CHAPTER 10

Does Spruce Aphid Defoliation Alter Engelmann Spruce Resistance to Spruce Beetle?

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INTRODUCTION

Nonnative species are a major threat to the composition and functioning of global forests (Parry and Teale 2011). Impacts of nonnative tree-feeding insects often occur in concert with impacts of native insects, yet interactive effects between nonnatives and natives on tree performance are poorly understood and have rarely been investigated. Nonnative insects could make trees more or less susceptible to native insects, depending on the magnitude of impacts of nonnatives on tree defense, vigor, and host quality.

At the very southern extent of its range in Arizona, Engelmann spruce (*Picea engelmannii*) is being attacked by the nonnative spruce aphid (SA; *Elatobium abietinum*. The SA was first found in the Southwestern United States in 1976 in urban settings, and then in wildland settings in Arizona beginning in 1989 (Lynch 2004). Outbreak frequency increased beginning in the early 2000s, especially in high-elevation spruce-fir-dominated forests of eastern Arizona (Grady 2019, Lynch 2009). Attacks from the native spruce beetle (SB; *Dendroctonus rufipennis*) on Engelmann spruce and the intensity of regional drought also increased during this period, which led to high tree mortality (Grady 2019). The SB has been observed attacking SA-defoliated trees (Lynch 2004, 2009), although whether SB attacks are facilitated by SA defoliation is uncertain. The potential for SA to incite SB outbreaks is of great concern for managers as spruce populations are already declining across the West and SA outbreaks may increase with warmer winters (Straw and others 2019). No previous studies have investigated impacts of SA defoliation on SB performance or defenses of Engelmann spruce. This project addressed impacts of SA defoliation on SB performance and tree defenses with a novel experiment during an exceptional multidecadal megadrought (2000–2021).

METHODS

This study included an experiment to evaluate whether defoliation by the nonnative SA affects resistance of Engelmann spruce to the native SB in a natural mixed-conifer forest near Greens Peak in the Apache-Sitgreaves National Forests in the White Mountains of east-central Arizona (34.067017, -109.553811) between elevations of 2895 and 2987 m. Selection of this location was based on a well-documented history of SA defoliation of Engelmann spruce by annual aerial surveys and site visits by U.S. Department of Agriculture, Forest Service, Forest Health Protection personnel in the vicinity of Greens Peak (Grady 2019). Spruce in the area incurred defoliation between 2015 and 2018, with a particularly severe defoliation event during winter 2017–2018 (USDA Forest Service 2019). SA defoliation varied substantially among individual trees, ranging from low to high (see next paragraph).

In October 2020, researchers selected 30 Engelmann spruce trees with a range of recent SA defoliation to represent a gradient of SA attack and impact. This approach assumed that the amount of tree defoliation approximated the severity of SA attack. Direct data on the number of aphids attacking each tree were lacking. Criteria for selection was diameter at breast height (d.b.h.) between 30 and 43 cm and location within 50 m of a forest road to facilitate access. A team of four experienced observers scored SA defoliation of each tree using a crown rating system conceptually based on the dwarf mistletoe (*Arceuthobium* spp.) rating system (Lynch 2004). Briefly, the live tree crown of each tree was divided into thirds with each section receiving a rating from 0 to 3: 0 = no evidence of defoliation, 1 = 1–33 percent of foliage missing or affected (chlorotic), 2 = 34–66 percent, and 3 = 67 percent or more. The scores were summed to give each tree a rating ranging from 0 to 9. These scores were used to group trees into three defoliation classes, with 10 trees per class: low (score of 3), medium (score between 4 and 6; 2 trees with score of 4, 3 trees with score of 5, and 5 trees with score of 6), and high (score between 7 and 8; 8 trees with score of 7 and 2 trees with score of 8).

In April 2021, samples of phloem and resin were taken from each tree at two breast-height locations at north and south aspects. A 2.54-cm arch punch extracted a disk of phloem that was immediately put in a plastic bag and frozen (-20 °C) until extraction of terpenes. Thickness of each phloem disk was measured with a digital micrometer. Resin that flowed from the phloem wounds over 7 days after wounding was collected using a small aluminum funnel and test tube and then its mass was measured.

In May 2021, one SB pheromone bait (containing frontalin; item # 3300, spruce beetle/Douglas-fir beetle bait; purchased from Synergy, Delta, BC, Canada) was attached to each tree in an attempt to instigate mass SB attack. Baits were replaced in July 2021 and remained on the trees until September 2021. All trees were surveyed in September 2021 to assess SB success by removing a small (3.8 x 7.6 cm) section of bark above four to six pitch tubes per tree to assess whether galleries were established and if beetles were developing. For each tree, the percentage of pitch tubes with successful attacks was determined based on galleries and larval development.

In the second fall after baiting of trees in 2021 with SB pheromones (November 2022), three increment cores (4- or 5-mm diameter) were collected from each tree after cessation of annual growth. Cores were collected at a height of 1.3 m and evenly distributed around the tree circumference. Because this study's focus was on recent growth and resin ducts, core depth in sapwood was 5 cm to obtain rings from the last decade.

After drying and mounting, cores were prepared for measurement of annual ring widths by progressively sanding to a final grit of 600, and then scanned using a flatbed scanner (Epson America, Inc.) at 2,400 dots per square inch. The width of each annual ring was measured to 0.1 mm on scanned images with ImageJ software, aided by inspection under higher magnification (up to × 40) under a scope (Omano Inc). The number of traumatic resin ducts in each annual ring was counted under × 40 magnification but were not measured due to their small size. Most ducts were formed in 2021 and/or 2022 during the pheromone-mediated bark beetle attacks. They occurred in distinct lines of 8 to 26 ducts in areas darkened by resin. Ducts in years before 2021 were rare constitutive ducts that were excluded from statistical analyses.

Dating of years of ring formation was informed by knowledge of the date of core collection (late fall 2022) and the occurrence of traumatic resin ducts starting in 2021 when pheromone lures induced SB attacks. Assumptions were that one ring was formed in each of the 10 focal years of the study (2013 to 2022) and that no rings were absent. Absent rings in Engelmann spruce can occur but are uncommon in Arizona (O'Connor and others 2015), and Engelmann spruce does not show a strong response of tree ring growth to regional drought compared to lower elevation species on drier sites (Adams and Kolb 2005).

The frequency of traumatic resin ducts formed during the pheromone-mediated SB attacks relative to annual tree ring growth was calculated. First, the area of the combined 2021 and 2022 annual rings was calculated as: (ring growth year 2021 + ring growth 2022) × core width. Duct frequency (#/mm^2) was then calculated as the number of ducts over both years divided by the combined area of 2021 and 2022 rings. Values from multiple cores per tree were averaged to produce one value for each tree for statistical analysis. Tests for differences among SA defoliation classes used one-way analysis of variance (ANOVA) and Tukey honest mean comparisons, supplemented by nonparametric Wilcoxon tests.

Annual basal area increment (BAI) in mm^2 was calculated for each tree. To reconstruct tree radius for each year, calculations used d.b.h. in November 2022 and annual radial increments from cores (assuming no change in bark thickness). These annual radii were used to calculate BAI using the usual geometric approach: $BAI_{year\ x} = 3.14159 \times ((radius_{year\ x}^2) - (radius_{year\ x-1}^2))$. Values from multiple cores per tree were averaged to produce one value for each tree for statistical analysis. BAI was averaged over the 5 years ending with the year of pheromone baiting (2017 to 2021) and differences compared among SA defoliation levels with ANOVA. JMP Pro® 16 was used for all analyses.

Terpenes in phloem were extracted and analyzed using gas chromatography and mass spectrometry. Approximately 30 mg of frozen phloem from each tree was cut into small pieces (ca. 2 mm^3) and placed in 1 mL of 95-percent n-hexane in 2-mL glass gas chromatograph (GC) vials and agitated on a shaker plate for 24 hours (20 °C, 250 rpm). After shaking, the solvent was transferred to new GC vials using a pipette. The phloem vial was rinsed twice with 0.25 mL of hexane for a final volume of 1.5 mL and 100 µg of 2-nonanone was added as the internal standard. Phloem was dried in an oven at 30 °C for 1 week and then weighed. Quantifications were made relative to the internal standard by using ChemStation software. Compounds were identified by comparison of retention times and mass spectra with those of commercially available standards or classified using mass spectra as monoterpenes

(MT) or sesquiterpenes (ST). Terpene concentrations were analyzed on a dry phloem weight basis (ug/g phloem dry weight).

RESULTS

Tree mortality over 18 months after SB baiting (May 2021 to November 2022) was greater for trees with high SA defoliation (40 percent) than trees with medium (10 percent) or low defoliation (0 percent) (table 10.1). BAI differed among SA defoliation classes (p = 0.0402) and was greatest in lightly defoliated trees, intermediate in moderately defoliated trees, and lowest in highly defoliated trees (table 10.1). Resin duct frequency (p = 0.17) and resin flow (p = 0.363) did not differ among SA defoliation classes (table 10.1). Phloem thickness differed among defoliation classes (p = 0.034) and was lower in trees with high defoliation compared to trees with medium or low defoliation (table 10.1). Phloem concentration of total terpenes (p = 0.4680) and each of 34 constituent terpenes (p >0.05) did not differ among defoliation classes (table 10.1).

In September 2021, 5 months after baiting, an average of 67 percent of pitch tubes had SB galleries, but this percentage did not differ (p = 0.1446) over defoliation classes (table 10.1). The percentage of pitch tubes with larvae (9 percent overall) was lower than for galleries (67 percent) and differed among defoliation classes (p = 0.0156; table 10.1). Larvae were absent in trees with low defoliation, scarce in trees with moderate defoliation (6 percent), and most common in trees with high defoliation (20 percent). In November 2022, no SB exit holes or galleries with live beetles were observed in any of the trees (table 10.1), indicating that attacks were not successful.

DISCUSSION

An important caveat is that this study occurred during a period of declining SB activity in the study site region. In other words, the SB population was endemic during this study. For example, aerial survey data indicated that SB activity decreased between 2020 and 2021 (when trees were baited) on both the Springerville Ranger District of the Apache-Sitgreaves National Forests (decrease of 25 percent) and adjacent White Mountain Apache Tribal lands (decrease of 96 percent). The finding that SA defoliation of Engelmann spruce had little impact on tree defense against SB applies only to endemic SB populations. The degree to which these findings apply to higher SB populations, or outbreak levels, is not known and further investigation is recommended.

Elevated SB activity and mortality in SA-defoliated trees was documented in Engelmann spruce at Greens Peak (Grady 2019) and broadly across the White Mountains during 2015 to 2018 (Gaylord and others 2020). However, attack success of SB on all trees in this study was low despite lures with aggregation pheromone being on trees for the entire summer of 2021. Analysis of galleries beneath pitch tubes showed that SB attacked and started to reproduce similarly in trees over all SA defoliation levels. Most of these galleries did not produce larvae, yet larvae were more common in trees with high defoliation than lower levels of defoliation. This pattern is

Table 10.1—Results of experiment where Engelmann spruces in each of three spruce aphid defoliation classes (low, medium, high) were experimentally baited with spruce beetle pheromones in May 2021

Tree response; mean (SE)	Low defoliation	Medium defoliation	High defoliation	p-value ANOVA F-test[a]
(1) Mortality May 2021 to November 2022 (percent)	0	10	40	NA
(2) Mean 5-year (2017 to 2021) BAI (mm^2/year)	3168.5a (839.8)	2603.0ab (433.5)	1131.6b (144.5)	**0.0402**
(3) Resin duct frequency combined over 2021 and 2022 (#/mm^2)	2.081a (0.791)	5.75a (2.038)	5.76a (1.314)	0.17
(4) Resin flow (g)	0.102a (0.0381)	0.328a (0.2090)	0.106a (0.0502)	0.363
(5) Phloem thickness (mm)	2.29ab (0.109)	2.34a (0.132)	1.93b (0.101)	**0.034**
(6) Phloem total terpene concentration (ug/g)	1793.1a (361.52)	1338.0a (202.88)	1461.1a (202.57)	0.4680
(7) Phloem concentrations of 34 constituent terpenes[b]	Not listed for brevity	Not listed for brevity	Not listed for brevity	>0.05
(8) Percentage of beetle attacks with galleries, September 2021	56.0a (10.24)	82.0a (6.29)	64.5a (10.44)	0.1446
(9) Percentage of beetle attacks with larvae, September 2021	0.0b (0.0)	6.0ab (3.06)	20.0a (7.45)	**0.0156**
(10) Number of adult beetle exit holes	0	0	0	NA

ANOVA = analysis of variance; BAI = basal area increment; SE = standard error.

Number of trees per defoliation class was 10, except for row (1) where n = 9 for low defoliation and row (4) where n = 9 for medium defoliation and n = 6 for high defoliation.

Means with different letters are significantly different ($p < 0.05$) in Tukey honestly significant difference (HSD) comparisons.

[a] ANOVA results were similar to nonparametric Wilcoxon tests in all cases. Bold shows statistically significant differences among defoliation classes.

[b] Tricyclene, alpha-pinene, camphene, sabinene, beta-pinene, myrcene, alpha-phellandrene, 3-carene, terpinolene, cymene1, beta-phellandrene, limonene, gamma-terpinene, cymene2, terpinolene, linalool, methyl thymyl ether, terpineol acetate, bornyl acetate, alpha-terpineol acetate, alpha-longipinene, caryophyllene, beta-farnesene, cymene3, two unnamed monoterpenes, and eight unnamed sesquiterpenes.

surprising because highly defoliated trees had thinner phloem than less-defoliated trees, which suggest controls over SB larval development by factors not investigated in this study (e.g., moisture content, tissue sugar concentration). Despite this evidence of partial SB larval development in some highly defoliated trees in the fall of 2021, subsequent SB development over the next year was minimal. In November 2022 (the second year after baiting), no SB exit holes or galleries with beetles at any life stage were observed in any of the trees. These results suggest that tree mortality in this experiment was the result of SA defoliation, chronic drought, and other factors but not the pheromone-mediated SB attacks during the study.

The low 5-year BAI of trees with high SA defoliation shows that these trees were more stressed than trees with less defoliation for several years before the experiment, likely due in part to SA defoliation in 2018. The high mortality during the experiment for trees with high defoliation (40 percent) suggests that even a single year of heavy SA defoliation reduces tree survival under the conditions at the study site, which include the most severe multidecadal drought in the last thousand years (Williams and others 2022). Similar tree mortality rates have been reported during previous SA outbreaks in Arizona (Lynch 2004, 2009). The lower mortality for trees with either light (0 percent) or moderate (10 percent) SA defoliation compared to high defoliation (40 percent) shows that trees can survive light SA defoliation for at least several years, whereas heavy defoliation results in fast mortality for some trees, and this generally occurs within the first 2 to 4 years following severe defoliation (Lynch 2004).

Root disease is another site factor that likely influenced results. Near the end of the experiment (August 29, 2022), the study site was surveyed for root disease during a period of heavy rainfall. Evidence of tomentosus root rot (*Onnia tomentosa*) was widespread on the site. Fruiting bodies were present within a 3-m radius of every tree in the study; several snapped trees in the study area exhibited "honeycomb" rot at the base, which is typical of tomentosus. Furthermore, evidence of armillaria (fungal mats) was present on several trees. Root disease was suspected to have contributed to tree mortality. Continued study of relationships among root disease, SA, and SB is highly recommended.

Trees with high or medium SA defoliation still have some defense against SB despite their slow growth. These trees were still able to form traumatic resin ducts in response to SB attack. Resin flow and terpene concentrations of moderately or highly defoliated trees were similar to lightly defoliated trees, suggesting similar quantitative and qualitative defenses among SA defoliation levels.

In summary, the results of this study suggest that, under endemic conditions, SB does not gain a reproductive advantage from Engelmann spruce trees defoliated by SA, and SB outbreaks likely do not initiate from SA defoliation. In other words, the results suggest that trees heavily defoliated by SA act as a sink for SB. Further monitoring and investigation of the interaction between SA defoliation and SB performance under outbreak, epidemic conditions are needed.

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