

ASSOCIATIONAL SUSCEPTIBILITY OF COTTONWOOD TO A BOX ELDER HERBIVORE

JENNIFER A. WHITE¹ AND THOMAS G. WHITHAM

Department of Biological Sciences, Box 5640, Northern Arizona University, Flagstaff, Arizona 86011 USA

Abstract. Associational resistance, which refers to decreased herbivory experienced by a plant growing with heterospecific neighbors, is a well documented ecological phenomenon. In contrast, studies that describe increased herbivory due to heterospecific neighbors (associational susceptibility) are relatively rare. In this study we document associational susceptibility among hosts of the fall cankerworm (*Alsophila pometaria*). Cottonwoods (*Populus angustifolia* × *P. fremontii*) located under box elder (*Acer negundo*) were colonized by two to three times more cankerworms, and suffered two to three times greater defoliation than cottonwoods growing under mature cottonwoods, or cottonwoods growing in the open. This associational pattern reflects fall cankerworm's strong preference for box elder over cottonwood: egg densities were 26 times greater on box elder than cottonwood, first instar larvae consumed 75 times more box elder than cottonwood in larval palatability trials, and fourth instar larvae consumed three times more box elder than cottonwood. In terms of larval performance, first instar larvae exhibited approximately six times greater mortality and 40% slower development time on cottonwood relative to box elder, whereas fourth instar larval performance did not differ between the hosts. Based on these and other findings, we predict that, when generalist herbivores reach outbreak proportions and consume their preferred hosts, they will then move to nearby less-preferred hosts to complete their life cycle. This "spillover" effect will result in associational susceptibility for less-preferred hosts and is likely common in forest outbreak situations where herbivore densities are high. With increased emphasis on diversified plantings in agriculture and forestry, it is important to understand potential drawbacks such as associational susceptibility.

Key words: *Acer negundo*; *Alsophila pometaria*; associational resistance; associational susceptibility; box elder; cottonwood; dietary breadth; fall cankerworm; plant–herbivore interactions; *Populus*; preference hierarchy; spillover.

INTRODUCTION

Atsatt and O'Dowd (1976) argued that the susceptibility of a plant to herbivory is affected by the identity and proximity of its neighbors. Most ecological and agricultural studies have focused on the benefits a plant can gain by having heterospecific neighbors (e.g., Pimentel 1961, Janzen 1970, Root 1973). This interaction is known as "associational resistance," and refers to the reduction in herbivory experienced by a plant associated with taxonomically diverse plant species (Tahvanainen and Root 1972, Andow 1991). Many studies have documented reduced herbivore numbers in response to increased vegetational diversity, resulting in patterns consistent with associational resistance (see Kareiva 1983, Risch et al. 1983, Stanton 1983, and Andow 1991 for reviews). However, higher vegetational diversity does not always equate with lower herbivore density. Studies from both agricultural and natural systems have reported plant species that are subject to greater herbivory when spatially associated with het-

erospecifics (e.g., McClure et al. 1982, Hjältén et al. 1993, Karban 1997). This has been called "associational susceptibility" (Brown and Ewel 1987), "associational damage" (Thomas 1986), or "shared doom" (Wahl and Hay 1995). We prefer the term associational susceptibility, because it contrasts most intuitively with associational resistance. Note that neither term refers to resistance or susceptibility in a genetic sense.

Associational susceptibility is probably more common than generally appreciated in the ecological literature. Forestry studies frequently report that in outbreak situations nonfavored host species become defoliated in the vicinity of the pests' favored hosts (e.g., Hodson 1941, Cuming 1961, Fedde 1964). For these less preferred hosts that would otherwise be ignored by the pest, the probable result is associational susceptibility: greater defoliation when associated spatially with heterospecifics than with conspecifics. Although these systems have generally not been incorporated into the theoretical literature dealing with the consequences of plant spatial association (but see Futuyma and Wasserman 1980), they represent an important exception to the "rule" of associational resistance.

Current ecological theory does not systematically ac-

Manuscript received 4 January 1999; revised 26 May 1999; accepted 1 June 1999.

¹ Present address: Plant Biology Department, University of Minnesota, 220 Bioscience Center, 1445 Gortner Avenue, St. Paul, Minnesota 55108 USA. E-mail: white066@tc.umn.edu

count for both associational susceptibility and associational resistance, although some effort has been made to determine the characteristics that might encourage alternative outcomes. For example, herbivore dietary breadth has been recognized as an important factor. In a survey of agricultural studies, Andow (1991) found a marked difference between monophagous and polyphagous herbivores. The majority of monophagous herbivore species (59%) had lower densities per host plant in polycultures, whereas only 8% had higher densities in polycultures (the remaining 33% either showed no difference or variable results). In contrast, only 28% of polyphagous herbivore species had lower densities in polycultures, versus 40% with higher densities in polycultures.

Brown and Ewel (1987) have further suggested that relative palatability among plant species may determine whether a plant receives associational susceptibility or associational resistance. Supporting this, Wahl and Hay (1995) found that a marine alga associated with more palatable algal species experienced associational susceptibility, whereas association with less palatable algae caused associational resistance. However, the opposite pattern has also been proposed, wherein association with more attractive hosts leads to lowered herbivory levels (the attractant/decoy hypothesis, Atsatt and O'Dowd 1976; Hjältén et al. 1993). Consequently, the role of herbivore host preference in determining associational herbivory patterns is not clear (Andow 1988, Hjältén and Price 1997).

The first goal of this paper is to document an example of associational susceptibility using the hosts of a common forest pest, the fall cankerworm (*Alsophila pometaria*). The second goal is to examine how the host preferences of a generalist herbivore might be an important factor in predicting associational susceptibility.

METHODS

Natural history

Fall cankerworm (*Alsophila pometaria* Harr., Lepidoptera: Geometridae) is a univoltine pest species native to North America (Porter and Alden 1924). Our study was conducted along the Weber River, northern Utah, USA, where localized areas have been consistently defoliated for the past 15 years (T. G. Whitham, *personal observation*). Larvae emerge from overwintering eggs in mid- to late April, coincident with bud burst, and newly hatched larvae passively disperse through wind-borne ballooning. Once an acceptable host is reached, larvae begin feeding and only relocate when disturbed or when food is depleted (Balch 1939). Late instar larvae are heavier, and restricted in their dispersal ability. Fall cankerworm is broadly polyphagous, consuming plant species in at least 17 genera distributed among 9 families (Porter and Alden 1924). Within our study area, early larval feeding is restricted primarily to box elder (*Acer negundo*). Once box elder

is defoliated, late instar larvae disperse and defoliate other tree species such as cottonwoods (*Populus* spp.), hawthorn (*Crataegus douglasii*), willow (*Salix exigua*), and ash (*Fraxinus americanus*). At the end of the fourth and final instar (usually late May or early June), larvae drop to the ground, where they burrow 3–6 cm into the soil and pupate. Adult cankerworms emerge in late fall to mate, and the wingless females oviposit eggs at the base of small twigs of nearby vegetation.

Observational studies

To examine the patterns of associational host use (i.e., resistance, susceptibility, and/or no differences), we first quantified herbivory on cottonwoods (naturally occurring backcross hybrids of *Populus angustifolia* × *P. fremontii*) (Keim et al. 1989) growing in association with box elder. We compared cankerworm densities and defoliation levels of small trees (0.5–3.0 m in height) located either under a mature box elder, under a mature conspecific, or in the open and relatively isolated from other trees that could serve as sources of cankerworms. Eight trees in each location were chosen in early May 1995, before secondary cankerworm dispersal had begun. Cankerworm density (larvae/shoot) was calculated for each tree by taking a visual census of larval numbers on ~50 shoots and correcting for number of shoots sampled. If less than 50 shoots were present on a tree, all shoots were examined. Percentage defoliation was calculated by visually estimating the damage on the sampled shoots and placing each into one of seven damage categories: 0%, 0–5%, 5–25%, 25–50%, 50–75%, 75–100%, or 100% (if part of the stem was left, but no leaf material remained). We then generated the mean percentage defoliation for each tree using the midpoint of each category.

The timing of late instar cankerworm dispersal is heavily dependent on box elder infestation levels, which varied considerably from tree to tree. To standardize for this time effect, we measured both cankerworm density and percentage defoliation at multiple points in time. However, because the time effect was not inherently of interest to us, we chose to simplify statistical analyses by performing analysis of variance on the maximum values of larval density and defoliation, rather than performing repeated-measures ANOVA. Cankerworm density and percentage defoliation values were transformed before statistical analysis to homogenize variance among groups and linearize the relationship between density and defoliation values. A square root transformation was performed on cankerworm densities, and an arcsine square root transformation was made for proportion defoliation measurements (Neter et al. 1990). A Kruskal-Wallis one-way ANOVA by ranks was performed, followed by Dunn's Multiple Contrasts to separate means.

Experimental test of associational susceptibility

Using greenhouse propagated potted cottonwoods in a randomized block design, we performed an experi-

mental version of the associational study described above. To partially control for genetic effects, we used a blocked design (three potted cottonwoods per block) in which all members of a block were either clones of the same parent (11 blocks), or were full sibs derived from controlled crosses (8 blocks). One member of each block was placed under box elder, one under a mature cottonwood, and one in the open. These trees were <1 m tall, and supported a mean \pm 1 SE of 23.8 \pm 1.4 shoots. The experiment was started on 19 April 1996, before cankerworm egg hatch began. Each pot was sunk into the ground, and watered at 3-d intervals throughout the experiment. Percent defoliation and cankerworm densities were measured at \sim 5-d intervals beginning 14 May until 8 June, when the majority of larvae had completed their development. Larger sample sizes and conformity to normality assumptions allowed use of parametric statistics in this experiment. Transformed values of maximum cankerworm density and maximum proportion defoliation were analyzed using blocked ANOVA, followed by Tukey's hsd to separate means.

Distance from sources

A second experiment was performed to determine how cankerworm attack on cottonwood decreases as a function of distance from "source" box elders. We placed potted cottonwoods in lines from source box elders at distances of 0, 1, 2, 4, and 8 m from the source tree's canopy. There were six blocks corresponding to six different source trees. All blocks were placed on the west/southwest side (downwind) of the source tree, to standardize for prevailing winds that might affect ballooning larvae. Again, the trees were positioned before cankerworm eggs hatched, and were monitored at 5-d intervals for cankerworm numbers and percentage defoliation. Small sample size dictated the use of non-parametric statistics, hence results were analyzed using Page's test for ordered alternatives (Siegel and Castellan 1988).

Cankerworm preference and performance

To document the host preferences of fall cankerworm, we performed observational and experimental tests of cankerworm preference. Observationally, we evaluated host preference by estimating fall cankerworm egg densities on box elder and cottonwood. Twenty individuals of each species were chosen at random within our study site, and one branch weighing \sim 200 g was clipped from each using a pole pruner. Foliage was stripped from each branch, and the branch was reweighed to obtain branch mass. The total number of egg casings on the branch was counted, to yield egg density per gram of branch mass. Due to non-normality in the data, egg densities were compared using a Mann-Whitney *U* test.

We experimentally tested larval host preference in first and fourth instar larvae using a procedure based

on Jermy et al. (1968). To prevent any potential biases in host preference due to maternal effects (Rossiter 1995), or host induction (Greenblatt et al. 1978, de Boer and Hanson 1984), eggs and fourth instar larvae were collected from Gambel's oak (*Quercus gambelii*) in the field, a host that is not present in our study area but is common at higher elevations. Scarcity of cottonwood and box elder at this elevation makes previous exposure to these hosts unlikely. In the first instar experiment, leaf disks were cut from box elder and cottonwood using a #1 cork borer (\sim 9.6 mm² leaf area), and one disk from each species was placed on a moistened paper towel in a closed petri dish, randomized with respect to orientation. Newly hatched larvae were placed singly in the center of each petri dish and allowed to feed for 48 hr. This experiment was repeated for fourth instar larvae, using larger leaf disks (#3 cork borer \approx 44.2 mm²), and a shorter duration (16 hr). For each experiment, the percentage leaf material eaten was estimated for each disk and, due to lack of normality, compared using a Wilcoxon signed ranks test. Note that each larval preference experiment was undertaken when larvae of that instar were prevalent in the field, using contemporaneous leaf material. Consequently the leaf disks for the first instar preference experiment came from younger leaves than leaf disks for the fourth instar experiment.

We also tested larval performance on box elder vs. cottonwood. First instar larvae were lab-reared in petri plates on either box elder or cottonwood. Seven petri dishes were used per food source, each starting with 5–10 larvae. Larvae had a constant supply of field-collected fresh leaf material, and were not food limited. Larvae were monitored throughout development for percentage mortality. As larvae neared the end of the fourth instar, we placed field-collected soil in half of the dish. Larval censuses were taken twice a day; any larvae that had burrowed into the soil were considered to have completed feeding, and this timepoint was used to calculate larval development time.

Performance experiments for fourth instar larvae were conducted in the field. Larvae that had just molted to fourth instar were collected off box elder, and randomly placed in mesh bags (six bags, 10 larvae/bag). The bags were placed on branches of different box elder and cottonwood trees in the field (three bags per tree species). Larvae were rebagged onto a different branch of the same tree after 3 d to insure fresh food availability. After 7 d some larvae had nearly completed development, so the experiment was ended, larval mortality was determined, and larvae were weighed to obtain an estimate of growth. Larval development times and larval masses were compared using a Mann-Whitney *U* test, due to lack of normality. Percentage mortality data were compared using chi-squared analysis.

RESULTS

Observational study

Cottonwoods under box elder supported 30 \times more cankerworms per shoot than trees in the open, with

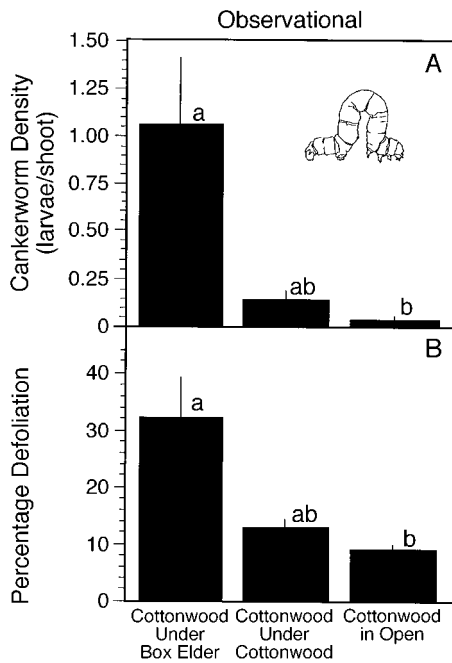


FIG. 1. (A) Mean maximum cankerworm densities + 1 SE and (B) mean maximum percentage defoliation + 1 SE of cottonwoods located under box elder ($n = 8$), under mature cottonwood ($n = 8$), and in the open ($n = 8$). Columns with the same letter did not differ significantly at $\alpha = 0.05$.

cottonwoods under conspecifics showing statistically intermediate cankerworm densities (Kruskal-Wallis $H = 13.82$, $P = 0.001$; Fig. 1A). These observational data suggest that the distribution of cankerworms is contingent on the distribution of box elder, and that cottonwoods growing with box elder are more susceptible to fall cankerworm than cottonwoods located in the open.

Increased cankerworm densities translated into higher defoliation levels for cottonwoods associated with box elder. Cankerworm density and percentage defoliation were highly correlated (Spearman rank correlation $r_s = 0.838$, $P < 0.001$), and cottonwoods located under box elder suffered three times greater defoliation than trees located in the open (Kruskal-Wallis $H = 10.14$, $P = 0.006$; Fig. 1B). As with cankerworm densities, defoliation levels of cottonwood trees located under conspecifics were statistically intermediate. The overall pattern of defoliation is very similar to the pattern of cankerworm distribution, and suggests that fall cankerworm is responsible for associational susceptibility in cottonwoods; cottonwoods growing with a heterospecific suffer greater herbivory than cottonwoods growing in the open.

Experimental test of associational susceptibility

Our experimental results confirmed our observational results; cottonwoods growing in association with box elder are more likely to be colonized by fall canker-

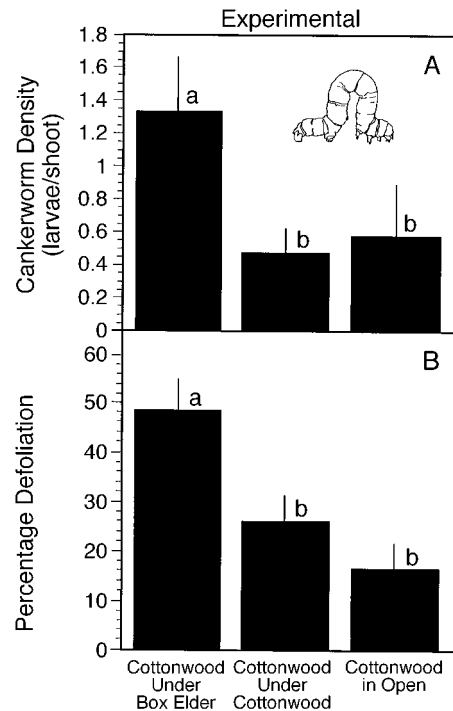


FIG. 2. (A) Mean maximum cankerworm densities + 1 SE and (B) mean maximum percentage defoliation + 1 SE of potted cottonwoods placed under box elder, under mature cottonwood, and in the open ($n = 19$ blocks). Columns with the same letter did not differ significantly at $\alpha = 0.05$.

worm and suffer greater defoliation than cottonwoods growing in other associations (Fig. 2). Potted cottonwoods placed under box elder had almost three times greater cankerworm densities than trees placed under mature cottonwoods, and two times greater cankerworm densities than trees located in the open (treatment $F = 15.445$; $df = 2, 36$; $P < 0.001$; Fig. 2A). Similarly, potted cottonwoods placed under box elder suffered defoliation levels that were nearly two times greater than those under cottonwood, and three times greater than those placed in the open (treatment $F = 9.480$; $df = 2, 36$; $P < 0.001$; Fig. 2B). The correlation between cankerworm densities and percentage defoliation was again highly significant ($r_s = 0.826$, $P < 0.001$), demonstrating that fall cankerworm densities accounted for most of the differences in defoliation levels.

Distance from sources

When potted cottonwoods were experimentally placed varying distances from box elder trees, we found that cankerworm numbers significantly declined with increasing distance from source box elders, showing that increased distance from box elder resulted in decreased susceptibility to fall cankerworm (Page's $L_a = 309$, $P < 0.001$; Fig. 3A). Potted cottonwoods placed directly under box elder always acquired the most cankerworms, and typically supported nearly $3\times$ more lar-

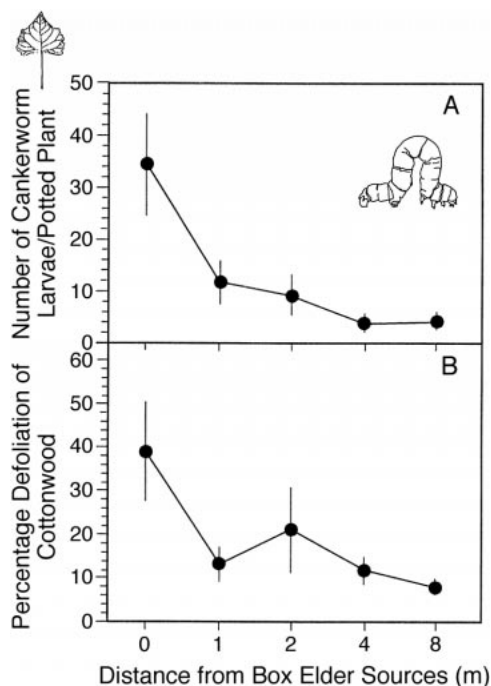


FIG. 3. (A) Mean maximum cankerworm numbers ± 1 SE and (B) mean maximum percentage defoliation ± 1 SE of potted cottonwoods placed various distances from source box elders ($n = 6$ blocks). Both cankerworm numbers and percentage defoliation decreased significantly with distance at $\alpha = 0.05$.

vae than trees placed only 1 m from the box elder canopy.

Likewise, percentage defoliation (which was strongly correlated to larval numbers; $r_s = 0.872$, $P < 0.001$), also dropped significantly with increased distance from box elder, showing that associational susceptibility is a function of distance from box elder ($L_a = 300$, $P < 0.01$; Fig. 3B). Cottonwoods located under box elder suffered about two times greater defoliation than trees farther from the source. Clearly, associational susceptibility to fall cankerworm occurs when cottonwoods grow in the immediate vicinity of box elder.

Cankerworm preference and performance

Observationally, cankerworm egg densities were 26 times greater on box elder than cottonwood ($U = 8$, $n = 39$, $P < 0.001$; Fig. 4A). Likewise, larval preference experiments showed that both first and fourth instar larvae preferred box elder to cottonwood. First instar consumption of box elder was significantly greater than consumption of cottonwood, which was essentially zero ($Z = -3.896$, $n = 22$, $P < 0.001$; Fig. 4B). Only two of 22 first instar larvae that were tested ate any cottonwood. Similar preference experiments with second and third instar larvae revealed equally strong preferences in the same direction (J. A. White and T. G. Whitham, unpublished data).

Fourth instar larvae ate three times more box elder

than cottonwood ($Z = -3.950$, $n = 30$, $P < 0.001$; Fig. 4C), and generally consumed box elder prior to consuming cottonwood (25 of 30 larvae ate box elder first, or ate only box elder). However, 20 of 30 larvae consumed at least some cottonwood, indicating that even though cottonwood is not preferred, it is a potential host for fall cankerworm.

Performance studies confirmed that cottonwood is an inferior host for first instar larvae. First instar larvae suffered six times greater mortality on cottonwood (73.1%) than box elder (11.4%; $\chi^2 = 27.6$, $df = 1$, $P < 0.001$). Surviving larvae reared on cottonwood ($n = 7$) took 19.1 ± 1.3 d (mean ± 1 SE) to reach pupation, significantly longer than larvae reared on box elder (13.9 ± 0.2 d, $n = 39$; $U = 264$, $P < 0.001$).

In contrast to the high mortality exhibited by first instar larvae on cottonwood, fourth instar larvae that were switched from box elder to cottonwood did not exhibit increased mortality over larvae that remained on box elder. In fact, no larvae died on either food source in this experiment. Moreover, larval mass did not significantly differ between fourth instar larvae on cottonwood and box elder (cottonwood larvae = 0.36 ± 0.02 g, box elder larvae = 0.41 ± 0.01 g; $U = 358.5$, $n = 60$, $P = 0.178$). In combination, these experiments show that first instar larvae have more restricted food options than fourth instar larvae.

DISCUSSION

Associational susceptibility of cottonwoods

Both experimental and observational results support the conclusion that cottonwood suffers associational susceptibility to fall cankerworm when growing under box elder. The contrast between cottonwoods under box elder and cottonwoods under cottonwood is particularly important. Associational susceptibility is best demonstrated by comparing the "under heterospecific" to "under conspecific" treatments, because this contrast controls for neighbor proximity (vegetational density), and allows any differences to be attributed purely to the effect of neighbor identity (vegetational diversity). For trees in the open, vegetational density and vegetational diversity are confounded. By experimentally demonstrating increased herbivory for cottonwoods under box elder relative to cottonwoods under conspecifics, our results show that association with a heterospecific neighbor results in associational susceptibility in and of itself, independent of issues of isolation. Moreover, cottonwoods in the experimental study were blocked in terms of genetic relatedness, largely eliminating the possibility that innate genetic differences in the plants caused the observed pattern of defoliation.

Fall cankerworm larvae do not shift from box elder to cottonwood as a result of changes in larval host preferences. Rather, associational susceptibility appears to result purely from host shifting to less preferred resources as the preferred host becomes un-

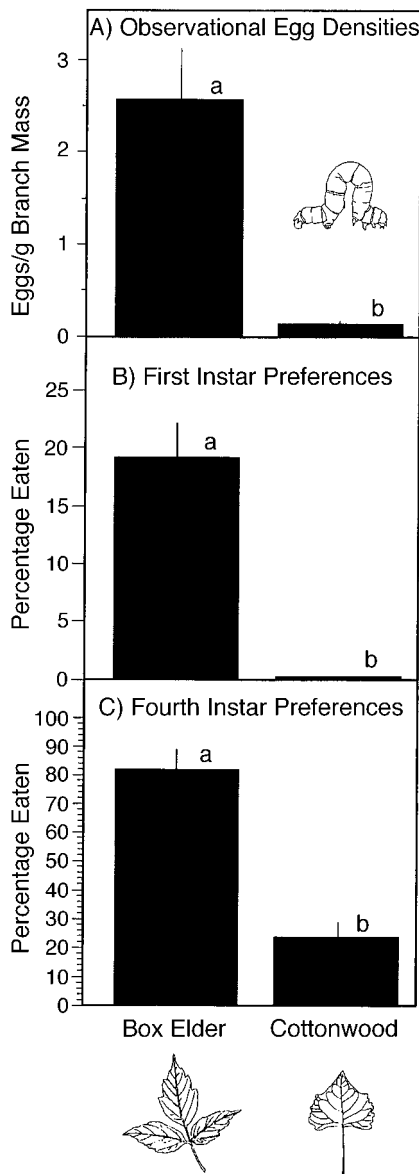


FIG. 4. (A) Mean fall cankerworm egg density + 1 SE on box elder ($n = 19$) and cottonwood ($n = 19$) trees in the field. (B) Mean percentage leaf area eaten + 1 SE by first instar larvae ($n = 22$) after 48 hr given a choice between equal amounts of box elder and cottonwood leaf material. (C) Mean percentage leaf area eaten + 1 SE by fourth instar larvae ($n = 30$) after 16 hr.

available. Experimental results from both first and fourth instar larvae demonstrate that fall cankerworm retains a strong preference for box elder over cottonwood throughout larval development. However, the "preference differential" between box elder and cottonwood decreases with time, such that late instar larvae are not as reluctant to eat cottonwood as early instar larvae, and the consequences for larval performance are not as great. This greater willingness to consume cottonwood may arise either from changes in larval

tolerances as larvae age (Barbosa et al. 1979) or changes in host leaf quality as the season progresses (Meyer and Montgomery 1987).

Despite cottonwood's status as a relatively minor host of fall cankerworm, fall cankerworm can have an important impact on this plant. Cottonwood defoliation averaged 30–50% for individuals growing in close proximity to box elder, and some suffered 100% defoliation. The high correlation between defoliation and fall cankerworm density in both observational and experimental studies, as well as a lack of other prominent herbivores, argues that the observed defoliation is caused by fall cankerworm. Local areas of fall cankerworm defoliation have occurred consistently during this 3-yr study (1995–1997), and although not quantified, chronic defoliation by fall cankerworm has been observed for the last 15 yr at our study sites. Given that repeated defoliation can result in reduced tree vigor and health, particularly for understory trees (Kulman 1971, Campbell and Sloan 1977), it seems likely that cottonwoods suffer long-term population consequences of associational susceptibility. For example, Parker and Root (1981) have found that associational susceptibility to a herbivore limits the habitat distribution of a forb species. Furthermore, we have found that other tree species within this riparian community (hawthorn, willow, and ash) show similar patterns of associational susceptibility to fall cankerworm, indicating potentially community-wide consequences of associational susceptibility (J. A. White and T. G. Whitham, unpublished data).

Where should associational susceptibility be expected?

According to the resource concentration hypothesis (Root 1973) herbivores should accumulate where their resources are most concentrated due to increased immigration to (Elmstrom et al. 1988), decreased emigration from (Kareiva 1985), or increased reproduction within (Bach 1980) the area of most concentrated resources. Under these circumstances, the expected outcome for the host species is associational resistance, with more isolated individuals suffering lower levels of herbivory than individuals growing with conspecifics (Tahvanainen and Root 1972). There is much support for these predictions (Stanton 1983, Andow 1991). At the opposite end of the spectrum, our findings of associational susceptibility can be attributed to three factors.

First, fall cankerworm is a generalist herbivore with respect to box elder and cottonwood. In his original statement of the resource concentration hypothesis, Root (1973) noted that the proposed mechanisms were most applicable to specialist herbivores. Andow's (1991) review upholds this conclusion; generalist herbivores show a wide array of responses to vegetational diversity. In part, this may be attributed to the intrinsic difficulty in determining resource concentration when

multiple host species are involved. For specialist herbivores, all surrounding vegetation acts to decrease the favored host's apparency by decreasing the probability of encounter (Feeny 1976). In contrast, for generalist herbivores, the effect depends on the exact composition of the surrounding vegetation.

Second, cottonwood, the species that experienced associational susceptibility, ranked lower in fall cankerworm's preference hierarchy than box elder. "Preference hierarchy" simply refers to a herbivore's ranking of its potential hosts within a site, and can incorporate nondietary components of preference such as microhabitat (Rossiter 1987), or phenological availability of hosts (Futuyma and Wasserman 1980), in addition to relative palatability of hosts. Assuming that selection favors herbivores that choose their "best" resources first; herbivores should primarily utilize host species that rank higher in their preference hierarchy. Consequently, for less-preferred host species such as cottonwood, susceptibility to herbivory may be a function of proximity to preferred host species, which act as epicenters of herbivore abundance. For preferred host species, association with species that rank lower in the herbivore's preference hierarchy is likely to confer associational resistance, just as with specialist herbivores.

Third, herbivore density was high. During all three years of our study, locally high densities of fall cankerworm depleted the preferred resource, box elder, and then "spilled over" onto the less-preferred host, cottonwood. Yet in areas where fall cankerworm densities were lower, larvae completed development on box elder, and associational susceptibility did not occur. This pattern argues that associational susceptibility is closely tied to herbivore density. At low herbivore densities, herbivores should selectively consume only their preferred hosts, allowing nearby, less-preferred hosts to escape attack (the attractant/decoy hypothesis; Atsatt and O'Dowd 1976). This concept has been utilized in agriculture by planting a favored host as a "trap crop," to attract a herbivore away from an economically important host that is less preferred (Stride 1969, Trenbath 1993). However, when herbivore densities are high and the preferred host is depleted, spill over to less-preferred hosts is likely to occur (see also Brown and Ewel 1987). Unfortunately, extant studies of vegetational diversity rarely mention overall herbivore density, much less quantify it in any way (but see Futuyma and Wasserman 1980). Further studies are needed that explicitly test the role of herbivore density in determining associational herbivory patterns.

Although resource depletion is a common cause of host shifting when population densities of generalist herbivores are high, other factors may also trigger host shifts. For example, the herbivore's preference hierarchy may shift, such that a formerly nonfavored host becomes more attractive. This may occur due to switches in the phenological availability of hosts (Futuyma

and Wasserman 1980, Floate et al. 1993) or because the herbivore favors one host for oviposition and another for feeding (McClure et al. 1982). Sequentially polyphagous species, whose life cycles involve obligatory host shifting (e.g., heteraceous aphids), would also be likely to inflict associational susceptibility on secondary hosts located near primary hosts, even at relatively low herbivore densities (Andow 1988).

The likelihood of spill over onto marginal hosts is also influenced by the mobility of the herbivore. Late instar lepidopterous larvae often have limited mobility and perception (Doane and Leonard 1975). With the low dispersal ability of late instar fall cankerworm, it is not surprising that associational susceptibility was evident at the scale of only a few meters (Fig. 3). Other factors that restrict herbivore movement would also tend to encourage use of nearby less-preferred hosts. Associational susceptibility patterns have been described as a result of a herbivore's need to remain near shelter (Bartholomew 1970) or in a preferred microhabitat (Burger and Louda 1994). Although mobile herbivores are likely to search further to find preferred hosts (Messina 1982), tradeoffs should still exist such that at some point, acceptance of nearby less-preferred hosts is favored.

Associational susceptibility is likely to be common among less-preferred hosts of forest pest species, because these insects often consume a wide array of plant species (Furniss and Carolin 1977), exhibit preference hierarchies (Fedde 1964, Gansner and Herrick 1985), and achieve high densities. For example, outbreaks of gypsy moth, *Lymantria dispar*, are most likely in stands dominated by preferred oak species (Herrick and Gansner 1986). Less-preferred species within these stands are often consumed as well, whereas in stands where the less-preferred species dominate, outbreaks are unlikely to occur (Gansner and Herrick 1985, Herrick and Gansner 1986). Thus, it appears that less-preferred hosts are most susceptible to attack when growing in oak-dominated stands. Because associational susceptibility is a pattern that applies to less-preferred hosts, however, it is often overlooked due to the more obvious interactions between the herbivore and its favored host species. Furthermore, the historic emphasis on specialized crop herbivores in simplified agroecosystems tends to overshadow the host use patterns of generalist herbivores in more complex settings. Consequently, the prevalence and importance of associational susceptibility has yet to be fully explored. Additionally, the recognized importance of diversification in agroecosystem and forest management practices (Vandermeer 1989, Tonhasca and Byrne 1994) makes it seem especially important to gain a clear understanding of associational susceptibility, a potential repercussion of vegetational diversity.

ACKNOWLEDGMENTS

We thank D. Andow, C. Bach, K. Charters, N. Cobb, S. Ferrier, K. Gehring, G. Martinsen, K. Ogle, P. Price, R. Root,

J. Schweitzer, R. Scott, R. Swaty, T. Theimer, and G. Wimp for their constructive comments on the manuscript. Special thanks go out to R. Swaty for field assistance and R. O'Reilly for figure production. This research was supported under a National Science Foundation Graduate Research Fellowship, as well as NSF grant DEB-9726648 and USDA grant 95-37302-1801.

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