rank as covariate) to separate these two effects on spruce budworm survival: source effects were insignificant ($P < 0.65$) after adjusting for the covariate. This suggests that seed source and tree effects are small relative to balsam twig aphid effects (immediate and long term).

Table 4. Two-way analysis of variance* of spruce budworm survival rates (arcsin-transformed) in 1985 using aphid and predator level classifications per sleeve cage as main effects

Source	Degrees of freedom	Mean square	F value
Aphid level	4	258.98	3.02†
Predator level	3	83.17	0.96
A × P	7	115.02	1.34
Error	121	85.76	—

*Due to unbalanced experimental design (observations unequal in all cells) the degrees of freedom for the interaction term is smaller than usual.

† $P \leq 0.05$.

A fourth hypothesis is aphid enhancement of aphid natural enemies which secondarily kill spruce budworm. For example, heavily infested aphid branches may contain substantially more aphid predators (e.g. coccinellids) than lightly infested branches. Hence spruce budworm survival is lowered. We discount this hypothesis as the main explanation for "aphid effects" in our sleeve cages, because there was no relationship between spruce budworm survival per bag and predator abundance in all 3 years after accounting for aphid abundance (Table 4).

A fifth and rather intriguing hypothesis is aphid enhancement of phylloplane microorganisms that may incidentally have allelopathic effects on spruce budworm (Jones 1984). For example, it is common that heavily infested trees have blackened foliage due apparently to saprophytic sooty mold fungi. Some phylloplane fungi can produce mycotoxins which may be toxic to spruce budworm (Miller *et al.* 1985; Strongman *et al.* 1988). Unfortunately, we have no evidence to evaluate this interesting hypothesis.

With respect to the negative correlation between spruce budworm developmental rates and balsam twig aphid in 1985, we hypothesize that the causal agent is long-term, cumulative changes in foliar chemistry that lowered developmental rates on the heavily and chronically infested trees. These trees have been infested since at least 1983 based on our casual records. We could not detect this effect in 1986 and 1987 because all experimental trees were chronically infested.

Community-level Balsam Twig Aphid Effects. Our data suggest that balsam twig aphid, under some circumstances, can influence spruce budworm population dynamics. One influence occurs only in those years when aphids directly out-compete budworms for new shoots (or trigger an ephemeral, local defense). Another occurs over several years because of the long-term impact of aphid feeding on foliage architecture and perhaps foliage chemistry that could reduce the suitability of foliage for oviposition, or obligatory mining and feeding by second-instar budworm larvae. Nettleton and Hain (1982) concluded that 45% of the severe needle curling in *Abies fraseri* (Pursh) Poir. was permanent. Recovery was most likely in the vigorous upper portions of the crown and in vigorous trees. Still another influence is the effect of aphid honeydew as food for increasing populations of some phylloplane fungi and prolonging the lives and increasing the fecundity of natural enemies of spruce budworm such as ants, and parasitic wasps and flies (Downes and Dahlem 1987). On the other hand, Miller (1987) has demonstrated that such sources of food might also very well enhance the longevity and the fecundity of spruce budworm moths.

These data pose questions about the importance of the many and often opposing kinds of community-level interactions which occur not only horizontally (e.g. spruce budworm versus balsam twig aphid), but also vertically (among plants, phytophages, symbionts, and natural enemies) (see Faeth 1987 for an overview) (Fig. 5). The general question is whether plant susceptibility to one phytophage species can consistently and substantially lower contemporaneous or sequential susceptibility to others, and thereby eventually

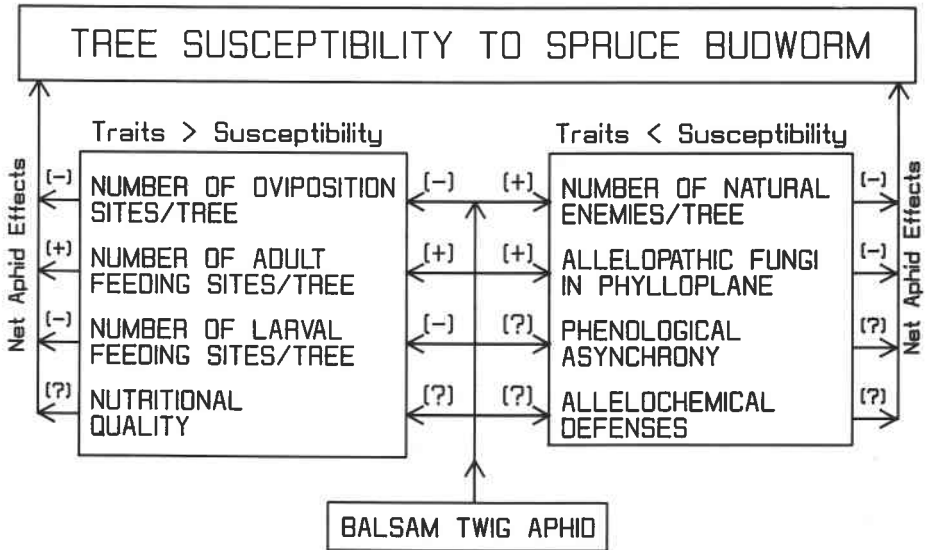


FIG. 5. Examining the effects of balsam twig aphids on tree susceptibility to spruce budworm through aphid impact on key tree traits. > = increasing susceptibility; < = decreasing susceptibility.

become an integral part of the plant's defensive "package" against other potentially serious phytophages. Neuvonen *et al.* (1988), Faeth (1986, 1987), Karban *et al.* (1987), Harrison and Karban (1986), and Kuc (1983) have provided evidence that plant invasion by one phytophage can significantly lower the success of later ones. But such a "defense" can only be a viable evolutionary option if (a) the other phytophages are much more debilitating to plant fitness than the first, and (b) the first is abundant and ubiquitous enough to consistently "defend" the plant. If such systems were to evolve, we believe that aphids, and perhaps scales too, may uniquely qualify for the "defending" phytophage position, as long as they do not transmit plant pathogens. First, their method of feeding is one of the least disruptive to the plant's physiological make-up, as opposed to those that remove both vital tissues and nutrients, as do chewing types (Mattson *et al.* 1988). Second, their insertion of mouth parts intercellularly along with the protein sheath may trigger some of the plant's more specific defensive reactions because foreign insect molecules will be brought into intimate contact with living plant cells (Mattson *et al.* 1988). Such plant defensive reactions might then be inimical to other phytophages even if not to the aphids. Third, even if defenses were inimical to the aphids, their chances of overcoming them through evolutionary processes are probably much greater than for many other kinds of phytophages because of their unusual and prolific breeding systems. In both parthenogenetic and nonparthenogenetic aphid species there has been very rapid development of novel, resistance-breaking biotypes in agricultural ecosystems (Buckley 1987). Moreover, there are several cases of sympatric speciation or incipient speciation of Homoptera on a single host (Buckley 1987). All of this is testimony to the hypothesis that aphids may be among the most likely and consistent early successful colonizers of novel plant genotypes. Finally, aphids may be more likely, owing to their honeydew production, to establish mutualistic bioassociations (enhanced allelopathic microorganisms and natural enemies hypotheses) that may simultaneously benefit the plant. Although we discounted the natural enemy hypothesis earlier, it was only because in our sleeve cage enclosures, generalist predators were not the main factor reducing spruce budworm survival. However, we recognize that enhancement of generalist and specialist natural enemies may be even more

important than direct balsam twig aphid effects. For example ants, predaceous wasps, parasitoid wasps, and flies which are attracted to and utilize aphid and scale honeydew (Way 1963; Buckley 1987; Elliot *et al.* 1987; Downes and Dahlem 1987) and flower nectar (Lieux 1967), may concomitantly lower populations of contemporaneous herbivores. Ants in particular are conspicuous for their ability to reduce herbivore populations in their foraging zones (Laine and Niemela 1980; Campbell *et al.* 1983; Larsson 1985; Schaupp 1986; Buckley 1987; Strauss 1987). Bentley (1977) suggested that aphids and other honeydew-secreting Homoptera might be the ecological analogues in temperate zones of the extra-floral nectaries that attract predaceous "body guards" such as ants to so many plant species in the tropics. Furthermore, the presence of honeydew may cause less obvious but highly significant effects through the enhancement of parasitoid wasps and flies (Downes and Dahlem 1987) and perhaps allelopathic phylloplane fungi (Jones 1984; Strongman *et al.* 1988). So we argue here, as did Strauss (1987), that aphids and scales may be "keystone" species in the structure of the total community. In fact, Strauss (1987) provided evidence that increases in honeydew-producing aphids on a perennial, *Artemisia ludoviciana* Nuttall, brought about subsequent decreases in chrysomelid folivores via aphid-tending ants.

Depending on the frequency and duration of balsam twig aphid outbreaks during stand ontogeny, they could be important in rendering balsam forests less susceptible to spruce budworm outbreaks.

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