SELECTION OF DWARF MISTLETOE–INFECTED PONDEROSA PINES BY *IPS* SPECIES (COLEOPTERA: SCOLYTIDAE) IN NORTHERN ARIZONA

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ABSTRACT.—Following an *Ips* bark beetle outbreak in 2002, mortality of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) was evaluated in 2 study areas infested with southwestern dwarf mistletoe (*Arceuthobium vaginatum* [Willd.] Presl subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens) in the Coconino and Tonto National Forests, Arizona. A pair-wise comparison of dwarf mistletoe ratings for live and dead ponderosa pines was conducted to determine whether dead ponderosa pines had higher dwarf mistletoe ratings than pines that were not attacked. In both study areas, dead ponderosa pines had significantly higher dwarf mistletoe ratings, indicating an association between the severity of dwarf mistletoe infection and susceptibility to attack by *Ips* spp. We suggest that the probability of ponderosa pine mortality is greater in stands severely infested with southwestern dwarf mistletoe in northern Arizona.

Key words: Arceuthobium vaginatum, *dwarf mistletoe, bark beetles, ponderosa pine,* Ips.

In 2002 a bark beetle epidemic severely impacted ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson.) forests in northern Arizona. Ponderosa pine mortality occurred over approximately 211,000 ha statewide (USDA 2002). *Ips* spp. (*Ips pini* Lecontei and *I. lecontei* Swaine, Coleoptera: Scolytidae) predominated within infestations and accounted for approximately 99% or about 208,000 infested hectares statewide (McMillin 2003, S.C. Kenaley personal communication). High rates of infestation and tree mortality occurred within the Coconino (24,400 ha), Prescott (30,600 ha), and Tonto National Forests (27,000 ha). In the Tonto National Forest alone, 47% of the ponderosa pine forest type was infested, and many stands had mortality rates of 80%–90%. Western pine beetle (*Dendroctonus brevicomis* Leconte), roundheaded pine beetle (*Dendroctonus adjunctunus* Blandford), and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have also been detected within infested areas in northern Arizona, but these bark beetle populations have not yet reached epidemic levels.

In many areas where bark beetle infestations occurred, ponderosa pine mortality was greatest in areas infested with southwestern dwarf mistletoe (*Arceuthobium vaginatum* [Willd.] Presl subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens). Southwestern dwarf mistletoe is considered to be the most important disease agent of ponderosa pine in the Southwest (Hawksworth 1961, Hawksworth et al. 1989, Hawksworth and Wiens 1996). Severely infected ponderosa pines exhibit an overall decline in tree vigor as expressed via reductions in diameter and height growth, seed and cone production, and longevity (Korstian and Long 1922, Hawksworth 1961, Hessburg et al. 1985, Hawksworth and Geils 1990, Hawksworth and Wiens 1996). Ponderosa pine has a constitutive (preformed) wound response and therefore relies on its primary resin system for defense against bark beetle attack (Matson and Hain 1985). Ponderosa pines severely infected with southwestern dwarf mistletoe may not have the necessary resources to initiate a wound response proportional to bark beetle attack; therefore, the probability of successful bark beetle attack and subsequent mortality of the affected pines increases.

The incidence of bark beetle infestations in areas infested with southwestern dwarf mistletoe has been reported previously for mountain pine beetle (Johnson et al.1976, McCambridge 1980, McCambridge et al. 1982) and for roundheaded pine beetle (Stevens and Flake

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1974, Negrón 1997, Negrón et al. 2000). Johnson et al. (1976) observed no relationship between dwarf mistletoe and mountain pine beetle attack at low stand mistletoe ratings; however, with increased dwarf mistletoe severity and stand mistletoe rating, bark beetle attacks significantly increased on ponderosa pines infected with dwarf mistletoe. Similarly, McCambridge et al. (1982) found that mortality due to mountain pine beetle was greatest in areas where dwarf mistletoe was most abundant. They found that the percentage killed by mountain pine beetle was greater in ponderosa pine stands infested with southwestern dwarf mistletoe (30.8%) than in uninfested stands (20.5%). Additionally, losses due to mountain pine beetle attack, as measured by percent of stems killed, merchantable cubic foot volume, and basal area, were significantly higher in study plots infested with dwarf mistletoe. Although these studies were descriptive postmortem evaluations of dwarf mistletoe infection ratings of trees killed by bark beetles, Negrón (1997) constructed predictive models for roundheaded pine beetle infestation in ponderosa pine forests in the Sacramento Mountains, New Mexico, and suggested that the average dwarf mistletoe rating of live ponderosa pines in plots infested with roundheaded pine beetle was slightly higher than in uninfested plots.

No specific studies have examined the relationship between bark beetle attack and ponderosa pine mortality in areas infested with southwestern dwarf mistletoe in northern Arizona. Wagner and Mathiasen (1985) conducted a study comparing dwarf mistletoe ratings (Hawksworth 1977) of live and dead ponderosa pine following a pandora moth (*Coloradia pandora pandora* Blake, Lepidoptera: Saturniidae) outbreak in 1979 and 1981 on the Kaibab Plateau in northern Arizona. They reported that ponderosa pine mortality primarily occurred among trees severely infected with southwestern dwarf mistletoe. We used methodology similar to Wagner and Mathiasen (1985) to compare attacked and unattacked ponderosa pines to determine if a similar association exists for *Ips* spp. and dwarf mistletoe–infected ponderosa pines. Our hypothesis was that ponderosa pines attacked and killed by *Ips* spp. during 2002 were more severely infected with southwestern dwarf mistletoe than pines that were not attacked.

STUDY SITES

Two study sites were selected, one approximately 4.8 km north of Strawberry, Arizona (UTM: 12S 467163E, 3811025N), and the other 12.9 km northwest of Flagstaff, Arizona (UTM: 12S 430668E, 3811025N), within the Tonto and Coconino National Forests, respectively. The study sites were selected using insect and disease aerial detection survey maps and were ground-checked for dwarf mistletoe severity (USDA 2002). The sample areas had significant ponderosa pine mortality following the *Ips* bark beetle outbreak in 2002, ranging in size from 36 ha on the Coconino National Forest to 784 ha on the Tonto National Forest. Both study sites were severely infested with southwestern dwarf mistletoe.

METHODS

The sampling and statistical methods followed those of Wagner and Mathiasen (1985). We sampled the study areas using a systematic distribution of plots with a random start. Plot centers were placed at 40.4-m intervals along a single transect, and plots had a 20.2-m radius. Within each sample plot, a pair consisting of 1 live and 1 dead tree nearest the plot center was selected for comparison. Tree pairs were of similar diameters (±10.2 cm). If tree mortality could not be attributed to attack by *Ips* spp. or if a suitable pair was not found, the sample plot was rejected. Diameter at breast height (dbh; 1.4 m above the ground on the uphill side of the tree) and dwarf mistletoe rating (DMR; Hawksworth 1977) were determined for each tree in all pairings. The dwarf mistletoe rating was applied by dividing the live crown into thirds and rating each third as follows: 0 for no visible dwarf mistletoe infections, 1 for light dwarf mistletoe infection (less than half of the branches were infected), or 2 for severe dwarf mistletoe infection (more than half of the branches were infected). Ratings for each third were then summed to obtain the total rating for the tree. For example, if the bottom third of the live crown was severely infected, the middle third was lightly infected, and the top third had no visible infection, the overall tree rating was 3 (i.e., $2 + 1 + 0 = 3$). We examined 22 and 26 sample plots within the Coconino and Tonto National Forests, respectively.

TABLE 1. Mean diameters (dbh) and dwarf mistletoe ratings (DMR) of live and dead ponderosa pines with corresponding ranges, standard errors of the means ($s_{\overline{x}}$), and sign test results (P-value, $\alpha = 0.05$), Coconino and Tonto National Forests. Note that ponderosa pine trees killed by *Ips* spp. (Dead) had significantly higher dwarf mistletoe ratings compared to the paired live trees (Live).

| | Coconino National Forest | | | | Tonto National Forest | | | |
| | Live | | Dead | | Live | | Dead | |
	dbh (cm)	DMR	dbh (cm)	DMR	dbh (cm)	DMR	dbh (cm)	DMR
Mean	11.2	3.5	11	5.8	13.7	1.6	13.1	4.4
Range	5.0–18.3	2.0–6.0	4.0–20.0	4.0–6.0	4.4–26.1	0.0–5.0	5.6–24.4	1.0–6.0
$s_{\overline{x}}$	0.82	0.30	0.94	0.10	0.97	0.31	0.91	0.32
P-value	$P < 0.0001$				$P < 0.0001$			

Data Analysis

We used a nonparametric paired sign test ($\alpha = 0.05$; Zar 1999) to compare DMRs of live and dead trees for each study area. (Because we could not assume a normal distribution of the DMRs [nominal-scale data] the paried-sample *t* test was not appropriate.) Quantitative differences between members of each pair are not important to the sign test, but rather the direction or sign of each difference (+ or –). This test is best used to observe the pronouncement and/or trend of a random variable between members of each pair. The null hypothesis was that there would be no difference in DMR between dead and live ponderosa pines within each study site.

RESULTS

Because of the pairing criteria, no difference in mean dbh for live and dead trees was detected (Table 1). Dead ponderosa pines had a consistently higher DMR than their live counterparts in both the Tonto (sign test: df = 25, $P < 0.001$; Table 1) and Coconino National Forests (sign test: df = 21, $P < 0.001$; Table 1). Furthermore, in only 1 pair per study site did the live tree have a greater DMR than its dead paired member. Overall, dead ponderosa pines were severely infected (mean DMR = 5.8) in the Coconino National Forest and moderately infected (mean DMR = 4.4) in the Tonto National Forest (Table 1).

DISCUSSION

In ponderosa pine forests of northern Arizona there is a clear association between the severity of southwestern dwarf mistletoe infection and mortality attributable to *Ips* spp.

In both study areas, ponderosa pine mortality occurred in moderately (DMR = 4) and severely (DMR = 5–6) infected trees. However, those trees that escaped successful attack by *Ips* spp. had significantly lower mean DMRs. Thus, we suggest that during an *Ips* spp. outbreak, the risk of ponderosa pine mortality will be greater in trees moderately or severely infected with southwestern dwarf mistletoe.

The sampling scheme and statistical analyses we employed do not allow for the determination of causal relationships; however, southwestern dwarf mistletoe was clearly associated with ponderosa pine mortality during the *Ips* spp. outbreak in the study areas. The physiological constraints and decline in host vigor imposed by southwestern dwarf mistletoe infection probably contribute to the predisposition of ponderosa pine to bark beetle attack (Hawksworth 1961, Fisher 1983, Hawksworth et al. 1989, Hawksworth and Wiens 1996). Southwestern dwarf mistletoe directly influences the allocation of water and carbohydrates within its host by redistributing water, nutrients, and various organic and inorganic assimilates to infected parts of the tree at the expense of uninfected parts (Hawksworth 1961, Hull and Leonard 1964a, 1964b, Leonard and Hull 1965, Fisher 1983, Knutson 1983, Hawksworth and Wiens 1996, Kolb 2002). With increasing dwarf mistletoe infection, the proportions of carbohydrates partitioned to roots, shoots, reproduction, stem storage, and defensive compounds in ponderosa pine likely decline (Waring and Pitman 1985, Hawksworth and Wiens 1996, Kolb 2001, 2002). This decline is expressed by reductions in diameter and height growth, reduced seed and cone production, and decreased longevity (Korstian and Long 1922, Hawksworth 1961, Hessburg et al. 1985,

Hawksworth and Geils 1990, Hawksworth and Wiens 1996).

The competition for available carbohydrates between dwarf mistletoe and its host is most apparent in the reduction of diameter growth observed with increasing dwarf mistletoe infection. Across dwarf mistletoe rating classes, Hawksworth (1961) compared the periodic growth rates (last 5 years) in ponderosa pine and found that growth reductions corresponded directly with the degree of infection. Compared to uninfected ponderosa pines (DMR = 0), trees with a DMR = 4, 5, and 6 sustained a 9%, 23%, and 53% reduction in growth, respectively. Poor growth has been associated with bark beetle attacks and the onset of bark beetle outbreaks (Sartwell and Stevens 1975, Larson et al. 1983, Shrimpton and Thompson 1983, Negrón 1997, Negrón et al. 2000). In a model developed to estimate the probabilities of roundheaded pine beetle infestations in ponderosa pine, Negrón (1997) reported that roundheaded pine beetles preferred stands or trees with reduced growth, particularly over the 5 years prior to infestation. Furthermore, Negrón and Wilson (2003) examined the attributes associated with pinyon ips (*Ips confusus* Leconte) infestation in pinyon pine (*Pinus edulis* Englem.) in northern Arizona and found that *Ips*-infested plots had significantly higher pinyon dwarf mistletoe (*Arceuthobium divaricatum* Engelm.) infection levels, and the probability of pinyon ips attack increased with increasing pinyon dwarf mistletoe infection.

Southwestern dwarf mistletoe is a natural and endemic component of ponderosa pine forests in the Southwest, but in the last century its distribution and intensity of infestation have increased (Andrews and Daniels 1960, Maffei and Beatty 1988). In a survey of National Forest lands in Arizona and New Mexico in 1958, Andrews and Daniels (1960) reported that 30% of the ponderosa pine forest type was infested with dwarf mistletoe. Maffei and Beatty (1988) reevaluated the survey of Andrews and Daniels (1960) to estimate changes in the incidence of dwarf mistletoe and reported an 8% increase from 1958 to 1988 and a mean increase of 11% for the national forests they resampled. Factors contributing to the increased incidence and intensity of southwestern dwarf mistletoe include single tree selection, high-grading, ineffective cultural control, and fire suppres-

sion (Alexander and Hawksworth 1975, Maffei and Beatty 1988, Hawksworth et al. 1989). Without appropriate attention and management, southwestern dwarf mistletoe infestations will continue to spread and intensify within ponderosa pine forests of the Southwest. These infestations will then contribute to development of highly susceptible populations of ponderosa pine and increase the risk of ponderosa pine mortality during *Ips* epidemics as indicated by this study.

Although significant ponderosa pine mortality occurred in northern Arizona in 2002, the current bark beetle outbreak may have beneficial effects in areas infested with southwestern dwarf mistletoe. Southwestern dwarf mistletoe is an obligate parasite of ponderosa pine, and requires a living host to reproduce and persist (Hawksworth 1961, Hawksworth and Wiens 1996). Because *Ips* spp. are more likely to successfully kill moderately to severely dwarf mistletoe-infected ponderosa pines, we may expect the density of dwarf mistletoe–infested stands to be reduced to some extent. As demonstrated in this study, *Ips* spp. served as natural thinning agents by selectively killing ponderosa pines moderately to severely infected with dwarf mistletoe. Therefore, the resource environment of surviving trees would probably improve via reductions in both tree density and tree–tree competition for available water and nutrients (Kolb et al. 1998, McMillin and Allen 2004). With the death and ultimate downing of trees both infested with *Ips* and infected with dwarf mistletoe, healthy or lightly infected trees (DMR = 0–2) could experience increased vigor and thus survive (Hawksworth 1961).

Although the susceptibility of individual ponderosa pine trees and ponderosa pine stands to bark beetle attack is also influenced by the interaction of biotic and abiotic factors such as stocking levels, crown class, phloem thickness, resin flow, site quality, and climatic stress (Larson et al. 1983, Lorio 1993, Negrón 1997, Feeney et al. 1998, Kolb et al. 1998, Negrón et al. 2000, Sánchez-Martínez and Wagner 2002), our study demonstrated that southwestern dwarf mistletoe infection was correlated with ponderosa pine mortality during an *Ips* spp. outbreak in 2 areas in northern Arizona. However, our knowledge regarding southwestern dwarf mistletoe and bark beetle associations is still limited. Future research

should be devoted to a large-scale examination of the influence(s) of southwestern dwarf mistletoe on ponderosa pine defensive capabilities, and to a spatial analysis of bark beetle infestation in areas containing several different infection levels of southwestern dwarf mistletoe.

ACKNOWLEDGMENTS

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