Bird Dissemination of Dwarf Mistletoe on Ponderosa Pine in Colorado

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ABSTRACT: Dwarf mistletoe [*Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksworth and Wiens] distribution and the role of birds as vectors of the parasite were studied in a Colorado ponderosa pine (*Pinus ponderosa* Laws.) forest. Occurrence of the parasite at distances from a source greater than those attributable to explosive seed discharge was erratic and infrequent. In 24 cases, ages of initial infections in single or multiple tree infection centers were determined. Age analyses indicated that long-distance seed transmission followed by successful infection occurred on an average once every 4 years in 150 ha of healthy ponderosa pine. A total of 411 birds representing 21 species were trapped in an infected pine stand during dwarf mistletoe seed dispersal in 1974-1976. Mountain chickadees (*Parus gambeli* Ridgway) and pygmy nuthatches (*Sitta pygmaea* van Rossem) were primary vectors of the parasite. Field observations and laboratory experiments suggested that birds ingested dwarf mistletoe seeds infrequently but such seeds were not viable when voided in feces. Viable seeds apparently were transported by birds only when they adhered to feathers and were transferred to foliage as birds subsequently foraged.

INTRODUCTION

Dwarf mistletoe [*Arceuthobium vaginatum* subsp. *cryptopodum* (Engelm.) Hawksworth and Wiens] is a serious pest of ponderosa pine (*Pinus ponderosa* Laws.). Annual losses through mortality and growth reduction resulting from dwarf mistletoe infection may exceed 12.5 million ft^3 in Arizona, New Mexico and Colorado (Flake *et al.*, 1972).

The parasite spreads to adjacent trees and within a single tree by explosively discharged seeds. Seed discharge usually occurs from mid-July to mid-August in Colorado and is most frequent in forenoon each day. Seeds are propelled a maximum of 20 m by the explosive discharge mechanism (Hawksworth, 1961b), but new infections are found at distances considerably greater than 20 m.

Casual observations of birds and mammals frequenting dwarf mistletoe-infected trees suggested that they played a role in long-distance transport of the parasite (Hawksworth, 1961b; Marshall, 1957; Keith, 1965; Patton, 1975; Taylor, 1935). Hudler *et al.* (1974) found that seeds of a related species, *Arceuthobium pusillum* Peck, readily stuck to feathers of grey jays [*Perisoreus canadensis* (L.)] in Minnesota.

The objectives of this investigation were to document the frequency of long-distance dissemination of dwarf mistletoe and to examine the possible role of birds in its dissemination.

METHODS

Examination of stomach contents of birds.—Prior to field investigations, a collection of bird stomach contents preserved by the Department of Zoology and Entomology at Colorado State University was examined. The collection was made in July-August 1962 and 1963 as part of a study of bird predation of ponderosa pine bark-beetles (*Dendroctonus ponderosae* Hopk.) near Bailey in central Colorado. Birds had been collected randomly in and near dwarf mistletoe-infected pines. Initially,

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all contents which had been noted by the original investigator to contain vegetation were reexamined for dwarf mistletoe seeds. Subsequently, all mountain chickadee and pygmy nuthatch stomach contents were examined.

Study area description.—Fieldwork was done at the Manitou Experimental Forest (elev. = 2400 m) located 40 km NW of Colorado Springs in Teller County, Colo.

An area 4.3 x 0.8 km was selected for study of dwarf mistletoe distribution and bird dissemination of the parasite (Fig. 1). This relatively large area was selected to insure that long-distance dissemination could be assessed even if rare. Preliminary observations indicated that pines on the eastern edge were heavily infected and supplied ample inoculum for dissemination into adjacent healthy timber. The area was on a gentle (<5%) W-facing slope on the E side of a broad valley drained by Trout Creek. Two major drainages, Hotel and John's gulches, as well as several minor drainages ran from E to W through the area. The area was divided into four subunits numbered from N to S.

Ponderosa pine, in uneven-aged, multistoried stands, was the dominant tree in the study area. Analysis of 63 0.1-ha plots in subunits 3 and 4 indicated that the species occurred at a mean density of 380 stem/ha and a mean basal area of 8.6 m^2/ha. The largest pines averaged 17-m tall, 50-cm diam at breast height (dbh) and were 125-150 years old. Aspen (*Populus tremuloides* Michx.) and douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] occurred either singly or in small (< 0.5 ha) stands, particularly on N-facing slopes and in drainage bottoms.

Understory vegetation was limited to kinnikinnik [*Arctostaphylos uva-ursi* (L.) Spreng.] and dwarf juniper (*Juniperus communis* L. var. *depressa* Pursh.) in most forested areas, but mountain mahogany (*Cercocarpus montanus* Raf.) and numerous herbs and grasses were present in sparsely stocked or nonforested areas or where pine mortality from dwarf mistletoe was severe.

Dwarf mistletoe distribution.—The extent of dwarf mistletoe infection in the study area was surveyed by walking the edges of large (>1 ha) infection centers and plotting the route on acetate overlaid on 1:7920 infrared, false-color aerial photographs. Additional, smaller infection centers (which in several cases were single trees) were located by a thorough visual examination of "healthy" stands in the study area. This examination was conducted throughout the term of the study. When smaller infection centers (satellite centers) were located, they were also plotted on aerial photographs. Areas of satellite centers were measured, and numbers of infected and healthy trees recorded. Where possible, the tree containing the oldest dwarf mistletoe infection—hence, the original infection site in the satellite center—was located. Age, height and dbh of each tree containing the first infection in a center, and height and age of oldest infections were determined. The latter measurement was determined by cutting through branches at points of maximum swelling and counting rings from the outside in to the oldest ring containing mistletoe endophytic tissue. Distances from oldest infections in satellite centers to nearest potential seed sources were measured.

Explosive seed discharge.—Dwarf mistletoe seed dispersal was quantified in 1974 by a daily estimate of the number of seeds discharged from 10 dwarf mistletoe plants, each with 50-100 mature berries. In 1975 and 1976, six 1.0 x 2.5-m muslin sheets spread on ground beneath infected trees were used to quantify seed dispersal. Sheets were located in the same place in both years, and the number of seeds found on all six sheets was recorded daily.

Bird dissemination.—Birds were captured by mist nets in or near infection centers from 24 July to 23 August 1974; 17 August to 10 September 1975, and 1 August to 23 August 1976. Trapping periods coincided with dwarf mistletoe seed dispersal and 1 week thereafter in 1974 and 1975. In 1976, trapping ceased the same day that the last seed was found on the sheets.

Birds were examined for seeds as soon as possible, usually within 15 min, after being caught. Each bird was placed in a 0.3 x 0.3 x 0.3-m holding cage for 3-6 hr, and released. Feces voided in holding cages were collected and examined immediately for dwarf mistletoe seeds or were stored in vials with 95% ethyl alcohol until examination.

Trapping results and observations in 1974 suggested that mountain chickadees and pygmy nuthatches were vectors of dwarf mistletoe. In 1975 and 1976, those species were observed more closely and additional information on their behavior was obtained.

To further test the possibility that birds could pass viable dwarf mistletoe seeds, five mountain chickadees, five pygmy nuthatches, five gray-headed juncos [*Junco canniceps* (Woodhouse)] and five chipping sparrows [*Spizella passerina* (Bechstein)] were each fed 10 dwarf mistletoe seeds. The seeds were consumed readily by juncos and sparrows but were ingested by the other two species only when concealed within the exoskeletons of live mealworms. After eating all 10 seeds, each bird was held for 4-12 hr and released. Fecal matter voided during that time was examined immediately for dwarf mistletoe seeds. A seed was considered to have been passed if the endosperm and embryo were intact. Viability of passed seeds was determined by immersing them in 0.2% w/v aqueous 2,3,5-triphenyl tetrazolium chloride (TTC) for 24-48 hr. Viable seeds stained pink to red while nonviable seeds remained unstained (Scharpf, 1970).

To identify factors which caused seeds to lose viability, seed survival was tested in temperature and *p*H ranges including those encountered in birds' digestive tracts. Differences in seed survival within each of the following experiments were tested for significance ($P = 0.05$) with analyses of variance and, where appropriate, Duncan's Multiple Range Test (Steele and Torrie, 1960).

Seed survival was tested in aqueous HCl at each of six acidities: $pH = 0.7$, 1.4, 1.9, 2.8, 4.1 and 5.7. For each test, 50 fresh seeds were added to 10 ml of acid solution and incubated for 3 hr at 25 C or 40 C. In one set of tests, entire seeds, including endocarp and viscin cells were used. In a second set, the endocarp was removed from each seed prior to exposure to an acid solution. Each test was replicated once. After exposure to its respective acid solution, each lot of seeds or seed parts was rinsed for 20 min in each of two changes of 125 ml of distilled water and tested for viability with TTC.

Seed survival was also tested at 25 C, 40 C, 55 C and 70 C. Lots of 50 fresh seeds were placed in 10 ml of distilled water in test tubes which were capped and immersed for 1 hr in 900 ml of water at the desired temperature. Seeds were then air-dried for 2 hr, and tested for viability with TTC.

RESULTS

Examination of stomach contents.—Stomach contents of 131 birds representing 15 species were examined. Whole dwarf mistletoe seeds or seed fragments were found only in stomach contents of mountain chickadees (nine of 44 birds) and a pygmy nuthatch (one of 11 birds). In most cases, three or fewer seeds were found, but one mountain chickadee had 16 seeds.

Dwarf mistletoe distribution in the study area.—Ponderosa pines in the eastern portion of the study area were severely and extensively infected with dwarf mistletoe. A total of 47 ha were included in several large infection centers in that region. In addition, 32 satellite centers were found in otherwise healthy timber W of the main infection centers (Fig. 1). The frequency of occurrence of satellite centers increased markedly from N-S such that there were nine times as many satellite centers in subunit 4 as in subunit 1.

Satellite infection centers ranged in size from the area occupied by one tree to

0.3 h (Table 1). The 32 satellite centers occupied a total of 1.2 ha. Most (84%) satellite centers were located within 100 m of the nearest possible source of dwarf mistletoe seeds, but five were more than 100 m away.

Original infections were located in 27 satellite centers. Of those, 22 branches were still living and infection ages were determined. Infections ranged in age from 17-120 years. All but two of 22 original infections bore shoots with pistillate flowers.

Explosive seed discharge.—Explosive discharge of dwarf mistletoe seeds began on 25 July 1974, and was complete by 16 August. In 1975, seed discharge began on 17 August. Freezing temperatures on 21 August damaged much of the fruit crop, and seed discharge was negligible thereafter. In 1976, seed discharge began on 3 August and was complete by 26 August.

Bird dissemination.—A total of 411 birds representing 21 species were captured in 530 hr of trapping during dwarf mistletoe seed dispersal in 3 years (Table 2). Gray-headed juncos, Audubon's warbler [*Dendroica coronata auduboni* (Townsend)], mountain chickadees and pygmy nuthatches were trapped most frequently.

Dwarf mistletoe seeds were found on feathers of 16 (3.4%) birds, most frequently on mountain chickadees, pygmy nuthatches and gray-headed juncos. All but one of the birds carried only one seed. The exception was a pygmy nuthatch with three seeds.

Additional information about seed transport by birds was obtained through observation. On eight occasions, mountain chickadees foraging on infected branches and in dwarf mistletoe shoots were observed to be struck by discharging seeds which adhered to their feathers. After flying to other branches, the chickadees either continued foraging or stopped to preen seeds from their feathers. In the latter case,

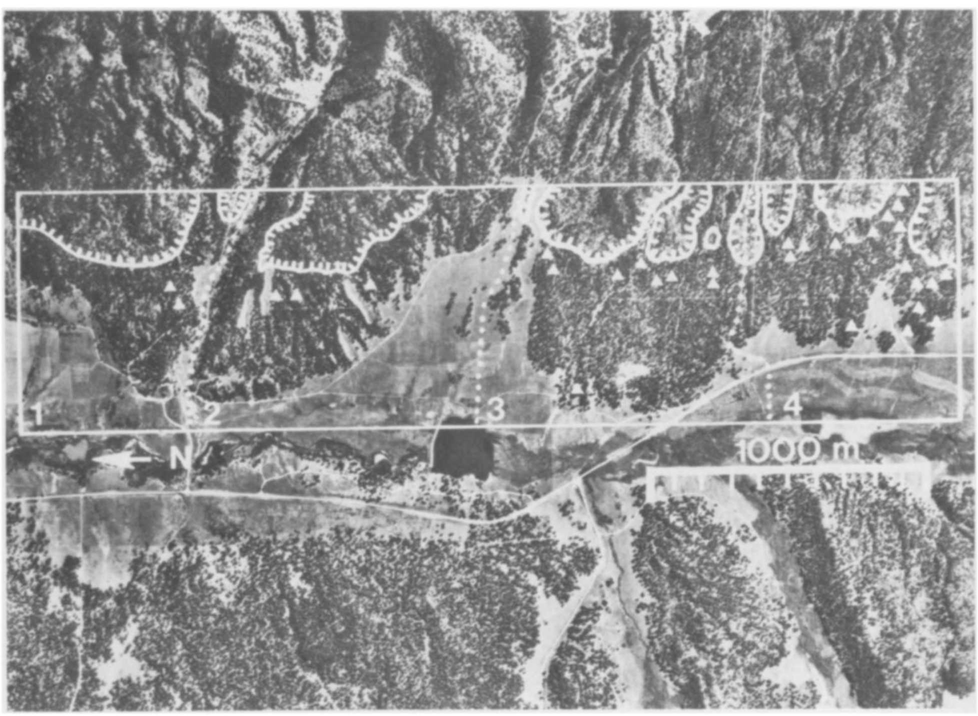

Fig. 1.—Aerial photograph of the study area showing dwarf mistletoe distribution. Hatched lines bound heavily infected areas. White triangles mark locations of satellite centers

TABLE 1.—Characteristics of satellite infection centers

Center no.	No. inf. trees	Distance & direction from seed source (m)	Age of center (yr)	Sex of original infection
1	1	49 W	33	F
2	1	150 W	28	F
3	100+	68 W	......	....
4	3	76 S	......	....
5	6	126 W	36	F
6	7	47 W	71	F
7	34	63 W	......	....
8	23	58 W	......	....
9	24	46 NW	......	....
10	27	46 W	42	F
11	1	76 W	60	M
12	8	458 W	52	F
13	42	76 W	26	F
14	55	20 W	58	F
15	1	263 N	32	F
16	2	76 E	......	....
17	4	64 W	120	F
18	2	65 S	22	F
19	48	28 SW	70	F
20	35	45 W	20	F
21	175	126 SW	......	....
22	49	53 NW	......	....
23	3	42 S	......	....
24	1	55 S	43	F
25	39	88 S	82	F
26	21	41 NW	35	F
27	1	55 W	17	F
28	1	55 W	48	M
29	17	84 NE	75	F
30	6	24 E	38	F
31	1	22 E	......	....
32	11	79 W	113	F

TABLE 2.—Birds trapped during dwarf mistletoe seed dispersal in 1974, 1975 and 1976. The number of individuals with seeds on feathers is shown in parentheses

Species	Number trapped
Pygmy nuthatch	105 (6)
Mountain chickadee	63 (4)
Gray-headed junco	53 (4)
Chipping sparrow	31 (1)
Audubon's warbler	72
Vesper sparrow	22
Lincoln's sparrow	15
Broad-tailed hummingbird	8
Western tanager	7
Western wood pewee	5
Hermit thrush	5
White-breasted nuthatch	5
Empidonax flycatcher	4
Williamson's sapsucker	4 (1)
Western bluebird	4
Stellar's jay	2
American robin	2
Mountain bluebird	1
Northern three-toed woodpecker	1
House wren	1
Common nighthawk	1
Total	411 (16)

activities such as bill-wiping, by which birds might actively place seeds on branches, were not observed. Thus, preened seeds were presumably eaten. In five instances, chickadees hit by discharged seeds continued foraging in tips of ponderosa pine branches, and seeds were transferred from birds to pine needles. Pygmy nuthatches were also observed to be struck by discharging seeds on six occasions, although transfer of seeds from their plumage to pine needles was not observed. The habit of foraging in dwarf mistletoe shoots was not observed with chipping sparrows, gray-headed juncos, Audubon's warblers, Steller's jays [*Cyanocitta stelleri* (Gmelin)], white-breasted nuthatches (*Sitta carolinensis* Latham) or robins (*Turdus migratorius* L.).

Pygmy nuthatches foraged in pine foliage and on branches and stems, spending approximately equal time with each. They were observed occasionally foraging in dwarf mistletoe plants, but such activity amounted to less than 1% of the total effort. Mountain chickadees spent ca. 75% of their time foraging in pine foliage and usually perched on branches only to preen or eat. When chickadees foraged in dwarf mistletoe-infected pines, as much as 25% of their effort was directed toward dwarf mistletoe plants. That insects, and not dwarf mistletoe seeds, were their primary objective was evidenced by the fact that they always searched at the bases of shoots and not in the aerial portions.

Flocks of chickadees and nuthatches encountered during seed dispersal comprised 10-30 individuals. When the two species were together, there were two to three times as many nuthatches as chickadees. The birds would forage in an area of 0.3-0.5 ha for 10-30 min and then move as a group to a new area 50-200 m away.

Seeds were rarely found in the excrement of trapped birds and then only in that of pygmy nuthatches and mountain chickadees. A total of three seeds were found in feces of two pygmy nuthatches, and one seed in feces of a mountain chickadee. None of the 50 seeds ingested by captive gray-headed juncos or chipping sparrows were passed in a recognizable condition. Seeds fed to those birds were presumably digested. Mountain chickadees passed 12 of 50 seeds, and pygmy nuthatches passed seven of 50 seeds. However, none of the 19 seeds were viable when tested with TTC. The endocarp and viscin of the seeds were missing, but each seed retained the yellow-green color characteristic of healthy seeds.

Viability of whole dwarf mistletoe seeds with endocarps and viscin intact was unaffected by exposure to any of the HCl solutions at 25 C, but was affected adversely at 40 C (Table 3). When only the endosperm and embryo were incubated in acid solutions, mortality increased with decreasing *p*H. Solutions of *p*H 0.7 and 1.4 were lethal to all seeds tested at either temperature.

Seed survival at 25, 40, 55 and 70 C averaged 78, 30, 2 and 0%, respectively.

TABLE 3.—Survival of dwarf mistletoe seeds incubated for 3 hr in solutions of HCl at 25 C or 40 C. Means of two replicates of 50 seeds are shown. Within each column, means followed by common letters are not significantly different at $P = 0.05$

	Endocarp and viscin intact		Endocarp and viscin removed	
*p*H	25 C	40 C	25 C	40 C
0.7	37	0 a	0 a	0 a
1.4	41	4 ab	0 a	0 a
1.9	36	10 bc	5 ab	1 a
2.8	39	11 c	11 bc	2 a
4.1	40	19 d	16 cd	5 a
5.7	42	23 d	18 d	12 b
6.8 (water)	44	19 d	42 d	21 c

DISCUSSION

The occurrence of dwarf mistle infection centers at distances up to 450 m from the nearest potential seed source indicates that some agent in addition to explosive discharge was involved in seed dispersal. However, analysis of the ages of satellite centers reflected the relative infrequent occurrence of long-distance dissemination. On the average, new infection centers were established only once every 4 years in 150 ha of healthy ponderosa pine.

Wind has only a limited effect on dwarf mistletoe seed dispersal (Hudler and French, 1976; Smith, 1966; Scharpf and Parmeter, 1971) and was considered to be an unlikely factor in establishing satellite centers. Most satellite centers were W of nearest inoculum sources. Prevailing winds during the season of seed dispersal are from the W or NW and strong E winds are rare. Even if strong E winds were present, seeds would have to penetrate successfully a moderately dense canopy if they were to travel far. That possibility seems remote.

Rodents are known to frequent infected trees and feed on dwarf mistletoe plants (Keith, 1965; Patton, 1975; Taylor, 1935). Abert squirrels (*Sciurus aberti* Woodhouse) and chipmunks (*Eutamias* spp.) were seen frequently in the study area and could serve as vectors of the parasite. It was observed, however, that Abert squirrels and chipmunks rarely travelled more than 30 m from one tree to another in less than 15 min. Viscin from freshly discharged seeds was observed to dry in 6-10 min on cotton cloth. Drying may take slightly longer on rodent fur because it is water repellent to some extent. They may aid in intensifying infections within trees, but their ability to spread the parasite over longer distances is questionable.

Birds were the most likely agents of long-distance dispersal of dwarf mistletoe in this investigation. Trapping data and observations suggested that mountain chickadees and pygmy nuthatches were the most important species. Not only were they most often found carrying seeds, but they also were seen foraging repeatedly in dwarf mistletoe shoots where seeds could be obtained, and in tips of pine branches where seeds could be deposited in positions that could lead to infection.

Other less easily trapped species or those less abundant in the study area could also function as vectors. Several gray-headed juncos, a chipping sparrow and a Williamson's sapsucker (*Sphyrapicus thyroideus* Cassin) were trapped with seeds on their feathers.

Although mountain chickadees and pygmy nuthatches were found to eat dwarf mistletoe seeds and void them intact, voided seeds were not viable. Viability was probably lost due to combined effects of temperature and HCl in birds' digestive tracts. Incubation of seeds in acidic environments and at temperatures including those of birds' digestive tracts caused significant losses in viability and suggested that birds rarely, if ever, disseminate viable seeds by eating and voiding them.

By the time seed dispersal started in 1975, many nonresident birds had begun their southward migration. Species such as mountain bluebird (*Sialia currucoides* Bechstein), western bluebird (*S. mexicana* Ridgway), vesper sparrow (*Pooecetes gramineus* Baird), chipping sparrow, robin and Audubon's warbler were observed in large flocks of 20 or more individuals. The flocks were observed for only a short time, usually less than 1 day, in any one area, before continuing S and E to lower elevations and more favorable weather. In years such as 1975, when seed discharge occurs during bird migration, it is conceivable that migratory species could disseminate dwarf mistletoe over distances far greater than those reported in this study.

Freezing injury to maturing fruit may reduce the likelihood of bird dissemination. Damage to dwarf mistletoe fruits by freezing has been reported for *Arceuthobium laricis* and *A. americanum* (Baranyay and Smith, 1974) in British Columbia, *A. americanum* and *A. douglasii* in Montana (*Tunnock et al.*, 1966) and *A. pusillum* in Minnesota (Hudler and French, 1976), but this is the first report for *A. vaginatum* subsp. *cryptopodum*. Seeds oozed from frozen and thawed berries and remained attached to the pedicel rather than being forcibly discharged. Although viscin on such seeds was still sticky, the chance of seeds adhering to birds is presumably diminished with loss of explosive discharge capability.

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