Take Me to Your Leader: Does Early Successional Nonhost Vegetation Spatially Inhibit *Pissodes strobi* (Coleoptera: Curculionidae)?

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ABSTRACT The spatial influences of host and nonhost trees and shrubs on the colonization patterns of white pine weevil *Pissodes strobi* (Peck) were studied within a stand of planted interior hybrid spruce [*Picea glauca* (Moench) Voss × *Picea engelmannii* (Parry) ex Engelm.]. Planted spruce accounted for one third of all trees within the stand, whereas the remaining two thirds were comprised of early-successional nonhost vegetation, such as alder (*Alnus* spp.), paper birch (*Betula papyrifera* Marsh.), black cottonwood [*Populus balsamifera* ssp. *trichocarpa* (T. Ng.) Brayshaw], lodgepole pine [*Pinus contorta* (Dougl.) ex Loud.], trembling aspen (*Populus tremuloides* Michx), willow (*Salix* spp.), and Canadian buffaloberry [*Shepherdia canadensis* (L.) Nutt.]. Unlike the spruce trees, nonhost vegetation in the stand was not uniformly distributed. Spatial point process models showed that Canadian buffaloberry, paper birch, black cottonwoood, and trembling aspen had negative associations with damage caused by the weevil, even though the density of the insects' hosts in these areas did not change. Moreover, knowing the locations of these nonhost trees provided as much, or more, inference about the locations of weevil-attacked trees as knowing the locations of suitable or preferred host trees (i.e., those larger in size). Nonhost volatiles, the alteration of soil composition, and overstory shade are discussed as potential explanatory factors for the patterns observed. New research avenues are suggested to determine whether nonhost vegetation in early successional stands might be an additional tool in the management of these insects in comercially important forests.

KEY WORDS nonhost volatiles, angiosperm volatiles, plant–insect interactions, Engelmann spruce weevil, spatial point processes

The white pine weevil *Pissodes strobi* (Peck) (Coleoptera: Curculionidae), native to North America, is a herbivorous insect that reproduces in the terminal leaders of young spruce and pine. In the spring, females oviposit in leaders of host trees generally >5 yr of age (He and Alfaro 2000). Developing larvae girdle the shoots, often leading to creases, crooks, and forks in the tree (Silver 1968). Although mortality of trees is uncommon, stem defects and associated growth reductions may reduce lumber yield by as much as 40% in commercially important forests (Alfaro et al. 1997). After a brief pupation within the leader, adults emerge between July and September to overwinter in the duff layer or on the tree itself in coastal areas (Silver 1968). White pine weevils complete their life cycle in 1 yr (Silver 1968). Infestations may continue in stands of spruce for up to 50 yr (He and Alfaro 2000).

Past research on the distribution and impact of white pine weevils on host trees has focused primarily on defensive mechanisms of the trees, including chemical responses and genetic variation therein (King et al. 1997, 2004; Alfaro et al. 2000, 2008; Tomlin et al. 2000). Physical characteristics, such as thickness of the primary cortex and the size of trees and their leaders, also influence host selection (VanderSar and Borden 1977, Kiss and Yanchuk 1991, Turnquist and Alfaro 1996, King et al. 1997, van den Driessche 1997, Manville et al. 2002). Spatial factors that potentially influence insect distribution have received less attention, however (He and Alfaro 1997). Some of these factors affect the vigor of young spruce, including overstory composition, sun exposure, soil drainage, and edge vegetation (Lavallee et al. 1996, Taylor et al. 1996, Simard and Hannam 2000). Certain properties of these factors may be exploited in silvicultural recommendations to reduce impacts of white pine weevil.

Influences of spatial distribution and diversity of nonhost species, and their impacts on the host-selection behavior, distribution, and abundance of white pine weevil, has not yet been studied to our knowledge. New spruce forests are typically established as the result of natural or anthropogenic disturbances and therefore may contain diverse early successional species (Denslow 1980), such as alder (*Alnus* spp.), trembling aspen (*Populus tremuloides* Michx), willow (*Salix* spp.), and paper birch (*Betula papyrifera*

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Marsh.), as well as various shrub species. Recent work has suggested that the presence of nonhost vegetation such as red alder (*Alnus rubra* Bong.) may affect the levels of white pine weevil abundance (McLean 1989, Almond 2006). Increased plant diversity may decrease impacts by herbivores that exhibit narrow host breadths (Bianchi et al. 2006) but also may increase impacts by more generalist herbivores (Koricheva et al. 2006).

In this study, we explore spatial factors that may influence host selection and distribution of *P. strobi*. We fit spatial point process models to a data set from a population census of >1,000 trees in a stand containing moderate levels of white pine weevil. We seek to answer two questions regarding the pattern of weevil distribution. First, does nonhost vegetation have either a positive or negative association with distribution of white pine weevil attack? Second, if such an association exists, how does it compare with known predictors of weevil attack distribution, including physical attributes of colonized spruce trees such as size? Expanding our understanding of insect interactions with host and nonhost vegetation, in combination with existing knowledge of spruce defense mechanisms, may yield new silvicultural tools for contending with this herbivore in commercially important forests.

Materials and Methods

Site Selection and Data Collection. We censused a 0.154-ha stand of interior hybrid spruce with relatively even-aged trees displaying a moderate level of *P. strobi* abundance near Prince George, British Columbia, Canada (53°52′ N, 122°47′ W). The spruce had been hand-planted and were 12 yr of age at the time of study. The stand also contained a variety of other nonhost vegetation from natural regeneration. With the exception of willow (*Salix* spp.), trees and shrubs were identified to the species or subspecies level. For the purposes of analysis, alder, which consisted of green alder [*Alnus viridis* ssp. *crispa* (Ait.) Turrill], sitka alder [*Alnus viridis* ssp. *sinuata* (Regel) A. and D. Löve], and mountain alder [*Alnus incana* ssp. *tenuifolia* (Nutt.) Breit.] were grouped together at the genus level. Every live tree with >1-cm root collar diameter was censused.

Spatial location data for each tree was determined using a compass, vertex, and corresponding distance transponder (Haglöf Sweden Vertex III v.1.4; Haglöf, Madison, MS), with slope values and horizontal distance measurements corrected based on the internal clinometer. Tree species with multiple stems emerging from a single root collar, such as alder, were mapped at a single point location central to all of the stems and were recorded as a single tree with the corresponding number of stems as a stem density. Stems without a well-defined root collar, yet that appeared to be connected and were growing within a 10-cm radius of each other, were also recorded as a single tree.

Measurements for spruce and pine [lodgepole pine *Pinus contorta* variety *latifolia* (Engelm.) ex S. Wats.] trees included age, root collar diameter, height, evidence of white pine weevil activity, and the presence of other insects. The ages of spruce trees were estimated by counting the number of whorls and confirmed by counting growth rings on a randomly selected subset of trees destructively sampled poststudy. Root collar diameter was measured with a 150-mm caliper, and tree height was measured with a standard 8-m tape measure. Weevil activity was identified by the presence of oviposition punctures, fecal plugs, emergence holes, larval cavities on broken leaders, and wilted (i.e., shepherd's crooks) or dead leaders (Lavallee et al. 1996). In this paper, we refer only to those trees possessing dead or dying leaders as successfully colonized. Four categories of weevil colonization were identified: 1, 2, and 3 yr of colonization or never colonized. Spruce trees were judged to have multiple years of weevil colonization if they showed damage on the initial leader with subsequent attack of new shoots vying for apical dominance. An elevation grid was developed by recording elevation values at 10-m intervals along the transect and at two to four locations on the horizontal axis using a GPS (Meridian Gold Magellan; Thales Navigation, San Dima, CA). Data were collected from 26 May to 17 June 2008.

Data Analysis. Maps for the locations of all trees, including weevil-colonized trees, were created using the "spatstat" package v.1.13–3 in R v.2.6.2 (Ihaka and Gentleman 1996, Baddeley and Turner 2005, R Development Core Team 2008). Spatial trends in the x and y directions of height and root collar diameter of colonized versus uncolonized spruce trees were studied using linear regression. Further effects of weevil colonization status on height and diameter of spruce trees were studied by examining the significance of such a term added to the prior regression models that accounted for spatial trends.

Spatial point process models were used to examine the effects of spatial trends (i.e., x and y, as well as elevation), spatial attributes of host plants (i.e., height and diameter at root collar), and locations of nonhost plants on the prevalence of white pine weevil attack. The response variable for each model, intensity (λ), a spatially explicit estimated density of weevil attacks, was measured as the number of trees with damaged (i.e., dead or dying) leaders per square meter. Covariates were converted to either density surfaces (for point processes such as locations of trees or shrubs) or a smoothed interpolation (for the marks of a point process) before fitting. Both types of surfaces incorporated a Gaussian kernel density smoother as a representation of the point process defined within the boundary (Cressie 1991, Baddely and Turner 2000). Border corrections were tested, but not applied in the final analyses, because the trees and boundary were well defined, and our results proved robust compared with various edge corrections (results not shown).

Parameters in these spatial point process regression models were estimated using maximum pseudolikelihood methods. Significance of individual variables was

Table 1. Composition of a stand planted with interior hybrid spruce near Prince George, British Columbia

Species	Common name	Code	n
Picea glauca × *engelmanni*	Spruce	Sx	365
Alnus spp.	Alder	Al	361
Betula papyrifera	Paper birch	Be	210
Salix spp.	Willow	Sa	56
Populus tremuloides	Trembling aspen	Pt	36
Shepherdia canadensis	Canadian buffaloberry	Sc	25
Populus balsamifera ssp. *trichocarpa*	Black cottonwood	Pb	11
Pinus contorta	Lodgepole pine	Pl	5

A code for each species is provided for reference in Fig. 1 (n_{total} = 1,069).

judged by statistical comparison to a homogenous model (i.e., one estimating only an intercept or a constant intensity of weevil attack across the site), by examining the change in deviance relative to a χ^2 reference distribution. Similarly, when we sought to examine additive effects of a second (or third) variable while accounting for the effect of a previous variable, a comparison of nested models was performed by examining the change in deviance relative to a χ^2 reference distribution. Models were compared using Akaike's Information Criterion (AIC), and models with the lowest AIC values were judged to fit the best (Akaike 1973).

Results

Distribution of Trees and Shrubs. A population census of the stand yielded 1,069 trees and shrubs from seven different genera (Table 1). Interior hybrid spruce comprised one third of the site's population (34%), whereas alder comprised another third (33.6%). The remaining third of the population consisted of six other species of trees and shrubs, predominantly young paper birch (19.6%).

The location and identity of each tree species mapped within the stand is shown in Fig. 1. Spruce were evenly distributed throughout the entire site without spatial trends in either the *x* or *y* direction ($P > 0.05$). The mean density of spruce was 0.24 stems/m^2, (i.e., ~2 by 2-m spacing). Alder was present across the majority of the site with the exception of the upper right section. Canadian buffaloberry, black cottonwood [*Populus balsamifera* ssp. *trichocarpa* (T. Ng.) Brayshaw], willow, and trembling aspen were found predominantly in the top half of the site (as depicted in Fig. 1), particularly in areas where alder was absent. There were also more paper birch in the top half of the site, although a few small clusters of stems were noted in the central and lower regions. Only five lodgepole pine trees were present across the site.

Distribution of Weevil Colonization. Figure 2 shows the distribution of all spruce trees according to their four categories of colonization by white pine weevil, with a numerical summary in Table 2. Nearly one quarter of the 365 spruce trees, i.e., 87 trees, had been colonized by white pine weevil. The 76% of
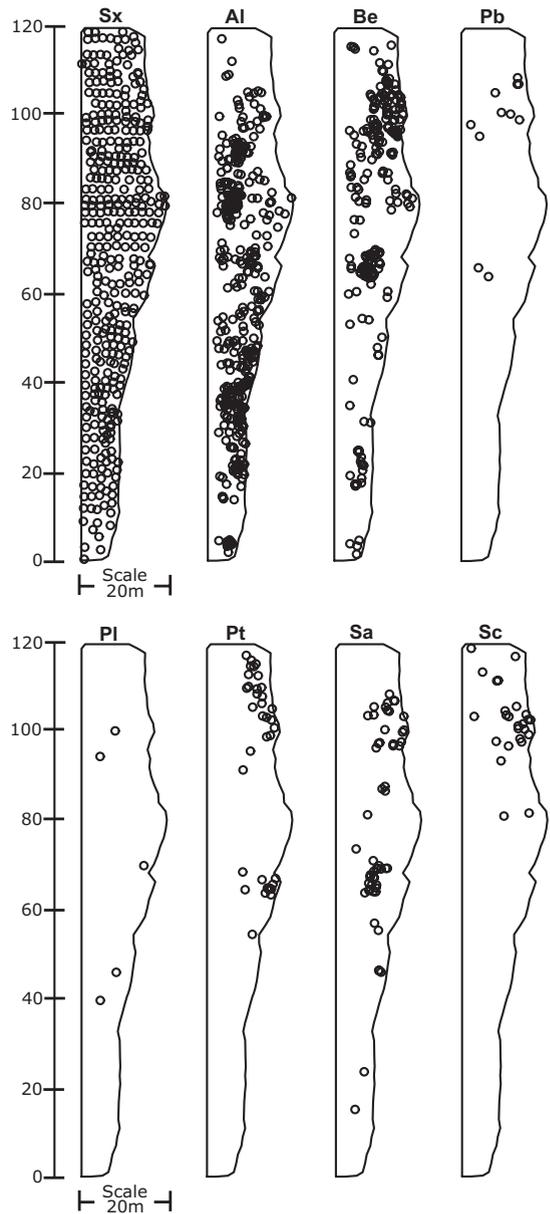
Fig. 1. Stem maps of all trees and woody shrubs found within stand. Each tree is represented by an open circle. Sx, *P. glauca* × *engelmanni*; Al, *Alnus* spp.; Be, *B. papyrifera*; Pb, *P. balsamifera* ssp. *trichocarpa*; Pl, *P. contorta*; Pt, *P. tremuloides*; Sa, *Salix* spp.; Sc, *S. canadensis.* For ease of graphical representation, the top of the figure is oriented east (rather than due north).

spruce trees that were not colonized by white pine weevil were distributed throughout the entire stand (Fig. 2A). Nineteen percent of trees had been colonized once. These trees were distributed throughout the stand except for a small pocket within the uppermost section (Fig. 2B). Fifteen of the 87 trees with weevils had been colonized twice (Table 2) and were distributed in two clusters near 10 and 75 m on the
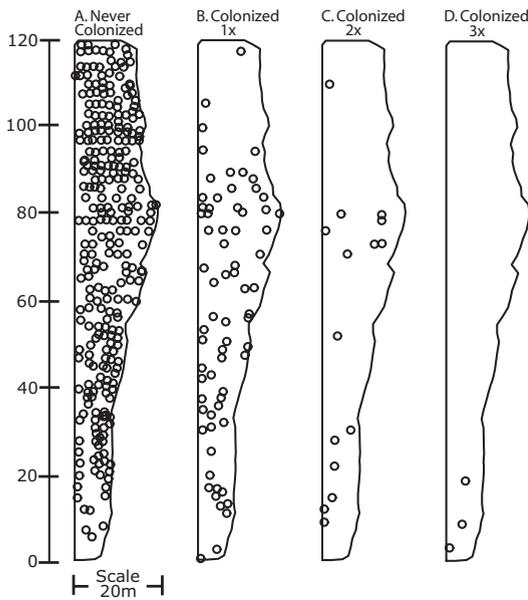
Fig. 2. Map of all spruce trees within the stand according to level of white pine weevil colonization. Each tree is represented by an open circle. (A) Trees that have not been colonized. (B) Trees showing 1 yr of colonization, (C) 2 yr of colonization, and (D) 3 yr of colonization. For ease of graphical representation, the top of figure is oriented east (rather than due north).

vertical axis (Fig. 2C). Spruce trees with three leaders colonized by *P. strobi* represented <1% of the total spruce population and were located exclusively in the lower portion of the stand between 0 and 20 m on the vertical axis (Fig. 2D). When examined collectively, Fig. 2B–D, shows reduced activity by white pine weevil in the upper third of our site from the 90- to 120-m marks. One hundred eighteen spruce trees (i.e., nearly one third of all spruce) existed between 90 and 120 m. Of these trees, only eight (6.8%) had been colonized.

Table 3 summarizes the association of individual variables, such as spatial directions, spruce hosts, and nonhost vegetation, with the prevalence of weevil colonization in the stand. Weevil abundance was measured as an estimated density, λ, or trees with killed leaders per square meter. Models with lower AIC

Table 2. Mean (±SE) root collar diameter and height of trees categorized by colonization of white pine weevil in a 12-yr-old stand of planted interior hybrid spruce near Prince George, British Columbia

Colonization classification	n	Root collar diameter (mm)	Height (cm)
All spruce trees	365	31.9 (0.5)	138 (2)
Never colonized	278	30.0 (0.6)	136 (2)
All colonized	87	38.1[a] (1.0)	144 (3)
Colonized one time	69	37.3 (1.3)	143 (4)
Colonized two times	15	41.5 (1.9)	153 (7)
Colonized three times	3	39.4 (4.3)	142 (17)

[a] Significantly different from trees that had never been colonized ($P < 0.0001$, see text).

values were judged to have the best explanatory power. Despite the fact that spruce were spatially homogenous throughout the stand, Table 3A indicates that there was a significant spatial trend in weevil attack in the vertical (y) direction, with more insect colonization present toward the lower portion of the plot (Fig. 2). Colonization of leaders by the white pine weevil did not vary across the stand with respect to the moderate elevational differences or the horizontal (x) direction.

Association of Weevils With Spruce Attributes. The average diameter of all spruce trees was 32 mm at the root collar (Table 2), with larger trees being found toward the lower and left sides of the plot (diameter in mm = $44 - 0.470x - 0.125y$, where the x and y axes are measured in meters and are the same as in Fig. 1; $F_{2,362} = 54.74$; $P < 0.0001$). After accounting for this spatial trend, we found that, on average, spruce trees with signs of weevil colonization were almost 1 cm larger in root collar diameter than those that had not been colonized ($F_{1,361} = 25.81$, $P < 0.0001$; Table 2). Increased densities of white pine weevil colonization were associated with areas containing trees with larger diameter at root collar, as indicated by the significant positive slope for the diameter term in Table 3B.

Spruce trees were 138 cm tall on average (Table 2). Similar to root collar diameter, there was a significant spatial trend in height in the y direction, with taller trees predominantly located toward the lower portions of the stand (height in cm = $168 - 0.43y$; $F_{1,363} = 50.59$; $P < 0.0001$). Greater evidence of weevil colonization was noted in areas of the plot with taller trees (Table 3B). Uncolonized trees were an average of 8 cm shorter than spruce colonized by the weevil; however, this difference was not statistically significant after accounting for the spatial trend in height ($F_{1,362} = 0.002$, $P = 0.96$; Table 2). Spruce within the stand had been hand-planted, and, aside from a few trees that had regenerated naturally, were 12 yr of age. As such, there were no spatial trends in age nor were there any associations between weevil colonization and the age of the trees ($P > 0.05$).

Association of Weevils With Nonhost Vegetation. Table 3C shows the effect of each nonhost species on the intensity of white pine weevil activity (trees with leaders killed/m²) across the stand, as well as the total stem density of all species including and excluding spruce. The stem density of vegetation did not explain any variation in the distribution of white pine weevil attack. Of the six nonhost species listed (i.e., excluding lodgepole pine), five exhibited negative slope estimates, indicating that the presence of these trees among the spruce was correlated with lower weevil colonization densities. Four of these five nonhost species, Canadian buffaloberry, paper birch, black cottonwood, and trembling aspen, were statistically significant ($P < 0.05$). The model for Canadian buffaloberry exhibited the best explanatory power for the presence (or absence) of white pine weevil colonization, because it had the lowest AIC value (653.3). Incorporating other variables in multiple regression equations containing a term for Canadian buffaloberry

Table 3. Regression equations for single variables describing directional trends, host, and nonhost associations with distribution of white pine weevil colonization in a stand of interior hybrid spruce near Prince George, British Columbia

Term	Intercept		Slope		χ^{2a}	P	AIC^b
	Estimate	SE	Estimate	SE			
Intercept only[c] (i.e., constant intestity)	−2.87	0.11					676.2
A. Directional trends[d]							
Elevational trend	19.29	21.36	−0.033	0.032	1.05	0.31	677.2
Trend in x direction	−2.59	0.19	−0.044	0.025	3.19	0.07	675.1
Trend in y direction	−2.03	0.21	−0.013	0.003	16.94	0.0021	661.3
B. Spruce characteristics							
Diameter (mm)	−5.32	0.60	0.073	0.017	18.34	<0.0001	659.9
Height (cm)	−5.48	0.75	0.018	0.005	12.44	<0.0001	665.8
C. Nonhost species[e]							
Alder	−3.05	0.17	0.73	0.48	2.17	0.14	676.1
Paper birch	−2.68	0.14	−1.57	0.85	4.05	0.04	674.2
Black cottonwood	−2.70	0.11	−41.42	14.83	14.00	0.0002	664.3
Lodgepole pine	−2.82	0.12	−16.87	17.77	0.99	0.32	677.3
Trembling aspen	−2.70	0.11	−12.78	4.78	12.92	0.0003	665.3
Willow	−2.80	0.12	−2.20	2.05	1.30	0.25	677.0
Canadian buffaloberry	−2.59	0.12	−40.89	12.09	24.99	<0.0001	653.2
Stem density (all trees)	−3.36	0.50	0.22	0.22	0.98	0.32	677.3
Stem density (nonhosts)	−3.26	0.38	0.11	0.12	1.14	0.29	677.1

The response variable for each equation is log(λ), where λ is the density estimate of female adult weevils measured by leaders killed per square meter. For example, the estimated density of weevils in locations with spruce 40 mm in diameter at root collar would be $\exp^{(-5.32 + 0.073 \times 40)}$ or 0.09 leaders killed/m².

[a] Change in deviance from a homogenous model tested against a χ^2 distribution with 1 degree of freedom (i.e., does the variable explain more spatial variation in weevil abundance than a surface with constant density?).

[b] Akaike information criteria. Lowest numbers are judged to be best models.

[c] Average density of insects is $\exp^{(-2.87)}$ or 0.06 insects/m², or approximately one in four spruce (density of spruce is 0.24 trees/m²; see text).

[d] Mean elevation for the site was 670 m. Ranges for x and y are 0–18.9 and 0–120.1 m, respectively.

[e] Terms for trees and shrubs are listed as a density in trees per square meter.

did not significantly improve that model's fit. Knowing the locations of trembling aspen or black cottonwood provided as much inference on the locations of weevil-damaged trees through negative spatial associations as knowing the location of larger spruce trees positively associated with increased weevil colonization density (as judged by the similar AIC values of ≈665, among these models).

Discussion

Our results showed that patterns of spatial inhibition indicated by nonhost vegetation can provide as much, or more, inference on the location of white pine weevil–damaged trees as simply knowing the locations and attributes of their host trees such as height and diameter, which along with leader size, are often positively correlated with white pine weevil distribution (VanderSar and Borden 1977, Kiss and Yanchuk 1991, Turnquist and Alfaro 1996, King et al. 1997, van den Driessche 1997, Manville et al. 2002). Although spatial correlations do not imply causation, and manipulative experiments are required to establish mechanistic links between pattern and process, several potential mechanisms between nonhosts and white pine weevil exist.

For example, nonhost volatiles may alter, enhance, or reduce mate or host finding, as shown in numerous and diverse insect systems such as the diamondback moth (*Plutella xylostella* L.), cotton bollworm (*Helicoverpa armigera* Hubner), Colorado potato beetle (*Leptinotarsa decemlineata* Say), ambrosia beetles (*Gnathotrichus retusus* LeConte), and bark beetles

(Coleoptera: Curculionidae) (Dickens et al. 1992; Schroeder 1992; Deglow and Borden 1998a, b; Huber and Borden 2001; Deng et al. 2004; Dickens 2006; Broad et al. 2008). *P. strobi* shows attraction to host volatiles such as monoterpenes and ethanol (Chenier and Philogene 1989), as well as a response to the pheromone grandisol and its aldehyde grandisal (Booth et al. 1983, Hibbard and Webster 1993). Therefore, the potential for disruption of host species recognition by nonhost volatiles is certainly plausible. For example, in laboratory bioassays, feeding of *P. strobi* is inhibited by the oil extract of western red cedar [*Thuja plicata* (Donn) ex D. Don] when present at levels similar to those found in nature (Alfaro et al. 1979, 1981). The quantity of isoprenes and monoterpenes emitted by western red cedar are ≈0.02 ± 0.01 and 0.07 ± 0.05 μg/g leaf dry weight/h, respectively (Kesselmeier and Staudt 1999). Trembling aspen and black cottonwood, both of which showed significant negative spatial associations with weevils in our study, emit isoprenes at a rate of ≈50 μg/g leaf dry weight/h (Benjamin et al. 1996, Kesselmeier and Staudt 1999). These emission rates are two orders of magnitude greater than the emission rates of western red cedar and also higher than the emission rates found in Engelmann or white spruce (16 and 7–15 μg/g leaf dry weight/h, respectively; Kesselmeier and Staudt 1999). Paper birch also exhibited a significant negative spatial association with weevils on our site. Emission rates of paper birch are unknown; however, silver birch (*Betula pendula* Roth) may emit 5.4 μg/g leaf dry weight/h of monoterpenes (Hakola et al. 1998), again, far greater than the amount found in western red cedar.

Although the chemical profile of Canadian buffaloberry is unknown, isoprene emissions of redberry, also within *Rhamnaceae*, may exceed the 50 μg/g leaf dry weight/h emitted by trembling aspen or black cottonwood (Kesselmeier and Staudt 1999).

Aside from nonhost volatiles potentially acting on host finding or feeding behaviors above ground, alteration of nutrient regimens by nonhosts below ground may affect the defensive chemistry of proximate host plants (Stamp 2003, Cortini and Comeau 2008). For example, we know little of the mycorrhizal communities associated with nonhost species, which may influence the defensive mechanisms of proximate trees by altering nutrient availability (Read 1991, Gange and West 1994, Hartnett and Wilson 1999, Langley and Hungate 2003). The most statistically significant nonhost species, Canadian buffaloberry, fixes nitrogen and may be a key source of this nutrient for the development of maturing pine stands (Wei and Kimmins 1998). It is possible that Canadian buffaloberry influences the defensive mechanisms of young spruce, leading to a differential distribution of white pine weevil colonization. We might expect, however, that nitrogen enhancement would increase growth, shifting resources away from plant defenses and increasing susceptibility to insect colonization (Herms and Mattson 1992). Indeed, the preference *P. strobi* exhibit for large, vigorously growing leaders suggests that host trees allocating less resources toward growth and more toward defense may not be colonized. Like Canadian buffaloberry, however, alder conditions soil by fixing nitrogen (Cortini and Comeau 2008), and we did not find evidence of spatial inhibition between alder and white pine weevil attack in the stand.

Another potential mechanism of inhibition between host and nonhost trees is direct competition for water, nutrients, and sunlight among neighboring trees. Competition may, for example, reduce spruce leader size and hence attractiveness to white pine weevil and lodgepole terminal weevil *P. terminalis* Hopping (Alfaro and Omule 1990, Maclauchlan and Borden 1996). Although nonhost vegetation on the site was not distributed evenly, we found no association between stem density (either including or excluding nonhosts) and the presence or absence of weevil attack. Trees proximate to spruce may increase overstory shade, which is also known to reduce the prevalence of weevil attack (Taylor and Cozens 1994, Taylor et al. 1996). Alder may act as a shade source for spruce, potentially decreasing the likelihood of weevil attack (McLean 1989, Almond 2006), although no spatial correlations between alder and trees with white pine weevil attack were evident in our stand. Trembling aspen, paper birch, and black cottonwood offered fractional overstory cover for spruce within the stand, because none of the host trees exceeded 3.5 m in height, and deciduous trees, excluding alder, did not exceed 3 m. Canadian buffaloberry is a low-growing shrub and did not provide any shade for spruce. Hence, any potential inhibition processes by the deciduous vegetation and spruce selected by adult female weevils were likely limited to either above-ground

volatiles or below-ground competitive interactions. Therefore, the significance of these nonhosts species on weevil colonization in early stages of stand development is likely from the presence of nonhost volatiles and possibly the alteration of constitutive or induced defenses through nitrogen fixation and macronutrient uptake in below-ground processes.

It is possible that the area of decreased weevil abundance found within our stand was caused solely by a lag in weevil dispersal, with avoidance of areas of nonhosts strictly a statistical artifact. Weevil activity on our site seems to be increasing annually, as is typical in early stand development (King et al. 1997). However, movements of *P. strobi* recorded during spring flight have shown that the insects are capable of flying 50 m or more (Godwin et al. 1957, Silver 1968, Harman 1975). Hence, dispersal ability does not seem to be a limiting factor in the patterns observed. Likewise, it seems unlikely that the current pattern of colonization across the stand reflects stand saturation, because both stand age (He and Alfaro 2000) and the directional gradient observed (Table 3) instead of a regular pattern (He and Alfaro 1997) suggests that the level of white pine weevil colonization across the site has likely not yet reached its peak (He and Alfaro 2000).

Settlement patterns of white pine weevil in conifers are likely caused by multiple and interacting processes. Our findings that some species of nonhost vegetation in regenerating stands may be associated with areas of reduced weevil activity provides new avenues for research. For example, it is unknown whether the present patterns of weevil colonization distribution in early stand development persist into later successional stages. Our work also highlights research avenues exploring potential mechanisms responsible for the patterns we observed. These opportunities include examining the alteration of host seeking behaviors by insects through exposure to nonhost volatiles, and examining how competition in plant communities affects herbivore population dynamics by altering host plant defenses.

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