

FATE AND CHARACTERISTICS OF *PICEA* DAMAGED
BY *ELATOBIMUM ABIETINUM* (WALKER) (HOMOPTERA: APHIDIDAE)
IN THE WHITE MOUNTAINS OF ARIZONA

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ABSTRACT.—Spruce aphid, *Elatobium abietinum* (Walker), is a new invasive pest in high-elevation forests of southwestern USA. Plots in the White Mountains of Arizona were evaluated over several years to assess the extent and severity of damage in high-elevation forests and to identify tree and site characteristics associated with defoliation and mortality. Large areas were defoliated in each of 4 recent outbreaks. Impact from a single defoliation episode included an overall mortality of 10.3% to *Picea engelmannii* Parry, 24%–41% in severely defoliated trees. Defoliation severity was much greater on *P. engelmannii* than on *P. pungens* Engelm. and was more severe in the lower canopy layers. Retention of foliage in the upper-crown third of individual trees was a critical factor in tree survivorship. Mortality was associated with defoliation severity and severe infection by *Arceuthobium microcarpum* (Engelmann) Hawksworth & Wiens. *Picea pungens* was much more susceptible to *A. microcarpum* than was *P. engelmannii*. The combined effects of high levels of defoliation and mistletoe infection were lethal, resulting in almost 70% mortality. Mortality continued to occur at least 3 years after defoliation. This aphid will affect natural disturbance regimes and tree population dynamics in mixed-conifer and spruce-fir forests of the American Southwest.

Key words: *Elatobium abietinum*, *Arceuthobium microcarpum*, *Picea engelmannii*, *Picea pungens*, *invasive species*, *exotic*, *disturbance ecology*, *insect impact*.

Spruce aphid, *Elatobium abietinum* (Walker) (Homoptera: Aphididae), is a new invasive pest in the interior southwestern United States (Lynch 2003). This species probably originated in northern Europe (Hanson 1952, Bejer-Petersen 1962, Carter and Halldórsson 1998), where it is known as green spruce aphid. It has been known from the Pacific Northwest coastal areas of North America since 1916 (Koot and Ruth 1971, Carter and Halldórsson 1998). It was found in urban Santa Fe, New Mexico, in 1976, where it has been an intermittent pest in the urban forest. The first wildland outbreak in the Southwest occurred over the 1989–90 winter in the White Mountains of Arizona, causing defoliation on more than 100,000 acres (USDA Forest Service 1997). Three subsequent outbreaks occurred over the winters of 1995–96, 1996–97, and 1999–2000 (USDA Forest Service 1997, 1998, 2001). The range has expanded to include the Mogollon Mountains (just east of the White Mountains) and Sacramento Mountains in New Mexico, and the Pinaleño Mountains and San Francisco Peaks in Arizona. The last outbreak was very extensive, causing

defoliation on 156,800 acres in the White Mountains (USDA Forest Service 2001).

Elatobium abietinum feeds on dormant, mature *Picea* needles (Parry 1976, Jackson and Dixon 1996). Epizootics of this insect occur during the spring in the Pacific Northwest and other areas with maritime climate (Bejer-Petersen 1962, Parry 1973, Heie 1989, Day and Crute 1990, Carter and Halldórsson 1998) and during the fall in high-elevation forests of the Southwest (Lynch 2003). Relatively minor population increases can occur in maritime climates in the fall (Hussey 1952, Bevan 1966). The host species in the Southwest are *Picea engelmannii* Parry (Engelmann spruce) and *P. pungens* Engelm. (Colorado blue spruce). The insect sucks sap from needle phloem cells, causing needle necrosis, dehydration, and premature drop (Bevan 1966). Tree mortality is uncommon in maritime areas, where the most important host species are *P. sitchensis* (Bong.) Carr. (Sitka spruce), *P. glauca* (Moench) Voss (white spruce), and *P. abies* (L.) Karst (Norway spruce; Bevan 1966, Carter 1977, Day and McClean 1991, Seaby and Mowat 1993, Thomas

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and Miller 1994, Straw et al. 1998). *Elatobium abietinum* has been a chronic pest in the Pacific Northwest, but occasionally it causes severe tree mortality in local areas (Koot 1992).

I conducted this study to evaluate the extent and severity of damage in high-elevation forests and to identify tree and site characteristics associated with defoliation and mortality. Emphasis was placed on identifying tree characteristics associated with damage and mortality because the annual Aerial Detection Surveys indicated extensive defoliation with little apparent site or stand variability within the defoliated areas (Fig. 1; USDA Forest Service 1998, 1999). This approach will allow assessment of potential damage in subsequent outbreaks and in other mountain ranges.

Western spruce dwarf mistletoe, *Arceuthobium microcarpum* (Engelmann) Hawksworth & Wiens (Viscaceae), is a localized parasite of *Picea* in Arizona and New Mexico. The most damaging disease agent in southwestern mixed-conifer forests dominated by *Picea*, it is noted for causing an unusually high rate of mortality in *P. pungens* (Mathiasen et al. 1986, Hawksworth and Wiens 1996). Evaluation of *A. microcarpum* effects was included in the study after analyses indicated that it plays an important role in the fate of trees defoliated by *E. abietinum*.

STUDY SITES

Thirty-seven 0.20-acre (0.08-ha) study plots were surveyed in 1997, 1999, 2000, and 2001. The plots include considerable variation in elevation, species composition, density, diameter distribution, and dominance by spruce. Elevation ranges from 8174 feet to 9698 feet (2491 m to 2956 m), with a mean of 9130 feet (2783 m). The sampled area excludes some of the highest-elevation spruce-fir forest in the White Mountains, which is in the Mount Baldy Wilderness Area, and a 10,000-acre (4047-ha) area defoliated in 1995–1999 by *Nepytia janetae* Rindge (Lepidoptera: Geometridae; USDA Forest Service 1999, 2000, Lynch and Fitzgibbon 2004). Density varies from 15 tpa to 590 tpa (37 tph to 1458 tph), with spruce density varying from 5 tpa to 155 tpa (12 tph to 383 tph). Plots include variable and relatively uniform diameter distributions, indicating that even- and mixed-aged stands were represented.

The range of species composition includes mixed-conifer (5 species were present on 14

plots), *Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco-dominated, spruce-fir (almost all *P. engelmannii*–*A. lasiocarpa* var. *arizonica*), and pure spruce (either pure *P. engelmannii* or a mix of both *Picea* species). Plots of relatively pure spruce were above 9100 feet in elevation and composed of medium- to large-sized trees (mean dbh of 8–14 inches) with fairly uniform diameter distributions (usually with coefficient of variation of the mean [CVM] of dbh < 30%). Spruce dominance (based on density) ranged from 2% to 100%, with a mean of 32%. *Picea pungens* was present on 14 plots but was the major component on only 4 of those.

METHODS

The plots consist of high-elevation plots from the Fort Apache Indian Reservation Continuous Forest Inventory (CFI) plot system. The CFI system and spruce-fir population dynamics were described by Moran-Palma and McTague (1997). The CFI is designed to provide data on growth, yield, and mortality of the entire forest rather than of individual sites or stands. The CFI consists of 3-plot clusters on a 100-chain (2012-m) grid. Within each cluster, circular plots of 0.20 acres (0.08 ha) are usually located on a north–south line, 5 chains (101 m) apart. For this study individual plots are considered individual observations without regard to cluster. Variance of tree density, stocking, and dominance by *P. engelmannii* was as great between plots as between clusters, which is not surprising given the distance between plots.

Tree- and plot-level effects were evaluated. Individual tree measurements taken in 1997 on live *Picea* greater than 5 inches dbh included species, dbh, activity of defoliators and spruce beetle (*Dendroctonus rufipennis* Kirby [Coleoptera: Scolytidae]), defoliation index, and dwarf mistletoe rating. Defoliation index was computed as the sum of 3 crown-third ratings, where each crown-third was rated as 0, 1, 2, or 3, by 33% defoliation classes (an index of 9 indicates that each crown-third was 67%–100% defoliated). Trees or plots with defoliation indices of 0–3, 4–6, and 7–9 were considered lightly, moderately, and severely defoliated, respectively. Severity of *A. microcarpum* infection was assessed using the Hawksworth (1977) 6-class dwarf mistletoe rating index (DMR). Trees or plots with DMR values of 4, 5, and 6

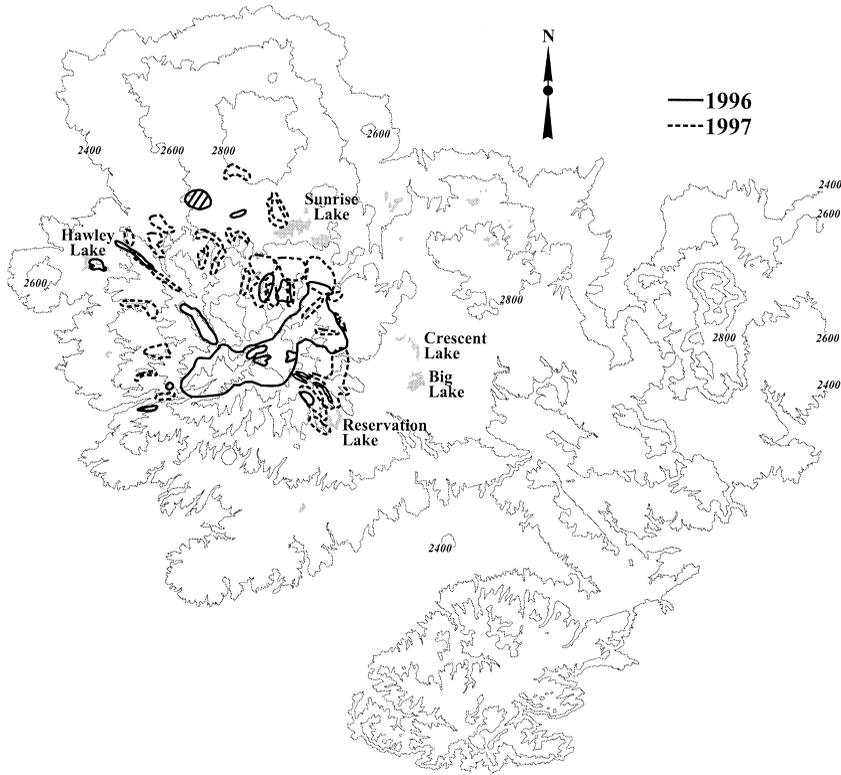


Fig. 1. High-elevation areas mapped during the 1996 and 1997 Aerial Detection Surveys as defoliated by *E. abietinum* in the White Mountains in the 1995–96 and 1996–97 defoliation episodes, respectively, or burned (hatched). Contour intervals are 200 m (656 feet).

were considered severely infected. *Picea* were reassessed in 1999, 2000, and 2001 for bark beetle activity, defoliation, and mortality. Additionally, the size of individual *Picea* relative to the size of neighboring *Picea* was evaluated as the dbh of the individual tree divided by the plot mean dbh for *Picea*, such that the smaller and larger *Picea* on the plot had values $<$ or $>$ 1, respectively.

For each plot, elevation was recorded with a GPS unit and aspect was estimated from U.S. Geological Survey 7.5-minute quadrangle maps. Plot data of tree density, dominance by individual species, and mortality were computed from tree data. Density data were converted to per-acre units for analysis and presentation. Density and species dominance data for species other than *Picea* were taken from the 1994 and 1995 CFI measurements. Standard deviations and CVM of dbh were used at plot level to evaluate uniformity of tree size, with the

assumption that a uniform diameter distribution indicates a relatively even-aged stand.

Foliage damage on *P. engelmannii* and *P. pungens* from *E. abietinum* is difficult to evaluate with precision. Stippling and banding observed on *E. abietinum*-damaged *P. sitchensis* foliage in Europe and the Pacific Northwest are not always found on *P. engelmannii* and *P. pungens* in Arizona. Although fading and yellow or red discoloration do occur, they are not reliable indicators of *E. abietinum* feeding. Foliage usually changes color very little, losing some of its brightness and looking slightly grayer than healthy foliage. This change is small, uncertain, and unobservable under many conditions (dusk, cloudiness, bright sun). Many needles are gray-green when they fall. Minimal fading of foliage of *P. engelmannii* is known to delay the detection of *D. rufipennis* outbreaks (Furniss and Carolin 1977). I suspect that some aphid-damaged foliage is retained

for a year or longer after foliage or tree death, as considerable feeding by Piciformes birds on bark beetles and wood boring beetles was observed on trees with green foliage. A significant amount of woodpecker feeding indicates the presence of wood-boring beetles in dead wood or the presence of a large number of bark beetles, such that the tree is already dead or dying. Defoliation estimates made during this study include lost foliage and foliage discolored yellow or red, and are probably conservative. Also, defoliation from a sap-sucking insect is not the same as defoliation from a leaf-chewing insect such as *Choristoneura occidentalis* Freeman (Lepidoptera: Tortricidae) and *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae). 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.

Defoliation episodes occurred over the fall and winter seasons of 1995–96, 1996–97, and 1999–2000. The 1996–97 episode was more severe and extensive than the earlier episode, and very little acreage was defoliated twice (Fig. 1). Mortality and defoliation were surveyed in 1997, 1999, 2000, and 2001. Reconnaissance in 1998 indicated that little if any mortality occurred that year. Defoliation estimates taken in 1997 therefore represent a single defoliation event for most trees and plots. I evaluated mortality from 2000 rather than 2001 to avoid the complication of the 1999–2000 episode. Usually, mortality to individual *P. engelmannii* and *P. pungens* is not positively detectable until 2 years after the fatal event, so mortality estimates made during 2000 include few if any trees that were killed by the 1999–2000 defoliation episode.

Contingency analyses with likelihood ratios (*G*-statistics) were used to evaluate associations between mortality and dbh class, DMR, and defoliation index (Sokal and Rohlf 1995). Kolmogorov-Smirnov 2-sample tests (*Z*-statistics), which are sensitive to the shape of the frequency distribution as well as to central tendency, were used to evaluate associations between species or live/dead groups and individual tree measurements such as dbh class, DMR, and defoliation index (Sokal and Rohlf

1995). Paired Student sample *t* tests were used to compare defoliation severity by crown-thirds.

I used Principal Component Analysis to summarize vegetation and site data. Scores of the first 3 components were subsequently computed for each plot and assessed for association with defoliation and mortality (Isebrands and Crow 1975, Nichols 1977, Gauch 1982). Principal components are no longer a favored method for devising predictor models but remain a good tool for summarizing multi-dimensional data prone to multicollinearity, particularly when the components are easy to interpret and normally distributed and the predictor variable is exclusive of those used in the components (Ludwig and Reynold 1988, Jackson 1991). This is the case here, where the vegetation-descriptor components are assessed for association with insect damage. The 1st component distinguished between mixed-conifer plots (especially those with *Populus tremuloides* Michx. present) and those dominated by *P. engelmannii*. The 2nd component distinguished between the plots from highest elevations with variable-diameter stems dominated by *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm. and those dominated by *Picea*. The 3rd component summarized variability associated with warmer habitats and non-host species, primarily *Pinus ponderosa* Laws and *Abies concolor* (Gord. & Glend.) Lindl. Each of the first 3 components described 15% to 20% of the shared linear variability in the plot data. I analyzed the component scores, as well as other plot-level statistics, for associations with defoliation and mortality using Pearson correlation coefficients (*r*). Significance of all tests was evaluated at 0.10.

RESULTS

Elatobium abietinum Defoliation

Picea engelmannii was significantly more defoliated than *P. pungens* ($Z = -5.46$, $P < 0.000$; Figs. 2a, 2b). For all trees in the sample, mean 1997 defoliation index was 5.0 on *P. engelmannii* and 2.3 on *P. pungens*. Thirty-three percent of *P. engelmannii* were severely defoliated, compared with 8% of *P. pungens*. Fewer than 15% of *P. pungens* lost more than 33% of their foliage. All age classes of needles were affected except the most recently produced cohort. Some of the most recent needle cohort were lost, but the amount was minimal.

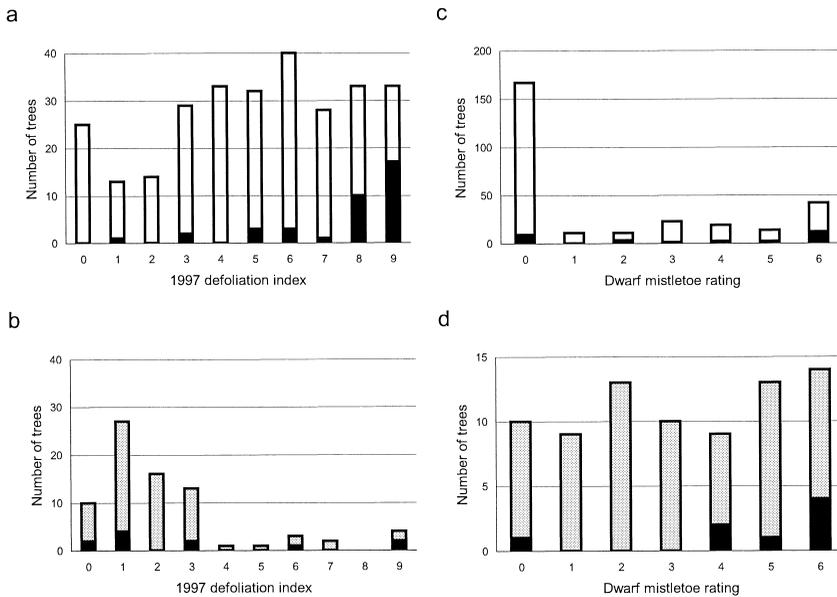


Fig. 2. Frequency of *P. engelmannii* (white) and *P. pungens* (gray) in 1997, and dead spruce (black) in 2000 by 1997 defoliation index (a,b) and dwarf mistletoe rating (c,d). Note that scale is the same for a and b, but different for c and d.

Defoliation severity of trees 5 inches dbh and larger was not directly associated with dbh class ($G = 6.85$, $P = 0.553$) or DMR ($G = 65.3$, $P = 0.140$). There was a weak, negative correlation ($r = -0.204$, $P = 0.00$) between *P. engelmannii* defoliation index and relative diameter, such that defoliation index was generally greater on those trees with dbh smaller than the species' average dbh on the same plot. Inspection of the data showed that few *P. engelmannii* with diameters less than 50% of the plot *Picea* dbh average were lightly defoliated. Defoliation severity of larger trees did not appear to be associated with relative size.

Defoliation was more severe in the lower portions of the tree crowns (upper < middle, and middle < lower; $P < 0.02$). For example, of trees with defoliation index of 7, 48% retained at least 2/3 of the upper-crown foliage, while 97% lost at least 2/3 of the lower-crown foliage. This pattern was consistent in the other defoliation index classes.

On a plot basis, distribution of plot frequency by mean defoliation index was very similar to that shown in Figures 2a and 2c for tree frequency by defoliation index. Twenty-six percent of plots with *P. engelmannii* were severely defoliated. *Picea engelmannii* mean defoliation

index was weakly correlated ($|r| \leq 0.4$, $P \leq 0.10$) with increased density and dominance by *Populus tremuloides* and *A. lasiocarpa* var. *arizonica*, decreased density and dominance by *Pinus ponderosa* Laws., and the 2nd principal component (which distinguished fir-dominated plots from *Picea*-dominated plots). Within-plot variability in defoliation was low: 54% CVM on average with a range from 8% to 128%.

The estimates above, made in 1997, include defoliation from the 2 defoliation episodes in the 1995–96 and 1996–97 fall–winter seasons (Fig. 1). The latter was more extensive than the former, and there was little overlap in the areas defoliated in the 2 episodes. A later outbreak in 1999–2000 was orders of magnitude more severe and extensive. Because of the 2-year (or greater) lag between defoliation and tree mortality, tree fate after the 1999–2000 outbreak cannot be evaluated yet; only defoliation patterns can be evaluated. Severity of defoliation estimates made in 2000 correlated weakly but significantly ($|r| < 0.4$, $P < 0.10$) with increased tree and *Abies* density and with decreased *Pinus ponderosa* density and dominance by *Pinus*. Additionally, defoliation estimates made in 2001 (there is also a lag between aphid feeding and needle drop) correlated with increased *Populus tremuloides*

density and dominance, decreased elevation, and *P. engelmannii* density and dominance.

Dwarf Mistletoe Effects

Eighty-seven percent and 48% of *P. pungens* and *P. engelmannii*, respectively, were infected by *A. microcarpum*. *Picea pungens* was significantly more severely infected by *A. microcarpum* than was *P. engelmannii* ($Z = -5.5$, $P < 0.001$), with mean DMR values of 3.2 and 1.8, respectively (Figs. 2c, 2d). *Picea pungens* was present on 14 plots, 10 of which also had *P. engelmannii*, so numbers shown here reflect greater susceptibility to *A. microcarpum* and not a sampling bias in favor of *P. pungens* representation. Thirteen of 14 plots had *A. microcarpum*-infected *P. pungens* (93%).

Arceuthobium microcarpum was found over the entire elevational range (8174–9698 feet) covered by the study plots. Mean plot DMR of each species was not significantly correlated with elevation, aspect, tree density, or density and dominance of *P. pungens*.

Fate of Individual Trees

Picea engelmannii mortality was significantly associated with defoliation index ($G = 62.1$, $P = 0.000$; Fig. 2a) and with *A. microcarpum* infection ($G = 25.0$, $P = 0.000$; Fig. 2c). Mean 1997 defoliation index was significantly higher for trees that died than for those that survived (7.9 and 4.7, respectively; Table 1). Mortality of lightly, moderately, and severely defoliated *P. engelmannii* was 4%, 6%, and 30% (3.4%, 24.2%, and 41% for trees with defoliation indices of 7, 8, and 9, respectively). Mean DMR of survivor *P. engelmannii* was 1.5, compared with 3.4 for those that died (Table 1). DMR was 4 or higher for 50% of the *P. engelmannii* that died.

Picea pungens mortality was significantly associated with DMR ($G = 18.2$, $P = 0.006$). Mean DMR of survivors was 2.8, compared with 4.6 for those that died (Table 1). Less than 3% of *P. pungens* with DMR of 3 or less died, but 19% of trees with DMR of 4 or higher died (Fig. 2d). *Arceuthobium microcarpum* was one of the causal agents for 75% of *P. pungens* that died (Fig. 3a). There were too few heavily defoliated *P. pungens* to determine if mortality was significantly associated with defoliation index (Fig. 2b).

The combined effects of high levels of defoliation and mistletoe infection were lethal: 66%

and 67% of *P. pungens* and *P. engelmannii* with DI of 8 or 9 and DMR of 5 or 6 died by 2000. Most *P. engelmannii* mortality was due to spruce aphid damage or to the combined effects of aphid damage and mistletoe infection, while recent *P. pungens* mortality has been mostly due to dwarf mistletoe infection (Fig. 3a). To date, bark beetle activity has not increased substantially in *Picea* in the White Mountains.

The pattern of crown defoliation affected tree survivorship: mortality rates of 3.4%, 24.2%, and 41.2% were associated with defoliation indices of 7, 8, and 9, respectively. Invariably, the difference between class-7 trees and class-8 and -9 trees was that the top crown-third was less severely defoliated. Likewise, class-8 trees were less severely defoliated in the top crown-third than were class-9 trees. Lack of defoliation in the top third of the crown was a good predictor of survivorship.

Mortality continued to occur until at least 2001 (Fig. 3b), 3 or 4 years after the 1995–96 and 1996–97 defoliation episodes. The *P. engelmannii* trees that died in 2001 had high DMR values or high defoliation indices or both in 1997 or 2000, but few had high defoliation indices in both events. Based on patterns seen after the 1995–96 and 1996–97 outbreaks, additional mortality should occur in 2002 and 2003.

Plot Characteristics Associated with *P. engelmannii* Mortality

Mean plot mortality in 2000 of *P. engelmannii* on lightly, moderately, and heavily defoliated plots was 4.8%, 9.5%, and 29.2%, respectively. The mean for all plots was 10.3%. Mean plot mortality of *P. engelmannii* was positively correlated ($P \leq 0.10$) with mean *P. engelmannii* defoliation, mean plot DMR, density and dominance of both *Pinus ponderosa* and *P. strobiformis* Engelm. (both individually and combined), and the 3rd principal component, which described warm habitats with *Pinus* (Table 2). Linear regression with 1997 defoliation index (97DI), DMR, and pine dominance (Pine) explained 54% of the variability in plot mortality of *P. engelmannii* ($F = 13.7$, $P = 0.000$, $n = 32$):

$$\text{Percent mortality} = -14.0 + (2.9 * 97DI) \\ + (3.2 * \text{DMR}) + (2.0 * \text{Pine}).$$

TABLE 1. Mean 1997 defoliation index and dwarf mistletoe rating (DMR) of trees that died or survived.

	Survivors mean (s)	Dead mean (s)	<i>n</i>	<i>Z</i>	<i>P</i>
<i>P. engelmannii</i>					
1997 defoliation index	4.7 (2.7)	7.9 (1.6)	285	-6.332	0.000
DMR	1.5 (2.2)	3.4 (2.6)	285	-4.299	0.000
<i>P. pungens</i>					
1997 defoliation index	2.2 (2.0)	3.7 (3.8)	78	-0.244	0.807
DMR	2.8 (2.1)	4.6 (2.1)	89	-1.987	0.047

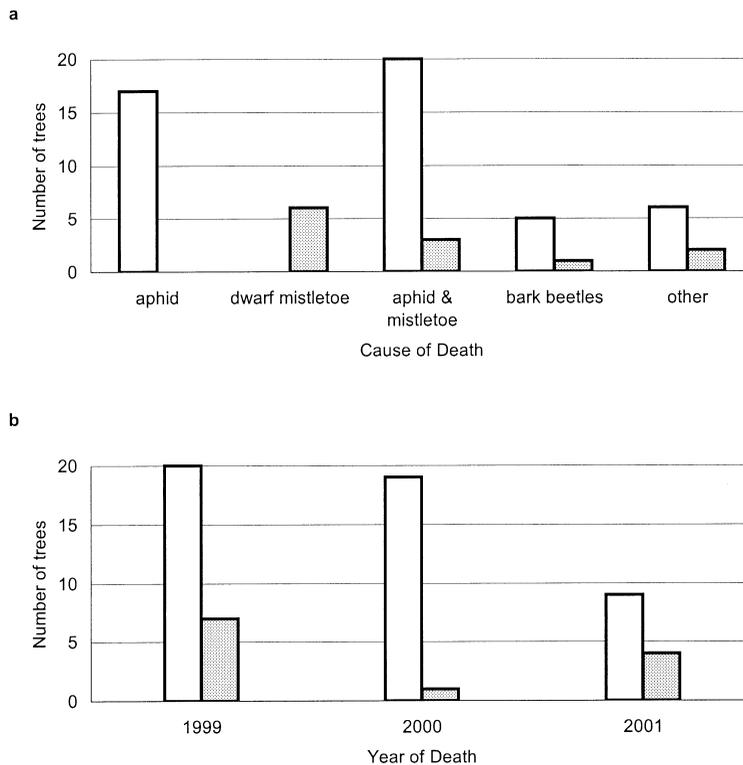


Fig. 3. Cause (a) and year (b) of death for *P. engelmannii* (white) and *P. pungens* (gray). Some trees noted as killed by bark beetles were also defoliated or had high dwarf mistletoe ratings or both.

Mortality of each spruce species was not significantly related to aspect, dbh class, or variability, or to a variety of vegetation character variables ($P > 0.25$; Table 2). *Dendroctonus rufipennis* was active in only 8% of the dead trees prior to death (Fig. 3a).

Interpretation of the results shown here must include recognition of the dry winter conditions that have prevailed in recent years. Mean annual precipitation at McNary, Arizona (National Climate Data Center Station McNary

2 N, AZ, located at 7340 feet [2237 m] elevation in the White Mountains), has been 21% less since 1994 than it was during 1980–1994 (23.2 inches vs. 29.1 inches [59 cm vs. 74 cm]; NCDC 1995). Wintertime precipitation has changed the most. On average, winters from 1994–95 to 2000–01 received 38% less precipitation than did winters from 1980–81 to 1993–94 (8.3 inches vs. 14 inches [21 cm vs. 36 cm]). Autumn *E. abietinum* outbreaks in the southwestern mountains may be preceded by dry

TABLE 2. Correlation (r) between 1997 defoliation index and 2000 mortality of *P. engelmannii* and plot characteristics. Correlations significant at 0.10 and 0.01 are marked by * and **, respectively.

	Defoliation index	Percent mortality
Aspect	0.113	0.133
Elevation	0.207	0.006
Mean dbh	0.091	0.098
Mean dbh of spruce	0.063	0.053
s (dbh)	0.213	0.105
s (dbh of spruce)	0.267	0.127
1997 defoliation index (of <i>P. engelmannii</i>)	0.389 *	0.429 **
DMR (<i>Arceuthobium microcarpum</i>)	0.003	0.494 **
Density of		
All trees	0.390 **	0.100
<i>Abies concolor</i>	-0.053	-0.238
<i>Abies lasiocarpa</i> var. <i>arizonica</i>	0.347 *	0.109
<i>P. pungens</i>	-0.205	0.094
<i>P. engelmannii</i>	0.233	-0.182
<i>P. engelmannii</i> + <i>P. pungens</i>	-0.001	-0.305 *
<i>Pinus ponderosa</i>	-0.381 *	0.515 **
<i>Pinus strobiformis</i>	0.088	0.320 *
<i>Populus tremuloides</i>	0.337 *	0.043
<i>Pseudotsuga menziesii</i>	0.094	0.168
Dominance by		
<i>Abies concolor</i>	0.264 *	-0.066
<i>Abies lasiocarpa</i> var. <i>arizonica</i>	0.270 *	-0.024
<i>P. engelmannii</i>	0.064	-0.260
<i>P. pungens</i>	-0.242	0.071
<i>P. engelmannii</i> + <i>P. pungens</i>	-0.039	-0.205
<i>Pinus ponderosa</i> + <i>P. strobiformis</i>	-0.409 *	0.634 **
<i>Populus tremuloides</i>	0.287 *	-0.017
<i>Pseudotsuga menziesii</i>	-0.246	0.313 *
PC 1 (mixed-conifer vs. <i>P. engelmannii</i>)	0.273	0.113
PC 2 (<i>A. lasiocarpa</i> vs. <i>P. engelmannii</i>)	0.321 *	0.067
PC 3 (warm habitats with <i>Pinus</i>)	-0.101	0.443 **

winters (Lynch 2003). More importantly, moisture stress undoubtedly contributes to tree mortality. Little moisture is received from April through June, so dry winters mean that soil moisture is also very low for the early part of the growing season.

DISCUSSION

Prior to the 1989–90 outbreak in the White Mountains, *E. abietinum* was known as a pest only in areas with mild maritime winter climate, primarily on *P. sitchensis* and *P. glauca* (Bejer-Petersen 1962, Carter and Halldórsson 1998). In most areas where *E. abietinum* is considered a pest species, both the aphid and the host are exotic (Bevan 1984, Carter and Halldórsson 1998). Population increases and damage occur in the spring in maritime areas, while outbreaks develop in the fall and winter in the southwestern U.S., perhaps persisting through mild winters. The White Mountains

of Arizona incurred 3 outbreaks in 6 years, each with extensive, serious levels of defoliation. Impacts documented in this study indicate that this insect will affect natural disturbance regimes and tree population dynamics in mixed-conifer and spruce-fir forests.

In the hosts' native habitats, *P. engelmannii* is more susceptible to *E. abietinum* than is *P. pungens*. Both species can be damaged in European maritime habitats (Theobald 1914, Hanson 1952), and the North American species of *Picea* are generally considered to be more susceptible than *Picea* from Europe and Asia (Theobald 1914, Nichols 1987, Jensen et al. 1997). Trees can withstand light to moderate amounts of defoliation, but a large proportion of heavily defoliated trees will die. *Elatobium abietinum* damage causes more mortality to *P. engelmannii* in high-elevation habitats than it does on the most important host in Europe, *P. sitchensis*. In maritime habitats *E. abietinum* impacts height growth, radial growth, and seed

and cone crops (Bevan 1966, Carter 1977, Day and McClean 1991, Seaby and Mowat 1993, Thomas and Miller 1994, Straw et al. 1998), although mortality to *P. sitchensis* occurs in New Zealand (Nicol et al. 1998) and British Columbia (Koot 1992) and has occurred at least occasionally in Europe in the past (Theobald 1914).

Defoliation was most severe on the smallest trees of each plot and on the lower portions of the tree crowns, a pattern apparently related to canopy position, not to tree size. Retention of foliage in the top crown-third was strongly associated with survivorship, probably because these trees retain a proportionally large amount of the most recently produced foliage. At the onset of this study, severe defoliation was defined as defoliation index ≥ 7 . In future work severe defoliation should be defined as defoliation index ≥ 8 . Also noteworthy is that about half of the dead trees did not die until 2 to 3 years after defoliation—a factor that should be considered in future damage surveys.

Only one-third of trees both severely defoliated by *E. abietinum* and heavily infected by *A. microcarpum* survived. *P. pungens* was more frequently and more severely infected by *A. microcarpum* than was *P. engelmannii*. Mortality of heavily infected *P. pungens* was 6 times greater than that of noninfected and lightly to moderately infected trees, as observed by Mathiasen et al. (1986). With pine-infesting *Arceuthobium* species, mortality is primarily associated with DMR class 6 (Hawksworth and Lusher 1956). Here, mortality was 19% in class 4 and higher. Mathiasen et al. (1986) found 13%, 30%, and 47% mortality in class-4, -5, and -6 trees. They surveyed live and dead trees, and mortality was not dated nor identified per species. The mortality observed in this study is quite high for a 4-year period, indicating that defoliation accelerates mortality of dwarf mistletoe-infected trees, and that dwarf mistletoe-related mortality is accelerated in droughts.

While *A. microcarpum* infection rates were much lower on *P. engelmannii*, Acciavatti and Weiss (1974) observed even lower levels (3.4%). Acciavatti and Weiss (1974) surveyed the entire elevational range of *P. engelmannii* and seldom found *A. microcarpum* above 10,000 feet. Data reported here are from plots at 9640 feet and lower, and Mathiasen et al. (1986) stated that their survey was of mixed-conifer

stands, which would be from even lower elevations. Acciavatti and Weiss did not survey *P. pungens* and did not evaluate mortality.

Beyond the clear patterns of species difference in susceptibility to both the insect and disease agents, increased defoliation in the lower canopy layers, and strong relationships between tree mortality and severe mistletoe infection and defoliation, risk and hazard patterns associated with site and vegetation character were indistinct. Patterns of increased defoliation severity with cooler habitats, increased presence of *Abies*, and decreased defoliation severity with increased presence of *Pinus* or warmer habitats were weak, but worthy of consideration, because they were consistent among the different defoliation episodes and analytic methods (both individual variables and the relevant principal components were significant). These patterns suggest that aphid populations are greater, or persist longer, in cooler habitats. *Elatobium abietinum* requires mature, dormant foliage for populations to increase to damaging levels (Parry 1976, Jackson and Dixon 1996), and perhaps trees in colder habitats enter dormancy earlier in the fall. Though weak, the patterns seen here are consistent enough to warrant further study. Although a different approach might clarify these relationships, factors such as autumn weather and *E. abietinum* population levels in early autumn are probably stronger factors contributing to outbreak severity. The association between mortality and warm, pine-supporting habitats, where defoliation was less severe, probably reflects greater drought stress on those sites.

Picea engelmannii and *P. pungens* co-occur in many stands. The greater susceptibility of *P. engelmannii* to *E. abietinum* will probably favor the reproduction of *P. pungens* in these stands. Because *P. pungens* is much more susceptible to *A. microcarpum*, the severity of that problem could increase over time. In other stands *P. engelmannii* would be replaced by other species depending on habitat, but primarily by *Abies lasiocarpa* var. *arizonica* at higher elevations and by *Pseudotsuga menziesii* at lower elevations.

Accumulation of fine fuels from dehydrated and dead needles, dead twigs and branches, and dead trees will increase fire hazard. The recurrence of even fairly frequent outbreaks will result in a near-constant presence of dehydrated fine fuels distributed throughout the

forest canopy and on the ground. This will further destabilize ecosystem processes in southwestern high-elevation forests that have already been affected by grazing, logging, and fire exclusion, especially with regard to fire regimes in lower-elevation forests and the likelihood of stand-replacement fires in high-elevation forests (Baisan and Swetnam 1990, Swetnam and Betancourt 1990, Bahre 1991, Grissino-Mayer et al. 1995).

Elatobium abietinum outbreak severity varies from one episode to another. This study evaluated the damage from a single episode (a few plots may have been defoliated twice). Outbreak severity may vary from year to year and from place to place, but the general findings of greater susceptibility of *P. engelmannii*, greater defoliation in the lower canopy layers, and high probability of mortality to severely defoliated or severely *A. microcarpum*-infected trees or both will probably be reasonably consistent.

If *E. abietinum* outbreak frequency is low, then many trees should be able to survive and reproduce. However, 3 of 6 autumn/winter seasons incurred outbreaks. If outbreaks continue at this frequency, then this insect will impact natural disturbance regimes and tree population dynamics in mixed-conifer and spruce-fir forests. Large areas were defoliated in each outbreak, and significant portions of the areas were defoliated severely. Eighteen percent, 10%, and 24% of plots assessed in 1997, 2000, and 2001, respectively, had mean defoliation ratings of 7.5 or higher. Repeated defoliation episodes with 10% overall *P. engelmannii* mortality, 30% in severely defoliated areas, will lead to reduced representation of *P. engelmannii* in the ecosystem. More severe defoliation and subsequent mortality in the smaller size classes will mean a gradual reduction of ingrowth within the forest. Also, repeated defoliation episodes will likely prevent viable seed from being produced. If this is the case, *P. engelmannii* representation in the forest will diminish over time.

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