COMPARATIVE SUSCEPTIBILITY OF CONIFERS TO KNOBCONE PINE DWARF MISTLETOE

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ABSTRACT.—Seventeen mixed conifer stands infested with knobcone pine dwarf mistletoe (*Arceuthobium siskiyouense*) were sampled to evaluate host susceptibility to this parasitic plant. Temporary circular plots (radius 6 m) were established around dominant, severely infected knobcone pines (*Pinus attenuata*). Within plots, species, diameter at breast height, and dwarf mistletoe rating (6-class system) were determined for each live tree taller than 1.4 m. More than 2000 trees were sampled in 140 plots. Based on the incidence of infection, tree species were assigned to host-susceptibility classes. Although Jeffrey pine (*Pinus jeffreyi*) and shore pine (*Pinus contorta* var. *contorta*) have been classified as rare hosts of knobcone pine dwarf mistletoe, my results suggest that Jeffrey pine should be classified as a principal host and shore pine should be classified as an occasional host. No infection was observed on western white pine (*Pinus monticola*), Douglas-fir (*Pseudotsuga menziesii*), or incense-cedar (*Calocedrus decurrens*), indicating that these species should be classified as immune.

Key words: *Arceuthobium siskiyouense*, host susceptibility, *Pinus attenuata*, *Pinus jeffreyi*, *Pinus contorta* var. *contorta*.

Knobcone pine dwarf mistletoe (KPDM; *Arceuthobium siskiyouense* Hawksw., Wiens & D. Nickrent) severely parasitizes knobcone pine (*Pinus attenuata* Lemmon) in northwestern California and southwestern Oregon (Hawksworth and Wiens 1996). This dwarf mistletoe had been classified as *Arceuthobium campylopodum* Engelm., a common parasite of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and knobcone pine, but in 1992 it was described as a separate species (Hawksworth et al. 1992). Hawksworth et al. (1992) and Hawksworth and Wiens (1996) reported that KPDM rarely parasitized Jeffrey pine, ponderosa pine, and shore pine (*Pinus contorta* Douglas ex Loudon var. *contorta*) and that sugar pine (*Pinus lambertiana* Douglas) and western white pine (*Pinus monticola* Douglas ex D. Don) were immune to this dwarf mistletoe.

Hawksworth and Wiens (1970, 1972, 1996) established a host-susceptibility classification system for dwarf mistletoe infection based on the percentage of trees of the tree species in question that were infected within 6 m of principal hosts of a dwarf mistletoe with a dwarf mistletoe rating of 5 or 6 (Hawksworth 1977). In addition, Hawksworth and Wiens recommended that infection incidence determinations only be made in stands older than

20–30 years to ensure that trees had been exposed to infection long enough to express their relative susceptibility. Hawksworth and Wiens established 5 host-susceptibility classes as follows: principal host (at least 90% infected), secondary host (50%–90% infected), occasional host (5%–50% infected), rare host (>0% but <5% infected), and immune (0% infected).

Although knobcone pine is the most widely distributed of the closed-cone pines in California, it is not economically important because of its small size, wood qualities, and distribution, which is primarily outside of the principal commercial forests of California and Oregon (Vogl et al. 1977). However, knobcone pine is a common component of the low- and mid-elevation forests of northwestern California and southwestern Oregon because of its adaptations to frequent fire intervals and its ability to grow on serpentine soils (Whittaker 1954, 1960, Vogl et al. 1977). Because of the low economic value of knobcone pine and the limited distribution of KPDM, little quantitative data is available regarding the susceptibility of conifers to this parasitic plant. Although knobcone pine has been classified as the only principal host of KPDM (Hawksworth et al. 1992, Hawksworth and Wiens 1996), my field observations have consistently indicated that both Jeffrey pine and shore pine are more susceptible to

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Fig. 1. Approximate location of study sites sampled in California and Oregon. Dark circles represent locations where knobcone pine dwarf mistletoe was sampled on Jeffrey pine. Open circles represent locations where knobcone pine dwarf mistletoe was sampled on shore pine. Dark triangles represent locations where knobcone pine dwarf mistletoe was sampled on both Jeffrey and shore pines. Numbers correspond to the following locations: 1, Lookout Gap; 2, Eight Dollar Mountain; 3, Bain Station; 4, Crazy Peak; 5, Black Butte; 6, Holiday Road, Elk Camp Ridge Trailhead; 7, Old Gasquet Toll Road, Elevenmile Creek; 8, Old Gasquet Toll Road, Twelvemile Creek; 9, Old Gasquet Toll Road, near Danger Point; 10, Gasquet; 11, 7 km south of Low Divide; 12, 5 km south of Low Divide; 13, 8 km south of High Divide; 14, 2 km south of High Divide; 15, 7 km east of Low Divide; 16, Pine Flat; 17, 3 km west of Smith River.

KPDM than previously reported. Therefore, this study was initiated to provide additional quantitative data on the susceptibility of Jeffrey pine and shore pine to KPDM in northwestern California and southwestern Oregon. Because western white pine, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and incense-cedar (*Calocedrus decurrens* [Torrey] Florin) were common in the forests sampled, infection data were also collected for these species.

METHODS

Seventeen mixed conifer stands where severely infected knobcone pines occurred near a variety of conifers were sampled (Fig. 1). At each site, temporary circular plots with a 6-m radius (0.012 ha) were established around dominant or codominant, severely infected knobcone pines. At each study site an attempt was made to establish at least 10 plots, but at

TABLE 1. Percent infection of hosts frequently infected by knobcone pine dwarf mistletoe by 5-cm diameter classes.

Diameter class (cm)	Knobcone pine		Jeffrey pine		Shore pine		Western white pine		Incense cedar		Douglas-fir	
	n	% Inf. ^a	n	% Inf.	n	% Inf.	n	% Inf.	n	% Inf.	n	% Inf.
1–5	138	91	125	83	140	29	98	0	58	0	38	0
6–10	106	93	96	92	104	37	62	0	37	0	21	0
11–15	157	97	63	95	112	46	46	0	22	0	19	0
16–20	112	98	39	92	51	43	26	0	9	0	11	0
21–25	72	100	45	96	31	42	21	0	15	0	9	0
26–30	56	100	29	97	13	54	14	0	7	0	7	0
31–35	21	100	19	100	3	67	6	0	1	0	1	0
36–40	3	100	12	100	—	—	—	0	2	0	3	0
>40	—	—	5	100	—	—	—	0	1	0	1	0
ALL TREES	665	96	433	91	454	38	273	0	152	0	101	0

^aPercent infection

Table 2. Mean dwarf mistletoe ratings (DMRs) of 3 hosts, in nine 5-cm diameter classes, that are frequently infected by knobcone pine dwarf mistletoe.

Diameter class (cm)	Mean DMR ^a		
	Knobcone pine	Jeffrey pine	Shore pine
1–5	2.9	1.4	0.6
6–10	3.1	1.9	0.7
11–15	3.0	2.4	1.2
16–20	3.4	3.1	1.4
21–25	3.8	3.5	1.7
26–30	4.1	3.3	2.2
31–35	3.7	3.4	2.0
36–40	5.3	3.3	—
>40	4.8	2.9	—
ALL TREES	3.3	2.3	1.0

^aDwarf mistletoe rating (6-class system), Hawksworth 1977. Mean DMR was calculated using infected and uninfected trees in each diameter class for each species.

some locations more than 10 plots were established, and at other locations fewer than 10 plots were completed because only a few large, severely infected knobcone pines were present.

A dwarf mistletoe rating (DMR) was assigned to each severely infected knobcone pine that was used as a plot center. The plot radii were measured from the base of plot-center trees. Infection of the selected knobcone pines was severe—only trees with a DMR of 5 or 6 were used—but no attempt was made to assess their vigor or the relative number of mistletoe seeds that might be produced by the individual trees. It was assumed these severely infected trees had exposed the trees growing within 6 m of their bases to a large number of mistletoe seeds throughout most, if not all, of the life of the neighboring trees (Hawksworth

and Wiens 1972, 1996). Because most seeds that are disseminated from severely infected trees fall within 5–6 m from the tree (Hawksworth 1978), 6 m has been the standard radius used for plots used to estimate host susceptibility, based on percentage of infection for trees greater than 20–30 years old (Mathiasen 1984, 1998, 1999, Hawksworth and Wiens 1996, Mathiasen and Daugherty 2005).

The following data were collected for each live tree taller than 1.4 m within a plot: species, diameter at 1.4 m above the ground (breast height, measured to the nearest cm), and DMR. Dead trees were not sampled, because frequently they could not be assigned an accurate DMR. A total of 140 plots were completed and a total of 2083 trees examined for infection by KPDM. Host species classification and identification were based on *Flora of North America* (Flora of North America Editorial Committee 1993).

Percent infection of sampled live trees for 6 species was calculated by 5-cm diameter classes and for all size classes combined. Percent infection of all trees sampled for each species was used for determining host susceptibility classifications. The mean DMR was also calculated using all of the trees for a species in each diameter class, including uninfected trees (Hawksworth 1977). Using the mean DMR of trees by diameter classes is another method of comparing relative host susceptibility, because mistletoe infection usually increases rapidly for highly susceptible host species as size increases and less rapidly for less susceptible species (Mathiasen 1984, 1998, 1999, Mathiasen and Daugherty 2005).

Fig. 2. Witches' brooms associated with infection by knobcone pine dwarf mistletoe on knobcone pine.

RESULTS

Knobcone pine is clearly the most susceptible host of KPDM. Ninety-six percent of the 665 knobcone pines sampled were infected (Table 1). Trees >20 cm in diameter were 100% infected and more than 90% of the knobcone pines in the smallest diameter class (1–5 cm) were infected. Mean DMR for knobcone pine was 3.3, but for trees >20 cm in diameter, mean DMR was >3.5 (Table 2). Although Hawksworth et al. (1992) and Hawksworth and Wiens (1996) reported that knobcone pine did not form witches' brooms in response to infection by KPDM, I commonly found that witches' brooms formed after infection, particularly on large, severely infected knobcone pines (Fig. 2).

Although Jeffrey pine was classified as a rare host of knobcone pine dwarf mistletoe, in this study it would be classified as a principal host because $>90\%$ of the Jeffrey pines in plots were infected (Table 1). It is much more susceptible than previously reported. Over

Fig. 3. Witches' brooms associated with infection by knobcone pine dwarf mistletoe on Jeffrey pine.

80% of Jeffrey pines in the 1–5 cm diameter class were infected, which also demonstrated its high susceptibility to KPDM. Jeffrey pines also formed witches' brooms in response to infection by KPDM (Fig. 3).

Shore pine was also reported as a rare host of KPDM, but in this study shore pines growing near severely infected knobcone pines were commonly infected. Thirty-eight percent of shore pines were infected, and infected shore pines had a mean DMR of 1.0. Therefore, shore pine should be reclassified as an occasional host of KPDM. Twenty-nine percent of shore pines sampled in the 1–5 cm diameter class were infected. Severely infected shore pines often formed witches' brooms in response to infection (Fig. 4).

No infection was observed on western white pine, Douglas-fir, or incense-cedar, which indicated that these species were immune to infection by KPDM (Table 1). Table 3 summarizes the host susceptibility classification for knobcone pine dwarf mistletoe based on the

Fig. 4. Witches' brooms associated with infection by knobcone pine dwarf mistletoe on shore pine.

results of this study and results reported by Hawksworth and Wiens (1996).

DISCUSSION

The classification of the dwarf mistletoes parasitizing pines in California and Oregon has been controversial since Gill (1935) initially classified these dwarf mistletoes as *Arceuthobium campylopodum* host form *typicum*. Hawksworth and Wiens (1972) rejected Gill's host form concept and classified the dwarf mistletoes severely parasitizing ponderosa pine, Jeffrey pine, knobcone pine, Bishop pine (*Pinus muricata* D. Don), and Monterrey pine (*Pinus radiata* D. Don) in California as *A. campylopodum*, but classified the dwarf mistletoe parasitizing gray pine (*Pinus sabiniana* Douglas ex D. Don) as *A. occidentale* Engelm. Hawksworth et al. (1992) reclassified the dwarf mistletoe parasitizing knobcone pine in northwestern California and southwestern Oregon as *A. siskiyouense* and the dwarf mistletoe parasitizing Bishop and Monterrey pines along the Cali-

TABLE 3. Host susceptibility classification for knobcone pine dwarf mistletoe based on the results of this study and reported by Hawksworth and Wiens (1996).

Host susceptibility class ^a
Principal
<i>Pinus attenuata</i> ^{b,c}
<i>Pinus jeffreyi</i> ^c
Secondary
—
Occasional
<i>Pinus contorta</i> var. <i>contorta</i> ^c
Rare
<i>Pinus ponderosa</i> ^b
Immune
<i>Calocedrus decurrens</i> ^c
<i>Pinus lambertiana</i> ^b
<i>Pinus monticola</i> ^b
<i>Pseudotsuga menziesii</i> ^c

^aSusceptibility classes are explained in the text.

^bClassification reported in Hawksworth and Wiens (1996).

^cClassification based on the results of this study.

fornia coast as *A. littorum* Hawksw., Wiens, & D. Nickrent. Although Nickrent and Butler (1990, 1991) demonstrated, using isozyme analysis, that *A. siskiyouense* and *A. littorum* were genetically distinct from *A. campylopodum* and *A. occidentale*, Nickrent et al. (2004) were unable to distinguish between any of the species of dwarf mistletoes parasitizing pines in California using the DNA sequences they analyzed. They proposed a classification system that combined most species of dwarf mistletoe recognized by Hawksworth and Wiens (1996) in their section "Campylopoda" as one species, *Arceuthobium campylopodum*. Nickrent et al. (2004) did not consider the morphological characters or host susceptibility differences described by Hawksworth and Wiens (1972, 1996) and Hawksworth et al. (1992) for the species of *Arceuthobium* parasitizing pines in California. I consider these morphological characters and host susceptibility differences important taxonomic characters that must be considered in the taxonomic classification of dwarf mistletoes. They are particularly important if the classification system is to prove practical and useful for forest managers, whose objectives often include management of dwarf mistletoe populations. Therefore, I recognize the classification of Hawksworth and Wiens (1996), which treats KPDM (*A. siskiyouense*) as a distinct species.

As expected, this study demonstrated that knobcone pine is a principal host of KPDM.

Severity results further indicated that knobcone pine is extremely susceptible to infection. Mistletoe infections on knobcone pine were easy to observe because most infections had visible aerial shoots and/or basal cups present on infected branches. Infected branches without aerial shoots or basal cups were also easily observed because they usually had large fusiform swellings around the point of infection. An additional factor which assisted with identification of infections on knobcone pines was the consistent formation of witches' brooms on large trees. Although Hawksworth et al. (1992) reported that KPDM does not induce witches' brooms on knobcone pine and although they used this characteristic for separating it from *Arceuthobium campylopodum*, I frequently observed witches' brooms on knobcone pines infected by KPDM (Fig. 2).

Jeffrey pine is much more susceptible to KPDM than its prior classification as a rare host indicates. My infection data demonstrated that it should be classified, along with knobcone pine, as a principal host of KPDM. However, my severity (mean DMR) data indicated that Jeffrey pine is slightly less susceptible than knobcone pine. Large, distinct witches' brooms were also frequently formed on Jeffrey pines (Fig. 3). Jeffrey pines were often so severely infected that they were killed by the mistletoe, and dead trees often had numerous large witches' brooms still on the trees and/or on the ground around them. Many of these dead trees also had evidence of attack by the Jeffrey pine bark beetle (*Dendroctonus jeffreyi* Hopkins).

My results demonstrated that shore pine should be reclassified as an occasional host of KPDM, but infection incidence varied a great deal for shore pines between study sites. For example, 54% of shore pines were infected in plots near Bain Station, while only 12% were infected at Elevenmile Creek. However, at least 5% of shore pines were infected at all of the study areas. Infection exceeded 50% only at Bain Station. Most shore pines had a DMR of 1 or 2. Infections on shore pines were more difficult to detect than on knobcone or Jeffrey pines because many infected shore pines had only 1 or 2 infections. When aerial shoots were absent, it was even more difficult to detect infections, even though most shore pines sampled were <10 m tall.

Although I sampled more than 100 trees of western white pine, Douglas-fir, and incense-cedar, none of these species were infected by KPDM. I consider these species to be immune to KPDM. This agrees with Hawksworth and Wiens' (1996) conclusion that western white pine was immune to infection by this mistletoe. Hawksworth and Wiens (1996) did not report that Douglas-fir is immune to infection by knobcone pine dwarf mistletoe. It is unlikely that KPDM will infect Douglas-fir, because most dwarf mistletoes that primarily parasitize pines seldom parasitize Douglas-fir (Hawksworth and Wiens 1996). Dwarf mistletoes have not previously been reported as parasites of incense-cedar (Hawksworth and Wiens 1972, 1996), and my results support this apparent immunity.

Knobcone pine dwarf mistletoe often produced many aerial shoots on both Jeffrey and shore pines. Hawksworth et al. (1992) specifically noted that KPDM could be identified using morphological characters when it was found parasitizing other hosts, which they believed was further support for its taxonomic classification as a separate species. However, I have observed that although the mistletoe's aerial shoots formed on Jeffrey pine were usually the same color as those found on knobcone pine, they were frequently much larger than those on knobcone or shore pine. For example, I measured some male aerial shoots on Jeffrey pine that were taller than 20 cm and female aerial shoots that were taller than 15 cm. The maximum aerial shoot height measured by Hawksworth et al. (1992) for KPDM on knobcone pine was only 10 cm. Thus far, I have concluded that at each of the locations where I sampled KPDM severely parasitizing knobcone and Jeffrey pines, the mistletoe on these hosts was the same species, even though plant sizes were frequently larger on Jeffrey pine than those observed on knobcone pine. In addition, the mistletoe infecting Jeffrey pine in areas where knobcone pine was not present also appears to be KPDM. This determination was based on similarities in plant color for this mistletoe on all of its hosts. However, additional morphological studies of KPDM populations are needed, and this future work should include additional molecular analyses comparing *A. siskiyouense* with *A. campylopodum* and with additional dwarf mistletoes (i.e., *A. occidentale* and *A. littorum*) on pines in California.

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