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EFFECTS OF FOREST FUEL SMOKE ON DWARF MISTLETOE SEED GERMINATION

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ABSTRACT.—Seeds of three species of dwarf mistletoe, *Arceuthobium americanum* Nutt. ex Engelm., *A. cyanocarpum* Coulter & Nelson, and *A. vaginatum* subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens, were exposed to smoke from burning forest fuels. Premeasured amounts of coniferous needles and branch wood were burned in a small incinerator with smoke passing through a closed chamber containing the seeds. Following three different smoke treatments and one high-temperature treatment, tests were conducted to evaluate the effects of these treatments on seed germination. Germination was inhibited for all species when the seeds were exposed to smoke for 60 minutes or longer. Seeds of *A. americanum* were unaffected by exposures of up to 40 minutes from fuels with high moisture contents, but enhanced germination occurred after 30 minutes of exposure to smoke from drier fuels. The percentage of germinating seeds of *A. cyanocarpum* and *A. vaginatum* showed little effect from exposures of up to 30 minutes.

Dwarf mistletoe species (*Arceuthobium* spp.) are the most serious of diseases in coniferous forest communities of western North America (Alexander and Hawksworth 1975). These plants are obligate parasites that attack specific coniferous host tree species and appropriate water, minerals, and other nutrients from the host. Injury to infected trees results in a continual reduction of host assimilatory leaf-surface area (Weir 1916, Korstian and Long 1922), decreased growth, reduced vigor, and increased mortality (Hawksworth 1961, 1975, Wicker and Leaphart 1976). Hawksworth and Wiens (1972) discuss dwarf mistletoe biology and host reaction extensively.

Wildfires, which occurred repeatedly in coniferous forest communities prior to the advent of organized fire suppression (Weaver 1951, Wellner 1970, Arno 1976, McBride and Laven 1976, Stokes and Dieterich 1980), are a major ecological force that influenced forest structure and development and also significantly affected dwarf mistletoe population dynamics (Gill and Hawksworth 1964, Baranyay 1970, Wicker and Leaphart 1976, Tinnin 1981). Fire affects dwarf mistletoes directly by killing and consuming host tissues and parasitic plants. These effects are dramatic, immediate, readily observable, and well known. The indirect relationships of fire to dwarf mistletoes, such as reduction of growth or vigor in hosts and parasites, loss of parasite seed viability, or predisposition of hosts to other damaging agents, may be caused by exposure to smoke or elevated temperatures. These effects are subtle, gradual, and difficult to observe. The effects of forest fire smoke exposure on dwarf mistletoe growth and development are unknown and constitute an area of necessary research (Alexander and Hawksworth 1975, Hardison 1976, Koonce and Roth 1980, Smith 1981).

Several workers have reported the effects of smoke on various disease-causing agents. Long (1922) observed that mistletoe (*Phoradendron* spp.) parasitizing one seed juniper (*Juniperus monosperma* [Engelm.] Sarg.) died after exposure to smelter smoke. Spore germination, mycelial growth, and infection of several species of fungi are inhibited after exposure to pine needle and grass smoke (Parmeter and Uhrenholdt 1975). Koonce and Roth (1980) suggested that heat and smoke may affect dwarf mistletoe plants (*Arceuthobium campylopodum* Engelm.) more severely than the associated host plants (*Pinus ponderosa* Laws.).

This study will improve our understanding of the indirect relationships of fire and dwarf mistletoe. The primary objective was to evaluate the effects of various durations of forest fuel smoke exposure on seed germination of three dwarf mistletoe species.

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MATERIALS AND METHODS

Dwarf mistletoe, *A. americanum*, seeds were collected from lodgepole pine (*Pinus contorta* Dougl.), *A. cyanocarpum* were collected from limber pine (*Pinus flexilis* James), and *A. vaginatum* were collected from ponderosa pine in a manner similar to that discussed by Scharpf and Parmeter (1962). These seeds were then placed in petri dishes (50 per dish) and stored in a refrigerator at 6 C for equal time periods until ready for treatment.

A smoking apparatus, similar to that described by Parmeter and Uhrenholdt (1975), was constructed from a small wood stove, uninsulated duct pipe, and a refrigerator. Smoke from burning fuels in the wood stove passed into a 10-cm-diameter duct pipe and traveled 5.5 m through this uninsulated pipe to allow cooling and to minimize heat effects. The pipe entered the bottom of the refrigerator, permitting smoke movement through shelves supporting the petri dishes upward and outward through the refrigerator roof. Use of wire mesh shelves and a small electric fan promoted a somewhat even distribution and movement of smoke through the chamber.

Three smoke treatment experiments were conducted. First, samples of seeds of all three dwarf mistletoe species were exposed to smoke for 0 (control), 60, and 180 minutes. Second, samples of all three species were exposed to smoke for 0, 1, 5, 15, and 30 minutes. Third, samples of only *A. americanum* seeds were exposed to smoke for 0, 10, 20, 30, 40, 50, 60, and 90 minutes.

Ponderosa pine, lodgepole pine, and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) needles and branch wood were used to generate smoke. This fuel was collected from the forest floor duff layer. Moisture content and weight of fuels consumed were determined prior to each experiment. Air temperatures inside and outside the smoking chamber were recorded during the exposure periods. Chemical composition of smoke was analyzed for polynuclear aromatic hydrocarbons (PAH), a common pollutant in combustion emissions. Analysis methods are reported in Tan et al. (1985).

Separate germination tests were conducted with *A. americanum* seeds in an attempt to assess the effects of high temperatures on germination. Only *A. americanum* seeds were used in this test as well as in the third smoke treatment experiment because seeds of the other species were not available in sufficient quantities for collection and treatment. The *A. americanum* seeds were exposed to elevated temperatures for selected time periods in a portable heating apparatus.

The heat treatment chamber was constructed of lightweight aluminum and insulated with 2.54-cm insulation board. A small electric fan was attached to the bottom of the box along with the heat source, a 750-watt ceramic heating coil screwed into a 110-volt electric light socket. An aluminum shelf, insulated on the upper side, was placed directly above the heating element to shield petri dishes and dwarf mistletoe seeds from direct heat. This shelf was open on both sides, and the continuously operating fan promoted movement of heated air around the shield into the space occupied by the dishes and seeds.

Air temperatures inside the treatment chamber were controlled by a separate control box. This device possessed time and temperature control features which enabled the setting of a desired temperature and time period on the dial panel. The control box automatically activated the heating element as needed to attain the desired temperature. After the preset temperature was achieved, the timer engaged and the heating element operated as needed to maintain the internal temperature. Following operation for the preset time period, the control box disengaged both the timer and the heating element, allowing the chamber to cool down. A solid-state, two-terminal, integrated circuit temperature transducer attached to the control box circuit board monitored the chamber air temperature. This transducer permitted the control box to maintain the chamber temperature within ± 0.5 degrees C. A thermometer placed inside the treatment chamber provided a check of the temperature controller.

Elevated temperature treatments included time periods of 30 and 45 minutes for both 35 and 40 C, and 2, 5, and 10 minutes for 45 and 50 C. An unexposed group was used for comparison. These temperatures and durations were selected to correspond to the temperature environments within the smoke treatment chamber during smoke experiments.

TABLE 1. Air temperature (°C) during smoke treatment experiments.

Experiment number	Temperature[1] location	Time (minutes) 0	1	5	10	15	20	30	40	50	60	90	120	150	180
1	0	12	—	—	—	—	—	—	—	—	12	14	13	12	12
	I	17	—	—	—	—	—	—	—	—	40	40	43	46	41
2	0	17	17	17	—	19	—	21	—	—	—	—	—	—	—
	I	21	21	21	—	23	—	31	—	—	—	—	—	—	—
3	0	10	—	10	11	12	13	16	18	18	18	23	—	—	—
	I	9	—	25	30	35	32	35	37	37	38	44	—	—	—

[1]Temperature locations are signified as 0 = outside ambient air temperature, 1 = air temperature inside smoke treatment chamber.

TABLE 2. Average percent germination of *A. americanum* seeds after exposure to temperatures and durations that occurred during smoke treatments.

Temp (°C)	Time (minutes) 2	5	10	30	40
35	—	—	—	35.6	18.8
40	—	—	—	38.8	6.4[3]
45	30.8	28.8	26.4	—	—
50	50.8[2]	24.0	6.0[3]	—	—

[1]Average germination of the untreated group used for comparison = 26.8%.
[2]Average percent germination significantly higher than untreated group.
[3]Average percent germination significantly lower than untreated group.

After exposure to smoke or high temperatures, treated and untreated seeds were immersed in a 2% hydrogen peroxide solution to inhibit fungal attack and facilitate maximum germination (Wicker 1974). The seeds were then placed in a standard germination chamber for 30 days and maintained at 16 C with an 8-hour light treatment during each 24-hour period. A visible radicle that ruptured the endocarp was taken as positive evidence of germination (Knutson 1969). Statistical analyses that compared average percent germination of treated and untreated groups were conducted with one-way analysis of variance and Duncan's Multiple Range Test. The .05 level of statistical probability was selected as significant.

RESULTS

During the initial experiment, 3,235 g of fuel averaging 8% moisture content (oven-dry basis) was consumed. In the second experiment, 1,816 g of fuel having a moisture content of 25% was burned, while in the final experiment 4,225 g of fuel with an average moisture content of 34% was consumed.

Maximum air temperatures outside the treatment chamber varied from 12 to 23 C for the three experiments (Table 1). Inside chamber temperatures showed a gradual increase in all experiments, with the maximum reaching as high as 46 C (Table 1). Although inside air temperatures exceeded outside air temperatures throughout most of the experiments, the maximum inside temperature persisted for a relatively short time.

Analyses of smoke particulates to assess PAH composition were conducted on both the wood and duff fuel used in the study. Composition of PAH from wood burning was found to resemble that from other environmental samples such as air particulates and sediments where parental PAH are the predominant components (Tan et al., unpublished manuscript). Duff burning, however, illustrated a PAH composition markedly different from the composition in environmental samples such as air, sediments, and wood-burning emitted particulates.

In typical environmental samples, parental PAH generally make up the major components. In smoke particles from duff burning, phenanthrene, alkylated phenanthrene, alkylated cyclopenta(def)phenanthrene, and dodecahydrochrysene clearly stood out as the predominant components (Tan et al., unpublished manuscript). In addition, the concentration of individual PAH in smoke particles varied with moisture content of burning duff, but not in a systematic way for all components (Tan et al., unpublished manuscript). No ready explanation is available for this occurrence.

Exposure of dwarf mistletoe seeds to elevated temperatures for different periods of time resulted in variable seed germination (Table 2). While average percent germination of seeds did not continually decrease as time and temperature increased, it was lowest after treatment. After heating at temperatures of 40

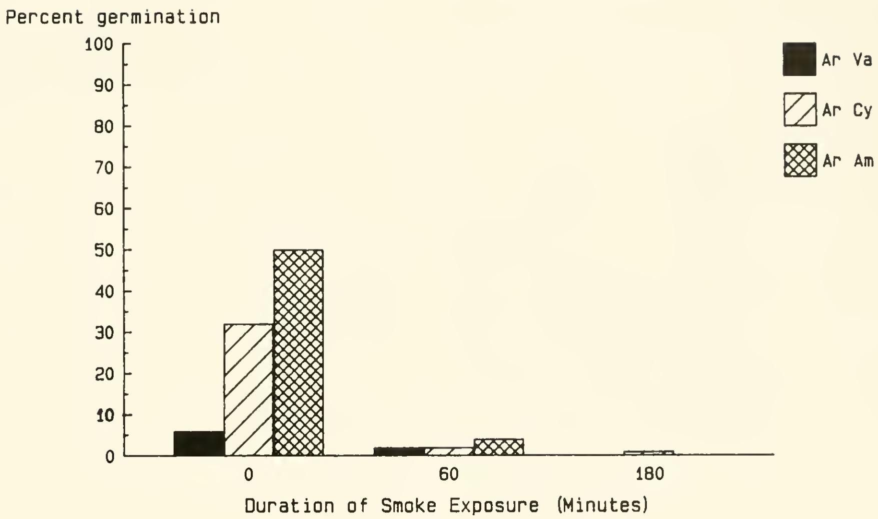

Fig. 1. Average percent germination of *Arceuthobium vaginatum* (Ar Va), *A. cyanocarpum* (Ar Cy), and *A. americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 25% moisture content.

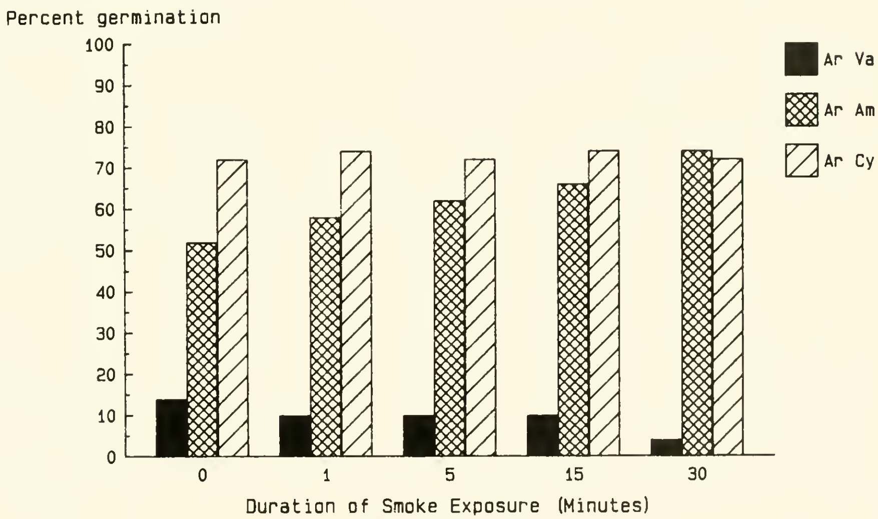

Fig. 2. Average percent germination of *Arceuthobium vaginatum* (Ar Va), *A. cyanocarpum* (Ar Cy), and *A. americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 8% moisture content.

C for 40 minutes, average percent germination was significantly reduced (Table 2). Germination was unaffected when exposed to 45 C. Treatment at a still higher temperature (50 C) appeared to stimulate germination at low durations (2 min), while inhibiting germination after 10 minutes (Table 2).

Exposure of dwarf mistletoe seeds to different smoke durations caused varying results, depending on the moisture content of the fuels consumed (Figs. 1–3). Average percent seed germination of all dwarf mistletoe species was markedly reduced after smoke exposure of 60 minutes or more regardless of the fuel moisture content (Figs. 1, 3).

Average percent germination of *A. americanum* seeds varied with both duration of smoke exposure and fuel moisture content (Figs. 1–3). Smoke exposure of 20 minutes or less had no effect on germination in all

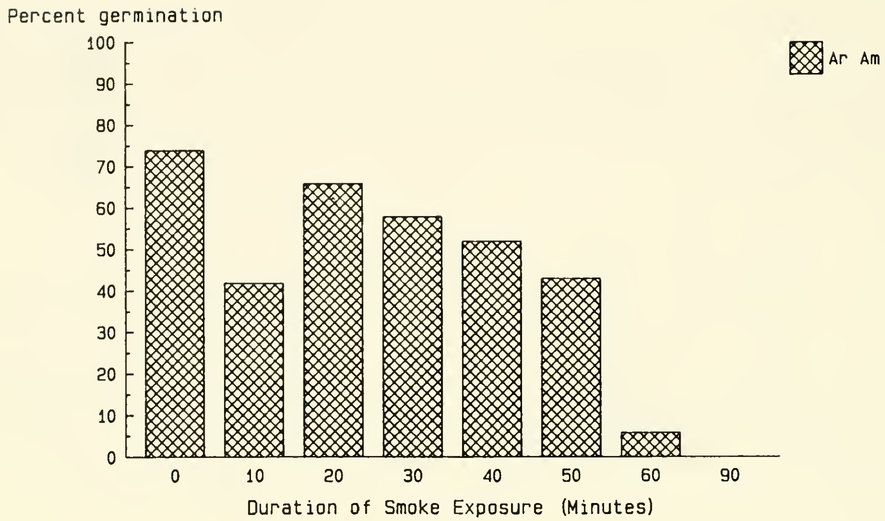

Fig. 3. Average percent germination of *Arceuthobium americanum* (Ar Am) in relation to duration of smoke exposure from fuels with 34% moisture content.

experiments except that exposure to smoke from moist fuels for 10 minutes resulted in significantly lower average percent germination (Fig. 3). However, this trend was not consistent because both untreated seed groups and groups exposed for longer duration had significantly higher germination percentages (Fig. 3). This apparent anomaly may have resulted from factors other than exposure to forest fuel smoke. Exposure of seeds of this species to smoke for 30 minutes from fuels with a low moisture content resulted in average percent germination levels significantly higher than seeds in the unexposed group (Fig. 2). However, 30 minutes of smoke exposure from fuels with high moisture contents resulted in no significant differences in average percent germination (Fig. 3). Exposure to smoke from fuels with high moisture content for longer than 40 minutes caused a significant decrease in the germination of *A. americanum* seeds (Fig. 3). The percentage of germinating seeds exposed to 60 minutes of smoke was less than one-twelfth of the average germination for the untreated groups in both the first and third experiments (Figs. 1, 3). No *A. americanum* seeds germinated after smoke exposure reached 90 minutes (Figs. 1, 3).

Average percent germination of *A. cyanocarpum* seeds exposed to smoke for 0, 1, 5, 15, and 30 minutes did not differ markedly (Fig. 2). However, average percent seed germination was significantly reduced after exposure to smoke for at least 60 minutes (Fig. 1).

Germination percentages of *A. vaginatum* were considerably lower than those of the other species for all treatments including the controls (Figs. 1, 2). Germination of *A. vaginatum* seeds decreased slightly as smoke exposure increased but was not significant until exposure periods exceeded 30 minutes.

Discussion

Substantially lower seed germination percentages of all dwarf mistletoe species when smoke exposures exceeded 30 minutes may result from several factors: (1) a threshold level of smoke toxicity to seeds, (2) chemical toxicity of various fuel types, (3) temperature, and (4) lack of air mixing around the plants.

The occurrence of PAH in the combustion products of carbonaceous fuels agrees with Sandberg et al. (1979). In a study of PAH production from laboratory burning of pine needles with moisture contents ranging from 18 to 27%, McMahon and Tsoukalas (1978) report that heading fires appear to produce higher total particulate matter but lower PAH values than backing fires. Within heading fires, PAH levels also vary as the fire phase varies. Flaming phases produce lower levels of both total particulate matter and PAH than smoldering phases. Specific causes of these effects are hard to pinpoint, but apparently the longer residence times associated with backing and smoldering fires are more conducive to PAH-compound formation.

Increasing moisture in fuels should result in lower combustion efficiency, thereby increasing residence time and PAH production. But, fuels burned with the lowest moisture content (8%) caused the greatest total PAH production (Tan et al., unpublished manuscript). Total PAH production was lowest in smoke produced from the fuels having the highest moisture content. Since individual PAH concentrations varied in an unsystematic fashion as fuel moisture content increased, the influence of specific compounds on seed germination appears to be more important than the influence of total PAH production.

Exposure duration is a major factor determining the degree of injury from compounds contained in or formed as a result of smoke (Jensen and Dochinger 1974, Dochinger and Jensen 1975). Smoke contains or results in formation of numerous compounds, primarily oxidants (Cramer 1974, Evans et al. 1977), which are toxic at relatively low levels to vegetation. Smoke in low doses can have minor effects on plant physiological processes, while high doses can result in acute toxicity and tissue necrosis (Sandberg et al. 1979).

Structure of the smoke treatment chamber failed to remove all possible effects of high-temperature exposure on seed germination. Separate tests completed with the heating apparatus, however, did effectively isolate this source of variation. Average percent germination of those seeds exposed only to elevated temperatures did not follow any consistent trends. Although differential viability may have been responsible for these inconsistencies, it was not assessed in either the smoke or temperature treatments. The fact that differential viability had an equal probability of influencing the percent of seeds germinating after exposure to smoke or high temperatures indicates that it had little effect on the observed outcome.

Seeds exposed to temperature environments in the heating apparatus (which correspond to temperature environments within the smoke treatment chamber) showed reductions in average percent germination only after long exposure. Thus, it appears that at these temperatures for exposures of less than 60 minutes, smoke was the major factor influencing dwarf mistletoe seed germination. As exposure exceeded 60 minutes, the temperature treatment became an increasingly important factor affecting seed germination. After longer durations (90 minutes), the combined effects of the temperatures used in this study and smoke appear lethal to dwarf mistletoe seeds.

Average percent germination of *A. vaginatum* seeds was significantly lower than the other species for all treatments, including the control. Conceivably, lower germination percentages of *A. vaginatum* seeds may indicate that the other species have evolved ecological adaptations to smoke exposure. Seeds of *A. vaginatum* commonly mature four to six weeks before the seeds of *A. americanum* and *A. cyanocarpum*. Upon reaching maturity, *A. vaginatum* seeds are expelled from the fruit and germinate within a short period of time. Seeds of *A. americanum* and *A. cyanocarpum* mature in late August or early September and are expelled onto the host material. They then overwinter on the twig and germinate the following May. Consequently, *A. vaginatum* seeds are susceptible to smoke exposure for a much shorter period of time than those of the other species. Frequent smoke exposure may have permitted seeds of *A. americanum* and *A. cyanocarpum* to evolve mechanisms that promote successful germination in the presence of smoke of low concentrations for short durations.

SUMMARY

Fire is one of the principal agents preventing parasitic species from overrunning host populations (Tinnin 1981). Smoke from fire is a common occurrence in many coniferous forest communities. Although the preservative properties of smoke are well known (Frazier 1967), the specific effects of smoke exposure on dwarf mistletoe growth and development have not been documented.

Results reported here indicate that prolonged smoke exposure inhibits dwarf mistletoe seed germination. After continuous exposure for more than 60 minutes, smoke, and the accompanying increase in temperatures, both severely limit dwarf mistletoe seed germination. Brief exposure to smoke from fuels with low moisture contents causes increased germination of *A. americanum* seeds but has little effect on *A. cyanocarpum* and *A. vaginatum* seed germination.

Other relationships between fire and dwarf mistletoes are still not well understood. Fumigation of coniferous forests by smoke from wildfires may affect plant development, pollination, fruit maturation, and infection by dwarf mistletoes. Smoke may have secondary effects on these parasites by affecting host vigor.

Although this paper by no means addresses all of the relationships between fire and dwarf mistletoe, it does provide new ecological information concerning the effects of forest fuel smoke on dwarf mistletoe seed germination.

Literature Cited

Alexander, M. E., and F. G. Hawksworth. 1975. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. USDA For. Serv. Gen. Tech. Rept. RM-14. Rocky Mtn. For. Range Expt. Sta., Fort Collins, Colorado. 12 pp.

Arno, S. F. 1976. The historical role of fire on the Bitterroot National Forest. USDA For. Serv. Res. Pap. INT-187. Intmtn. For. Range Expt. Sta., Ogden, Utah. 29 pp.

Baranyay, J. A. 1970. Lodgepole pine dwarf mistletoe in Alberta. Canada Dept. Fish. and Forest., Canadian Forest. Serv. Publ. 1286. 22 pp.

Cramer, O. P. 1974. Air quality influences. *In:* Environmental effects of forest residues management in the Pacific Northwest. USDA For. Serv. Gen. Tech. Rept. PNW-24.

Dochinger, L. S., and K. F. Jensen. 1975. Effects of chronic and acute exposure of sulfur dioxide on the growth of hybrid poplar cuttings. Environ. Pollut. 9: 219–229.

Evans, L. F., I. A. Weeks, A. J. Eccleston, and D. R. Packham. 1977. Photochemical ozone in smoke from prescribed burning of forests. Environ. Sci. Tech. 11: 896–900.

Frazier, W. C. 1967. Food microbiology. McGraw-Hill Book Co., New York. 537 pp.

Gill, L. S., and F. G. Hawksworth. 1964. Dwarf mistletoe of lodgepole pine. USDA For. Pest Leafl. 18 (rev.). 7 pp.

Hardison, J. R. 1976. Fire and flame for plant disease control. Ann. Rev. Phytopathol. 14: 355–379.

Hawksworth, F. G. 1961. Dwarf mistletoe of ponderosa pine in the Southwest. USDA Tech. Bull. 1246. Washington, D.C. 112 pp.

______. 1975. Dwarf mistletoe and its role in lodgepole pine ecosystems. Pages 342–358 *in* D. M. Baumgartner, ed., Management of lodgepole pine ecosystems. Vol. 1. Washington State University, Pullman. October 1973.

Hawksworth, F. G., and D. Wiens. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). USDA Agric. Handb. 401. Washington, D. C. 234 pp.

Jensen, K. F., and L. S. Dochinger. 1974. Responses of hybrid poplar cuttings to chronic and acute levels of ozone. Environ. Pollut. 6: 289–295.

Knutson, D. M. 1969. Effect of temperature and relative humidity on longevity of stored dwarf mistletoe seeds. Phytopathology 59: 1035 (abstract).

Koonce, A. L., and L. F. Roth. 1980. The effects of prescribed burning on dwarf mistletoe in ponderosa pine. Pages 197–203 *in* Proc. Sixth Conf. on Fire and Forest Meteorol. Seattle, Washington.

Korstian, C. F., and W. H. Long. 1922. The western yellow pine mistletoe: effect on growth and suggestions for control. USDA Bull. 1112. Washington, D.C. 35 pp.

Long, W. H. 1922. Mistletoe and smelter smoke. Phytopathology 12: 535–536.

McBride, J. R., and R. D. Laven. 1976. Scars as an indicator of fire frequency in the San Bernardino Mountains, California. J. Forest. 74: 439–442.

McMahon, C. K., and S. N. Tsoukalas. 1978. Polynuclear aromatic hydrocarbons in forest fire smoke. Pages 61–73 *in* P. W. Jones and R. I. Friedenthal, Carcinogens. Vol. 3, Polynuclear aromatic hydrocarbons. Raven Press, New York.

Parmeter, J. R., Jr., and B. Uhrenholdt. 1975. Some effects of pine needle or grass smoke on fungi. Phytopathology 65: 28–31.

Sandberg, D. V., J. M. Pierovich, D. G. Fox, and E. W. Ross. 1979. Effects of fire on air: a state-of-knowledge review. USDA For. Serv. Gen. Tech. Rept. WO-9. Washington, D.C. 40 pp.

Scharpf, R. F., and J. R. Parmeter, Jr. 1962. The collection, storage, and germination of seeds of a dwarf mistletoe. J. Forest. 60: 551–552.

Smith, W. H. 1981. Air pollution and forests. Springer-Verlag, Inc., New York. 379 pp.

Stokes, M. A., and J. H. Dieterich. 1980. Proceedings of the fire history workshop. USDA For. Serv. Gen. Tech. Rept. RM-81. Rocky Mtn. For. Range Expt. Sta., Fort Collins, Colorado.

Tan, Y. L., J. F. Quanci, R. D. Borys, and M. J. Quanci. 1985. Polynuclear aromatic hydrocarbons and smoke particulates from wood and duff burning. Unpublished manuscript in file of U.S. Department of Energy, Environmental Measurements Laboratory, New York, New York.

Tan, Y. L., J. F. Quanci, M. J. Quanci, and R. D. Borys. 1985. Polynuclear aromatic hydrocarbons in duff burning particulates. Page 555, abstract. Proc. 33d Ann. Conf. on Mass Spectrometry and Allied Topics.

Tinnin, R. O. 1981. Interrelationships between *Arceuthobium* and its hosts. Amer. Midl. Nat. 106: 126–132.

Weaver, H. 1951. Fire as an ecological factor in the south-western pine forests. J. Forest. 49: 93–98.

Weir, J. R. 1916. Mistletoe injury to conifers in the Northwest. USDA Bull. 360. Washington, D.C. 39 pp.

WELLNER, C. A. 1970. Fire history in the northern Rocky Mountains. Pages 41–64 *in* The role of fire in the Inter-mountain West, Symp. Proc. Missoula, Montana.

WICKER, E. F. 1974. Ecology of dwarf mistletoe seed. USDA For. Serv. Res. Pap. INT-154. Intmtn. For. Range Expt. Sta., Ogden, Utah. 28 pp.

WICKER, E. F., AND C. D. LEAPHART. 1976. Fire and dwarf mistletoe (*Arceuthobium* spp.) relationships in the northern Rocky Mountains. Tall Timbers Fire Ecol. Conf. Proc. 14: 279–298. Missoula, Montana. October 1974.