CHAPTER 22

# Spruce Aphid, *Elatobium abietinum* (Walker)

## *Life History and Damage to Engelmann Spruce in the Pinaleño Mountains, Arizona*[1]

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SPRUCE APHID IS AN EXOTIC INSECT recently introduced to the Pinaleño Mountains. It feeds on dormant Engelmann spruce, and possible effects include tree-growth suppression, tree mortality, and reduction in seed and cone production. Potential longer-term effects include changes in forest structure and species composition—primarily through reduction in Engelmann spruce dominance in spruce-fir and mixed-conifer forests. These effects would impact Mt. Graham red squirrel food resources, cache sites, and general habitat requirements.

Spruce aphid is folivorous on spruce species, with known infestations previously restricted to coastal areas (Koot 1991). Historically, economically important damage has occurred on Sitka spruce (*Picea sitchensis*), white spruce (*P. glauca*), and Norway spruce (*P. abies*) in areas with mild maritime winter climates: Britain, Iceland, Norway, Denmark, southern Sweden, northwestern Germany, Holland, New Zealand, and the northwestern North America coast (Bejer-Petersen 1962; Day et al. 1998). Spruce aphid was first reported in North America in 1916 in British Columbia (Koot and Ruth 1971; Carter and Halldórsson 1998), probably originating from European infestations (Bejer-Petersen 1962; Carter and Halldórsson 1998). The insect was found in Santa Fe, New Mexico, in 1976, although no wildland outbreak occurred in the Southwest until 1988, in the White Mountains of Arizona (U.S. Forest Service 1997; Lynch 2003, 2004). Numerous outbreaks of this insect have recently occurred on Engelmann spruce and Colorado blue spruce (*P. pungens*) in the subhumid mountains of the southwestern United States. Defoliation episodes, sometimes exceeding 11,000 ha, have occurred in the White Mountains, Pinaleño Mountains, and San Francisco Peaks of Arizona, and in the Mogollon Mountains and Sacramento Mountains of New Mexico (U.S. Forest Service 1997, 2001; Lynch 2004).

Spruce aphid was first found in the Pinaleño Mountains near High Peak in early winter 1999 by staff with the University of Arizona's Mt. Graham Red Squirrel Monitoring Program (MGRSMP). The majority of the Engelmann spruce on the mountain was severely defoliated by spring 2000. In the White Mountains, severe defoliation resulted in 24–41 percent mortality of Engelmann spruce (Lynch 2004). The extent and severity of spruce aphid damage in such a short period in the Pinaleño Mountains raised concerns about the insect's potential effects on Mt. Graham red squirrel habitat. Additionally, the timing of defoliation raised questions about the seasonal history of this insect in high-elevation southwestern ecosystems. Previous damaging outbreaks of this insect have been in maritime environments in the spring and early summer, with only infrequent and mild population increases being recorded in the autumn (Carter and Halldórsson 1998). Almost complete defoliation of many Engelmann spruce stands, and the nearly undetectable levels of aphid populations by April, indicated that the epizootic event occurred prior to spring in the Pinaleño Mountains.

Extensive European literature (see Day et al. 1998) describes spruce aphid maritime populations as increasing on dormant spruce in late winter through late spring, with occasional modest increases in the autumn. The aphids suck sap from host needle phloem cells, attacking the most recently produced needles after the foliage matures and hardens. Needles die and fall from the tree.

The insect's ability to over-winter is facilitated through supercooling ability, but aphid mortality does occur from ice nucleation (Carter 1972; Powell 1974), and populations are limited by cold winter temperatures. Aphids reared in cool conditions acquire cold-hardiness (Day and Kidd 1998), which varies seasonally and is lost in the spring (Carter 1972; Day and Kidd 1998). Spruce aphid epidemics have been restricted to areas with maritime climates, which moderates winter temperatures (Ohnesorge 1961; Bejer-Petersen 1962; Carter and Halldórsson 1998). Developing outbreaks in Britain are checked by sudden late spring frost (-11°C) after mild winters (Carter 1972). Epidemics in Denmark correspond to years with all monthly mean temperatures above 0°C (Bejer-Petersen 1962) and in Britain to regions where ambient temperatures do not fall to −8°C (Carter 1972). Some mild winters in Britain are not followed by outbreaks, and this is thought to be due to ambient temperatures falling below a limiting level at some point (Carter 1972; Day and Crute 1990), to an abrupt onset of cold conditions (Carter 1972), or to overcompensating density dependence (Day and Kidd 1998). The coldest temperature recorded for aphid survival is −23°C (Carter 1972). Using weather station data, Ohnesorge (1961, as summarized by Bejer-Petersen 1962) found that temperatures below −10°C to −14°C prevented or diminished outbreaks, with 0.5°C the lowest monthly mean in winters before an outbreak. Powell and Parry (1976) reported that in Scotland over-wintering populations are noticeably reduced when ambient temperatures fall below −7°C. In the North American Pacific Northwest, springtime populations collapse when temperatures fall below −5°C or −6°C (D. Overhulser and M. Schultz, personal communication). Temperatures often fall below these population limits in southwestern high-elevation forests, raising additional questions about the insect's life history.

Research was initiated in 2000 to determine the life history and potential frequency of outbreaks of the insect and the severity of damage to Engelmann spruce in Mt. Graham red squirrel habitats in the Pinaleño Mountains.

## Methods

### *Seasonal Life History*

Aphid populations were sampled 15 times between August 2000 and July 2001 to determine the seasonal abundance of the species in southwestern high-elevation ecosystems. On each sample date, one branch encompassing the 1996–2000 foliage was collected from 10 different trees and bagged individually at each of two sites, one on Emerald Peak and one near the Vatican Advanced Technology Telescope. Branches and trees were haphazardly selected each sample date within a 1 ha area. Branches were taken to the laboratory, where aphids were washed off in a lukewarm, weak saltwater bath. Straight-edged artists' brushes were used to gently brush tenacious aphids from the upper- and under-sides of the needles and twigs. When aphids were numerous, coffee filters in fast-flow funnels were used to filter them from the water bath. Aphids were placed in 85 percent ethyl alcohol and counted later. The distribution of aphids by foliage cohort was not obtained. Aphid count data is reported here as the mean number of aptera (wingless forms) and alates (winged forms) per branch.

Contemporary temperatures in the Pinaleño spruce-fir forest, and population increase and decline with respect to temperature, were assessed using temperature data from two sources. Temperature data for 1995–2000 were obtained from the MGRSMP weather station located in an opening on Emerald Peak. Temperature data for 2000–2003 were obtained from Onset optic temperature data loggers approximately 0.4 km away in the forest. In both cases, the ambient temperature was recorded at 2–3 m above ground. The MGRSMP weather station recorded minimum and maximum diurnal temperatures, from which a diurnal midpoint temperature was computed. The optic data loggers recorded temperature every 15 minutes, and mean daily temperatures were computed from 96 observations. Humidity and rainfall affect spruce aphid when rime ice is formed (Carter 1972; Carter and Nichols 1989; Carter and Halldórsson 1998), but the effect of snow is not known. In maritime populations, freezing of individual aphids of instars II through adult occurs when ice nucleation begins in the needles in which the aphid stylets are inserted (Powell 1974). During several sample dates over the 2002–2003 autumn–winter (data not reported here), aphids were observed to be alive and well when branches were covered by snow. Rather than damaging the aphids, snow may insulate them from nighttime low temperatures.

### *Tree Defoliation and Mortality*

Temporary and permanent impact assessment plots were established and assessed on a grid for the area of the Pinaleños above 2,600 m. The primary objective was to determine if defoliation and mortality in the Pinaleños will be more or less severe than in the White Mountains of Arizona, as reported by Lynch (2004). Forty-three plots of 0.0314 ha (10 m radius) were measured in summer 2000 on a grid pattern above 2,600 m, including 34 temporary and 9 permanent plots. In 2001, the plots with few Engelmann spruce were expanded to 0.126 ha (20 m radius), and one additional permanent plot was added in the mixed-conifer zone. All live trees 10 cm or larger diameter at breast height (dbh) were assessed for species and diameter. All Engelmann spruce 10 cm dbh or larger were assessed for spruce dwarf mistletoe (*Arceuthobium microcarpum*) infection using the six-point Hawksworth DMR system (Hawksworth 1977), attack by bark beetles (spruce beetle and spruce ips [*Ips hunteri* Swaine], both Coleoptera: Scolytidae), and defoliation by spruce aphid. A defoliation index (DI) was computed as the sum of three crown-third ratings—where each crown-third was rated as 0, 1, 2, or 3—by 33 percent defoliation classes (an index of nine indicates that each crown third was 67–100 percent defoliated) (Lynch 2004). Trees or plots with defoliation indices of 0–3, 4–7, and 8–9 were considered lightly, moderately, and severely defoliated, respectively. DI class 7 trees were considered moderately rather than severely defoliated because Lynch (2004) found that significant mortality after spruce aphid defoliation occurred only in trees with DI 8 and 9.

Eight permanent plots were compared with nearby plots of the same size containing occupied Mt. Graham red squirrel middens. Midden plots were of the same size (10 m radii), approximately centered on the midden, and assessed in the same manner as non-midden plots. Statistical comparison of midden and non-midden plots utilized paired-comparison t-tests.

It should be noted that defoliation caused by a sap-sucking insect such as spruce aphid is not the same as defoliation from a defoliator such as western spruce budworm (*Choristoneura occidentalis* Freeman [Lepidoptera: Tortricidae]). The needle replenishes and subsequently loses fluid removed by the aphid. Eventually, the needle may die from necrosis or dehydration. Therefore, defoliation estimates made here are not directly comparable to similar levels of defoliation from a leaf-chewing insect.

## Results

### *Aphid Populations and Temperatures*

Aphids were found from early August 2000 through late March 2001, and again in July 2001, though population densities were very low after November 2000 (table 22.1). Aphid densities were high in autumn, from sometime in July through October 2001, and increased rapidly between

Table 22.1. Mean number of aphids collected on the 1996–2000 foliage of 10 branches at Emerald Peak and near the Vatican telescope over the 2000–2001 winter*

| | Emerald Peak | | | Vatican | | |
|---|---|---|---|---|---|---|
| Date | Aptera | Alates | Percent alates | Aptera | Alates | Percent alates |
| 7 Jul 00 | present | present | unknown | | | |
| 5 Aug 00 | 57.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| 24 Aug 00 | 49.6 | 1.2 | 2.3 | 0.0 | 0.0 | |
| 21 Sep 00 | 50.6 | 1.8 | 3.4 | 1.5 | 0.0 | 0.0 |
| 11 Oct 00 | 318.9 | 8.1 | 2.5 | 7.3 | 0.3 | 4.1 |
| 5 Nov 00 | 8.7 | 0.0 | 0.0 | 4.0 | 0.4 | 0.1 |
| 22 Nov 00 | 2.4 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 |
| 13 Dec 00 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | |
| 3 Jan 01 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | |
| 1 Feb 01 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | |
| 7 Mar 01 | 0.0 | 0.2 | 100.0 | 0.1 | 0.0 | 0.0 |
| 29 Mar 01 | 0.0 | 0.4 | 100.0 | 0.0 | 0.0 | |
| 12 Apr 01 | 0.0 | 0.0 | | 0.0 | 0.0 | |
| 8 May 01 | 0.0 | 0.0 | | 0.0 | 0.0 | |
| 28 Jun 01 | 0.0 | 0.0 | | 0.0 | 0.0 | |
| 24 Jul 01 | 0.3 | 0.0 | 0.0 | 0.3 | 0.0 | 0.0 |

* Observations on 7 July 2000 are unquantified observations from a reconnaissance trip.

late September and mid-October (table 22.1; fig. 22.1). Populations were undetectable from April through June 2001, and barely detectable in July 2001 (table 22.1). Alates were found in autumn and spring. Population densities followed the same seasonal trends at both sample sites, but levels were much lower at the Vatican telescope site (table 22.1).

Aphid population density increased to detectable levels prior to the first sample date in early August 2000 (table 22.1; fig. 22.1). Population density was fairly stable from 5 August until 21 September, when mean daily temperatures were between 7°C and 14°C and minimum daily temperatures were above 2.7°C. Aphid population density increased 530

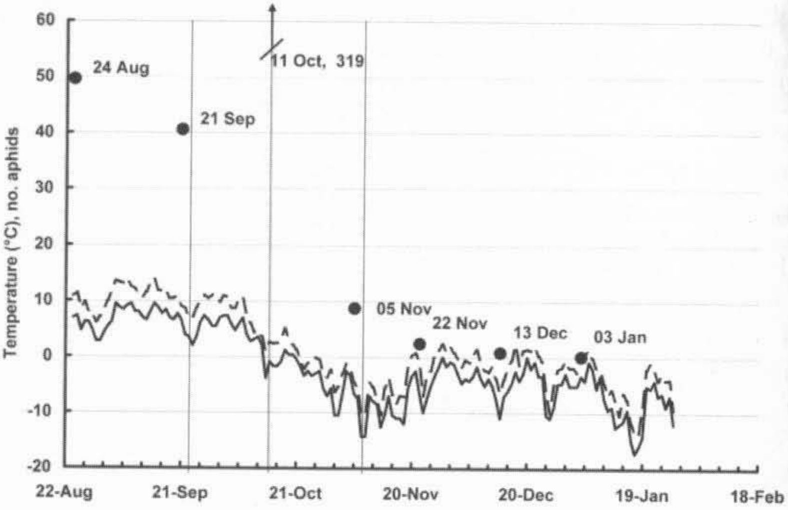

Figure 22.1. Minimum (solid line) and mean (dashed line) daily temperatures, and mean number of aphids per branch (dots, each computed as the mean of 10 branches including 1996–2000 foliage) at Emerald Peak, August 2000 through May 2001. Thin vertical lines are for guidance to the axis position.

percent in the 21-day period between 21 September and 11 October, when mean daily temperatures were somewhat cooler, between 7 and 10°C, with minimum temperatures never falling below 2°C (fig. 22.1). After the 2001 summer, aphid population density had increased to only barely detectable levels by the end of July 2001, much lower than by early August in the previous year (table 22.1).

Aphid population density decreased 97 percent between 11 October and 5 November 2000 (fig. 22.1). During the intervening 25-day period, minimum temperatures fell to −3.8°C, −7.0°C, and −10.5°C, and daily mean temperatures were below 0°C for 16 days. It is not known whether one of the cold events, or the extended cold period, caused the population to collapse. Populations were not quantified in 1999, the first year the insect was found in the Pinaleños, but populations were very high at least through December (collections were made for genetic assessment), when the mean daily temperature was −3.3°C and the minimum temperature was −12.1°C. The October and November 1999 minimum temperatures were −4.6°C and −8.7°C, respectively. Defoliation from the 1999–2000 episode was more severe and extensive than from the 2000–2001 episode, so aphid populations were either of higher density or present at damaging densities for a longer period of time during 1999–2000. Also, I have observed populations at damaging densities surviving temperatures as low as −13.6°C in the Pinaleños, during the 2002–2003 winter, and −15°C in the San Francisco Peaks, during the 2001–2002 winter.

Significant defoliation was observed in 2000, 2001, and 2003 from spruce aphid populations in the preceding autumn–winter periods of 1999–2000, 2000–2001, and 2002–2003, respectively. Monthly mean temperatures fell below 0°C three to five months each winter, and ambient temperatures fell below −12°C every autumn–winter period from 1996–1997 through 2002–2003. Spruce aphid population densities were not quantified in the Pinaleño Mountains the first winter that the species was present, but infested branch samples collected on Emerald Peak for identification purposes in November and December 1999 indicated that temperatures fell to at least −4.6°C and possibly below −10°C without terminating the outbreak.

The majority of aphids collected were aptera (table 22.1). A small portion of the collections from late August to November was male alates, and the collections in March at Emerald Peak were entirely dispersal females.

### *Tree Defoliation and Mortality*

Fifteen plots contained no Engelmann spruce 10 cm or larger dbh and were not evaluated further. The 29 remaining plots (19 temporary and 10 permanent) include 16 habitat types from corkbark fir, Douglas-fir, Engelmann spruce, and white fir series (Stuever and Hayden 1997). Site physiography varies from riparian to rocky ridge tops, ranging in slope from 3 to 72 percent and in elevation from 2,728 to 3,226 m, and encompassing the full range of aspect. Engelmann spruce density (trees 20 cm or larger) ranges from 32 to 795 trees per ha, and total tree density ranges from 64 to 954 trees per ha. Other tree species present include corkbark fir, white fir, Douglas-fir, ponderosa pine, southwestern white pine, quaking aspen, and willow (*Salix* sp.). The 10 stands in the permanent

Table 22.2. Character of the 10 stands sampled from 2000 through 2002 for spruce aphid defoliation and mortality

Habitat type abbreviations: Abco = White fir, Abla = Corkbark fir, Erex = Forest fleabane [*Erigeron eximius*], Pien = Engelmann spruce, Psme = Douglas-fir, Rone = New Mexico locust [*Robinia neomexicana*]

| | | | | | | | Engelmann Spruce | |
|---|---|---|---|---|---|---|---|---|
| Name | Aspect (deg) | Slope (%) | Elev (m) | Habitat Type | Physiography | Density (tph) | Dominance (%) | dbh ± SD (cm) |
| Shingle Mill | 320 | 27 | 2826 | Abla/moss | mid-slope, rocky soil | 72 | 36 | 28 ± 14 |
| Lower Webb Pk | 116 | 20 | 2961 | Abla/moss | lower slope | 863 | 100 | 36 ± 12 |
| Bible Camp | 12 | 53 | 2889 | Abla/moss | steep mid- to upper-slope | 401 | 37 | 17 ± 6 |
| Soldier Creek | 168 | 25 | 2910 | Pien/Erex | gentle mid-slope | 64 | 10 | 33 ± 10 |
| Rock Pile | 50 | 6 | 2947 | Abla/riparian | wetland | 223 | 50 | 33 ± 9 |
| Access Rd | 204 | 30 | 3140 | Pien/moss | upper slope | 863 | 96 | 31 ± 7 |
| Plain View | 188 | 30 | 3115 | Pien/moss | mid-slope, deep soil | 382 | 100 | 30 ± 9 |
| Crazy Horse | 310 | 3 | 2890 | Psme/Rone | ridge top, shallow soil | 401 | 49 | 20 ± 3 |
| Heliograph Peak | 250 | 36 | 2907 | Pien/Erex | mid-slope below steep slope | 159 | 19 | 46 ± 19 |
| Grant Hill Trailhead | 150 | 10 | 2800 | Abco/Carex | gentle drainage hollow | 374 | 75 | 22 ± 14 |

sample were a representative sample of the total sample, representing a wide range of density, dominance by Engelmann spruce, physiography, and Engelmann spruce size (table 22.2).

Defoliation from spruce aphid was moderate to severe (DI ≥ 5) on 55 percent of the total sample. Little or no defoliation occurred from the 1999–2000 episode on plots on, near, or east of the ridge that runs from Mt. Graham down towards Shannon Park. However, all plots in the permanent sample have subsequently had at least moderate defoliation from spruce aphid at least once (table 22.3). This indicates that aphids did not disperse from the original establishment area (probably near Highwater Cienega) to the east side of the mountain range with enough time for populations to increase and cause defoliation the first year. Mean plot defoliation in 2000 of plots within the 1999–2000 outbreak area was 7.1 ± 2.7 DI.

Mean mortality on plots was 21.2 percent ± 21.1 percent by 2002 (table 22.3). Many plots were defoliated two years in a row (table 22.3). Plots with a mean defoliation index in either 2000 or 2001 (or both) of 8 or greater incurred, on average, 32 percent mortality by 2002, while plots with mean defoliation indices of 7 or less each year incurred 5 percent mortality (table 22.3). The two plots with no mortality by 2002, which incurred no defoliation in the 1999–2000 episode, were located on the eastern side of the study area, as described earlier.

Of the trees that died, 10 percent died from aphid defoliation without additional attack from bark beetles or pre-existing severe mistletoe infection. Fourteen percent had pre-existing severe mistletoe infection, and 75 percent were attacked by bark beetles after being severely defoliated (DI ≥ 8) by spruce aphid. Fifty percent of trees with heavy defoliation (DI ≥ 8) and severe dwarf mistletoe (DMR ≥ 5) were dead by 2002. Much greater incidence of bark beetle attack in heavily defoliated trees was found in the Pinaleños than was found in the White Mountains, undoubtedly due to the fact that a spruce beetle epidemic was underway when spruce aphid first established in this mountain range (see Discussion). No tree in the sample died from spruce beetle attack that was not first severely defoliated by spruce aphid.

Paired-comparisons showed that midden plots were slightly less defoliated in 2000 than were non-midden plots (DI of 4.2 ± 3.7 vs. 5.1 ± 4.3, $t = 1.88$, df = 7, $P = 0.10$). Compared to non-midden plots, midden plots

Table 22.3. History of spruce aphid defoliation and mortality from 2000 through 2002

Note that defoliation in a given year results from aphid populations in the preceding autumn and winter.

| | Mean defoliation index (0 = none; 9 = complete) | | | Percent mortality of trees alive in 2000 | | |
|---|---|---|---|---|---|---|
| Site name | 2000 | 2001 | 2002 | 2001 | 2002 | Total |
| Shingle Mill | 9.0 | 7.3 | 2.0 | 0.0 | 16.6 | 16.6 |
| Lower Webb Pk | 5.3 | 6.9 | 2.7 | 0.0 | 5.9 | 5.9 |
| Bible Camp | 9.0 | 8.9 | 2.0 | 28.6 | 28.5 | 57.1 |
| Soldier Creek | 9.0 | 7.4 | 3.5 | 12.5 | 0.0 | 12.5 |
| Rock Pile | 2.4 | 4.8 | 2.7 | 0.0 | 14.3 | 14.3 |
| Access Rd | 8.1 | 7.6 | 1.6 | 0.0 | 47.1 | 47.1 |
| Plain View | 0.0 | 8.4 | 2.0 | 0.0 | 47.1 | 47.1 |
| Crazy Horse | 0.0 | 6.0 | 3.0 | 0.0 | 0.0 | 0.0 |
| Heliograph Peak | 0.0 | 3.6 | 3.3 | 0.0 | 0.0 | 0.0 |
| Grant Hill Trailhead | M | 8.0 | 2.6 | 0.0 | 11.1 | 11.1 |

had greater density (482 vs. 345 trees per hectare [tph]) and dominance (53.1 percent vs. 42.2 percent, by density) by Engelmann spruce. The Engelmann spruce were also larger on the midden plots (35.5 vs. 32 cm mean dbh).

## Discussion

In its native range in continental Europe, the spruce aphid life cycle is holocyclic, with parthenogenic population increases in autumn and spring, winged male and female forms, and sexual forms in autumn that produce an over-wintering egg stage (von Scheller 1963; Lampel 1968; Carter and Austarå 1994; Carter and Halldórsson 1998). The presence of autumn males in Arizona indicates that the life cycle is either holocyclic or paracyclic (both egg and parthenogenic forms over-winter). Winged females would account for rapid dispersal of the species throughout the mountain range; they rarely occur in maritime environments where the life cycle is usually limited to the parthenogenic apterous form. Sampling over several winters will be necessary to determine if the life cycle in the Southwest is holocyclic or paracyclic. Although eggs have not yet been found, the presence of males indicates that eggs are produced in Arizona. Very little is known about the egg stage, but since it is an over-wintering stage in continental Europe, it is probably very cold hardy.

Aphid populations in the Pinaleños appear to be more cold hardy than populations in maritime Europe and the Pacific Northwest. In maritime climates, temperatures below −10°C to −14°C prevent or diminish subsequent spring outbreaks, and outbreaks do not develop after a monthly mean of 0.5°C occurs in any winter month (Bejer-Petersen 1962; Day and Kidd 1998). Maritime populations collapse between −5°C and −7°C, and development of individual aphids occurs only above 5°C (Day and Crute 1990). Temperatures below these levels are reached in the Pinaleños almost every October, November, and December, and aphid populations continue to increase.

There may be considerable inter-annual variability in autumn–winter population dynamics. Aphid population densities in early autumn 2000 and 2001 were very different (table 22.1; fig. 22.1). Additionally, densities were quite high in late December 1999 and early January 2000, prior to this investigation, but very low in December 2000 and January 2001. Spring population dynamics in maritime Europe are influenced by the density of the pre-existing aphid population, and by temperatures during the previous winter (Day and Kidd 1998). Data here are not adequate to model population dynamics, but autumn temperatures show considerable variation, especially with respect to minimum temperatures. October minimum temperatures have ranged from −5°C to −14°C, which would undoubtedly affect spruce aphid population dynamics.

Even though the aphid sampling methodology was fairly crude, it is adequate to demonstrate that mean daily temperatures between 7°C and 10°C, and minimum temperatures above 2°C, are suitable for aphid population increase. However, aside from demonstrating that population increase occurs under late autumn environmental conditions typical of the Pinaleño Mountains, which are colder than temperatures that limit spruce aphid density in maritime environments, these data do not establish a direct relationship between temperature and population dynamics. Population growth and decline is associated with fecundity, which is strongly influenced by nutritional factors in the phloem fluid, as influenced by dormancy (Day 1984; Fisher and Dixon 1986; Day and Kidd 1998). Engelmann spruce dormancy would progress at different rates from year to year.

At some point, below-freezing temperatures limit aphid population growth and/or cause population decline. Several different cold events preceded a population crash in the Pinaleño Mountains during the course of this study. These events included temperatures falling to −3.8°C to −10.5°C, and mean and minimum diurnal temperatures remaining below 0°C for 16 days. However, damaging populations survived temperatures as low as −13.6°C the next year and −15°C in northern Arizona. This indicates some variability in the cold-hardiness of aphid populations, possibly associated with conditioning. Probably a sharp decline into cold temperatures is more damaging to aphid populations than a gradual decline. An extended cold period probably results in low developmental rates, starvation, and a low birth rate, such that dying individuals are not replaced.

Defoliation in the Pinaleño Mountains was more severe than what was seen in the White Mountains by Lynch (2004). Mortality levels are consistent with, or more severe than, those observed in the White Mountains, where 24–41 percent mortality was observed four years after a single defoliation episode in heavily defoliated trees (Lynch 2004). Here, mean plot mortality reached 21 percent by 2002 and 32 percent on severely defoliated plots within two years. These differences may be due to more severe defoliation, consecutive years of defoliation on some plots, or to spruce beetle activity in defoliated trees. Spruce beetle activity was high in the Pinaleño Mountains when spruce aphid was introduced, but has been low in the White Mountains. Based on patterns seen in the White Mountains, additional mortality from the 1999–2000 and 2000–2001 episodes may have continued through 2005 in the Pinaleño Mountains.

At the time that spruce aphid was first found in the Pinaleño Mountains, the spruce-fir forest was in the middle of outbreaks of both spruce beetle and western balsam bark beetle, both of which originated and developed slowly after damage from ice and snow in the winter of 1992–1993. About 160 ha of this area were subsequently severely defoliated in 1996–1999 by *Nepytia janetae* Rindge (Lepidoptera:Geometridae), and the beetle populations increased rapidly in the defoliated trees (Lynch et al. in press). Spruce beetle is an aggressive species, and during outbreaks, it kills most mature spruce over extensive areas of mature and over-mature spruce or spruce-fir forests, especially the larger trees (Furniss and Carolin 1977). Much greater incidence of bark beetle attack in heavily defoliated trees was found in the Pinaleño Mountains than was seen in the White Mountains, undoubtedly due to the coincidence of outbreaks. No trees on the study plots died from spruce beetle attack that were not first severely defoliated by spruce aphid. Spruce beetle hazard is high in dense stands composed primarily of large spruce (Schmid and Frye 1976, 1977), but defoliated trees in this study were attacked by spruce beetle in stands not dominated by large spruce, such as near the Bible Camp. Unfortunately, there were too few trees with light levels of defoliation (there were only 17 individual trees with DI ≤ 7) to definitively conclude that defoliation predisposes trees to spruce beetle attack.

The high level of mortality seen in trees that were both severely defoliated by spruce aphid and severely infected with spruce dwarf mistletoe (50 percent by 2002) is consistent with findings from the White Mountains, where almost 70 percent of such trees died within four years of aphid attack (Lynch 2004). Because the overall levels of defoliation were so high in the Pinaleños, site and vegetation factors could not be assessed for association with defoliation, other than to conclude that Engelmann spruce in the Pinaleño Mountains is susceptible to spruce aphid attack in the mixed-conifer, transition, and spruce-fir zones. The only other factor associated with increased likelihood of defoliation and mortality in the White Mountains was position in the lower-stand canopy (not tree size directly) (Lynch 2004). Future risk-assessment efforts should be directed towards weather factors rather than stand and site character.

Plots containing active Mt. Graham red squirrel middens in 2000 were slightly less severely defoliated than paired non-midden plots. Although I have seen Mt. Graham red squirrels feeding on spruce aphids, it is difficult to think that such activity would significantly reduce aphid populations on the entire plot. More likely, the less severe defoliation reflects an absence of smaller Engelmann spruce on the plots, which generally are the ones most severely defoliated (Lynch 2004). Average size of Engelmann spruce is larger on midden plots.

## Conclusions

The population dynamics information described here from the Pinaleño Mountains, repeated outbreaks two years in a row, as well as the frequency of outbreaks in the White Mountains, indicates that autumn and possibly winter temperatures are frequently suitable for spruce aphid population increase in the Pinaleño Mountains. Aphid populations in the southwestern United States are clearly surviving, increasing, and causing severe defoliation during periods when diurnal minimums are below −5°C, the point where ice nucleation occurs in Sitka spruce–attached aphids, and below −8°C to −14°C, the range of ambient temperatures below which subsequent epidemics are thought to be limited. Temperatures seldom fall below −15°C, and in some years do not fall below −10°C until December, while aphid population increase may begin as early as July. There is evidence that autumn spruce aphid outbreaks follow dry winter–spring periods, but the mechanisms are unknown (Lynch 2003). Further research is necessary to establish the temperature regimes that terminate autumn–winter spruce aphid outbreaks, and that limit and favor population increases in southwestern high-elevation environments. Such information will allow better estimation of outbreak frequency and severity.

There is little hope that spruce aphid will be eliminated from the ecosystem due to a severe cold event, as the species persisted in the White Mountains after December 1990 when temperatures fell to −25°C (NOAA 1990).

Unfortunately, if weather patterns seen in recent years continue, it appears that spruce aphid outbreaks will occur with some frequency. The severity of damage seen in both the Pinaleño Mountains and the White Mountains indicates that, given frequent outbreaks, Engelmann spruce populations will be diminished in all habitat types in which it occurs. Additional research is needed to determine the effect of aphid feeding on Engelmann spruce seed and cone production, seed viability, and established regeneration. Spruce aphid drastically reduces height growth of other spruce species (Carter 1977; Warrington and Whittaker 1990; Seaby and Mowat 1993; Thomas and Miller 1994; Straw et al. 1998), and similar growth loss effects would affect the ability of Engelmann spruce to compete with other species. Increased defoliation and mortality of the lower-canopy layers, seen in the White Mountains, indicates that regeneration size classes will be impacted the most by this insect. Though research reported here does not address impact to small trees, spruce aphid has heavily damaged Engelmann spruce seedlings and saplings in the Pinaleño Mountains.

The combined short-term effects of beetle, looper, and aphid outbreaks in the spruce-fir, transition, and mixed-conifer forests include an abundance of standing dead timber of all size classes, increased amounts of coarse woody debris, an abundance of desiccating and dead needles distributed throughout the forest canopy, and dramatically altered sunlight regimes within the forest. In stands with a large Engelmann spruce component, airflow and temperatures on the site have also changed. The abundance of dead and dying needles from repeated spruce aphid outbreaks represents a canopy ladder of fine fuels, affecting the risk and vulnerability to wildfire.

The combined effects of outbreaks of the multiple insect species have devastated the spruce-fir forest and pure spruce stands and individual Engelmann spruce in the mixed-conifer forest in the Pinaleño Mountains. Spruce beetle, western balsam bark beetle, and *N. janetae* drastically altered the character of the highest-elevation forest before spruce aphid established. Spruce aphid defoliation caused additional mortality to Engelmann spruce in both the spruce-fir and mixed-conifer forests (table 22.3), and will in all likelihood continue to cause mortality. The catastrophic insect-related damage was rapidly followed by a precipitous decline in the Mt. Graham red squirrel population (Koprowski et al. 2005). Severe outbreaks of bark beetles are catastrophic, but natural, disturbances in spruce and spruce-fir forests (Furniss and Carolin 1977). The geometrid is a native insect, and it has probably incurred outbreaks in the past as well (Lynch et al. in press). The Mt. Graham red squirrel, and red squirrel populations in other southwestern forests, have obviously survived such disturbances in the past, including catastrophic wildfire (Grissino-Mayer et al. 1995). However, spruce aphid is a new disturbance agent in the high-elevation forest, and the future cannot be assured by historical success.

Engelmann spruce is highly susceptible to fire damage (Fischer and Bradley 1987; Grissino-Mayer et al. 1995), but risk is somewhat mitigated by the relatively moist and cool habitat, except during very dry years

(Zwolinski 1996). Anthropogenic influences over the last century, especially fire exclusion, have produced dense, multi-storied canopies in the mixed-conifer forests that are now much more prone to catastrophic wildfire (Baisan and Swetnam 1995; Grissino-Mayer et al. 1995; Allen 1996; Touchan et al. 1996; Zwolinski 1996). Prior to European settlement, the relatively high frequency of surface fires and the heterogeneous nature of the mixed-conifer forest contributed to the formation of a buffer zone below the highly flammable spruce-fir forest, promoting long-term stability in the spruce-fir forest. The integrity of this buffer has been reduced by fire exclusion practices (Grissino-Mayer et al. 1995). Fine fuels produced by aphid feeding throughout the forest canopy may increase fire risk and hazard. Fire hazard will also be altered due to the significant amounts of mortality in the mature canopy from the combined effects of beetle, looper, and aphid outbreaks, and in the lower-canopy layers from spruce aphid. Wildfire concerns are heightened by an apparent association between aphid outbreaks and warm, dry winter weather (Lynch 2003), and the compromised ability of the lower-elevation forests to buffer the high-elevation forests from encroaching wildfires.

The time frames of the studies reported here, as well as those discussed from the White Mountains, are too short to predict the ultimate fate of Engelmann spruce in the ecosystem. However, in all likelihood, Engelmann spruce populations will be diminished in the future forest. Aphid-caused spruce mortality and altered seed production could have long-term effects on stand structure, species composition, and Mt. Graham red squirrel food resources and habitat.

## Acknowledgments

I am grateful to Genice Froehlich for reconnaissance and aphid sampling assistance, to Jill Wilson and Michelle Frank for helpful suggestions, and to Stephanie Jentsch, Brian Nowicki, and Jerry Snow for counting aphids and for assistance with the defoliation and mortality surveys. Funding for this study was provided by the University of Arizona through the Mt. Graham Red Squirrel Study Committee, which is comprised of representatives from the Arizona Game and Fish Department, the University of Arizona, the U.S. Forest Service, and the U.S. Fish and Wildlife Service; and by the U.S. Forest Service, Rocky Mountain Research Station.

## Note

[1] This manuscript was written and prepared by a U.S. government employee on official time, and therefore it is in the public domain and not subject to copyright.

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