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Mistletoes of North American Conifers

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Abstract

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Mistletoes of the families Loranthaceae and Viscaceae are the most important vascular plant parasites of conifers in Canada, the United States, and Mexico. Species of the genera *Psittacanthus*, *Phoradendron*, and *Arceuthobium* cause the greatest economic and ecological impacts. These shrubby, aerial parasites produce either showy or cryptic flowers; they are dispersed by birds or explosive fruits. Mistletoes are obligate parasites, dependent on their host for water, nutrients, and some or most of their carbohydrates. Pathogenic effects on the host include deformation of the infected stem, growth loss, increased susceptibility to other disease agents or insects, and reduced longevity. The presence of mistletoe plants, and the brooms and tree mortality caused by them, have significant ecological and economic effects in heavily infested forest stands and recreation areas. These effects may be either beneficial or detrimental depending on management objectives. Assessment concepts and procedures are available. Biological, chemical, and cultural control methods exist and are being developed to better manage mistletoe populations for resource protection and production.

Keywords: leafy mistletoe, true mistletoe, dwarf mistletoe, forest pathology, life history, silviculture, forest management

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Mistletoes of North American Conifers

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Preface

The mistletoes are serious disease agents affecting forests in all three countries represented by the North American Forestry Commission (NAFC 2002): Canada, Mexico, and the United States of America. For this reason, the Commission through its Insect and Disease Study Group has asked us to prepare a practical guide for field foresters. This publication provides basic information on the species of mistletoes, their hosts, distributions, effects, methods of evaluation, and management. This work updates and expands the several pages dedicated to mistletoes in the previous guide produced for the NACF (Davidson and Prentice 1967). This book covers the mistletoes (Loranthaceae and Viscaceae) that parasitize conifer hosts and occur in North America (Canada, United States, and Mexico). A similar management synopsis but from a different perspective is available for the mistletoes of eucalypts in Australia (Reid and Yan 2000).

The literature on mistletoes is large (over 5,700 articles on North American mistletoes) but widely scattered for some topics and rare for other topics. We intend this synoptic review as a guide to useful references for addressing management concerns from biological conservation to wood fiber production. Because many references have been already cited by Hawksworth and Wiens (1996) for the dwarf mistletoes, we give emphasis to general reviews, recent publications, and information on other mistletoes. An extensive, searchable, annotated bibliography (and other information) is available at the Mistletoe Center (2002). To facilitate use of this guide, we provide a glossary for specialized terms (see appendix D) and post the text online.

Many chapters in this book were first drafted by F. G. Hawksworth and D. Wiens as they were preparing botanical monographs for *Phoradendron* and for *Arceuthobium* (published as Hawksworth and Wiens 1996). Although information in this book has been selected, revised, and updated, the present authors and technical editors acknowledge Hawksworth and Wiens as the original source for many passages of text.

The systematics of *Psittacanthus*, *Phoradendron*, and *Arceuthobium* are the active subjects of current research; taxonomic revisions of these genera are expected in the near future. This book is not a systematics and taxonomic review of these mistletoes; no new species names or combinations are proposed. The nomenclature used in this book for mistletoes is adapted from several sources including taxonomic publications by Hawksworth, Wiens, and others (see Hawksworth and Wiens 1996), the International Plant Names Index (Plant Names Project 1999), the VAST database (Missouri Botanical Garden 2002), and the National PLANTS database (USDA, NRCS 2001).

The taxonomy of many host groups is also subject to uncertainty, disagreement, and revision. The names of many hosts cited in the literature are no longer accepted, and the proper name for a population in question may not be apparent. The host taxonomy accepted here follows the Flora of North America (Flora of North America Committee 1993) for Canada and the United States and Perry (1991) for Mexico. These sources also provide valuable host information including description, synonymy, and distribution. Nomenclatures for taxa not represented in these sources (and some authorities) are from the International Plant Names Index (Plant Names Project 1999).

Because this book has international readership in several languages (English and Spanish), we usually refer to plants by their scientific name. To accommodate those not familiar with these names, we provide appendix B, relating scientific and vernacular names for trees species; and we refer to common genera in the text as “pines” for *Pinus* and “dwarf mistletoes” for *Arceuthobium*. The formal nomenclature for mistletoes including authority, publication, and common synonyms is given for each mistletoe before its description.

The technical editors are grateful to the many supporters, contributors, reviewers, and editors who helped to prepare and publish this guide (see appendix C). We thank C. G. Shaw and Jerome Beatty, USDA Forest Service, Washington Office, for their helpful support to this project. We also thank the members of the NAFC, Insect and Disease Study Group for encouraging and supporting this work. The NAFC (2002) is a commission of the Food and Agriculture Organization of the United Nations and consists of the national forest agencies of Canada, the United States, and Mexico. Specialists from the represented countries meet in study groups to exchange technical assistance on insects and diseases, tree improvement, silviculture, fire management, and other topics.

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Author Profiles

Frank G. Hawksworth died in 1993 after starting this project and a monographic review of the genus *Arceuthobium*. He had been Project Leader and Supervisory Plant Pathologist with the Rocky Mountain Research Station in Fort Collins, CO. Beginning with his doctoral studies at Yale University, Dr. Hawksworth dedicated his professional life to the single question, "What is mistletoe?" He described numerous species (most with Del Wiens), authored over 275 articles on dwarf mistletoes, and compiled an extensive library on mistletoes of the world. He is commemorated by *Arceuthobium hawksworthii*.

Delbert Wiens is retired Professor of biology, University of Utah, Salt Lake City. He received a Ph.D. degree from the Claremont Graduate School, CA for his work on the taxonomy of *Phoradendron*. Dr. Wiens has investigated numerous aspects of plant biology including systematics, biogeography, cytology, reproductive biology, and mimicry. He has a particular interest in the Loranthaceae and Viscaceae and the flora of Africa and Southeast Asia. Dr. Wiens recently completed a popular book on the mistletoes of Africa and continues exploring the world.

John A. Muir is a registered professional Forester by the Province of British Columbia and serves as the Provincial Forest Pathologist for the Ministry of Forests, Victoria, B.C. Dr. Muir earned a Bachelor and Master degrees in forest pathology from the University of British Columbia; he has a Ph.D. degree in plant pathology from the University of California, Berkeley. His current activities include development of forest practices and regulations for diseases and development of models and decision aids for dwarf mistletoes and other pathogens. His work supports innovative disease management practices such as genetic resistance and intensive cultural techniques to enhance growth and sustainability of young forests.

Simon F. Shamoun is a research scientist with the Canadian Forest Service, Pacific Forestry Centre and adjunct professor at the University of British Columbia and at the University of Victoria. Dr. Shamoun obtained a Bachelor of Science degree in forestry from the University of Mosul, Nineveh, Mesopotamia (Iraq); Master of Science degree in plant pathology from North Carolina State University; and a Ph.D. degree in plant pathology from the University of Arkansas. His current research focuses on management of competing vegetation, forest weeds, and dwarf mistletoes using fungal pathogens. He is investigating the population structure and genetic diversity of several candidate biological control agents and their target plants.

Laura E. DeWald is an Associate Professor of forest genetics and conservation biology in the School of Forestry, Northern Arizona University, Flagstaff, AZ. She received a Bachelor of Science degree in forestry from Michigan Technological University, Master of Science degree in forest genetics from Pennsylvania State University, and a Ph.D. degree in forest genetics and physiology from Virginia Polytechnic Institute and State University. In addition, she completed postdoctoral studies in forest genetics and physiology at the University of Minnesota and the University of Florida. Her current research focuses on application of ecological genetics to forest management and restoration, insect and disease resistance of Southwestern tree species, and riparian restoration.

Ignacio Vázquez Collazo is a Research Investigator at the Centro de Investigaciones del Pácifico Centro in Uruapan, Michoacán, Mexico. He has published numerous articles on the biology, effects, and management of both dwarf mistletoes and leafy mistletoes in central Mexico.

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CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife—if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

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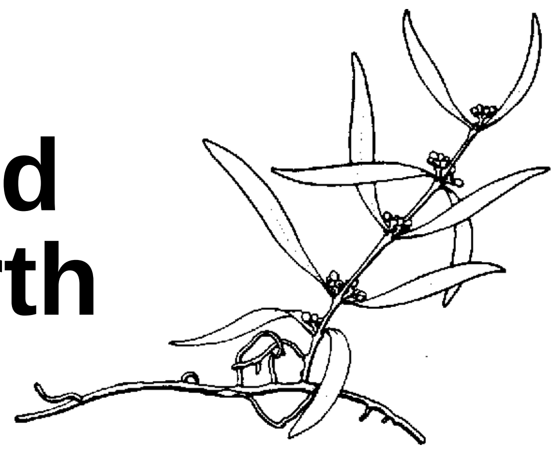

Loranthaceae and Viscaceae in North America

Mistletoes of Canada, Mexico, and the United States

The mistletoes are a diverse group in the order Santales of shrubby, usually aerial, parasitic plants with fruits possessing a viscid layer (Kuijt 1968, 1969a). They are widely distributed geographically and as a group have a broad host range on conifers and other woody plants (Calder 1983). Many mistletoes are specially adapted for avian pollination and dispersal, and several avian species make extensive use of these resources (Kuijt 1969a, Watson 2001). The mistletoes are damaging pathogens of trees; and in many parts of the world are serious forest pests (Hawksworth 1983, Knutson 1983). General information on mistletoes is available at Calder and Berhhardt (1983), Cházaro and others (1992), Geils (2001a, 2001b), Gill and Hawksworth (1961), Kuijt (1969a), Mistletoe Center (2002), Nickrent (2002), Sinclare and others (1987), and Vega (1976).

The principal families of mistletoe are the Loranthaceae and Viscaceae (Calder 1983). The Eremolepidaceae, Misodendraceae, and several genera of Santalaceae could also be included as "mistletoes," but these interesting parasites do not occur on North American conifers (Kuijt 1969a, 1988, Wiens and Barlow 1971). The loranthaceous and viscaceous mistletoes had been considered sub-families within the Loranthaceae but are now recognized as distinct, related families (Barlow 1964). There are several anatomical, embryological, and chromosomal differences between the two families (Kuijt 1969a, Wiens and Barlow 1971), but a practical difference is that the flowers in the Viscaceae are small and inconspicuous, whereas those in the Loranthaceae are large, colorful, and possess a calyculus (see Venkata 1963). The Viscaceae occur in tropical and temperate zones of the Northern Hemisphere; the Loranthaceae are generally tropical (Barlow 1983). The two families overlap in Mexico (Cházaro and Oliva 1987a, 1987b, 1988a).

The mistletoes of conifers in the New World are *Cladocolea*, *Struthanthus*, *Psittacanthus*, *Dendropemon* (Loranthaceae) plus *Arceuthobium*, *Phoradendron*, and *Viscum* (Viscaceae) (table 1-1). Scharpf and others (1997) review these genera and list the other mistletoes that infect conifers elsewhere. The most important genera to North American forestry are *Arceuthobium*, *Phoradendron*, and *Psittacanthus*. Field guides or keys for the identification of these mistletoes include: Bello (1984), Bello and Gutierrez (1985), Hawksworth and Scharpf (1981), Scharpf and Hawksworth (1993), Standley (1920), Tropical Agriculture Research and Training Center (1992), and Unger (1992).

The genus *Cladocolea* Tiegh. includes at least 23 little-studied mistletoes mostly of Central and Southern Mexico (Cházaro 1990, Kuijt 1975a). Plants are erect or vine-like shrubs (fig. 1-1); most species are parasites of oaks or other broadleaf trees. These mistletoes cause little damage to their hosts; their greatest importance is scientific, as rare species in a curious genus. The species reported to infect conifers (table 1-2) are:

- *Cladocolea cupulata* Kuijt [Journal Arnold Arboretum 56(3):285–286, 1975]
- *C. microphylla* (Kunth) Kuijt [Journal Arnold Arboretum 56(3):313–317, 1975]

Mistletoes of the genus *Struthanthus* Mart. are climbing vines to several meters long (fig. 1-2). These mistletoes ("mata palo" or "tripa de pollo") include 50 to 60 species from Mexico to Argentina (Bello 1984, Cházaro and Oliva 1988a, Kuijt 1964, 1975b). The *Struthanthus* mistletoes typically have broad host ranges that occasionally include a few conifers. The genus *Struthanthus* is a taxonomically chaotic and difficult group (Kuijt 1969a); applied names should be accepted with caution. The species reported to infect conifers (table 1-2) are:

- *Struthanthus deppeanus* (Schldt. & Cham.) Blume [Systema Vegetabilium 7:1731, 1830]
- *S. interruptus* (Kunth) Blume [Systema Vegetabilium 7:1731, 1830]
- *S. palmeri* Kuijt [Canadian Journal Botany 53(3):252. 1975]
- *S. quericola* (Schltdl. & Cham.) Blume [Systema Vegetabilium 7:1731, 1830]

Table 1-1—Mistletoes of North American conifers.

Family	Genus	Distribution in North America	Conifer hosts in North America
Loranthaceae			
	Cladocolea	Mexico	*Pinus*
	Struthanthus	Mexico	*Pinus, Taxodium*
	Psittacanthus	Mexico	*Abies, Pinus*
Viscaceae			
	Arceuthobium	Canada, Mexico, United States	*Abies, Larix, Picea, Pinus, Pseudotsuga, Tsuga*
	Phoradendron	Mexico, United States	*Abies, Calocedrus, Cupressus, Juniperus, Taxodium*
	Viscum	Canada, United States	*

*In North America, *Viscum* occurs as an introduced species only on angiosperms; elsewhere *Viscum* infects *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, and *Juniperus*.

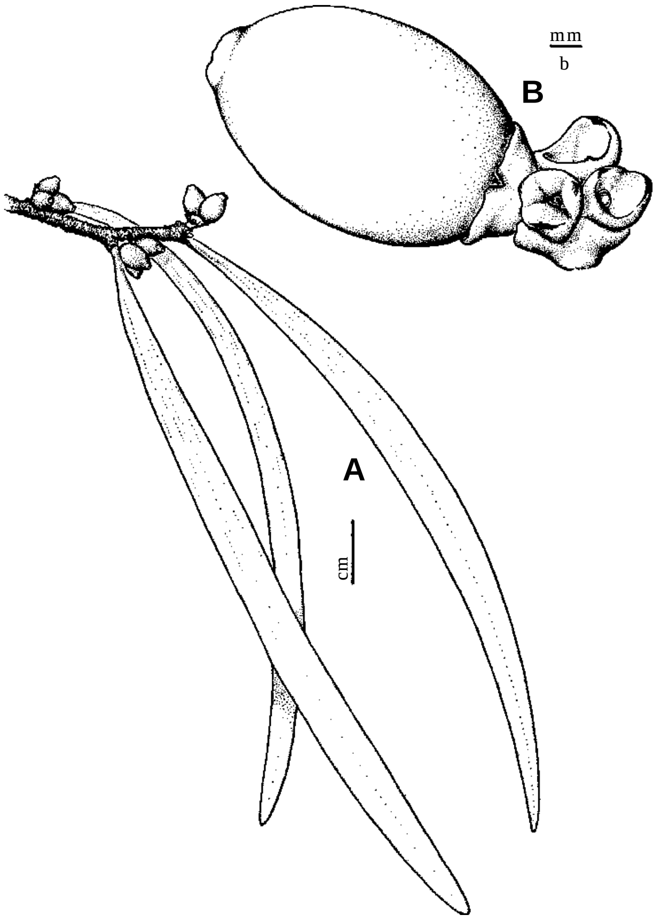

Figure 1-1—*Cladocolea cupulata*, **A** habit, pistillate plant and **B** fruit and supporting structure (three fruits removed). Illustration courtesy of Job Kuijt, edited from figure 9 in Journal Arnold Arboretum. 56(3): 285.

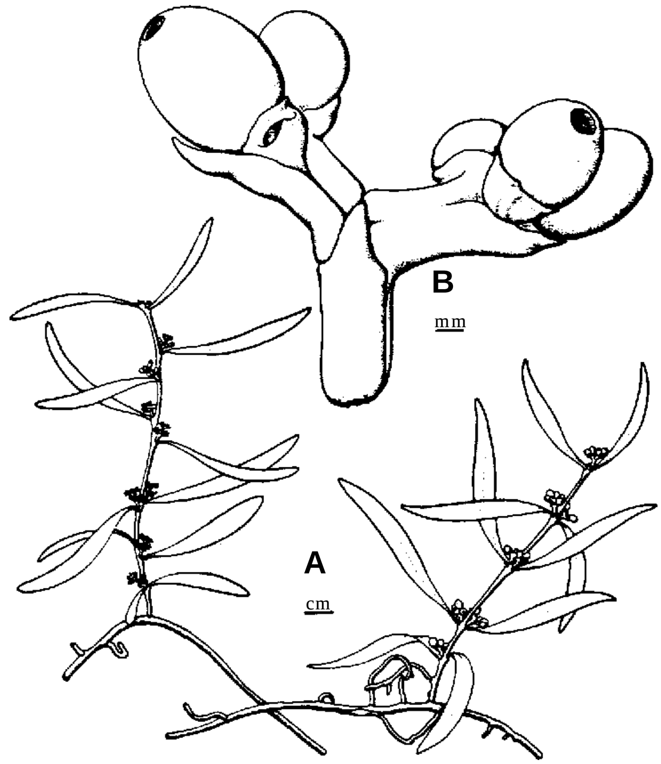

Figure 1-2—*Struthanthus palmeri*, **A** a habit, staminate plant and **B** fruit and supporting structure. Illustration courtesy of Job Kuijt, edited from figures 6 and 7 in Canadian Journal of Botany 53:252.

Table 1-2—*Cladocolea* and *Struthanthus* occurrence on conifers in Mexico.

Mistletoe	Distribution	Hosts	Reference
Cladocolea cupulata	Jalisco	*Pinus jaliscana* *P. lumholtzii*	Cházaro and others (1992)
Cladocolea microphyllus	Michoacán	*Pinus leiophylla*, *P. montezumae*, *P. pseudostrobus*	Bello Gonzalez (1984)
Struthanthus deppeanus	Chiapas, Oaxaca, Puebla, Veracruz	*Pinus patula*	Cházaro and Oliva (1988a)
Struthanthus interruptus	Michoacán	*Pinus lawsonii*	Bello Gonzalez (1984)
Struthanthus palmeri	Sonora	*Taxodium distichum* var. *mexicanum*[c]	Kuijt (1975b)
Struthanthus quericola		*Pinus* sp.	Cházaro and Oliva (1988a)

Note: These mistletoes are principally parasites of hardwoods over most of their distribution; this table presents only reports of the mistletoe on a conifer host and their joint distribution.

[a]Reported as *Struthanthus microphyllus*; determination by Kuijt (personal communication)

[b]Reported as *Struthanthus venetus*; determination by Kuijt (personal communication).

[c]Reported as *Taxodium mucronatum.*

Struthanthus palmeri (fig. 1-2) is found as far north as 60 km south of Nogales, AZ, and may be the most northern of the New World Loranthaceae (Kuijt 1975b). *Struthanthus* mistletoes cause little economic damage and are most important for scientific interest.

The genus *Psittacanthus* consists of 75 to 80 species, distributed from Mexico to Argentina on a wide range of angiosperm and gymnosperm hosts. In contrast to most of the other mistletoes of Mexico, the flowers are large and conspicuous-red, yellow, or orange (Cházaro and Oliva 1988a). Although about 10 species occur in Mexico, only four are parasites of fir or pine. These mistletoes are widely distributed but seriously damaging in only a few locations. The biology and management of these mistletoes are discussed in chapter 2.

The genus *Phoradendron* includes about 250 species, exclusive to the New World in tropical or temperate zones. Hosts include several genera of conifers, many broadleaf trees and shrubs, and other mistletoes. In some areas, *Phoradendron* mistletoes can be quite common and cause serious damage to conifers (Hawksworth and Scharpf 1981). The *Phoradendron* species on conifers are described in chapter 3.

The dwarf mistletoes, genus *Arceuthobium*, consist of 42 species of North and Central America, Europe, Asia, and Africa (Hawksworth and Wiens 1996). These mistletoes are restricted to conifers and usually quite damaging to their host. Descriptions, hosts, and distributions of 40 taxa are presented in chapter 4; damage, effects, and importance in chapter 5; survey methods in chapter 6; and management in chapters 7 and 8.

Two other genera of mistletoes are worthy of mention here. The European mistletoe, *Viscum album* L., was introduced to California by Luther Burbank about 1900 (Hawksworth and others 1991), and a recent introduction was discovered in 1988 for British Columbia (Muir 1989). Although subspecies of *Viscum album* are able to infect fir, spruce, pine, Douglas-fir, and juniper native to North America, *Viscum album* in Canada and the United States is only reported on broadleaf trees (Barney and others 1998). This mistletoe is not considered a threat to natural conifer stands in North America. Two additional species of mistletoes on conifers have been collected from Hispaniola in the Caribbean (Kuijt, personal communication). *Dendropemon constantiae* Krug & Urban is an uncommon species usually found on *Pinus occidentalis*; and *D. pycnophyllys* Krug & Urban is a common species, apparently restricted to pine hosts.

Although many mistletoe genera share host species in common, there are only a few examples of two genera of mistletoe infecting the same tree (Hawksworth and Wiens 1996). *Abies concolor* is coinfected by *Arceuthobium abietinum* and *Phoradendron pauciflorum* in California. *Pinus engelmannii* is coinfected by *A. vaginatum* subsp. *vaginatum* and *Psittacanthus macrantherus* in Durango, Mexico. *Pinus pseudostrobus* is coinfected by *A. globosum* subsp. *grandicaule* and *Psittacanthus macrantherus* in Michoacán, Mexico.

Economic and Ecological Importance

Mistletoes have long been held by many peoples as special. Their sacred, mythical role in numerous cultures is documented by Frazer (1930) in his classic study of magic and the golden bough. Mistletoes are an inspiration for art (Becker and Schmoll 1986); their haustoria produce woodroses. In traditional, agricultural societies, mistletoes provide fodder, dyes, and drugs. Mistletoes are used for holiday decoration and models for new pharmaceuticals. A few North American mistletoes are narrow endemics threatened with extinction. Rolston (1994) describes the values of such species and why they ought to be preserved. Most mistletoes, however, have

Key to Genera of Mistletoes in North America

1. Flowers with a calyculus, usually large and showy (Loranthaceae) 2
    2. Flowers less than 1 cm long, light green; leaves less than 5 cm long and 2 cm wide 3
        3. Inflorescence a determinate spike of monads .... *Cladocolea*
        3. Inflorescence generally indeterminate, dioecious .... *Struthanthus*
    2. Flowers 3–5 cm long, yellow or reddish; leaves 5–8 cm long and over 2 cm wide .... *Psittacanthus*
1. Flowers without a calyculus, less than 3 mm long, same color as the shoots; plants leafless or with leaves less than 5 cm long or 2 cm wide (Viscaceae) 4
    4. Fruit elongated and bicolored; seeds explosively dispersed (one exception); leafless; parasitic on pine, Douglas-fir, spruce, larch, fir, or hemlock .... *Arceuthobium*
    4. Fruit round, uniformly colored pink, reddish, or white; seeds dispersed by birds; leafless or with well-developed leaves, parasitic on juniper, cypress, incense-cedar, bald-cypress or fir .... *Phoradendron*

wide distributions, are locally abundant, and significantly alter the environment (Watson 2001). These mistletoes are important agents of disease, disturbance, and evolution. As pathogens, mistletoes affect host physiology (Knutson 1983, Kolb 2002). The results of tree disease are brooming, dieback, reduced growth, survival, and reproduction and increased susceptibility to other diseases and injuries. The consequences of an infestation are both economic and ecological. Mistletoes are forest pests for the commercial losses they cause and are influential symbionts for the many and complex interactions they affect. Assessing mistletoe importance revolves around two questions: how much (extent and abundance) and what effects.

Because mistletoes have major resources impacts (such as on timber yield), information is compiled regionally to describe their incidence and severity. North America consists of Canada, the continental United States of America, and the Republic of Mexico (fig. 1-3). North American mistletoes are found in most of the major coniferous forests and parasitize pine, fir, spruce, Douglas-fir, larch, hemlock, juniper, cypress, incense-cedar, and bald-cypress (table 1-1). The significant conifers not parasitized are arborvitae (*Thuja*), redwood (*Sequoia*), and giant sequoia (*Sequoiadendron*). The only mistletoes in Canada are dwarf mistletoes, but these occur across the country from Newfoundland to British Columbia. The most important are in eastern spruce bogs (Magasi 1984), central jack and lodgepole pine forests (Brandt and others 1998), and coastal hemlock forests (Alfaro 1985). Both *Phoradendron* and *Arceuthobium* occur in the United States. Although *Phoradendron* mistletoes are widely distributed across the Southern and Western States, the species that infect conifers are most common in the Western–Southwestern portion of the country (from western Texas to California, Colorado, and Oregon). *Phoradendron* mistletoes are abundant and damaging in some locations, but we know of no regional estimates of their incidence and severity. The dwarf mistletoes occur in the Northeastern States, Northern Lake States, Western States, and southeastern Alaska (see Forest Health Protection 2002). Drummond (1982) reports the infested area as 14 percent for the black spruce type in the Northern Lake States; 22 percent for the Rocky Mountain Douglas-fir type; 34 percent of the Rocky Mountain ponderosa pine type; 40 percent of the lodgepole pine type; and 22 percent of the commercial host type in Pacific states. Mistletoes including *Psittacanthus*, *Phoradendron*, and *Arceuthobium* are the principal cause of forest disease across Mexico. Mistletoes are most abundant in the cool or temperate coniferous forests and are found on more than 10 percent of the forest area (Hawksworth 1983). The forest area infected varies by State—Durango 15 percent, Nayarit 10 percent, Sonora 9 percent, Chihuahua 8.5 percent, Baja California 7 percent, Zacatecas 24 percent, Sinaloa 10 percent, and Jalisco 12 percent (Caballero 1968, 1970). Although the actual extent of infested area on a regional basis changes little from year to year, various definitions and data sources are used. These generate somewhat different estimates that are in broad agreement that mistletoes are common in some areas.

From an economic perspective, the effects of mistletoe infestation are described by Hawksworth (1993). Relevant to timber production, mistletoes reduce growth, yield, and quality and increase operation and protection costs for planning, harvesting, regeneration, and fuel management. Mistletoes are a concern in recreation areas for increased hazard from broom breakage (Hadfield 1999) and increased expense in vegetation management (Lightle and Hawksworth 1973).

From an ecological perspective, the effects of mistletoe infestations are complex because there are numerous criteria and relationships that might be considered relevant in a given situation. Allen and Hoekstra (1992) suggest describing ecological phenomena from alternative viewpoints or “criteria” of the population, species, community, landscape, and ecosystem. For a diseased tree, mistletoe infection means reduced competitive status and reproduction fitness (but see van Ommeren and Whitham 2002). The symbiotic relation between host and mistletoe has numerous population genetic and coevolutionary consequences that cannot be properly categorized as positive or negative (see Atsatt 1983, Norton and Carpenter 1998). Other species in addition to a host also are connected to the mistletoe by herbivory, pollination, use of the witches’ broom, or other relations. Watson (2001) recognizes mistletoes as keystone resources in many communities. Canopy effects are especially significant. Crown deformation and tree death affect composition of trees that compose the forest canopy and the structure of that canopy (Reid and others 1995). Numerous species, landscape, and ecosystem processes are consequently influenced—there are winner and losers, increases and decreases. Many indirect and long-term interactions involving mistletoes exhibit chaotic behaviors; a range of outcomes are likely rather than a single one determined (see Gleick 1988). The relevant fact is that mistletoes are often an important ecological and evolutionary agent driving that system (Holling 1992).

Management Strategies

The mistletoe literature indicates not only that mistletoes have important effects but also that infestations can be affected by management intervention to change their spread and intensification. Effective

Figure 1-3—North America, Canada, United States of America, and Mexico with political subdivisions.

Canadian Provinces, Territories and abbreviations

Province-Territory	Abbreviation
Alberta	Alta.
British Columbia	B.C.
Manitoba	Man.
New Brunswick	N.B.
Newfoundland	Nfld
Northwest Territories	N.W.T.
Nova Scotia	N.S.
Ontario	Ont.
Prince Edward Island	P.E.I
Quebec	Que.
Saskatchewan	Sask.
Yukon Territory	Y.T.

Mexican States and abbreviations

Mexican state	Abbreviation
Aguascalientes	Ags.
Baja California	B.C.
Baja California Sur	B.C.S.
Colima	Col.
Coahuila	Coah.
Chiapas	Chis.
Distrito Federal	D.F.
Durango	Dgo.
Guerrero	Gro.
Guanajuato	Gto.
Hidalgo	Hgo.
Jalisco	Jal.
Michoacan	Mich.
Morelos	Mor.
México	Edo de Mex.
Nayarit	Nay.
Nuevo León	N.L.
Oaxaca	Oax.
Puebla	Pue.
Quintana Roo	Q. Roo
Querétaro	Qro.
Sinaloa	Sin.
San Luis Potosí	S.L.P.
Sonora	Son.
Tabasco	Tab.
Tlaxcala	Tlax.
Tamaulipas	Tamps.
Veracruz	Ver.
Yucatán	Yuc.
Zacatecas	Zac.

U.S. states and abbreviations

Province-Territory	Abbreviation
Alabama	AL
Alaska	AK
Arizona	AZ
Arkansas	AR
California	CA
Colorado	CO
Connecticut	CT
Delaware	DE
Dist. of Columbia	DC
Florida	FA
Georgia	GA
Idaho	ID
Illinois	IL
Indiana	IN
Iowa	IA
Kansas	KS
Kentucky	KY
Louisiana	LA
Maine	ME
Maryland	MD
Massachusetts	MA
Michigan	MI
Minnesota	MN
Mississippi	MS
Missouri	MO
Montana	MT
Nebraska	NE
Nevada	NV
New Hampshire	NH
New Mexico	NM
New Jersey	NJ
New York	NY
North Carolina	NC
North Dakota	ND
Ohio	OH
Pennsylvania	PA
Rhode Island	RI
South Carolina	SC
South Dakota	SD
Tennessee	TN
Texas	TX
Utah	UT
Vermont	VT
Virginia	VA
Washington	WA
West Virginia	WV
Wisconsin	WI
Wyoming	WY

intervention is both purposeful and persistent. Tkacz (1989) describes an approach called Integrated Resource Management used in the Southwestern Region, USDA Forest Service, that incorporates forest insect and disease considerations into a planning, implementing, and monitoring process. Many other organizations have comparable management systems. Common elements of these systems include (1) formulation of objectives, (2) review of the expected performance of alternatives, (3) selection and implementation, and (4) monitoring and reaction. Holling and Meffe (1996) warn of the dangers from attempting rigid control in natural resource management; they advocate an adaptive process for complex environments with changing objectives and management options. Although management in mistletoe-infested stands has not always been successful for various reasons (Conklin 2000), management processes and techniques are available with the potential for producing desirable results.

A simplistic review of one management strategy that once dominated conifer forestry is instructive. A prevailing objective on public forests in the 20th century was sustained economic production of timber. Foresters knew that dwarf mistletoes were obligate parasites that died when the host tree was cut and had limited capability of spread (Weir 1916b). The preferred control technique was clearcutting in large blocks to remove the mistletoe and retard reinfestation (Stewart 1978). Where employed, it worked. A challenge to forest pathologists arose when objectives were expanded to include wildlife and aesthetic values, and treatments required or produced infrequent, selective removal that left infected trees. At least in the American Southwest, dwarf mistletoe infestations were not fading away (Conklin 2000, Maffei and Beatty 1988). Other control techniques based on biological, chemical, genetic, and silvicultural approaches were needed (Scharpf and Parmeter 1978, Muir 1993).

Hawksworth (1978) and Parmeter (1978) describe the epidemiological bases for control of dwarf mistletoes that can be extended with modification to other mistletoes. For technical and management reasons, silvicultural approaches have been used more commonly than chemical or biological control or genetic selection. Although there has been some success with chemical controls, phytotoxicity and need for reapplication have limited this approach (Adams and others 1993, Lichter and others 1991, Scharpf 1972). The concepts of control with biological agents are well developed (DeBach 1964), and use of insects and fungi on mistletoes has been considered (Cházaro and others 1992, Julian 1982, Mushtaque and Balock 1979). There is evidence for inherited variation in host resistance to infection by at least the dwarf mistletoes. Genetic selection may provide regeneration alternatives (Ringnes and others 1996). Silvicultural approaches include pruning, sanitation, species replacement, and other techniques that rely on cutting trees. As with chemical, biological, and genetic approaches, cultural methods must be adapted to fit the mistletoe and host combination in the context of specific management objectives and constraints.

Assessment and monitoring are essential elements of a strategy for managing mistletoes. Mistletoe infestations initially develop slowly but accelerate rapidly and cause significant departure from typical stand development. These facts suggest that early intervention provides greater flexibility and that a good model of stand response is useful for predicting what a treatment might produce in 20 to 40 years. Although the Dwarf Mistletoe Impact Model (Forest Health Technology Enterprise Team 2002) is primarily intended for assessing silvicultural alternatives, it (and other models) can be modified or developed for evaluating tactics of deploying biological agents or genetically selected stock (Robinson and others 2002).

The mistletoes of North American conifers range from obscure species in remote locations to major forest pests. Management varies from intensive timber production to biological conservation. Although these mistletoes can have significant impacts on forest conditions, they are also subject to management influence through various methods that alter rates of spread and intensification. Knowing which methods are appropriate and effective requires an understanding for each kind of mistletoe: its life history, hosts, distribution, effects, and ecology.

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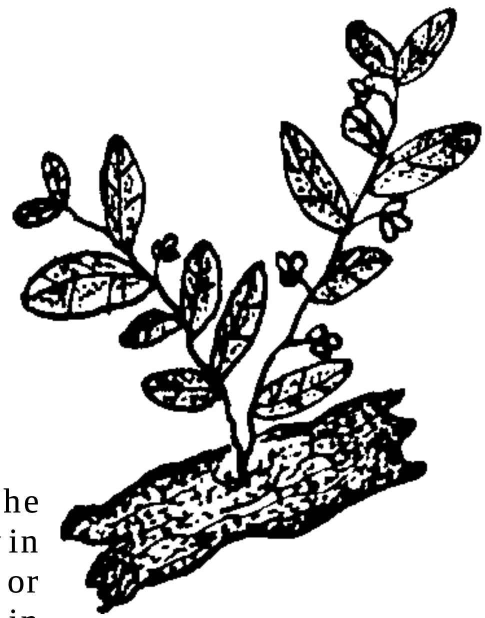
B. W. Geils

Chapter
2

Psittacanthus in Mexico



The *Psittacanthus*, parrot-flower, is the only genus of the family Loranthaceae that is significant to conifer forestry in North America. These mistletoes do not occur in Canada or the United States; and in Mexico, they are only important in central and southern portions. *Psittacanthus* also occurs in Central America (rarely on conifers) and other regions of the tropical New World where these mistletoes achieve their greatest diversity and abundance on numerous hardwoods. Plants are showy (fig. 2-1), become quite large, and are locally abundant. They are damaging to conifers, but they also provide special resource values. Because there are few studies for *Psittacanthus* on conifers (for example, Vázquez 1993a) and the taxonomy is confused, information on these mistletoes is sparse and difficult to interpret. This chapter reviews *Psittacanthus* on conifers with regard to life cycle, description, damage, importance, and management.

Figure 2-1—*Psittacanthus angustifolius*, **A** habit, leaves and flowers and **B** tip of petal. Illustration courtesy of Job Kuijt, edited from figure 10 in Annals Missouri Botanical Garden. 74:524.

General Life Cycle

The life cycle of *Psittacanthus* is divided into the fundamental processes of dispersal and development separated by inoculation and germination. Although some seeds are dispersed to the lower branches of an infested host by gravity, *Psittacanthus* is typically dispersed by birds feeding on fruits and defecating on branches. Incubation and production of the first flowers require several years. Once established, however, the infection is perennial, and the mistletoe produces a large haustorium with many long branches. Although *Psittacanthus* does photosynthesize, it is a parasite, and when it becomes large, it seriously interferes with host growth and reproduction.

Some of the *Psittacanthus* features that enhance bird-dispersal are time and duration of maturation, fruit size and attractiveness, adaptations for passage through the digestive tract, adhesion, and rapid germination after being voided (see Kuijt 1969a). Watson (2001) reviews the literature on coevolution of mistletoes and associates. Salas (1988) reports a study of *Psittacanthus* dispersal by birds at three sites in Michoacán (table 2-1). He observes that only eight out of 162 captured birds (4.9 percent, two crescent-chested warblers, a single Audubon's warbler, and two Bullock's orioles) carried mistletoe seeds in their feathers. Typical dispersal of *Psittacanthus* is for a passerine bird to feed on the fruit, fly to another tree, and void the seed to a suitable branch for infection. As with other mistletoes, those factors that influence bird abundance, distribution, and feeding behavior also affect the mistletoe's dispersal, population dynamics, host relations, and evolution (Lopez and Ornelas 1999).

Vázquez (1989) summarizes a 5-year study of *Psittacanthus calyculatus* on *Pinus douglasiana* in Michoacán. Additional data from that study are reported here (fig. 2-2) with observations of annual phenology (table 2-2). Bello (1984) provides photographs of an establishing seed, young plant, developing haustorium, and severely infested tree. *Psittacanthus* fruits are large (2.0 by 2.5 cm), and seeds have a sticky (viscous) layer that easily adheres them to a branch. When the basal portion of a mature seed makes contact, the seed germinates, opens its large cotyledons, and establishes an infection. Then 5 months later, the first true leaves are produced. Vegetative growth with more leaves and branches continues throughout the first year. Although shoot growth is determinate, the plant branches dichotomously expand its total length over the first 3 years at a rate of 30 cm per year. In May of the fourth year, shoot terminals begin producing flower buds. Full flowering is reached in 6 months; pollination occurs in November and December. The usual pollinators for most species are thought to be hummingbirds; but Freeman and others (1985) suggest passerine birds are the principal pollinators of *P. calyculatus* in Sinaloa. Senescing flowers are shed from November through March of the fourth year. Fruit maturation requires about 1 year and occurs from November to February of the fifth year. A generation therefore requires on average about 5 years to complete. Mature plants continue to flower and grow each year with an annual phenology that varies by host and elevation. On *Pinus douglasiana* at 1,700 m above sea level, full flowering occurs in November; on *P. pseudostrobus* at 2,400 m, flowering is delayed 3 months. Although an infection begins as a small plant growing *on* a host branch, it can

Table 2-1—Dispersal of *Psittacanthus calyculatus* at three sites in Michoacán, Mexico, for three guilds of bird species.

		Site		
Guild	**Species**	**Canoa alta**	**Capácuaro**	**Cicapien**
Insectivore				
	a Flycatcher	X	-	-
	Audubon's warbler	X	X	X
	Hermit warbler	-	-	X
	Common yellowthroat	X	-	-
	Black and white warbler	-	X	-
	Painted redstart	X	-	X
	Gray-sided chickadee	-	-	X
	Olive warbler	-	X	X
	Bushtit	-	X	X
	White-breasted nuthatch	-	-	X
	Warbling vireo	X	-	-
	Hutton's vireo	-	-	X
	Crescent-chested warbler	X	-	X
	Wilson's warbler	-	-	X
Omnivore				
	Bullock's oriole	X	X	X
	Gray silky-flycatcher	X	-	X
	American robin	-	X	X
Granivore				
	Rufous-capped brush-finch	-	X	X
	Black-headed grosbeak	-	X	X

Source: Salas (1988).

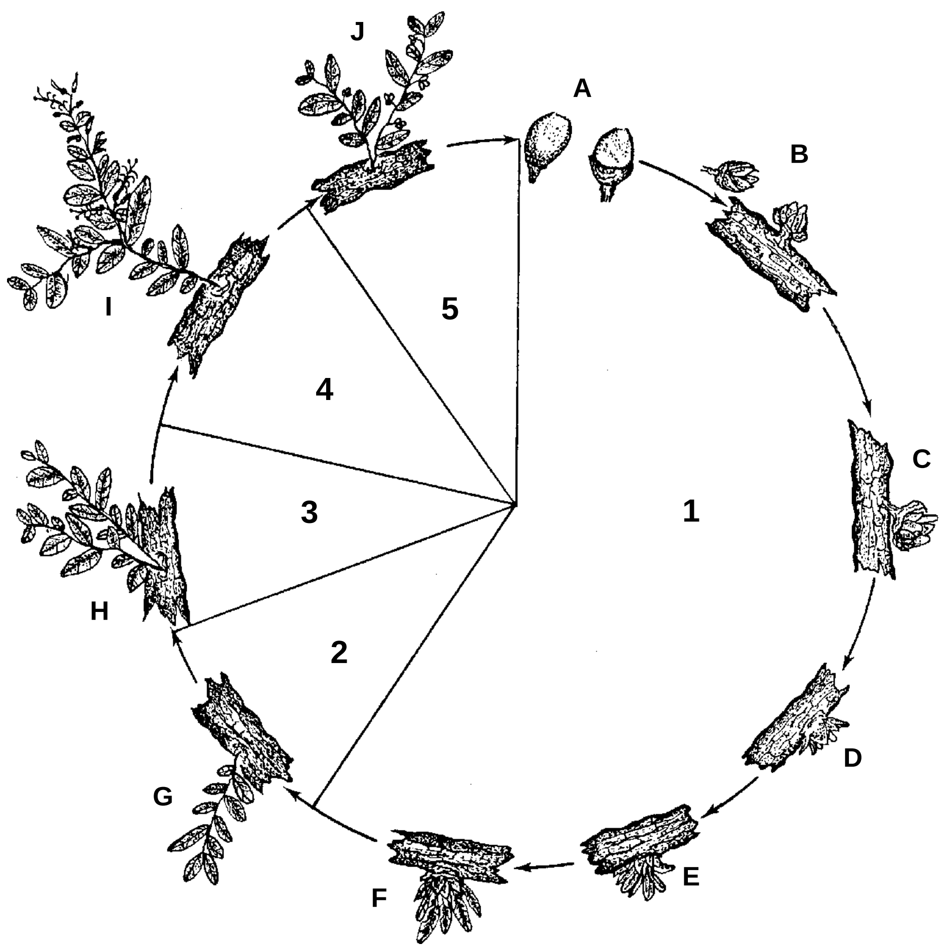


Figure 2-2—Life cycle of *Psittacanthus calyculatus*, from observations by Vázquez (1989) over a 5-year period. Year 1: A October, fruit matures; B November, infection; C November, cotyledons appear, D April, leaf buds appear; E October, leaves sprout; F October, leaves develop. Year 2: G continued vegetative growth. Year 3: H additional shoots develop. Year 4: I November, flowering. Year 5: J November, fruits mature.

Table 2-2—Phenology of *Psittacanthus calyculatus* on *Pinus douglasiana.*

Stage [b]	Month [a]											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
V1	X	X	-	-	-	-	-	-	-	-	-	-
V2	X	X	X	-	-	-	-	-	-	-	-	-
V3	X	X	X	X	X	X	X	X	X	-	-	-
FL1	X	X	X	X	X	X	X	X	-	-	-	-
FL2	X	X	-	-	-	-	-	-	-	-	-	-
FL3	X	X	-	-	-	-	-	-	-	-	-	-
FR1	X	X	X	X	-	-	-	-	-	-	-	-
FR2	X	X	X	X	X	X	X	X	X	X	X	X
FR3	X	X	X	X	-	-	-	-	-	-	-	-

[a] Month during which stages of life cycle are evident.
[b] V1 = early vegetative, V2 = full vegetative, V3 = final vegetative, FL1 = early flowering, FL2 = full flowering, FL3 = final flowering, FR1 = early fruiting, FR2 = full fruiting, FR3 = final fruiting.

ultimately *replace* the entire terminal portion of the host branch. With the vegetative growth of a single plant and sexual reproduction generating new plants, an infestation can eventually take over most of a tree's crown. Vázquez (1986) suggests a four-class system for rating infestation severity.

Kuijt (1967, 1970) describes the interesting anatomy and morphology of seedlings, seedling establishment, and the haustorium of *Psittacanthus*. Seedlings and the haustorium have several particular features that help construct a phylogeny for the genus (Kuijt 1983). The haustorium in *Psittacanthus* becomes quite large and is even harvested as a specialty product (see below).

Description of Genus

Psittacanthus
Mistletoe, parrot-flower, muérdago verdadero

Shrubby parasites of trees and other woody plants; stems brittle, erect, cylindrical or square, frequently ridged; epicortical root absent, primary haustorium often large; phyllotaxy opposite or whorled, leaves large (maximum 1 m in length), leathery or fleshy, green, persistent, opposite; leaf blade cordate, obovate, oval or lanceolate; leaf apex pointed; floral bracts short and stout; flower bisexual, six-partite, with a tubular perianth, 3 to 8 cm long, yellow, red, or orange, smooth; stamens dimorphic, as numerous as perianth lobes; anthers rarely more than 6 mm; ovary inferior, one-chambered; fruit berry, elliptical, green initially, developing into black or dark brown seed; endosperm lacking or apparently so (Standley 1920 but see Kuijt 1983).

Psittacanthus is endemic to the New World and ranges from Mexico to Argentina (Cházaro and Oliva 1988b). According to Reséndiz and others (1989), *Psittacanthus* is found in 25 Mexican States, absent only from Aguascalientes, Coahuila, Chihuahua, Hidalgo, Nuevo León, Tamaulipas, and Distrito Federal. Although *Psittacanthus* is distributed throughout Mexico, it is most common in the Central and Southern regions. Most species of *Psittacanthus* have broad host ranges on numerous woody hardwoods; some include conifers among their hosts. On conifers, *Psittacanthus* is limited to the cool temperate forests where conifers occur. The elevational distribution in Mexico ranges from 800 m on *Pinus oocarpa* to 3,300 m on *P. rudis*.

The taxonomy of *Psittacanthus* is quite confused; a comprehensive, monographic treatment would greatly benefit our understanding of the genus. Because of misidentification or subsequent taxonomic revision, numerous reports and publications refer to mistletoes using names that do not properly apply; sufficient information to identify the subject mistletoe is seldom given. These taxonomic difficulties are being overcome with projects such as Flora Mesoamericana (2002). Managers and researchers can reduce the confusion in the future by filing voucher specimens with a recognized herbarium for identification and future reference.

Standley (1920) initially describes only seven species of *Psittacanthus* for Mexico; Reséndiz and others (1989) later recognize 14 species for the country. Host data are frequently absent or sparse (genus only) on herbarium labels, but Reséndiz and others (1989) compile available data for Mexico from numerous collections. They report as hosts of *Psittacanthus* more than 50 genera of angiosperms and conifers, including trees, shrubs, and cactus. The primary angiosperm hosts are *Quercus*, *Acacia*, *Juglans*, *Ficus*, *Populus*, *Salix*, *Prunus*, *Prosopis*, *Annona*, *Bursera*, *Citrus*, *Nerium*, *Olea*, *Crataegus*, *Bacharis*, *Fraxinus*, *Eucaliptus*, *Persea*, *Cassuarina*, *Pseudosmondingium*, *Arbutus*, *Ulmus*, *Liquidambar*, *Psidium*, *Spondia*, *Phitecellobium*, *Amphipterigium*, *Pyrus*, *Mimosa*, and *Cydonia*. No monocots are known to be parasitized. *Psittacanthus* throughout its range is reported for conifers mostly on pine (table 2-3). In Mexico, the most common *Psittacanthus* species on conifers are *P. calyculatus* and *P. macrantherus* (Bello and Gutierrez 1985). Mathiasen and others (2000c) first report *P. angustifolius* on pine in Southern Mexico; this and other species (for example, *P. pinicola*) may be more widely distributed than apparent from the literature.

Description of Species

Only several species of *Psittacanthus* are reported as parasites of conifers in Mexico. Because of taxonomic uncertainty and the recent discovery of a new species for Mexico, we include in addition to frequently reported mistletoes several other species known or suspected to infect conifers in Mexico.

1. *Psittacanthus americanus*

Psittacanthus americanus (Mart.), Flora 13:108, 1830. =*Loranthus americanus* L

Description. Shrub 1 m tall; shoots erect and spreading, square or more or less angular, smooth; leaves fleshy, ovate, elliptical, rounded, 6 to 10.5 cm long by 3 to 6.5 cm wide, apex very obtuse; petiole short; perianth 6 cm long, bright red or orange; fruit berry, 0.8 by 1.0 cm, green initially, developing into reddish brown (Bello and Gutierrez 1985, Standley 1920).

Discussion. Vázquez and others (1986) refer to *Psittacanthus americanus* as abundant on *Pinus leiophylla*, *P. teocote*, and *P. montezumae* at sites in Michoacán. Standley (1920) adds Guerrero, and Bello and Gutierrez (1985) add Chiapas and Veracruz to the distribution. Reséndiz and others (1989) describe the species as having the smallest elevational range of the Mexican species. Kuijt (personal communication), however, reserves the name *Psittacanthus americanus* for a mistletoe of the Lesser Antilles that is not found in North or Central America. The collections of *Psittacanthus americanus* from Mexico should be reexamined.

2. *Psittacanthus angustifolius*

Psittacanthus angustifolius Kuijt, Ann. Missouri Bot. Gard. 74:523–525, 1987.

Description. Stems sharply angular; leaves paired, narrow, thin, 17 by 2.5 cm, base acute, apex attenuate; petiole to 5 mm long; inflorescences terminal, of four to six triads (groups of three); triad peduncles about 1 cm long, lowest with bracts to 2 cm long; bud stout, straight or somewhat curved; petals orange, 7.5 to 8 cm long, petal apices 4 mm wide, blunt, each with a

Table 2-3—Conifer hosts of *Psittacanthus* as reported in examined literature.

Host species	Reference
Abies religiosa	Bello (1984), Bello and Gutierrez (1985)
Cupressus sp.	MartÌnez 1983
Pinus caribaea var. *hondurensis*	Kuijt (1987), Mathiasen and Howell (2002)
Pinus douglasiana	Bello (1984), Bello and Gutierrez (1985), Vázquez (1989)
Pinus lawsonii	Bello (1984)
Pinus leiophylla	Bello (1984), Bello and Gutierrez (1985), Gibson (1978), Vázquez (1989), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)
Pinus maximinoi	Mathiasen and others (2000b)
Pinus michoacana	Bello (1984), Bello and Gutierrez (1985)
Pinus montezumae	Vázquez (1989), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)
Pinus oocarpa	Mathiasen and others (2000b)
Pinus oocarpa var. *ochoterenia*	Mathiasen and others (2000c)
Pinus pseudostrobus	Bello (1984), Gibson (1978)
Pinus tecunumanii	Melgar and others (2001)
Pinus teocote	Bello (1984), Bello and Gutierrez (1985), Vázquez and Pérez (1989), Vázquez and others (1982, 1985, 1986)

fleshy ligule-like median crest extending inwards (see fig. 2-1); anthers 6 mm long (Kuijt 1987).

Discussion. Kuijt (1987) only reports the host as pine, but the reported host range now includes *Pinus caribaea* var. *hondurensis*, *P. oocarpa*, *P. oocarpa* var. *ochoterenia*, *P maximinoi*, *P. tecunumanii*, and *Psidium guineese* (Mathiasen and Howell 2002, Mathiasen and others 2000b, Mathiasen and others 2000c, Melgar and others 2001). The mistletoe is known from Nicaragua, Belize, Honduras, Guatemala, and Mexico (Chiapas). Although the mistletoe appears to be more common and damaging in Central America (Mathiasen and others 2000c), it has only recently been described, and new populations are being discovered. With its wide host range, it may be more common in southern Mexico than presently reported.

3. *Psittacanthus calyculatus* (*sensu lato*)

Psittacanthus calyculatus (DC.) G. Don, Gen. Syst. 3:415, 1834.
Psittacanthus rhynchanthus (Bentham) Kuijt, Ann. Missouri Bot. Gard. 74:529, 1987
=*P. chrismarii*

Description. Shrub 1.0 by 1.5 m tall, herbaceous initially but becoming woody; stems green, quadrangular or ridged when young; leaves dark green, 5 to 14 cm long by 1.4 by 6 cm wide, leathery, lanceolate or elliptical to ovate, smooth; leaf blade asymmetric, margin undulating, with long attenuate apex and cuneate base, venation pinnate and prominent; inflorescence terminating the shoot; flower buds strongly incurved, 4 cm long, tip acute, base dilated, on peduncles up to 2 cm long, bracts fused to cup-like structure, in triads, perianth 3 to 5 cm long, red to orange, smooth; stamens as numerous as perianth lobes; fruit berry, 2.5 cm long by 2 cm wide, glabrous, with flaring calyculus (Bello and Gutierrez 1985, Hernandez 1991). Bello (1984) and Cházaro and Oliva (1988a) provide brief descriptions and illustrations.

Kuijt (1987) recognizes two similar taxa of *Psittacanthus* initially described as *Loranthus calyculatus* and *L. rhynchanthus.* He applies the name *P. calyculatus* to the Mexican species (Puebla and Morelia) in which the mature, unopened bud is nearly straight with a blunt tip, and the name *P. rhynchanthus* to a lowland, Mesoamerican (to Venezuela) species in which the bud is distinctively curved and beaked. He describes a number of additional characteristics that distinguish the two, such as symmetrical leaves 8 by 4 cm for *P. calyculatus* and asymmetrically curved, larger leaves 12 by 4 cm for *P. rhynchanthus*. Kuijt (1987) does not mention any host preference differences, but given the southern and lowland distribution of *P. rhynchanthus*, we suspect the more common parasite of conifers in Mexico is *P. calyculatus*. These differences, however, can only be resolved by examination of voucher specimens in light of Kuijt's interpretation of the type material.

Discussion. Bello (1984) lists the conifer hosts of *Psittacanthus calyculatus* as *Abies religiosa*, *Pinus douglasiana*, *P. lawsonii*, *P. leiophylla*, *P. michoacana*, *P. pseudostrobus*, and *P. teocote*. Vázquez here adds *Pinus montezumae*, *P. herrerai*, *P. pringlei*, and *P. rudis* and describes this as the species with the most number of conifer hosts, largest distribution, and most importance. Bello and Gonzales (1985) locate the mistletoe (without host distinction) as from Tamaulipas to Jalisco, Chiapas, Yucatan, Oaxaca, Valley of Mexico, Guanajuato, Morelia, and Michoacán. Freeman and others (1985) add Sinaloa, and Hernandez (1991) adds Tlaxcala. The mistletoe in Michoacán is widespread, mostly found in the subhumid temperate zones, from 1,300 to 2,750 m (Bello and Gonzales 1985). In natural stands of *P. leiophylla* and *P. pseudostrobus* in Michoacán, Gibson (1978) observes the mistletoe has a patchy distribution and some sites are severely infested. Vázquez (1989) describes the life cycle and phenology of this mistletoe. Vázquez (1994b) and Vázquez and others (1986) discuss control.

4. *Psittacanthus macrantherus*

Psittacanthus macrantherus Eichl., Mart. Flora Brasilense. 5(2):26, 1868.

Description. Shrub 1.0 m tall; shoots stiff, brown, cylindrical, glabrous; leaves 6 to 7.5 cm long, fleshy, elliptical, obovate, margin entire, apex obtuse, base attenuate; perianth 5.5 to 6.5 cm long, yellow or orange, large; anthers 18 mm long, as numerous as perianth lobes; fruit berry, green, glabrous (Bello and Gutierrez 1985, Standley 1920).

Discussion. Bello and Gutierrez (1985) only identify the hosts as pine and fir; but Vázquez (here) describes the pine hosts as *Pinus engelmannii*, *P. herrerai*, *P. lawsonii*, *P. lumholtzii*, *P. oocarpa*, and *P. pseudostrobus*. The mistletoe occurs locally in the Sierra de San Pedro Nolasco, Jalisco (Cházaro 1989b), Oaxaca and Michoacán (Bello and Gutierrez 1985), and Sinaloa (Gentry 1946). It ranges in elevation from 1,300 to 2,200 m. It is the second most important *Psittacanthus* on conifers in Mexico.

5. *Psittacanthus pinicola*

Psittacanthus pinicola Kuijt, Ann. Missouri Bot. Gard. 74:525–529, 1987.

Description. Stems terete, becoming fissured and black with age; leaves symmetrical, in irregular whorls of three 11 by 2.5 cm, elliptical to lanceolate; apex rounded, base tapered; inflorescences lateral, axillary, often on older leafless stems, an umbel of two or three dyads (groups of two); petals 4 cm long, red with yellow-green tip, orange in middle, ligulate at base; buds inflated at ovary to 5 mm, tapering to slender, curved tip at 1.5 mm; anther 3 to 4 mm long (Kuijt 1987, includes two illustrations).

Discussion. This attractive mistletoe is distinguished by the combination of parasitism on pine (*Pinus caribaea*) and inflorescences composed of pairs of flowers. The species is known from Central America at elevations below 650 m; it appears not to cause serious damage (Mathiasen and Howell 2002). Although we are aware of no collections from Mexico, other mistletoes (namely *Arceuthobium hondurense*) have recently been found to have widely disjunct distributions from Honduras to Mexico.

6. *Psittacanthus schiedeanus*

Psittacanthus schiedeanus (Schltdl. & Cham.) Blume, Sys. Veg. 7(2):1730, 1830.

Description. Shrub large, to 50 cm; stems, sharply quadrangular and four-winged until large lenticels develop; nodes flattened; haustorium very large; leaves bluish-green, 20 cm long by 8 cm wide; leaf blade asymmetric, ovate 6 to 16 by 1.4 by 4.5 cm; apex attenuate; petiole distinct and stout; venation pinnate; inflorescence terminal, leafless, forked; flowers 6.5 to 8 cm long in bud, on peduncles 1.5 to 2 cm long, perianth orange, 3 to 5 cm long, segments linear, separated to base, recurved; stamens dimorphic, very slender; fruit berry, 1.5 cm long by 1 cm wide (Bello and Gonzales 1985, Standley 1920). Bello (1984), Cházaro and Oliva (1988a), and Hernandez (1991) provide illustrations. Kuijt (1967) describes seedling structure and development in great and illustrated detail.

Discussion: The hosts most commonly reported for *Psittacanthus schiedeanus* are oaks and other hardwoods (Bello 1984, Lopez and Ornelas 1999). Vázquez and others (1982) name *Pinus leiophylla*, *P. montezumae*, and *P. teocote* as important, damaged hosts in Michoacán. Collections from Honduras (EAP) extend the hosts to include *P. oocarpa*. Standley (1920) reports this mistletoe as occurring in Central America and Mexico from Veracruz to Michoacán and Oaxaca. Hernandez (1991) describes its distribution in Tlaxcala, and it is collected from Chiapas (Flora Mesoamericana 2002).

Damage and Effects on Host

Damages produced by *Psittacanthus* to pine hosts include reductions of diameter increment, cone production, and seed viability. Vázquez and others (1982, 1985) report a series of studies from Michoacán to determine the effects of *Psittacanthus* to *Pinus leiophylla*, *P. montezumae*, and *Pinus teocote*.

Vázquez and others (1982, 1985) observe that the reduction in diameter increment for trees infected by *Psittacanthus* varies by host species and size class. The diameter increment of infected *Pinus leiophylla* trees is only 10 percent of uninfected trees (0.7:7.0 mm per year). The diameter increments of infected *P. montezumae* and *P. teocote* are both 47 percent of uninfected trees of the species, although the two species grow at different absolute rates (0.2:5.3 mm and 0.7:1.5 mm per year, respectively). Increment losses are greatest in the 20-cm diameter class for *P. leiophylla* and *P. montezumae* and in the 40-cm class for *P. teocote.* Reduction in diameter increment can also be expressed as loss in productivity or volume. Reduced volume production by infected *P. leiophylla* corresponds to half the annual productivity of 127 trees per ha or 0.0186 m^3 per tree per year. Infected *P. montezumae* lose the equivalent of 0.0843 m^3 per tree per year; infected *P. teocote* lose 0.0150 m^3 per tree per year. In terms of growth, *P. montezumae* is the species most severely impacted.

Vázquez (1986) uses a four-class rating system (table 2-4) to stratify *Psittacanthus*-infected trees by disease severity and to assess the effects on reproductive potential (Vázquez and Pérez 1989). They observe that severely infected trees of *Pinus montezumae* and *P. teocote* fail to produce cones, and *P. leiophylla* produces 23.8 percent fewer cones. Moderately infected trees of *P. montezumae* produce 37.5 percent fewer cones, and moderately infected *P. teocote* produce 19.4 percent fewer cones. No reduction in cone production is noted for moderately infected *P. leiophylla* or lightly infected trees of any species. They also note an effect on seed germination. Seeds from severely infected *P. leiophylla* exhibit only a 67 percent germination rate. Seed germination from moderately infected trees is reduced 25 percent for *P. montezumae* and 5 percent for *P. teocote*. In terms of reproductive loss, *P. montezumae* is the species most severely impacted.

Economic and Ecological Importance

Although *Psittacanthus* is established as a widespread and damaging parasite of conifers in Mexico, it is also important for medicine, crafts, and wildlife

Table 2-4—Four-class rating system for evaluating severity of diseases caused by *Psittacanthus.*

Disease index	Infection class	Percent of crown infected
0	uninfected	0
1	light	1–30
2	moderate	31–60
3	severe	61–100

(Cházaro and others 1992). Vázquez and others (1982, 1985) and Vázquez and Pérez (1989) document the impacts of *Psittacanthus* on conifer growth and reproduction. Martinez (1983) reports that 3,396 ha of *Pinus lumholtzii*, *P. montezumae*, *P. leiophylla*, *Cupressus*, *Quercus*, and *Alnus* in Jalisco, Mexico, and Michoacán are infested by *Psittacanthus*. Over most of its extensive range, however, *Psittacanthus* appears to occur as small patches of a few infected trees. Traditional medicines are produced from the mistletoe; Browner (1985) identifies some of these uses in Oaxaca. The large haustorium of an old *Psittacanthus* infection causes distorted growth of the host branch into an interesting form resembling a rose or similar flower after the mistletoe tissue is removed. Artisans use these woodroses to produce lamp stands and other decorative, craft items (Cházaro and others 1992). These mistletoes are also used and are important to numerous birds for nectar and fruit (Freeman and others 1985, Lopez and Ornelas 1999, Salas 1988).

Management Strategies

The *Psittacanthus* mistletoes are easily detected, obligate parasites, with long life cycles, and slow rates of spread and intensification. Because of these attributes, economic control is generally feasible. Chemical and silvicultural methods are used for mistletoe control; some biological control occurs naturally but has not been developed as management tool (Cházaro and others 1992, Hernandez 1991).

Biological Control

The principal insects that feed on *Psittacanthus* belong to the order Homoptera, including scale insects *Coccus*, *Saccharicoccus*, *Gascardia*, and *Aenidomytilus*, and the aphid *Macrosiphum* (Vázquez and others 1986). These homopterans feed exclusively on plant sap, infesting leaves, branches, flowers, and fruits. A heavy infestation weakens and may eventually kill a host mistletoe plant. *Macrosiphum* has the best potential as a biological control agent because aphids are excellent vectors of viruses (Horst 2002), which are themselves agents of biological control.

Vázquez and others (1986) report isolating the fungi *Alternaria*, *Ceratocystis*, and *Fumago* from *Psittacanthus*. The disease caused by *Alternaria* (see García 1977, Horst 2002) in *Psittacanthus* produces leaf spot of older leaves and blight of young branches. The fungus spreads quickly during wet periods and induces concentric dark lesions, which lead to extensive necrosis of mistletoe leaves and shoots. Because *Ceratocystis* causes much damage and is readily cultured, it has a good potential as a biological control agent. *Fumago* causes blights and sooty molds; these fungi are very common in tropical and subtropical agriculture around the world. The development of *Fumago* is promoted by the secretions of some Homopterans (aphids and scales). The resulting disease and infestation can produce reactions in the host plant similar to symptoms caused by mistletoe itself; severe leaf infestations reduce photosynthesis and therefore growth (García 1977, Horst 2002).

Chemical Control

Few studies for chemical control of *Psittacanthus* on conifers are published (for example, Vázquez 1994b). Vázquez and others (1986) describe an experiment in Michoacán on *Psittacanthus calyculatus* and *P. americanus* infecting *Pinus leiophylla*. They report 1-month and 6-month evaluations of commercial application of four herbicides: two 2,4-D derivatives (Esterón and Fitoamina), one pyridine (Gramoxone), and one urea derivative (Karmex). At neither observation time did Karmex appear to damage the mistletoe. At 1 month, Gramoxone appears to provide excellent control with high mortality rate (80 percent) of fruits, leaves, and branches and slight transient phytotoxicity in the pine. At 6 months, however, the mistletoe treated with Gramoxone recovers and produces new vigorous buds, flowers, and fruits. Therefore, Gramoxone only causes a temporary delay in mistletoe development. At 1 month, Fitoamina causes severe damage, 40 percent defoliation, to mistletoe leaves and tender buds but has less effect on the mistletoe fruits. At 6 months, Fitoamina affects 80 percent of the mistletoe with defoliation, leaf spotting, and fruit deformity. At 6 months, Esterón causes complete defoliation of the mistletoe and failure to set fruit. The 2,4-D derivative herbicides are the more effective chemical control agents, but their use must be consistent with local regulations.

Silviculture

Several silvicultural practices are useful for controlling *Psittacanthus* in severely infested stands. The appropriateness of a given method depends on numerous factors, including stand type and location, infection intensity, management objectives, and constraints. Sanitation, intermediate thinning, shelterwood, and clearfelling are available techniques. Sanitation consists of removing severely infected trees and leaving light and moderately infected trees. Periodic examinations are made to monitor disease intensification; trees are removed as they become heavily infected. Sanitation is usually conducted at the time of intermediate thinnings, but if intensification is rapid relative to the thinning cycle, early removal may be considered. During shelterwood regeneration cuts, mistletoe-infected trees are generally removed and not used as seed trees. Lightly infected, genetically superior trees are occasionally retained to provide seed and then removed after 5 years. Where more than 75 percent of trees are infected and most are severely infested, clearfelling is usually employed for stand regeneration. Replacement with species less damaged or resistant to mistletoe infection can be considered.

As with all mistletoes, the first decision on control is whether it is appropriate given the management objectives of the stand, values produced in the stand, and available options for treatment.

B. W. Geils
D. Wiens
F. G. Hawksworth

Chapter 3

Phoradendron in Mexico and the United States

The generally familiar mistletoes are the leafy *Phoradendron* that typically infest hardwood trees and are placed at doorways for winter celebrations. Several of these mistletoes, however, more resemble the dwarf mistletoes by their apparently leafless stems and presence on conifers; but their large, fleshy berries that are attractive to birds clearly identify them as *Phoradendron*, "the tree thief." For several reasons, the conifer-infecting *Phoradendron* (the group reviewed here) have not gotten the level of attention from forest managers that the *Arceuthobium* have. *Phoradendron* most typically cause slight damage to junipers in Southwestern woodlands. But these mistletoes include a number of different species, range from Oregon to Mexico, infect a variety of hosts, and provide an interesting model of host–parasite interactions.

Along with the other mistletoes, the taxonomy, biology, physiology, and ecology of the *Phoradendron* are reviewed by Gill and Hawksworth (1961) and Kuijt (1969a). Foresters have long been interested in the *Phoradendron* on incense cedar (Meinecke 1912).

Picture guidebooks are available by Walters (1978) for the Southwest and by Scharpf and Hawksworth (1993) for the Pacific States. General summaries of information including control are provided by Hawksworth and Scharpf (1981), Hernandez (1991), and Vega (1976). The taxonomy of the *Phoradendron* on conifers was first monographed by Trelease (1916) and then revised by Wiens (1964). Confusion over the position and ranking of several taxa (Hawksworth 1979) and recent evidence from molecular systematics (Ashworth 2000) suggest the group requires another taxonomic monograph.

Life History and Biology

The *Phoradendron* have a typical mistletoe life cycle characterized by bird dispersal of sticky seeds, internal parasitism of a woody host, and aerial shoots for flower and fruit production. *Phoradendron* biology, reproduction, and parasitism have received intense study from ecological and evolutionary perspectives.

Life Cycle

The most detailed but still comprehensive study and review of a *Phoradendron* life cycle is that by Felix (1970a) for the mistletoe on *Abies concolor*. A number of bird species feed on the mistletoe fruits and disperse seeds by excreting or regurgitating them. The most important birds for effective dispersal include cedar waxwings, euphonias, silky flycatcher, bluebirds, thrushes, robins, and solitaires (see Sutton 1951, Gill 1990). Seeds pass quickly, and because birds perch in trees, seeds are deposited at suitable sites for infection (often the top or warm side of a potential host, commonly one already infected). Germinating seeds produce a radicle, holdfast, and penetrate the host branch usually near a needle (Ruhland and Calvin 2001). The endophytic system consists of longitudinal strands and sinkers (Calvin and others 1991, Felix 1970a). Once aerial shoots are produced, the *Phoradendron* does photosynthesize, but it is a parasite (see below) not a simple epiphyte. Plants are either male or female. Although Dawson and others (1990a) report a male-bias and provide hypotheses why there might be such a bias, Daughtery and Mathiasen (1999) find the sex ratio is one to one. Flower production and reproduction is typical, except that natural hybridization occurs but rarely (Wiens and Dedecker 1972). Fruits are produced several years after infection; older plants produce more and larger fruits (Dawson and Ehleringer 1991, Dawson and others 1990a, 1990b). Although the shapes of shoots and leaves of *Phoradendron* might mimic their host, the biology behind the appearance is unclear (Atsatt 1993b). Endophytic systems are perennial, but plants of all ages are subject to mortality by extreme low temperatures (Wagener 1957).

Host–Parasite Physiology

The physiology of *Phoradendron* is generally reviewed by Fisher (1983), Knutson (1983), and Kolb (2002) as typical for most mistletoes (but different from that of the dwarf mistletoes). Many details of the nitrogen, carbon, and water relations of the "xylem-tapping" *Phoradendron juniperinum* are elucidated in a series of recent ecophysiology studies (Ehleringer and others 1986, Marshall and Ehleringer 1990, Marshall and others 1993, 1994). The mistletoes do fix some carbon but get much from their host; mistletoes transpire a lot of water (all from their host); and they get a lot of nitrogen from the host, as the inevitable consequence of the physiological relation (Marshall and others 1994). Lei (1997) concludes that heavy mistletoe infection increases host-plant water stress and reduces vigor, viability, and reproductive success of the host in favor of the mistletoe. McHenry (1934) reports that *Phoradendron* at the Grand Canyon kills juniper. Hawksworth and Wiens (1966) indicate that junipers may also form witches' broom in response to infection.

Host–Parasite Ecology

Numerous authors have studied the effects of *Phoradendron* parasitism on population dynamics and interactions with other species. Hreha and Weber (1979) compare pinyon dwarf mistletoe (*Arceuthobium divaricatum*) and juniper mistletoe (*Phoradendron juniperinum*) at the South Rim of the Grand Canyon, reporting more infection in bigger (older) trees, a lack of infestation in recently burned (young) areas, and general stability in the populations. They consider the pinyon dwarf mistletoe the more detrimental because it more readily kills its host. Juniper mistletoe often has a patchy distribution, with some trees heavily infested. Gregg (1991) concludes the critical difference between infested and uninfested sites is the need for a dependable moisture supply to maintain the high demand of infected trees. Moisture stress in firs infected by *Phoradendron* is associated with reduced resistance and increased successful attack by the fir engraver (Felix 1970a, Ferrell 1974). Gehring and Whitham (1992) report that on droughty sites, juniper severely infested by mistletoe have lower rates of beneficial mycorrhiza infection, and female junipers are more seriously affected than male junipers. Another three-way, conditional interaction is described by van Ommeren and Whitham (2002) for juniper, mistletoe, and their avian dispersers. Although mistletoe has a negative impact on the health of infected trees, mistletoe provides a more dependable food source than juniper for the shared avian dispersers of each species' seeds. By considering dispersal and reproductive success in the interaction model, they conclude that the net effect of mistletoe parasitism, depending on populations, shifts between favoring the mistletoe to favoring the juniper.

The *Phoradendron* also exhibit a curious phenomenon whereby a mistletoe is parasitized by another mistletoe of the same or different species (Hawksworth and Wiens 1966, Wiens and Calvin 1987). Although several of the conifer-infecting *Phoradendron* may be infected by other *Phoradendron* mistletoes (Felix 1970b), the occurrence is too rare to effect a significant biological control.

Description of Genus

Phoradendron

Mistletoe, injerto

Shrubby parasite of trees and other woody plants (fig. 3-1), woody at base, glabrous or hairy; shoots cylindrical, green or less often reddish, 20 cm in height, nodes constricted, lacking epicortical roots; phyllotaxy opposite or decussate; inflorescence a spike; perianth generally three-parted and persistent; anthers small, sessile and bilocular; fruit a berry, 3 to 6 mm, single color of white, pink, or reddish. A genus of about 200 species in temperate and tropical America. Type species: *Phoradendron californicum* Nuttall.

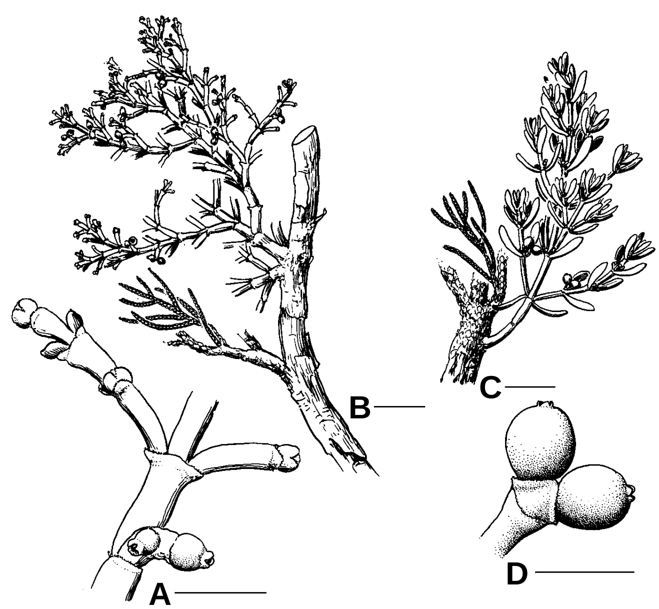


Figure 3-1—*Phoradendron* (all scales represent 5 mm). **A**, *P. juniperinum* on host; **B**, *P. juniperinum* with young fruit; **C**, *P. densum* on host; **D**, young fruits of *P. densum*. Adapted from Hitchcock and others (1964), p. 99, drawing by J.R. Janish. Our **C** and **D** originally labeled as *P. bolleanum* in figure, but accompanying text suggests figure represents *P. bolleanum* var. *densum* (Torr.) Fosberg, which we recognize as *P. densum*.

The genus *Phoradendron*, the largest genus of mistletoes, is in serious need of definitive taxonomic study. Trelease (1916) is the first monographic study of the genus, but Wiens (1964) revises many of Trelease's taxa that occur on conifers (see table 3-1). This taxonomy is further reconsidered by Hawksworth and Wiens (1993a, 1993b) for the flora of California, Nevada, and Arizona. Other floristic treatments with keys and illustrations include Hitchcock and others (1964) for the Pacific Northwest, McMinn (1939) for California, Standley (1920) for Mexico, and Wiggins (1980) for Baja California. Kuijt (1996) questions the significance and interpretation of many of the traditional morphological features used for the taxonomy of *Phoradendron*. Ashworth (2000) provides much insight to the relations among these mistletoes using techniques of molecular systematics.

Most of the taxa of *Phoradendron* that parasitize conifers are in the section *Pauciflorae* as described by Wiens (1964). Ashworth (2000) reports that these taxa (see table 3-1), delimited by morphological features, also form a single, related cluster based on molecular features. *Phoradendron rhipsalinum* is also a parasite of conifers but is apparently more closely related to a number of *Phoradendron* that typically infect hardwoods. A few other *Phoradendron* reportedly occur on conifers, but these are either rare cases or possibly misidentifications. Usual conifer host genera are *Abies*, *Calocedrus*, *Cupressus*, *Juniperus*, *Taxodium* (table 3-2). Martínez (1948) illustrates *Phoradendron velutinum* on *Pinus leiophylla* in Pueblo, but this is a rare host for a mistletoe with a wide host range, and we know of no other reports on pines.

In 1990, Wiens and Hawksworth drafted a further revision of *Phoradendron* section *Pauciflorae* that has never been completed and published (copy on file at Flagstaff Laboratory, Rocky Mountain Research Station). In that draft, they proposed recognizing seven new species on American conifers and raising to specific rank a previously submerged taxon not now generally accepted at that level. Although we do not describe any new species in this publication, we do suggest here that there may be differences in some populations that warrant recognition at the specific level. We leave it to other taxonomists using morphological and molecular techniques to judge these opinions. Specimens for these "ined" taxa are assembled for deposition at the U.S. National Herbarium.

Table 3-1—Taxonomic history of *Phoradendron* that parasitize conifers.

Trelease (1916)	Wiens (1964)	Accepted here
P. bolleanum Eichler *P. tequilense* n. sp.	*P. bolleanum* subsp. *bolleanum*	*P. bolleanum* (Seem.) Eichl.
P. capitellatum Torrey n. sp.	*P. capitellatum* Torr. ex Trel.	*P. capitellatum* Torr. ex Trel.[a]
P. densum Torrey n. sp. *P. guadalupense* n. sp.[c] *P. saltillense* n. sp.	*P. bolleanum* subsp. *densum* (Torr.) Wiens, comb. nov.	*P. densum* Torr. ex Trel.[a,b] *P. saltillense* Trel.[d]
P. juniperinum Engelmann *P. ligatum* n. sp.	*P. juniperinum* subsp. *juniperinum*	*P. juniperinum* Engelm. ex A. Gray[a,b]
P. libocedri Howell	*P. juniperinum* subsp. *libocedri* (Engelm.) Wiens, comb. nov.	*P. libocedri* (Engelm.) T.J. Howell[b]
P. longifolium Eichler	*P. longifolium* Eichler ex Trel.	*P. longifolium* Eichler ex Trel.
P. minutifolium Urban	*P. minutifolium* Urban	*P. minutifolium* Urban
P. pauciflorum Torrey	*P. bolleanum* subsp. *pauciflorum* (Torr.) Wiens, comb. nov.	*P. pauciflorum* Torr.[a,b]
		P. rhipsalinum Rzed.[e]

[a]Name used in Hawksworth and Wiens (1993a).
[b]Name used in Hawksworth and Wiens (1993b).
[c]Wiens (1964) indicates this taxon probably now extinct.
[d]Referred to by Hawksworth and Cibrián (1985) as *P. densum* subsp. *saltillense* (Trel.) Wiens.
[e]Taxon first recognized in 1972.

Description of Species

1. *Phoradendron bolleanum*
Bollean Mistletoe

Phoradendron bolleanum (Seem.) Eichl., Mart. Fl. Bras, v. II. 134.

Description. Plants 20 to 30 cm high, reddish; internodes 10 to 20 mm long; leaves spatulately linear-elliptical, 8 to 22 mm long and 1 to 4 mm wide, sessile, apex acute reddish, densely hairy; mature fruit is about 4 mm diameter, white to straw-colored (Trelease 1916, Cházaro and Oliva 1987b with illustration). This mistletoe is usually characterized by its bright reddish to brown color; however, some all-green populations have been found in central Chihuahua (Hawksworth and Cibrián 1985).

Hosts. Usual hosts are *Juniperus* and *Arbutus*. This is the only *Phoradendron* on *Arbutus* (*A. arizonica* and *A. xalapensis*); the closely related *Arctostaphylos* (*A. pungens*) is also rarely infected. Vega (1976) lists the hosts of "*Phoradendron bolleanum*" as not only *Juniperus* and *Arbutus* (*A. unedo*) but also *Quercus*,

Table 3-2—Host range and distribution of *Phoradendron* on conifers.

Phoradendron	Principal hosts	Mexico	United States
P. bolleanum	*Juniperus, Arbutus*	X	-
P. capitellatum	*Juniperus*	X	-
P. densum	*Juniperus, Cupressus*	X	X
P. juniperinum	*Juniperus, Cupressus*	X	X
P. libocedri	*Calocedrus*	X	X
P. longifolium	*Quercus, Pinus*	X	-
P. minutifolium	*Juniperus*	X	-
P. pauciflorum	*Abies*	X	X
P. rhipsalinum	*Taxodium, Quercus*	X	-
P. saltillense	*Juniperus, Cupressus*	X	-
	Total number of species	10	4

Pinus, and *Abies*. Given that he lists the distribution for this mistletoe to include Baja California, we suspect he is including *P. pauciflorum* and other *Phoradendron* under this name. *Cupressus benthami* is an unusual host in the pine–cypress woodlands of Veracruz (Cházaro 1989a).

Distribution. Mexico (Chihuahua, Durango, Hidalgo, Jalisco, Nayarit, Querétaro, Sonora, Sinaloa, Veracruz, and Zacatecas). Common in Sierra Madre Occidental, and Zacatecas to central Chihuahua (Hawksworth and Cibrián 1985). Cházaro (1989a) records *Phoradendron bolleanum* on *Cupressus* (*C. benthami*) in Veracruz. This is the most widespread *Phoradendron* on conifers in Mexico. Known elevational range is from 1,900 to 2,500 m. The mistletoe on junipers in eastern New Mexico, western Texas, and northern Coahuila are considered another taxa.

Discussion. *Phoradendron bolleanum* is a widespread and diverse mistletoe with a complicated taxonomic history. We are attempting here to include only reports of *P. bolleanum* subsp. *bolleanum* and populations resembling the type on juniper from the Sierra Madre Occidental and parasitizing both *Juniperus* and *Arbutus*. We describe other taxa under *P. densum* and *P. pauciflorum*.

Phoradendron bolleanum is unusual for mistletoes of section *Pauciflorae senus* Wiens (1964) in that it commonly parasitizes both gymnosperms and angiosperms (Hawksworth and Wiens 1966). Trelease (1916) questions whether one species of mistletoe would occur on such unrelated host genera; and without experimental evidence, the question is still open. However, no morphological grounds for a taxonomic separation of the populations on the two hosts have been found. Although infections of *Juniperus* and *Arbutus* frequently occur together, we have seen many situations from Chihuahua to Jalisco where only one host is infected, even though the other is present. For example, *P. bolleanum* has been found in Jalisco on *Arbutus* only, even though *Juniperus* occurs in the same areas (M. Cházaro B., personal communication). This suggests that there may be two host races of the mistletoe, one primarily parasitic on *Juniperus* and one on *Arbutus*. The areas where both types of hosts are infected may represent instances of sympatry of the two races. Carefully controlled, crossinfection experiments are needed to determine the status of the host populations of this mistletoe.

Various authors have attempted to sort out the systematic relations among taxa of *Phoradendron bolleanum* complex. Wiens (1964) revised the previous work by Trelease and Fosberg but later revised himself in floral treatments for Texas (Wiens 1970), Arizona (Hawksworth and Wiens 1993a), and California (Hawksworth and Wiens 1993b). Further changes by Hawksworth and Wiens are contemplated in an uncompleted draft. Ashworth (2000) identifies several sister groups for taxa of the complex: *P. bolleanum* subsp. *bolleanum* groups with *P. minutifolium*, *P. densum* and *P. pauciflorum* (both previously considered as subspecies of *P. bolleanum*) group together.

2. *Phoradendron capitellatum*
Hairy Mistletoe

Phoradendron capitellatum Torr. ex Trel., Genus *Phoradendron* 25, pl 17, 1916.

=*Phoradendron bolleanum* var. *capitellatum* (Torr. Ex Trel.) Kerney & Peebles

Description. Plants 30 to 80 cm tall, yellow–green; internodes 5 to 15 mm long, pendulous with age; leaves 6 to 14 mm long and 2 to 3 mm wide, densely hairy with stellate trichomes; flowers December to February; mature fruit is about 3 mm in diameter, pinkish–white (Hawksworth and Scharpf 1981with color picture and 1993a).

Hosts. Known hosts are *Juniperus deppeana*, *J. pinchotii*, *J. monosperma*, and *J. osteosperma*. It usually occurs at elevations below *Phoradendron juniperinum*, but the two species are sometimes sympatric and rarely even on the same host tree.

Distribution. United States (Arizona, New Mexico) and Mexico (Chihuahua, Sonora). This mistletoe has a restricted distribution and is known only in central and southeastern Arizona (nine counties), southwestern New Mexico (Grant, Hidalgo, Luna), northeastern Sonora, and northwestern Chihuahua (Hawksworth and Cibrián 1985). Hawksworth and Scharpf (1981) map its distribution in the United States and into Mexico. Known elevational range is 800 to 1,700 m.

Discussion. This highly distinctive parasite of junipers is characterized by its small, densely stellate–pubescent leaves. It is the only leafy mistletoe known to occur on junipers in Arizona and is poorly known. Ashworth (2000) finds that *Phoradendron capitellatum* is the most divergent taxa within the *Pauciflorae*, although there is some support for a sister group with *P. juniperinum*.

3. *Phoradendron densum*
Dense mistletoe

Phoradendron densum Torr. ex Trel., Genus *Phoradendron* 27, 1916.

=*Phoradendron bolleanum* var. *densum* (Torr. ex Trel.) Fosberg,

=*Phoradendron bolleanum* subsp. *densum* (Torr. ex Trel.) Wiens

Description. Plants 10 to 30 cm high, green (fig. 3-1); internodes 6 to 17 mm long; leaves 10 to 20 mm long and 2 to 4 mm wide, glabrous, sessile, apex obtuse; mature fruit is about 4 mm in diameter, white to straw-colored. (Hawksworth and Scharpf 1981with color photo, Hitchcock and others 1964 with illustration).

Hosts. *Cupressus arizonica, C. bakeri, C. goveniana, C. macnabiana, C. macrocarpa* (rare), *C. sargentii, Juniperus californica, J. monosperma, J. occidentalis, J. osteosperma, J. pinchotii*. The mistletoe is reported on *Pinus monophylla* at Mt. Pinos (Ventura, California) by McMinn (1939), but this has not been confirmed.

Distribution. United States (Arizona, California, Oregon) and Mexico (Baja California). The mistletoe ranges from southern Oregon (Klamath and Jackson) throughout California to the lower elevations of the Sierra San Pedro Mártir in Baja California, Mexico, and with outlying populations in central Arizona on *Cupressus* (Coconino, Yavapai, Maricopa, and Gila). Trelease (1916) reports *Phoradendron densum* from Sonora, and the Forest Pathology Herbarium-Fort Collins, CO, holds collections as well from Coahuila and Nuevo Leon, although these collections may more properly belong under *Phoradendron saltillense*.

The population in the Sierra San Pedro Mártir infects *Juniperus californica* but not *Cupressus*, which occurs at higher elevations (Hawksworth and Wiens 1966). The reciprocal situation occurs in Arizona; the mistletoe infects cypress but not junipers, even though junipers are widely distributed and abundant in the State. Hawksworth and Scharpf (1981) provide a distribution for Oregon, California, and Arizona. Known elevational range is 200 to 2,300 m.

Discussion. Ashworth (2000) illustrates the close systematic relationships among the taxa of section *Pauciflorae senu* Wiens. Her work, however, also brings out the taxonomic difficulty among *Phoradendron bolleanum*, *P. densum*, and the various taxa at one time or other considered subspecies of these (see table 3-1). For the reviewer (such as here), the problem is determining to which taxa various reports of hosts and distribution refer. Based on their descriptions and distributions, Hawksworth and Wiens (1993a, 1993b) restrict their interpretation of *P. densum* to include only certain populations from Oregon to Baja California on juniper and cypress and from central Arizona on cypress. Many of the mistletoes on either cypress or juniper from the Sierra Madre Oriental are now referred to *Phoradendron saltillense*. From eastern New Mexico, western Texas, and northern Coahuila (Wiens 1964), it is now referred to Hawksworth's mistletoe (see below). Several other populations usually referred to either *P. bolleanum* or to *P. densum* also have differences in morphology, life history, hosts, and distribution, so that they may warrant recognition at the specific level. Considering the difficulty of classifying these mistletoes using traditional criteria, molecular techniques (for example, Ashworth 2000) should be considered.

The population of *Phoradendron* on various junipers in western Texas, southern New Mexico, and Coahuila has been referred to as *Phoradendron bolleanum* subsp. *hawksworthii* (Wiens 1970) and *Phoradendron hawksworthii* (Hawksworth 1979, Hawksworth and Cibrián 1985, Hawksworth and Scharpf 1981). Although the name *Phoradendron hawksworthii* Wiens is accepted by the PLANTS database (USDA, NRCS 2001), it is not yet a validly published name and remains "ined." The Hawksworth's mistletoe plants are about 10 to 25 cm tall, dark green, with internodes 6 to 12 mm long. Leaves are 6 to 25 mm long, 2 to 2.5 mm wide and slightly hairy. The mature fruit is white and about 4 mm in diameter. The hosts are *Juniperus ashei, J. deppeana, J. flaccida, J. monosperma*, and *J. pinchotii*. This mistletoe is common throughout western Texas (Brewster, Culbertson, Edwards, Hudspeth, Presido, Terrell, Val Verde) and occurs in southern New Mexico (Dona Ana, Lincoln, Otero, Socorro?) and northern Coahuila (Sierra del al Encantada). [Note: the population collected from northwest of Carrizozo, NM, in 1969 could not be relocated and may be extinct.] The Hawksworth's mistletoe resembles *P. saltillense* but is distinguished by several features (table 3-3). Hawksworth's mistletoe is not sympatric with *P. capitellatum*, which also occurs on junipers in southern New Mexico. Hawksworth's mistletoe, however, is sympatric with *P. juniperinum* and may even infect

Table 3-3—Comparison of Hawksworth's mistletoe and *Phoradendron saltillense*.

Character	Hawksworth's mistletoe[a]	*Phoradendron saltillense*
leaf width	narrow, 2 mm or less	wide, more than 3 mm
leaf transection	upper surface flattened, lower rounded	dorsoventrally flattened
tip of mature leaf	abrupt, with point 0.2–0.3 mm or with the scar of such a point	never developing a point
internode length[b]	short, 6–12 mm, mean 9 mm	long, 6–17 mm, mean 11 mm
segments per staminate inflorescence	usually only one segment	typically two segments

[a] *Phoradendron densum* populations in western Texas and southern New Mexico.
[b] Internode length is correlated with total plant size.

the same tree; but Hawksworth's mistletoe usually extends to lower elevations than the distribution of *P. juniperinum*. Both *P. juniperinum* and Hawksworth's mistletoe appear to induce a witches' broom formation on its host (Hawksworth and Wiens 1966, D. Conklin, personal communication).

4. *Phoradendron juniperinum*
Juniper mistletoe

Phoradendron juniperinum Engelm. ex A. Gray, Mem. Am. Acad. N. S. iv. 59, 1849.

Description. Plants 20 to 40 cm tall, globose, green to yellow–green, glabrous; internodes 5 to 10 mm long; leaves reduced to minute scales; mature fruit is about 4 mm in diameter, pinkish–white colored (Hawksworth and Wiens 1993a, 1993b, Hichcock and others 1964 with illustration).

Hosts. Common hosts are *Juniperus californica*, *J. deppeana*, *J. pinchotii*, *J. flaccida*, *J. monosperma*, *J. occidentalis*, *J. osteosperma*, and *J. scopulorum*. *Cupressus arizonica* is commonly parasitized in central Chihuahua, but this tree is rarely infected in Texas (Hawksworth and Cibrián 1985), Arizona (Hawksworth and Wiens 1966), and New Mexico (Linnane 1987). Other rare hosts are *C. bakeri* in California (Hawksworth and Wiens 1966), *Chamaebatiara millefolium* (Rosaceae) in Arizona (Hawksworth 1952), and *Pinus monophylla* (Hawksworth 1979). Vega (1976) adds *Juniperus mexicanus* as a host.

Distribution. United States (Oregon, California, Nevada, Utah, western Colorado, Arizona, New Mexico, and western Texas) and Mexico (Baja California, Chihuahua, Durango, Sonora). It occurs in the Chisos Mountains in Big Bend National Park, Texas (Brewster), but is not yet known in adjacent Coahuila, Mexico. A collection in the Forest Pathology Herbarium-Fort Collins, CO, includes a single collection by J.R. Weir (no date) from Oakley, ID (Cassia) with a *Juniperus osteosperma* infected by *Phoradendron juniperinum*. Bunderson and others (1986) attempt to predict the distribution on the mistletoe from environmental site factors. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,000 to 2,600 m.

Discussion. The taxon described by Trelease (1916) as *Phoradendron ligatum* for its constricted scales is now included under *P. juniperinum* (Wiens 1964). This distinctive leafless species is the most widespread *Phoradendron* on conifers. *Phoradendron juniperinum* is geographically sympatric with *P. capitellatum* in Arizona, with Hawksworth's mistletoe in New Mexico, and with *P. densum* in California. In fact, natural hybrids of *P. juniperinum* x *P. densum* that appear to be sterile F1 plants have been found in the Inyo and San Bernardino Mountains in California (Wiens and DeDecker 1972). Vasek (1966) observes that *P. juniperinum* usually does not parasitize *Juniperus californica,* and *P. densum* usually does not parasitize *J. osteosperma*. *Phoradendron juniperinum* forms a sister group with *P. libocedri*, but there is also some evidence in support of another sister group with *P. capitellatum* (Ashworth 2000).

Phoradendron juniperinum is a widespread and common mistletoe on junipers in many of the Western States. It is the subject of numerous studies on ecophysiology (see below). Several curious observations (Hawksworth and Wiens 1966) on *P. juniperinum* include rarely occurring massive witches' brooms and parasitism by *Phoradendron villosum* subsp. *coryae* (normally on oak).

5. *Phoradendron libocedri*
Incense–cedar mistletoe

Phoradendron libocedri (Engelm.) T.J. Howell, Fl. N.W. Amer. 1:608, 1902.

=*Phoradendron juniperinum* Engelm. ex Gray var. *libocedri* Engelm.

=*Phoradendron juniperinum* Engelm. ex Gray subsp. *libocedri* (Engelm.) Wiens

Description. Plants 20 to 80 cm tall, woody only at base, older plants pendulous, green; internodes 10 to 29 mm long; leaves reduced to minute scales; pistillate inflorescences usually with one segment and two flowers (occasionally more); mature fruit 4 mm in diameter, pinkish white to straw colored (Hawksworth and Wiens 1993b).

Hosts. On *Calocedrus decurrens*. There is one collection by Platt and Felix (Dodge Ridge, Tuolumne, CA, 1968) of *Phoradendron libocedri* on *Abies concolor*. They report only a single fir tree was infected in a stand where the mistletoe was common on the associated incense cedar. Weir (*5995* from Del Norte CA in 1917) is a *Chamaecyparis lawsoniana* with a single infection of *P. librocedri*; he reports infected incense cedar are nearby.

Distribution. United States (California, Oregon, Nevada) and Mexico (Baja California). The main range of the mistletoe is from southern Oregon (Jackson, Josephine, Klamath) through the Cascade and Sierra Nevada Ranges to southern California. The population in Nevada (Douglas) is near the California border. Isolated known occurrences are in northern Oregon (Jefferson, Warm Springs Indian Reservation) and on San Benito Peak in the South Coast Range in Monterey County, California. It also occurs in the Sierra Juarez and Sierra San Pedro Mártir in Baja California (Wiggins 1980). Although the mistletoe has a wide range, it is not very common (McMinn 1939). Hawksworth and Scharpf (1981) provide a picture of an infested incense cedar and a distribution map. Known elevational range is 400 to 2,500 m.

Discussion. *Phoradendron libocedri* had been considered a subspecies of *P. juniperinum* (Wiens 1964) but is here recognized again at the specific level (Trelease 1916). *Phoradendron libocedri* and *P. juniperinum* are sympatric in the Sierra Nevada, but each remains restricted to it own host; *P. libocedri* has longer internodes and is more pendulous (mimicking its host? see Ashworth 2000). The two taxa, however, do form a very close sister group (Ashworth 2000). Meinecke (1912) describes the swellings and burls caused by *Phoradendron libocedri* and speculates on the age and parasitism of the mistletoe.

6. *Phoradendron longifolium*

Phoradendron longifolium Eichler ex Trel. Genus *Phoradendron* 53, 1916.

Description. Plants becoming generally woody; internodes 15 to 30 mm long; leaves linear, 32 to 84 mm long by 6 to 9 mm wide, apex rounded to acute; fruit 3 to 4 mm diameter, lightly puberulent (Wiens 1964, Bello 1984 with illustration, Bello and Gutierrez 1985).

Hosts. Usually *Quercus* but also *Alnus*, *Pinus pseudostrobus*, *P. michoacana* (Bello Gutierrez 1985).

Distribution. Mexico (Durango, Tamaulipas, Hidalgo, Mexico, Oaxaca).

Discussion. Wiens (1964) places *Phoradendron longifolium* in section *Calyculatae* but admits little material was available for morphological comparisons to other *Phoradendron*. Ashworth (2000) reports *P. longifolium* forms a sister group with *P. galeottii* with which it shares several morphological features, but not time of flowering, which Wiens uses as a taxonomic character. Although *P. longiflorum* occurs in pine woodlands of central Mexico, we have no information on how common or damaging it is.

7. *Phoradendron minutifolium*
Injerto de páraro

Phoradendron minutifolium Urban Bot. Jahrb. Syst 23, Beibl. 57:2, 1897

Description. Plants 30 to 80 cm tall, dull green; internodes 4 to 12 mm long; leaves 3 to 5 mm long and 1 to 1.5 mm wide, resembling scales, glabrous; spike one-jointed; mature fruit is about 4 mm in diameter, pinkish–white colored (Hernandez 1991 with illustration, Trelease 1916).

Hosts. *Juniperus deppeana* (Acosta and others 1992). Other juniper species are probably hosts, but our host collections are only identified as *Juniperus* sp. Depending on how populations in Colima and Jalisco are classified, also on *Cupressus*.

Distribution. Mexico (Chihuahua, Coahuila, Durango, Puebla, Tlaxcala, Veracruz). The mistletoe is most common in Tlaxcala (Hernández 1991) and Veracruz and in the Sierra Madre Occidental in southern Chihuahua and Durango. An apparently extreme outlier occurs in northern Coahuila in the Sierra del Carmen (across from Big Bend, TX). Depending on how populations on *Cupressus* are classified, also in Colima and Jalisco. Known elevational range is 2,000 to 2,750 m.

Discussion. *Phoradendron minutifolium* in Coahuila is sympatric with *Phoradendron saltillense* on juniper; the two mistletoes sometimes even coinfect the same tree. *Phoradendron minutifolium* and *P. bolleanum* subsp. *bolleanum* form a close sister group (Ashworth 2000).

A population of *Phoradendron* that appears similar to *P. minutifolium* occurs on *Cupressus* in the nearby vicinities of El Sauz and Terrero, Sierra de Mammitlan and Cerro Grande in Colima and Jalisco. Although these mistletoe are referred by the name *Phoradendron olivae* (Cházaro 1990, Cházaro and others 1992), we are unable to confirm that this name has been validly published, but the holotype is reported to be a collection by Wiens, Cházaro, Hawksworth, and Olivo (*7051*, 1 August 1989) deposited at IBUG (Universidad de Guadalajara). The hosts are variously identified as *Cupressus benthami* and *C. lusitanica*. The plants on *Cupressus* are larger and more open-formed because of longer internodes (15 to 25 mm) and smaller leaves (only 1 to 2 mm long). The mistletoes of *Cupresssus* have a distribution far to the west and south of those on *Juniperus*. Additional study of these mistletoes is needed.

8. *Phoradendron pauciflorum*
Fir mistletoe

Phoradendron pauciflorum Torr., Pacif. Rail. Rep. iv. 134.

=*Phoradendron bolleanum* (Seem.) Eichl. var. *pauciflorum* (Torr.) Fosberg

=*Phoradendron bolleanum* (Seem.) Eichl. subsp. *pauciflorum* (Torr.) Wiens

Description. Plants 20 to 40 cm high, green; internodes 10 to 21 mm long; leaves with short petiole, 5 to 30 mm long and 5 to 8 mm wide, glabrous; leaf apex obtuse; mature fruit is about 4 mm wide, pinkish white to straw colored (Hawksworth and Scharpf 1981 with color picture, Hawksworth and Wiens 1993a, 1993b).

Hosts. *Abies concolor* is usually the only host, although autoparasitism has been reported (Felix 1970b). It rarely parasitizes *Cupressus arizonica* var. *montana* in the Sierra San Pedro Mártir, Baja California, Mexico, where this tree is associated with infected *Abies* (Hawksworth and Wiens 1966).

Distribution. United States (Arizona, California) and Mexico (Baja California). This mistletoe is common in the central and southern Sierra Nevada (Calaveras) south to the Sierra San Pedro Mártir in Baja California, Mexico (Wiggins 1980). An extreme disjunct occurs in southern Arizona (Pima) in the

Santa Catalina and Rincon Mountains. Hawksworth and Scharpf (1981) provide a distribution map. Known elevational range is 1,400 to 2,600 m.

Discussion. This species was previously submerged under *Phoradendron bolleanum* (table 3-1) and confused with *P. densum* (Wiens 1964). Felix (1970a) provides a detailed study of the biology of *P. pauciflorum* including information on reproduction and dispersal, shoot growth, endophytic system, branch mortality, mistletoe mortality, effects on host, associated species, and epiparasitism.

A population of an unnamed *Phoradendron* occurs on the rare *Abies durangensis* in Chihuahua, Durango, and Jalisco. This mistletoe on fir is sometimes sympatric with *P. bolleanum*, but has yellow-green, linear leaves with an acuminate apex. The populations include a few widely scattered localities in the Sierra Madre Occidental; all the *A. durangensis* populations that we have visited in Durango are parasitized by this mistletoe.

9. *Phoradendron rhipsalinum*

Phoradendron rhipsalinum Rzed., Cact. Suc. Mex 17:102, 1972.

Description. Plants 2 to 4 m long, pendulous, bright green; leaves 4 to 6 cm long and 4 to 5 mm wide, glabrous; mature fruit yellow–green, 1.5 mm in diameter (Bello 1984 with illustration, and Bello and Gutierrez 1985 with picture and detailed description).

Hosts. *Taxodium distichum* var. *mexicanum*. *Quercus castanea* is also infected (Bello 1984, Bello and Gutierrez 1985).

Distribution. Mexico (Guanajuato, Jalisco, Mexico, Michoacán). Known elevational range is 1,600 to 2,300 m in pine-oak woodlands to subtropical matorral.

Discussion. This is one of the most distinctive Mexican mistletoes. Its 4 to 6 cm long "strap–like" leaves make it unusual. It forms huge pendulous masses hanging from the bald-cypress trees that look from a distance like masses of Spanish moss. Ashworth (2000) concludes this mistletoe does not fit with the other parasites of conifers in the section *Pauciflorae* but appears more closely related to *P. brachystachyum* rather than *P. bolleanum* as suggested by Kuijt (1996). It causes severe mortality to bald-cypress, for example in the vicinity of Zamora, Jalisco. Although approximately 120 species of mistletoe occur in Mexico, this is the only species described by a Mexican botanist (Cházaro and others 1992).

10. *Phoradendron saltillense*

***Phoradendron saltillense* Trel. Genus** *Phoradendron* 27, 1916.

=*P. bolleanum* subsp. *densum* (Torr.) Wiens, pro parte.

Description. Plants moderately long and stout; internodes 10 to 20 mm, papillate-hispid; leaves narrowly oblong, 20 to 30 mm long by 2 to 3 mm wide, sessile, apex acute; spike 50 to 60 mm long, with single joint and pistillate two-flowered (Trelease 1916, Standley 1920).

Hosts. *Cupressus arizonica, C. benthami, Juniperus deppeana, J. flaccida, J. monosperma*, and *J. saltillense*.

Distribution. Mexico (Coahuila, Nuevo Leon, San Luis Potosi, Puebla). Known elevational range is 1,850 to 2,850 m. This mistletoe is common the Sierra del Carmen, northern Coahuila, and it may occur in the Chisos Mountains, Texas. Hawksworth and Cibrián (1985) lists *P. densum* subsp. *saltillense* (Trel.) Wiens on *Cupressus arizonica* in Coahuila and on *Juniperus* in the Sierra Madre Oriental from Coahuila to Zacatecas.

Discussion. *Phoradendron saltillense* is first described by Trelease (1916), accepted by Standley (1920), submerged under *Phoradendron bolleanum* subsp. *densum* by Wiens (1964), and recognized here as a validly published name. It is separated from *P. densum* populations in Arizona by more than 1,000 km, but near to Hawksworth's mistletoe in the Sierra del Carmen. It is distinguished from Hawksworth's mistletoe by several morphological features (table 3-3). *Phoradendron saltillense* is sympatric in Nuevo Leon and Coahuila with populations of an unnamed *Phoradendron* that have longer, narrower, thinner leaves and a more open branching habit; these two contrasting mistletoes may even occur in the same tree.

Importance

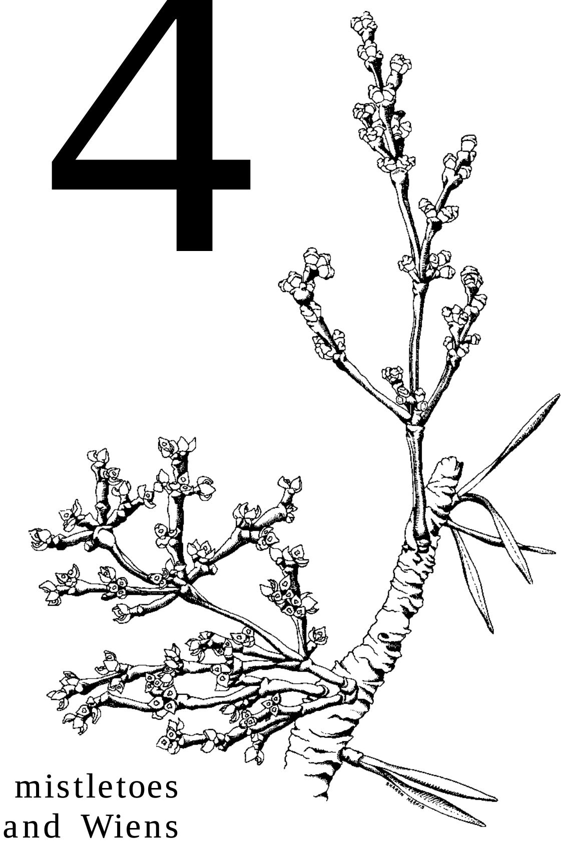
Although the *Phoradendron* mistletoes that infect conifers are widely distributed in the Western United States and in Mexico on a number of common and valuable hosts, their importance is mostly on a local basis and for special uses. In the United States, *Phoradendron* are most important in California on incense cedar and true fir in certain areas and important broadly across the Southwest (California to Texas) on junipers. In Mexico, *Phoradendron* (all species) are found throughout the Republic, but only recognized as a forest plague on about 4,000 ha in Jalisco, Mexico, and Michoacán (Martinez 1983). Hawksworth and Cibrián (1985), however, add that *Phoradendron* are damaging to junipers in the north (Sierra Madre Occidental, Oriental, and del Carmen). Although *Phoradendron* are a minor issue on a few forest species (see Felix 1970a, Meinecke 1912), they can be a serious concern in some recreation and other high-value sites (Frankel and others 1989, Linnane 1987). These mistletoes have a high nutritional value as animal forage (Urness 1969) and are utilized as such (Cházaro and Oliva 1988b, Gallina 1988). *Phoradendron* mistletoes are also consumed by humans as a stimulating beverage (Whiting 1950) and as a traditional medicine for childbirth and several ailments (Cházaro and Oliva 1988a, Moore 1979, Whiting 1950). A strong caution, however, is appropriate. Various compounds from *Phoradendron* and other mistletoes are being investigated for their pharmacological potential, but many of these compounds are present in toxic dosages to humans (Turner and Szczawinski 1991). Although it is the more leafy *Phoradendron* mistletoes on hardwoods that are usually harvested commercially for winter-festival greenery, the conifer mistletoe can still be enjoyed for attracting numerous, colorful birds (Sutton 1951).

Management Strategies

Phoradendron mistletoes seldom cause sufficient damage in an area that control is required; but where management objectives indicate that mistletoe control is justified, cultural methods are available. Although there are insects that feed on these mistletoes (Burke 1975) and fungi that caused disease (Horst 2002, Scharpf and Hawksworth 1966), there are no biological control programs for the *Phoradendron*. Chemical control has been tested using various herbicides (Quick 1963) and ethephon (Adams and others 1993), but none are recommended. We know of no genetic improvement programs to develop conifer resistance to *Phoradendron* mistletoes. Cultural methods are briefly discussed by Frankel and others (1989), Hawksworth and Scharpf (1981), and Hernandez (1991). Operations include regenerating with a nonhost tree, thinning trees to improve vigor and tolerance of the infestation, and sanitation by removing infected trees or branches or removing aerial shoots. Pruning infected branches is often sufficient; where the loss of infected branches cannot be accepted, the aerial shoots can be just knocked off. Removing the shoots does not eliminate the mistletoe infection but does reduce its reproduction and damage. Shoots will reappear after several years. Covering infected branches with tarpaper or creosote has not proven either attractive or effective. Perhaps the best way for discouraging additional bird-dispersal of mistletoe seeds is with branch pruning or shoot removal (since it is often the mistletoe fruits that initially attract the birds). Given the modest damage and slow rate of increase of these mistletoes, these methods are usually sufficient.

F. G. Hawksworth
D. Wiens
B. W. Geils

Chapter 4



Arceuthobium in North America

The biology, pathology, and systematics of dwarf mistletoes are recently and well reviewed in Hawksworth and Wiens (1996). That monograph forms the basis for the text in this and chapter 5 and should be consulted for more information (for example, references, photographs, and distribution maps). In addition to extracting the information that would be most relevant to forest managers and arborists, we here include new references on hosts, distributions, and ecology. The synonymy in this chapter is neither formal nor complete; rather, we provide additional names used in previous, significant literature (such as Gill 1935, Hawksworth and Wiens 1972, Kuijt 1955).

General Life Cycle

The life cycle of dwarf mistletoe is distinctive because of two features—obligate parasitism (shared with all mistletoes) and hydrostatically controlled, explosive dispersal (with one exception). The details of cytology, anatomy, embryology, genetics, and evolution that underlie these features are described by Hawksworth and Wiens (1996) and Kuijt (1960a, 1960b, 1969a).

Especially for dwarf mistletoes with their reduced morphologies, differences in reproductive phenology and host specificity are taxonomically decisive (Hawksworth and Wiens 1996). The life histories of several dwarf mistletoes are well studied (Gilbert 1984, 1988, Hawksworth 1961, 1965, Scharpf and Parmeter 1982, Strand and Roth 1976).

Life History

Dwarf mistletoe life history comprises four stages: dispersal, establishment, incubation, and reproduction (fig. 4-1). Dispersal begins when a mature fruit discharges its seed into ballistic flight. Establishment includes the time from the seed lodging at a safe-site until the parasitic relationship is initiated. Several years of incubation pass while an extensive, endophytic system develops under the host's bark. The reproductive stage continues with repeated, intermittent production of aerial shoots and flowers and continued expansion of the endophytic system. Reproduction ends with the death the mistletoe plant; this usually does not occur until the host itself dies. Various physical and biological factors affect the temporal and spatial unfolding of these processes into population consequences and afford an opportunity for management intervention.

Dispersal—Mistletoe dispersal is effected by the hydrostatic contraction of a mature fruit that propels a single, small seed upon ballistic flight to either a location where a host may be inoculated (safe-site) or elsewhere. Unlike other mistletoes that are primarily dispersed by birds consuming mature fruits and defecating viable seeds, the dwarf mistletoes rely almost exclusively on this ballistic mechanism. Birds and mammals are important, however, for the rare, long-distance dissemination of seeds to new infection centers (Nicholls and others 1984). The exception is *Arceuthobium verticilliflorum*, which is found in widely spaced pine forests of Mexico. This species has nonexplosive fruits twice the size of other dwarf mistletoes and is predominately dispersed by birds.

The special morphological and anatomical features that facilitate dispersal include the supporting structure for the fruit (pedicel) and characteristic, sticky, viscin cells (Wilson and Calvin 1996, Hawksworth and Wiens 1996). When the fruit matures, the pedicel elongates and water pressure increases. With separation of the fruit from the pedicel, the seed is ejected at nearly 24 m per second (Hinds and Hawksworth 1965) and tumbles in a short ballistic flight until it lands upon and sticks to a surface. The shape of the ballistic trajectory is influenced by height above the ground, pedicel–fruit orientation, seed shape and weight, discharge velocity, and gravity (Hawksworth 1961). Dwarf mistletoe seeds have a mass of 2 to 3 mg; wind affects the flight, but seeds fall to their destination within seconds. Although maximum horizontal displacement may reach 16 m, 10 m is a more typical, free-flight distance (see Escudero and Cibrián 1985). Most seeds are displaced horizontally only 2 to 4 m and deposited lower in the crown; some seeds, however, are shot

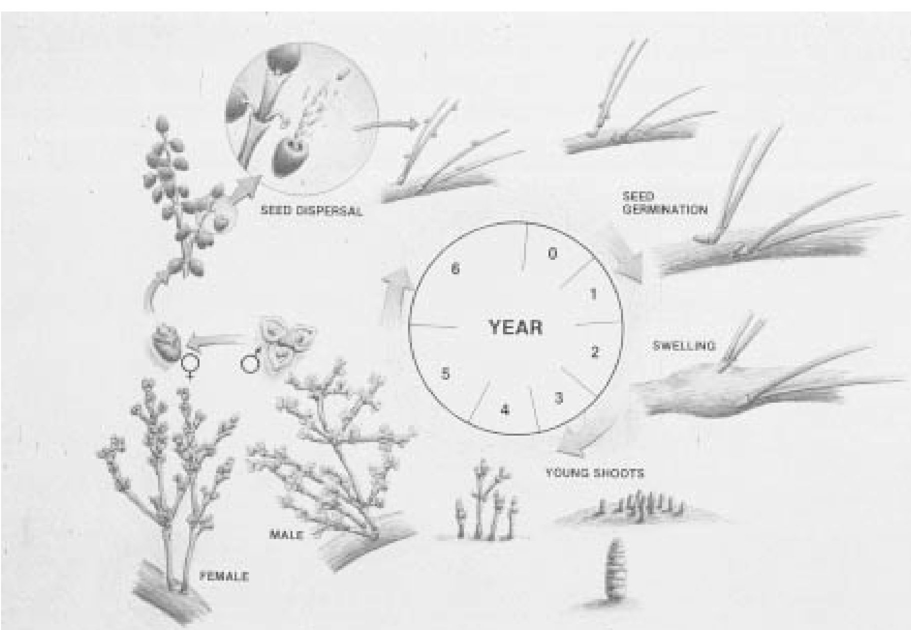


Figure 4-1—Generalized life cycle of a typical dwarf mistletoe. Illustration courtesy of W. R. Jacobi.

higher into the crown to effect vertical spread (Hawksworth and Geils 1985, Richardson and van der Kamp 1972, Shaw and Hennon 1991, Wicker and Hawksworth 1991). Because of variation in crown density, foliage display, and mistletoe position, the rate of seed interception within any tree crown is highly variable. Only about 40 percent of seeds are intercepted by any tree crown; 60 to 80 percent of seeds are retained in the crown from which they originated (reinfection); of those that escape, 90 percent may be intercepted by an adjoining tree (contagion) (Hawksworth 1965, Smith 1985).

After their ballistic flight, seeds continue to move by gravity or rarely by birds and mammals (Nicholls and others 1984). The viscin coating helps the seed adhere to any surface it strikes, including host foliage. After the initial interception, this viscin imbibes water, swells, loosens, and permits the seed to slide down the needle (see Hawksworth and Wiens 1996 for illustrations). If the needle points upward, the seed lodges on a twig at the base of a needle (a good safesite); otherwise, the seed slides off and relocates in the crown or falls to the ground. Most infections, but not all, occur on young branch wood (Sproule 1996a). Although only a few seeds reach safesites (less then 10 percent, according to Hawksworth 1965), large numbers of seeds are produced on heavily infected trees (Hawksworth 1965, Smith 1977, Wicker 1967a). Although it seems inefficient, for short range spread and intensification this dispersal mechanism is effective enough for dwarf mistletoes to have persisted since the Miocene, adapted to nearly a hundred host species, and spread throughout the conifer forests of North America.

Establishment—The physical process of dispersal brings the mistletoe seed within millimeters of establishing a new infection; biological growth completes the establishment phase. Although the embryo of some tropical species begins growth soon after dispersal, most temperate mistletoes do not resume growth (germinate) until the following spring when light, moisture, and temperature are suitable (Gill and Hawksworth 1961, Lamont 1983, Scharpf 1970, Wicker 1974).

Genetic factors, predation, and environmental conditions reduce the number of viable seeds; field germination varies from 7 to 90 percent (Hawksworth and Wiens 1996). The chlorophyllous endosperm helps maintain the embryo and permits growth of the hypocotyl (see Deeks and others 2001). If the germinating seed rests on a host shoot with thin bark and its growth encounters a needle base, it then develops an external holdfast structure and penetration wedge that grows into the host cortex (Scharpf and Parmeter 1967). From the penetration wedge, fine strings of mistletoe tissue — the endophytic system — ramifies throughout the host cortex and eventually becomes embedded in xylem as "sinkers" (Cibrián and others 1980, Calvin and Wilson 1996, Hunt and others 1996). With the establishment of the endophytic system, the parasitic nutritional relation is initiated. Although little is know about the mechanisms of host resistance (see chapter 7), a high degree of host specificity and inherited variation in susceptibility suggest that physiological compatibility is required for an infection to become established (Kolb 2002).

Incubation—The endophytic system expands within the cortex and becomes embedded in the xylem for a number of years before aerial shoots are produced (incubation period). The endophytic system both encircles the infected branch and grows along it. The nature of distal–proximal growth depends upon the dwarf mistletoe species and point of origin. When a species such as *Arceuthobium douglasii* infects the host's apical meristem, a systemic infection is established whereby the growth of the endophytic system keeps up with the growth of the host shoot. In other cases, growth of the endophytic system is limited, and a localized (nonsystemic) infection establishes. In nonsystemic infections, the infected branch develops a distinct fusiform swelling (except by a few host species). The incubation period extends from 2 to 12 years depending on mistletoe species and environmental conditions (Hawksworth and Wiens 1996). Typically, incubation periods range from 3 to 4 years.

Even after aerial shoots are produced, the endophytic system continues to grow (Calvin and Wilson 1996). Pathological effects of the mistletoe infection become evident as infected branches develop persistent witches' brooms, and the upper crown thins and dies. Although a single, systemic infection can eventually develop into a large witches' broom, most severe pathological effects result from multiple infections. Rarely, the endophytic system grows into the bole and establishes a main stem infection that persists as long as the host lives. Branch infections usually occur in the lower crown. These parasitized branches do not readily self-prune but are subject to breakage (especially large brooms in brittle hosts) and consumption by fire (brooms tend to be low and are highly flammable). Infections in the upper crown are lost as crown-dieback in severely diseased trees progresses.

Reproduction—Dwarf mistletoes are dioecious plants that only reproduce from seeds borne on shoots (see Gilbert 1988). Although dwarf mistletoe shoots have chlorophyll, they have no photosynthetic significance. Their function is primarily reproductive and secondarily in water regulation and synthesis of growth compounds (Wilson and Calvin 1996). Shoots range in size from several millimeters to 0.5 m, but most species are 2 to 10 cm tall. Generally, 1 to 2 years elapse from shoot appearance to the initial flowering. Several flower crops (range one to five) are usually produced, and shoots many be retained for 2 to 7 years. Meiosis may occur either immediately before flower production (direct flowering) or approximately 5 to 8 months before anthesis (indirect flowering). Most species exhibit definite annual flowering periods, but a few tropical species appear to flower continuously throughout the year. The sex ratio for most species is about 50:50 (Mathiasen and others 1998, Mathiasen and Shaw 1998, Wiens and others 1996). Pollen is either dispersed by wind or insects, and because of the clustered distribution of mistletoes, pollen is seldom limiting. Although fruit maturation in some tropical species occurs in as little as 4 to 5 months, most species require about 1 year (to 19 months) from flowering to seed dispersal. The number of fruits per infection is controlled by variation in the size of the endophytic system, host–parasite physiology, activity by pathogens and insects, and weather. Strand and Roth (1976) observe that the number of seeds produced by *Arceuthobium campylopodum* is related to plant age, but the coefficient of variation usually exceeds 100 percent (even greater than 200 percent). Wicker (1967a) estimates the number of mistletoe seeds produced on trees infected by *A. campylopodum* range from 800 to 2.2 million per year. Escudero and Cibrián (1985) report that *Arceuthobium globosum* produces more than 7.3 million seeds per hectare.

As parasites, dwarf mistletoes inhabit a relatively safe and constant environment and live for many decades. Because they rely upon a host for nutrition and because reproductive success does not require annual seed production, dwarf mistletoes can persist for years without producing aerial shoots (latent infections). Although little is known of the physiological mechanisms that regulate flowering, shoot production is apparently suppressed in the low light (Shaw and Weiss 2000) and in the nutrition environment of shaded lower crowns (Kolb 2002). Opening the canopy (removing trees) commonly results in a proliferation of mistletoe shoots on the residual trees (see chapter 8).

Spread and Intensification

Because ballistic dispersal and parasitism are important attributes of life history, these features are critical factors in determining population characteristics and dynamics (Bloomberg and Smith 1982, Hawksworth and Scharpf 1984, Parmeter 1978, Smith 1977). Ballistic dispersal is effective for short- range dissemination only, and parasitism requires a living host. Consequently, mistletoe plants are clustered within trees, and infected trees occur in patches (Robinson and others 2002). The spatial dynamics of mistletoe populations operate across a range of scales—the tree, neighborhood, stand, and landscape. Because mistletoes are clustered, infestations are usually described on the bases of incidence (percent of trees infected), severity (relative abundance), area distribution (extent), and spatial patterns (contagion). Successful reproduction leads to spread (Dixon and Hawksworth 1979) and intensification (Geils and Mathiasen 1990). In this context, spread refers to an increase in number of infected trees and the extent of an infestation (including the special case of vertical spread); intensification is increase in the abundance of mistletoe in an infested population. Stand development and management often generate grouping of trees whereby mistletoe disperses readily within groups but infrequently between groups. Even in stands with random or uniform patterns of tree distribution, the abundance of dwarf mistletoe plants often displays spatial autocorrelation. Spread and intensification, of course, are limited (Trummer and others 1998). Infected trees and the dwarf mistletoes they sustain eventually die from fire, insects, disease, or cutting, leading to fragmentation or local extinction of the dwarf mistletoe population.

Rating systems—There are numerous dwarf mistletoe rating systems for describing host susceptibility, mistletoe abundance, and witches' broom abundance (Hawksworth and Wiens 1972, Hawksworth 1977, Tinnin 1998). Each rating system provides a quantitative reference scale for indicating the population status of a mistletoe infestation and its potential for spread and intensification. New systems focus on potential use by wildlife (Parker 2001), fire ecology (Maffei 2002), and adaptations for woodland trees.

The host susceptibility system developed by Hawksworth and Wiens (1972) classifies candidate host species by the percentage expected to become infected where suitably exposed to an inoculum source. The classification is based on either direct field observations or general field experience. The system is meant to reflect the potential physiological susceptibility to infection and parasite development, not the distributional commonness or rarity of the host–pathogen combination. Species with greater than 90 percent infection where exposed to a mistletoe seed source are described as principal hosts; infestations on a principal host population are self-sustaining. Secondary, occasional, and rare hosts exhibit infection levels of 90 to 50 percent, 50 to 5 percent, or less than 5 percent, respectively. Infestations in populations of occasional or rare hosts usually occur where an infected principal host is present. Some species are recognized as hosts either by artificial inoculation or by natural infection of individuals planted beyond their normal range (extralimital hosts). Incompatible hosts are those species in which the dwarf mistletoe is able to establish a parasitic, nutritional relation but not to form aerial shoots. The physiological requirements necessary for parasitism are satisfied for only a few host and mistletoe combinations; most species are immune.

Although mistletoe abundance could be quantified by number of plants, biomass, or other indicators, mistletoe severity is usually described by a relative index for the amount of host crown affected, the dwarf mistletoe rating, DMR (Hawksworth 1977). By this system (fig. 6-1), the live host crown is divided into thirds; each third is rated as 0 if no live branches are apparently infected, 1 if not more than half of the branches are infected, or 2 if more than half of the branches are infected. The system allows a description of mistletoe distribution within crown thirds, or by summing values for crown thirds, abundance for the tree as a whole (DMR), or by averaging tree ratings, severity for a group or stand of trees. If tree ratings (0 to 6) are averaged over all susceptible trees in a stand, the result is stand-DMR; if tree ratings are averaged over infected trees only (1 to 6), the result is stand-DMI (Geils and Mathiasen 1990). The distinction is useful because of the computational identity among DMR, DMI, and the fraction of trees infected (incidence):

$$DMR = DMI \times (incidence).$$

DMR is a good single index of mistletoe severity; but DMI and incidence may be preferred to illustrate separately the severity of infection upon infected trees and relative abundance of infected trees in the population.

Although the DMR system applies well to many important hosts such as spruce, larch, and yellow and white pines, it is less practical for other hosts (Dooling 1978, Shaw and others 2000). In many hemlock and fir stands, the upper crown where much of the mistletoe would be found is obscured by height and foliage. The low, round, compact form of pinyons and general distribution of mistletoe throughout the crown make division into crown thirds impractical. In Douglas-fir, individual branches are difficult to count, but systemic witches' brooms are obvious. Tinnin (1998) suggests a variation to the DMR system, BVR for broom-forming hosts; in his system broom volume substitutes (in part) for number of infected branches in rating a crown third. Other variations are possible, but to avoid confusion, these other variations should not be referred to as DMR.

Spread and intensification are both strongly influenced by the same factors and are really just alternative views of the same basic life history processes—dispersal, establishment, incubation, and reproduction. Intensification of an infected host can occur from autoinfection, allo-infection, or both. The initial infection of a previously uninfected host (both spread and intensification) can only result from allo-infection. Dispersal is primarily affected by the physical configuration of the seed's environment—tree and crown density, vertical crown distribution (structure), and stand species composition. Establishment, incubation, and reproduction are determined by weather, genetic, and other biological factors, some of which are nearly fixed such as host susceptibility. Other factors such as host height growth and predation are extremely variable and difficult to predict. In most cases, the most valuable piece of information for predicting dwarf mistletoe behavior and response to management is knowledge of the mistletoe species. Although all dwarf mistletoes share a common genus morphology, most taxon are readily identifiable when size, branching pattern, color, and brooming response are considered together. Furthermore, most species can be determined based on host and distribution.

Description of Genus

Arceuthobium
Dwarf mistletoe

Arceuthobium M. Bieb. Flora Taurico-Caucasica 3(IV) Supplement, p. 629, 1819. Nom. Cons. 2091
= *Razoumofskya* Hoffman.

Herbs or shrubs from 0.5 cm to approximately 70 cm high (see fig. 4-2 and 4-3); parasitic on Pinaceae and Cupressaceae; plants glabrous, variously colored from greenish yellow to orange, reddish, or black; dioecious; stems with variant (anomalous) patterns of secondary growth; leaves reduced to minute, opposed, connate scales; internodes angled (at least when young); flowers generally decussate or rarely whorled on young shoots, 2 to 4 mm across; staminate flowers with a central nectary, perianth segments usually three to four (rarely two and up to seven) bearing a sessile, one-chambered, circular anther on each perianth segment; pollen spherical with six alternating spiny and smooth sections; pistillate flower manifestly epigynous with one style, perianth segments persistent, adnate to ovary, two-merous; ovary one-chambered; fruit an ovoid berry, one-seeded, mucilaginous and bicolored (distal and basal portions of different shades), explosive at maturity (one exception); seeds without true integuments, usually 3 to 5 mm long, ovate-lanceolate, containing one (rarely two) distal, cylindrical embryo, with copious endosperm.

A genus of 42 species in two subgenera. Subgenus *Arceuthobium* is characterized by verticillate (whorled) branching and occurring mostly in the Old World represented in North America by three species (*A. abietis-religiosae*, *A. americanum*, and *A. verticilliflorum*). Subgenus *Vaginata* occurs only in the New World and characterized by flabellate (fan-like) branching. Thirty-six taxa are described for North America (table 4-1). Type species: *Arceuthobium oxycedri* (DC.) M. Bieb.

Table 4-1—Dwarf mistletoes of Canada, Mexico, and the United States.

***Arceuthobium* taxon**	**Canada**	**United States**	**Mexico**
A. abietinum f. sp. *concoloris*	-	X	X
A. abietinum f. sp. *magnificae*	-	X	-
A. abietis-religiosae	-	-	X
A. americanum	X	X	-
A. apachecum	-	X	X
A. aureum subsp. *petersonii*	-	-	X
A. blumeri	-	X	X
A. californicum	-	X	-
A. campylopodum	-	X	X
A. cyanocarpum	-	X	-
A. divaricatum	-	X	X
A. douglasii	X	X	X
A. durangense	-	-	X
A. gillii	-	X	X
A. globosum subsp. *globosum*	-	-	X
A. globosum subsp. *grandicaule*	-	-	X
A. guatemalense	-	-	X
A. hondurense	-	-	X
A. laricis	X	X	-
A. littorum	-	X	-
A. microcarpum	-	X	-
A. monticola	-	X	-
A. nigrum	-	-	X
A. oaxacanum	-	-	X
A. occidentale	-	X	-
A. pendens	-	-	X
A. pusillum	X	X	-
A. rubrum	-	-	X
A. siskiyouense	-	X	-
A. strictum	-	-	X
A. tsugense subsp. *tsugense*	X	X	-
A. tsugense subsp. *mertensianae*	X	X	-
A. vaginatum subsp. *vaginatum*	-	-	X
A. vaginatum subsp. *cryptopodum*	-	X	X
A. verticilliflorum	-	-	X
A. yecorense	-	-	X
Total number of taxa	6	21	23

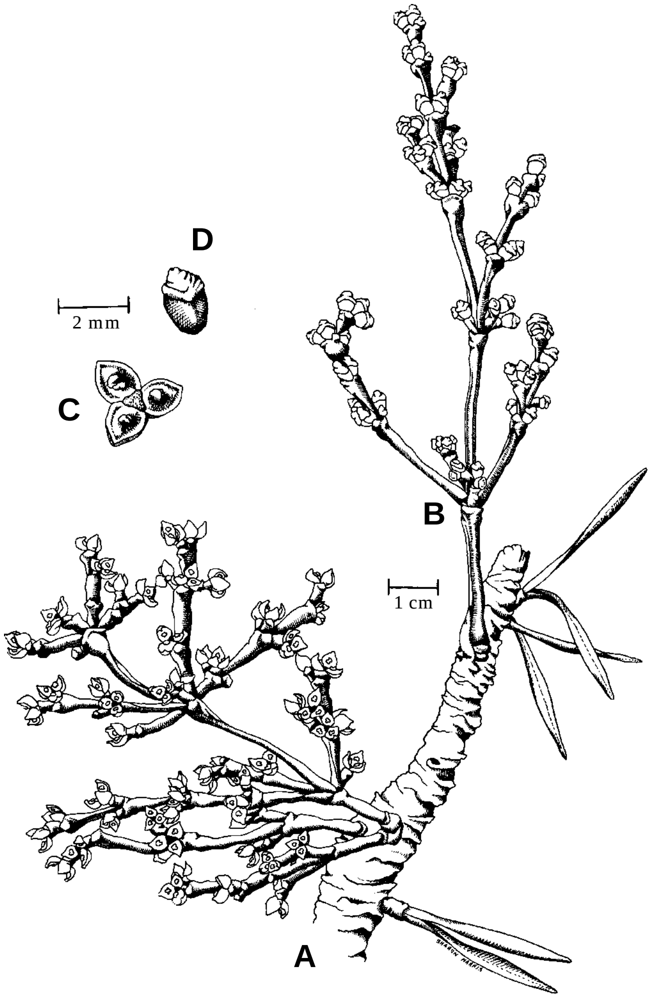


Figure 4-2—*Arceuthobium americanum* in spring, **A** staminate plant with verticillate (whorled) branching, **B** pistillate plant, **C** staminate flower, **D** pistillate flower. Illustration from Hawksworth and Wiens (1972).

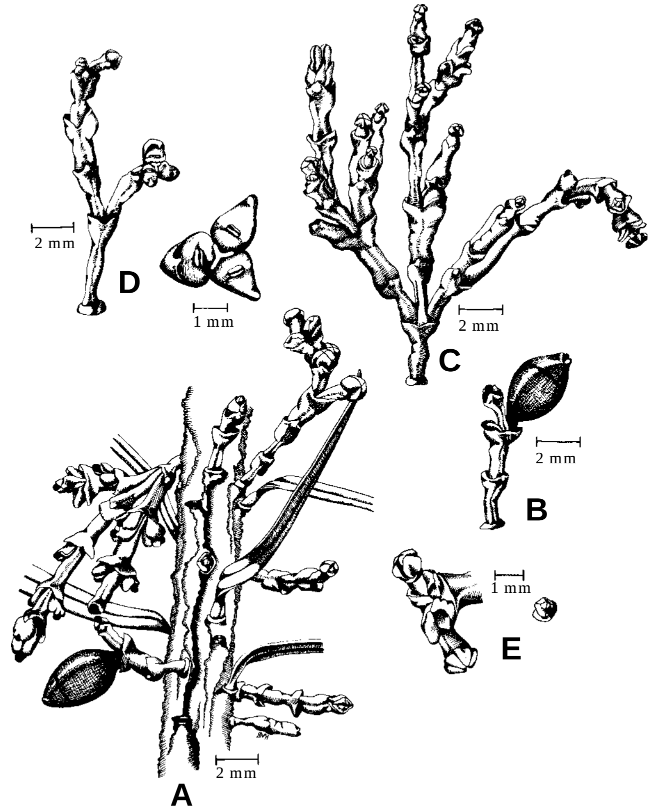


Figure 4-3—*Arceuthobium douglasii* in spring, **A** pistillate plant (left) and staminate plant (right), **B** detail of mature fruit, **C** staminate shoot, **D** staminate shoot with open mature buds (left) and detail of open flower (right), **E** staminate shoots with closed buds. Illustration from Hawksworth and Wiens (1972).

Key to North American Species of *Arceuthobium*

1. Distributed in Mexico 2
  2. Parasites of fir or Douglas-fir 3
    3. Shoots 1–3 cm high; parasites of Douglas-fir .... 11. *A. douglasii*
    3. Shoots more than 5 cm high; parasites of fir 4
      4. Shoots less than 10 cm high, not verticillate, greenish; Chihuahua .... 1. *A. abietinum*
      4. Shoots 10–20 cm high, some verticillate, yellow; Central Mexico .... 2. *A. abietis-religiosae*
  2. Parasites of pine 5
    5. Baja California 6
      6. Shoots olive–green, about 1–2 mm diameter; parasites of pinyon .... 10. *A. divaricatum*
      6. Shoots yellowish, about 2–4 mm diameter; parasites of *Pinus jeffreyi* or *P. coulteri* .... 8. *A. campylopodum*

5. Mainland Mexico 7
  7. Parasites of pinyon or white pine 8
    8. Parasites of pinyon .... 24. *A. pendens*
    8. Parasites of white pine 9
      9. Shoots greenish purple to purple; parasites of *Pinus ayacahuite* var. *ayacahuite*; southern Mexico .... 15. *A. guatemalense*
      9. Shoots yellow or gray; parasites of *Pinus strobiformis* or *P. ayacahuite* var. *brachyptera*; northern Mexico 10
        10. Shoots yellowish, usually less than 4 cm high; northern Coahuila .... 4. *A. apachecum*
        10. Shoots gray, usually more than 6 cm high; Chihuahua, Durango, or Nuevo León .... 6. *A. blumeri*
  7. Parasites of yellow pine 11
    11. Shoots dark, usually some shade of black, reddish (or dull brown when dried) 12
      12. Male and female plants similarly branched (little sexual dimorphism); fruits not glaucous 13
        13. Shoots usually more than 10 cm high and more than 1 cm diameter at base; fruits 4–5 mm long, not shiny .... 30a. *A. vaginatum* subsp. *vaginatum*
        13. Shoots usually less than 10 cm high and less than 1 cm diameter at base; fruits about 3 mm long, shiny .... 26. *A. rubrum*
      12. Male and female plants dissimilarly branched (sexually dimorphic); fruits markedly glaucous .... 21. *A. nigrum*
    11. Shoots yellow, brown, gray, or red 14
      14. Staminate flowers verticillate on deciduous spikes; mature fruits more than 10 mm long .... 31. *A. verticilliflorum*
      14. Staminate flowers not verticillate on deciduous spikes; mature fruits less than 6 mm long 15
        15. Plants of northern Mexico 16
          16. Male and female plants dissimilarly branched (sexually dimorphic) 17
            17. Male plants essentially non-branched and female plants densely branched .... 28. *A. strictum*
            17. Male plants with very open branches and female plants densely branched .... 13. *A. gillii*
          16. Male and female plants similarly branched (little sexual dimorphism) 18
            18. Shoots yellow or yellow–brown 19
              19. Shoots bright yellow, in globose clusters, usually more than 10 cm high .... 14a. *A. globosum* subsp. *globosum*
              19. Shoots yellow or brown, not in globose clusters, usually less than 10 cm high .... 32. *A. yecorense*
            18. Shoots some shade of orange 20
              20. Shoots dark–orange, usually more than 20 cm high; mature fruit 7 mm long; Durango or southward .... 12. *A. durangense*
              20. Shoots yellow–orange, usually less than 20 cm high; mature fruit 5 mm long; Chihuahua, Sonora, or Coahuila .... 30b. *A. vaginatum* subsp. *cryptopodum*
        15. Plants of southern Mexico (Chiapas and Oaxaca) 21
          21. Shoots glaucous, olive-brown to gray green; parasite of *P. oocarpa* or *P. maximinoi* .... 16. *A. hondurense*
          21. Shoots not glaucous; reddish, dark green, yellow, or orange 22
            22. Shoots reddish; Oaxaca .... 22. *A. oaxacanum*
            22. Shoots dark greenish yellow or orange; Oaxaca or Chiapas 23
              23. Shoots yellow, often over 2 cm in diameter at base; elevations above 2,700 m .... 14b. *A. globosum* subsp. *grandicaule*
              23. Shoots yellow–orange, usually less than 2 cm in diameter; elevations below 2,400 m .... 5. *A. aureum* subsp. *petersonii*

1. Distributed in the United States or Canada 24
 24. Parasites principally of pine 25
  25. Parasites of pinyon or white pine 26
   26. Parasites of pinyon .... 10. *A. divaricatum*
   26. Parasites of white pine 27
    27. Parasites of *Pinus strobiformis* 28
     28. Shoots usually less than 4 cm high, yellow; southern Arizona or southern New Mexico .... 4. *A. apachecum*
     28. Shoots usually more than 6 cm high, gray; Huachuca Mountains of Arizona .... 6. *A. blumeri*
    27. Parasites of white pines other than *Pinus strobiformis* 29
     29. Parasites of *Pinus aristata*; Arizona .... 19. *A. microcarpum*
     29. Parasites of pines other than *Pinus aristata* or if parasite of *Pinus aristata* then not Arizona 30
      30. Shoots usually less than 6 cm high, densely clustered around the host branch; parasites of *Pinus flexilis*, *P. albicaulis*, *P. aristata*, or *P. longaeva* .... 9. *A. cyanocarpum*
      30. Shoots usually more than 6 cm high, not densely clustered around the host branch; parasites of *Pinus monticola* or *P. lambertiana* 31
       31. Shoots dark brown; parasites of *Pinus monticola*; southwestern Oregon or northeastern California .... 20. *A. monticola*
       31. Shoots yellow to green; parasites of *Pinus lambertiana*; California .... 8. *A. californicum*
 25. Parasites of yellow pine 32
  32. Shoot branches verticillate; parasites principally of *Pinus contorta* or *P. banksiana* .... 3. *A. americanum*
  32. Shoot branches flabellate; parasites principally of pines other than *Pinus contorta* and *P. banksiana* 33
   33. Arizona, Utah, or eastward 34
    34. Fruits glaucous; male plants much more openly branched than female plants; parasites of *Pinus leiophylla* var. *chihuahuana* .... 13. *A. gillii*
    34. Fruits glabrous; male and female plants branch in similar manner; parasites of *Pinus ponderosa* var. *scopulorum*, *P. arizonica*, and *P. engelmannii*; north to Colorado .... 30b. *A. vaginatum* subsp. *cryptopodum*
   33. Pacific Coast States, Nevada, Idaho, or British Columbia 35
    35. Coastal areas (within 10 km of the Pacific Ocean) 36
     36. Shoots usually less than 10 cm high; staminate flowers mostly 3-merous; parasites of *Pinus contorta* var. *contorta*; Orcas Island, Washington or British Columbia .... 29a. *A. tsugense* subsp. *tsugense*
     36. Shoots usually more than 10 cm high; staminate flowers mostly 4-merous; parasites of *Pinus radiata* or *P. muricata*; California .... 18. *A. littorum*
    35. Inland areas 37
     37. Plants consistently forming witches' brooms; mature fruits about 6 mm long; shoots more than 3 mm diameter at base; parasites principally of *Pinus ponderosa* var. *ponderosa*, *P. jeffreyi*, or *P. coulteri*; California, Oregon, Washington, Idaho, or Nevada .... 8. *A. campylopodum*
     37. Plants not forming witches' brooms; mature fruits about 4 mm long; shoots less than 3 mm diameter at base; parasites principally of *Pinus sabiniana* or *P. attenuata*; California or southwestern Oregon 38
      38. Anthesis from late September to November; parasites principally of *Pinus sabiniana*; foothills surrounding Central Valley of California .... 23. *A. occidentale*
      38. Anthesis in August; parasites of *Pinus attenuata*; southwestern Oregon or northwestern California .... 27. *A. siskiyouense*

24. Parasites principally of hemlock, larch, Douglas-fir, fir, or spruce 39
 39 Parasites of hemlock, larch, or Douglas-fir 40
  40. Shoots usually less than 4 cm high; parasites of Douglas-fir .... 11. *A. douglasii*
  40. Shoots usually more than 5 cm high; parasites of larch or hemlock 41
   41. Parasites principally of larch .... 17. *A. laricis*
   41. Parasites principally of hemlock 42
    42. Parasites of *Tsuga heterophylla*; California to Alaska .... 29a. *A. tsugense* subsp. *tsugense*
    42. Parasites of *Tsuga mertensiana*; California to Idaho and British Columbia 43
     43. Host associated with infected *Larix occidentalis*; northern Idaho .... 17. *A. laricis*
     43. Host not associated with infected *Larix occidentalis*; central Sierra Nevada of California to southern British Columbia .... 29b. *A. tsugense* subsp. *mertensianae*
 39. Parasites of fir or spruce 44
  44. Parasites of fir 45
   45. Shoots usually more than 10 cm high, yellowish; staminate buds same color as the subtending bracts; host not associated with infected hemlock; Arizona, southern Utah, Nevada, California, Oregon, or Washington east of the Cascade Crest .... 1. *A. abietinum*
   45. Shoots usually less than 6 cm high, green to purplish; staminate buds conspicuously lighter than the subtending purplish bracts; host associated with infected hemlock; Oregon west of Cascade Crest to Alaska along Pacific Coast 46
    46. Host associated with infected *Tsuga heterophylla* .... 29a. *A. tsugense* subsp. *tsugense*
    46. Host associated with infected *Tsuga mertensianae* .... 29b. *A. tsugense* subsp. *mertensianae*
  44. Parasites of spruce 47
   47. Shoots less than 2 cm high; parasites of *Picea mariana*, *P. glauca*, or *P. rubens*; Saskatchewan and Great Lake region eastward to New Jersey and Newfoundland .... 25. *A. pusillum*
   47. Shoots usually more than 5 cm high; parasites on *Picea engelmannii* or *P. pungens*; Arizona or southern New Mexico .... 19. *A. microcarpum*

Several other keys and floristic treatments of the dwarf mistletoes are available. Scharpf and Hawksworth (1993) provide photographs and field descriptions for the mistletoe from Washington, Oregon, and California. Unger (1992) provides a similar, general coverage for Canada. Numerous but brief and partial descriptions describe the dwarf mistletoes of Mexico (Cházaro and Olivae 1987a, Hawksworth 1987, Hawksworth and Cibrián 1985, Najera and others 1987, Rodriguez 1983). Recent taxonomic notes include Hawksworth and Wiens (1965, 1977, 1989) and Hawksworth and others (1992b). Because the taxonomy of dwarf mistletoes has changed considerably in the past few decades, especially for some regions (Mexico) and some groups (*campylopodum*, *globosum*, *vaginatum*), care is required when reading the literature to relate the information presented to the proper taxa. Host and distribution information is ultimately derived from specimen collections and field observations. When the name applied to a specimen changes, the information also refers to a different taxa; published information goes out of date and may be associated with the wrong mistletoe.

Description of Species

1. *Arceuthobium abietinum*
Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz, Manual Southern California Botany: 114, 1935.
=*A. campylopodum* f. *abietinum*.

Description. Mean shoot height 8 (maximum 22) cm. Shoots yellow green to yellow, branches flabellate. Basal diameter of dominant shoots 1.5 to 6.0 (mean 2) mm. Third internode 4 to 23 (mean 14) mm long, 1.5 to 4.0 mm (mean 2) mm wide; length/width ratio is 7:1 to 9:1. Staminate flowers 2.5 mm across; perianth three-merous, sometimes four-merous, apex acute; same color as shoots; segments 1.2 mm long, 1.0 mm wide. Mature fruit 4 by 2 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Key to the Formae Speciales

1. Parasitic principally on *Abies concolor* or *A. grandis*; known in two areas in Chihuahua on *A. durangensis*. The primary distribution is from southern Washington southward through the Cascade and southern Coast Ranges in Oregon, and the North Coast and Cascade Ranges, Sierra Nevada to southern California. Isolated populations occur in southern Utah, northern and southern Arizona, and Chihuahua ....
.... 1a. *A. abietinum* f. sp. *concoloris*.
1. Parasitic principally on *Abies magnifica* from southwestern Oregon (Josephine) to the southern Sierra Nevada, California .... 1b. *A. abietinum* f. sp. *magnificae*.

Phenology. Meiosis in July. Anthesis usually August and September. Fruits mature in September or October of the year following pollination; maturation period averages 13 to 14 months. Seeds germinate from February through June.

Hosts. Fir.

Discussion. Parmeter and Scharpf (1963) first report that the dwarf mistletoe on *Abies concolor* does not infect associated *A. magnifica*, and conversely, the parasite of *A. magnifica* does not parasitize associated *A. concolor*. We are unable, however, to find any morphological, phenological, or chemical differences useful to distinguish between the two mistletoes. Because the host affinities of these two dwarf mistletoes are distinct and they are of considerable importance in forestry, we treat them as *formae speciales*. Branch death or “flagging” by the fungus *Cytospora abietis* is one of the most conspicuous field symptoms for infection by this dwarf mistletoe (Scharpf 1969a). The biology, pathology, and management of fir dwarf mistletoe are discussed by Filip and others (2000), Scharpf (1969b), and Scharpf and Parmeter (1967, 1982).

Hunt (1993) reorganizes the taxonomy of *Abies* and recognizes several combinations not previously used in the dwarf mistletoe literature. In his treatment, *Abies lasiocarpa* refers to west-side populations in the Pacific Northwest and British Columbia and *A. bifolia* to east-side and Rocky Mountain populations. Status of the corkbark fir (=*Abies lasiocarpa* var. *arizonica*) in the Southwest is left as uncertain. *Abies lowiana* is recognized as species rather than subspecies.

1a. *Arceuthobium abietinum*
White Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *concoloris* Hawksw. & Wiens, Brittonia 22:267, 1970.

Hosts. The principal hosts of this dwarf mistletoe are *Abies concolor*, *A. grandis*, *A. durangensis*, and *A. lowiana*. *Abies concolor* (Nevada, Utah, and Arizona) and *A. lowiana* (California) are about equally susceptible, although the dwarf mistletoe is more widely distributed on the latter. The rare *Picea breweriana* in Oregon is associated with infected *Abies concolor* and is heavy infected by *Arceuthobium abietinum*. On the North Rim of Grand Canyon, Arizona, *Abies bifolia* (usually referred to *Abies lasiocarpa* var. *arizonica*) is occasionally parasitized where this tree grows in association with infected *A. concolor*. *Abies amabilis* is a rare host of this dwarf mistletoe at Crater Lake, Oregon. *Pinus ayacahuite* var. *brachyptera, P. contorta* var. *murrayana, P. lambertiana*, and *P. monticola* are rare hosts.

Distribution. United States (Washington, Oregon, California, Nevada, Utah, and Arizona), and Mexico (Chihuahua). *Arceuthobium abietinum* f. sp. *concoloris* is widely distributed from southern Washington (Skamania, Wenatchee, and Klickitat) south through the Cascade Range and Sierra Nevada to the San Bernardino Mountains, California. A single, relict population is known in the Willamette Valley, Oregon. It also occurs along the coast ranges from Mendocino, California, to Curry, Oregon. Isolated populations are known in Nevada (Spring, Sheep, and Groom Mountains) and Utah (Kane). The parasite is known in Arizona from the Grand Canyon, the Chiricahua Mountains (Cochise), and the Santa Catalina Mountains (Pima). This dwarf mistletoe is reported on *Abies durangensis* from in two localities in Chihuahua 1,000 km south of Arizona. *Arceuthobium abietinum* f. sp. *concoloris* occurs from near sea level along the coast of northern California and southern Oregon to over 2,650 m in the Spring Mountains of southern Nevada.

Discussion. In the Northwest, two other species of *Arceuthobium* occur on fir: (1) *Arceuthobium tsugense* on *Abies amabilis*, *A. grandis*, and *A. lasiocarpa* and (2) *Arceuthobium laricis* on *Abies grandis* and *A. lasiocarpa*. However, insofar as we are aware, neither of these dwarf mistletoes is sympatric with *Arceuthobium abietinum*. *Arceuthobium tsugense* and *A. laricis* rarely infect pure stands of fir, but they may parasitize fir secondarily in stands where the principal hosts of these dwarf mistletoes are parasitized (for example, hemlock by *A. tsugense* and larch by *A. laricis*). *Arceuthobium tsugense* differs from *A. abietinum* by shorter (7 cm), green to purple shoots compared with the longer (10 cm), yellowish shoots of *A. abietinum*. *Arceuthobium* *laricis* is readily distinguished from *A. abietinum* by shorter, darker shoots (4 cm versus 10 cm) and shorter (in summer) staminate spikes (2 to 3 mm versus 5 to 7 mm). 1b.

Arceuthobium abietinum
Red Fir Dwarf Mistletoe

Arceuthobium abietinum Engelm. ex Munz f. sp. *magnificae* Hawksw. & Wiens, Brittonia 22:268, 1970.

Hosts. *Abies magnifica*.

Distribution. United States (Oregon and California). *Arceuthobium abietinum* f. sp. *magnificae* is distributed from Josephine, Oregon, to Kern, California, in the southern Sierra Nevada. Guyon and Munson (1991) record it within 3 km of the Nevada border. Elevational range is 1,500 to 2,400 m.

Discussion. *Arceuthobium abietinum* f. sp. *magnificae* is a common and serious disease agent of the *Abies magnifica* forests of the Sierra Nevada (Scharpf 1969b).

2. *Arceuthobium abietis-religiosae*
Mexican Fir Dwarf Mistletoe

Arceuthobium abietis-religiosae Heil, Zentralblatt f¸r Bakteriologie Abteilung 2:28, 1923 [and see Hawksworth and Wiens, Brittonia 17:231, 1965].

Description. Mean shoot height 10 (maximum 16) cm. Shoots olive green, older shoots typically with black variegations, occasionally with verticillate branching. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 8 to 24 (mean 15.4 ±5.3) mm long, 1 to 4 (mean 2.8) mm wide, length/width ratio 5.5:1. Staminate buds two to four per node. Staminate flowers 2 mm long, 2.4 mm across; perianth mostly three-merous, sometimes four-merous; apex obtuse-acute; same color as shoots on outer surface, reddish on inner surface distal to anther; segments 1.2 mm long, 0.9 mm wide. Pistillate flowers 1.0 mm long, 0.5 mm across. Mature fruit 3.5 by 2 mm; proximal portion 2.5 mm long. Seeds 2.2 by 1.0 mm.

Phenology. Meiosis in September. Anthesis poorly known but apparently flowering in March to April and September to October. Fruits probably mature in October or November.

Hosts. Known only on fir. *Abies religiosa* (including var. *emarginata*) is by far the most common host, but also this dwarf mistletoe also parasitizes *A. vejarii* and probably other Mexican firs.

Distribution. Mexico (Distrito Federal, Hidalgo, Jalisco, Mexico, Michoacán, Nuevo León, Puebla, Tamaulipas, Tlaxcala). This dwarf mistletoe is common in the *Abies religiosa* forests of Central Mexico and Sierra Madre Oriental (Hernandez and others 1992, Madrigal 1967). Elevational range is 2,500 to 3,350 m.

Discussion. This distinctive Mexican dwarf mistletoe is characterized by its large shoots, occasional verticillate branching, and exclusive parasitism of fir. With the exception of the rare occurrence of *Arceuthobium abietinum* in Chihuahua, this is the only dwarf mistletoe that parasitizes fir in Mexico.

3. *Arceuthobium americanum*
Lodgepole Pine Dwarf Mistletoe

Arceuthobium americanum Nutt. ex Engelm. in Gray, Boston Journal Natural History 6:214, 1850.

Description. Mean shoot height 5 to 9 (maximum 30) cm. Shoots yellowish to olive green, with verticillate branching (fig. 4-2). Basal diameter of dominant shoots 1 to 3 (mean 1.5) mm. Third internode 6 to 23 (mean 12 ±3.0) mm long, 1 to 2 (mean 1.2) mm wide (20 collections), length/width ratio 10.1:1. Staminate flowers borne on pedicel-like segments, 2 mm long, 2.2 mm across; perianth mostly three-merous, sometimes four-merous; same color as the shoots; segments 1.1 mm long, 1.0 mm wide. Pistillate flowers verticillate; 1.5 mm long, 1.0 mm across; two-merous. Mature fruit 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.5 (mean 2) mm wide; proximal portion about 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Meiosis in August. Anthesis usually from early April to early June, with extremes from late March to late June. Fruits mature in late August or September of the year following pollination; maturation period averages 16 months. Germination begins in May in Colorado.

Hosts. The principal hosts are *Pinus contorta* var. *latifolia*, var. *murrayana*, and *P. banksiana*; all are about equally susceptible. *Pinus contorta* var. *contorta* is infected in southern coastal British Columbia (Smith and Wass 1979). *Pinus ponderosa* var. *scopulorum* is frequently parasitized in Colorado, Utah, and Wyoming, usually where this tree is associated with infected *P. contorta* but also in pure stands of *Pinus ponderosa*. *Pinus ponderosa* var. *ponderosa*, however, is less susceptible and only occasionally infected. Other occasional hosts include *P. albicaulis*, *P. flexilis*, and *P. jeffreyi*. Rare, artificially inoculated, or extra-limital hosts are *Abies lasiocarpa* (Mathiasen and others 1996a), *Picea engelmannii*, *P. glauca* (incompatible), *P. pungens*, *P. mariana* (incompatible), *Pinus aristata*, *P. mugo*, *P. sylvestris*, and *Pseudotsuga menziesii* (incompatible).

Distribution. Canada (British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario) and the United States (Washington, Idaho, Montana, Oregon, California, Utah, Wyoming, Colorado, and possibly Nevada). *Arceuthobium americanum* has the most extensive distribution of any North American dwarf mistletoe. The distribution of *Arceuthobium americanum* is centered on the range of its principal host, *Pinus contorta*, and rarely occurs within the distribution of *Pinus contorta* var. *contorta* (shore pine). *Arceuthobium americanum* occurs in outlying populations of *Pinus* *contorta* var. *latifolia* in Southeastern Alberta and in north central Montana (Phillips, Hill, and Liberty). *Arceuthobium americanum* distribution maps include Alberta, British Columbia, Manitoba, Saskatchewan, Montana, Utah, Colorado, and California (see Brandt and others 1998, Hawksworth and Wiens 1996, Muir 2002). This dwarf mistletoe varies in elevation from 200 m near Lake Athabasca in northern Alberta and Saskatchewan to 3,350 m in central Colorado.

Discussion. *Arceuthobium americanum* induces characteristic systemic witches' brooms on *Pinus contorta* and produces the same type of broom on *P. ponderosa*. The witches' brooms formed on *Picea engelmannii*, however, are nonsystemic (Hawksworth and Graham 1963a). Kuijt (1960a) notes that *A. americanum* cannot perpetuate itself over time on *Pinus jeffreyi* or *P. ponderosa* var. *ponderosa* in California. In northern Colorado and southern Wyoming, however, the parasite is aggressive in pure stands of *P. ponderosa* var. *scopulorum* outside the range of *A. vaginatum* subsp. *cryptopodum*, which is the typical parasite on *P. ponderosa* in the Rocky Mountains. Hawksworth and Johnson (1989a) provide a synopsis of the biology and management of this mistletoe in the Rocky Mountains. Other general and silvicultural information is given by Baranyay (1970), Hawksworth and Dooling (1984), van der Kamp and Hawksworth (1985), and Van Sickle and Wegwitz (1978).

4. *Arceuthobium apachecum*
Apache Dwarf Mistletoe

Arceuthobium apachecum Hawksw. & Wiens, Brittonia 22:266, 1970.
=*A. campylopodum* f. *blumeri*

Description. Mean shoot height 3 to 4 (maximum 9) cm. Shoots yellow, green, or reddish, branches flabellate and densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.8) mm. Third internode 5 to 10 (mean 7.2 ± 2.0) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 4.8:1. Flowers axillary. Staminate flowers 2.7 mm across; perianth three- to four-merous; same color as shoots; segments 1.3 mm long, 0.9 mm wide. Mature fruit 4 by 2.5 mm; proximal portion 2.5 mm long. Seeds 2.8 by 1.2 mm.

Phenology. Meiosis in July. Anthesis from late July to mid-September, peak in mid-August. Fruits mature from mid-August to mid-October, peak in September; maturation period averages about 13 months.

Host. Known only naturally on *Pinus strobiformis*, but successfully inoculated by Mathiasen (1978) on *Pinus flexilis*.

Distribution. United States (Arizona, New Mexico) and Mexico (Coahuila). This dwarf mistletoe has a limited distribution in southern Arizona and central New Mexico, with an outlier in the Sierra del Carmen in northern Coahuila. In Arizona, it occurs in the White, Pinaleno, Santa Catalina, Santa Rita, and Chiricahua Mountains and in New Mexico in the Mangas, San Mateo, Magdalena, and Capitan Mountains. Elevational range is 2,000 to 3,000 m.

Discussion. The exclusive occurrence of two dwarf mistletoes species, *Arceuthobium apachecum* and *A. blumeri*, on a single host species, *Pinus strobiformis*, is unique in *Arceuthobium*. Geographically consistent morphological and broom differences indicate that separate taxonomic status is warranted (Mathiasen 1982). Although they are not sympatric, they approach 60 km of each other in southern Arizona. *Arceuthobium apachecum*, but not *A. blumeri*, frequently induces witches' broom formation.

5. *Arceuthobium aureum* subsp. *petersonii*
Peterson's Dwarf Mistletoe

Arceuthobium aureum Hawksw. & Wiens subsp. *petersonii* Hawksw. & Wiens, Brittonia 29:415, 1977.
=*A. globosum*

Description. Shoots 14 to 40 (mean 24) cm tall, golden to yellow-brown, branches flabellate. Basal diameter of dominant shoots 14 to 35 (mean 23) mm. Third internode 14 to 35 (mean 23) mm long and 2.5 to 8 (mean 5) mm wide.

Phenology. Anthesis in September. Fruits mature June and July; maturation period of 9 to 10 months, which is several months less than is common for many dwarf mistletoes.

Hosts. *Pinus michoacana*, *P. montezumae*, *P. oaxacana*, *P. oocarpa*, *P. patula*, and *P. pseudostrobus* are the principal and only hosts. *Pinus michoacana* is somewhat less susceptible and is infected only when it grows in association with the other principal hosts.

Distribution. Mexico (Oaxaca, Chiapas). This dwarf mistletoe is common between San Cristóbal de las Casas and Teopisabout (Chiapas). Its distribution in Oaxaca is poorly known by a few collections from Miahuátlan to Suchixtepec. Elevational range is 2,200 to 2,450 m.

Discussion. The taxon recognized here as *Arceuthobium aureum* had been in the *Arceuthobium globosum* complex (Hawksworth and Wiens 1972, 1977). *Arceuthobium aureum* includes two subspecies, but only subspecies *petersonii* is found in Mexico. This subspecies is characterized by tall, slender, brown to golden shoots, long fruits (5 mm), long pedicels (4 mm), and tendency to form witches' brooms.

6. *Arceuthobium blumeri*
Blumer's Dwarf Mistletoe

Arceuthobium blumeri A. Nels., Botanical Gazette 56:65, 1913.
=*A. campylopodum* var. *cryptopodum*
=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 6 to 7 (maximum 18) cm, gray to straw or light green, branches flabellate.

Basal diameter of dominant shoots 1 to 3 (mean 2.1) mm. Third internode 5 to 14 (mean 9.1 ±2.5) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 5.5:1. Staminate flowers 2.5 mm long, 2.5 to 3.0 mm across; perianth three- to six-merous (mostly three- or four-merous), segments 1.3 mm long, 1.0 mm wide, apex acute. Mature fruit 4 by 2.5 mm, proximal portion 2.5 mm long. Seeds 2.7 by 1.0 mm.

Phenology. Meiosis in July. Anthesis from mid-July to late-August, with a peak in early August (Mathiasen 1982). Fruits mature from late August to early October, with a peak in mid-September; maturation period averages 13 to 14 months.

Hosts. *Pinus strobiformis* and *P. ayacahuite* var. *brachyptera*. The host affinities of *Arceuthobium blumeri* are not clear because of the taxonomic confusion surrounding the white pine complex of *Pinus flexilis-strobiformis-ayacahuite* (Equiluz 1991, Hawksworth 1991, Perry 1991). Most host populations of this dwarf mistletoe are best referred to *P. ayacahuite* var. *brachyptera* in the Sierra Madre Occidental and *P. strobiformis* var. *potosiensis* on Cerro Potosí (Nuevo León). *Pinus flexilis* can be infected by inoculation (Mathiasen 1978).

Distribution. United States (Arizona) and Mexico (Sonora, Chihuahua, Durango, Nuevo León, and Coahuila). This dwarf mistletoe extends southward from the Huachuca Mountains in southern Arizona through the Sierra Madre Occidental in Chihuahua and Sonora to southern Durango. In the Sierra Madre Oriental, it is known only from Cerro Potosi (Nuevo León) and San Antonio de las Alazanas (Coahuila), but it probably occurs elsewhere over this extensive distribution (Cibrián and others 1980). Elevational range is 2,150 to 3,250 m.

Discussion. The parasitism of *Arceuthobium blumeri* and *A. apachecum* on *Pinus strobiformis* is discussed under *A. apachecum*. Distinctive features of *Arceuthobium blumeri* include its gray-colored shoots, four- to six-merous staminate flowers, and rare formation of witches' brooms.

7. *Arceuthobium californicum*
Sugar Pine Dwarf Mistletoe

Arceuthobium californicum Hawksw. & Wiens, Brittonia 22:266, 1970.
=*A. campylopodum* f. *cryptopodum*
=*A. campylopodum* f. *blumeri*.

Description. Mean shoot height 8 cm (maximum 12) cm, greenish to bright yellow, turning brown at base of older shoots, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 16 (mean 10.5 ±2.9) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 7.0:1. Flowers axillary. Staminate flowers 3.3 mm across; perianth three- or four-merous, segments 1.5 mm long, 1.1 mm wide. Mature fruit 4 by 2.5 mm; proximal portion 2.0 mm long. Seeds 3.2 by 1.2 mm.

Phenology. Meiosis in July. Anthesis usually in mid-July to mid-August, with extremes from early July to late August. Fruits mature from mid-September to mid-October, with extremes from late August to early November; maturation period averages 13 to 14 months.

Hosts. The only principal host is *Pinus lambertiana*. In association with infected *P. lambertiana*, *P. monticola* is secondarily parasitized (Mathiasen and Hawksworth 1988). Infected *P. lambertiana* produce large, compact witches' brooms.

Distribution. United States (California). This species is distributed from Mount Shasta southward through the North Coast Range, and through the Cascade Range south to Lake County and the west side of the Sierra Nevada to the Cuayamaca Mountains (San Diego). Elevational range is 600 to 2,000 m.

Discussion. *Arceuthobium californicum* is common in many areas and a serious pathogen of *Pinus lambertiana* (Scharpf and Hawksworth 1968).

8. *Arceuthobium campylopodum*
Western Dwarf Mistletoe

Arceuthobium campylopodum Engelm. in Gray, Boston Journal Natural History 6:214, 1850.
=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 13) cm, olive green to yellow, branches flabellate. Staminate plants brownish, and pistillate plants greenish. Basal diameter of dominant shoots 1.5 to 5.0 (mean 3) mm. Third internode 7 to 22 (mean 11.3 ±3.8) mm long, 1.5 to 2.5 (mean 2.0) mm wide, length/width ratio 5.6:1. Staminate flowers 3.0 mm across; perianth three-merous (occasionally four-merous), segments 1.4 mm long, 1.0 mm wide. Mature fruit 5.0 by 3.0 mm.

Phenology. Meiosis in July. Peak anthesis usually from mid-August to early October, with extremes from early August to late October. Fruits usually mature from early September to mid-November, with extremes from late August to late November; maturation period averages 13 months.

Hosts. The principal and most commonly infected hosts are *Pinus ponderosa* var. *ponderosa* and *P. jeffreyi*. *Pinus jeffreyi* is somewhat more susceptible than *P. ponderosa*, but both species incur considerable damage. Other trees frequently infected, particularly when associated with the above hosts, are *Pinus attenuata* and *P. coulteri*. In the Spring Mountains, Nevada, *P. ponderosa* var. *scopulorum* is a common and seriously damaged host, but this is the only known area where *Arceuthobium campylopodum* occurs naturally within the range of *scopulorum*. Occasional hosts for *A. campylopodum* are *P. contorta* var. *latifolia*, var. *murrayana*, and *P. sabiniana*. *Pinus lambertiana* is a rare host. Hosts by artificial inoculation are *Abies concolor*, *A. grandis*, *Picea abies*, *Pinus sylvestris*, *P. mugo*, *P. resinosa*, and *Larix occidentalis*. Although *Abies concolor*, *A. grandis*, and *Larix occidentalis* are commonly associated with *Pinus ponderosa* infected by *A. campylopodum*, they are not known to be naturally infected. *Pinus washoensis* is expected to be susceptible, but we know of no collections or reports on this species.

Distribution. United States (Washington, Idaho, Oregon, California, and Nevada) and Mexico (Baja California Norte). *Arceuthobium campylopodum* occurs from northern Washington and eastern Idaho, south through Oregon and California (but not the southern Coast Range) to the Sierra Juárez and Sierra de San Pedro Mártir (Baja California Norte). The distribution of this and other taxa in California is discussed by Kuijt (1960a). In Nevada, it occurs near Lake Tahoe and in the Spring Mountains (Clark). *Arceuthobium campylopodum* is distributed by elevation from 30 m along the Columbia River, near Hood River, Oregon, to 2,500 m in the Spring Mountains, Nevada.

Discussion. *Arceuthobium campylopodum* is a serious pathogen of *Pinus jeffreyi* and *P. ponderosa*. Our observations suggest that host damage is more severe in the southern or drier parts of the distribution. The most severely infested stands are in the California Laguna Mountains and on the east-side of the Sierra–Cascade forests. The biology, ecology, and management of this mistletoe are discussed by Kimmey and Mielke (1959), Schmitt (1996), and Stand and Roth (1976). The serious mortality caused by this mistletoe to pine in Oregon is described by Roth (2001).

9. *Arceuthobium cyanocarpum*
Limber Pine Dwarf Mistletoe

Arceuthobium cyanocarpum (A. Nels. ex Rydb.) A. Nels., New Manual of Botany of the Central Rocky Mountains, p. 146, 1909.

=*A. campylopodum* f. *cyanocarpum*.

Description. Mean shoot height 3 (maximum 7) cm, yellow–green, branches flabellate, densely clustered. Basal diameter of dominant shoots 1 to 2 (mean 1.4) mm. Third internode 2 to 14 (mean 5.2 ±2.0) mm long, 1.0 to 1.5 (mean 1.1) mm wide; length/width ratio 4.7:1. Staminate flowers 3.0 mm across; perianth three-merous (rarely four-merous), same color as shoots; segments 1.4 mm long, 1.0 mm wide, apex acute. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 b 0.9 mm.

Phenology. Meiosis in July. Peak anthesis from mid-July to early September, with extremes from early July to mid-September. Fruits mature from mid-August to late September; maturation averages 12 months. Seed germination mostly in June.

Hosts. *Pinus flexilis* is the most common host of this dwarf mistletoe throughout its extensive geographical range. *Pinus albicaulis, P. aristata*, and *P. longaeva* are also principal hosts even though they are not common within the range of *Arceuthobium cyanocarpum*. *Pinus albicaulis* is infected in western Wyoming, northern Nevada, central Oregon, and northern California. Infection of *P. aristata* is known from La Veta Pass, Colorado, in association with infected *P. flexilis*. *Pinus longaeva* is parasitized in many areas of Utah and Nevada. In northern California, *Pinus monticola* is a secondary host; and *Pinus balfouriana* is an occasional host (Mathiasen and Daughtery 2001). *Tsuga mertensiana* in central Oregon is another secondary host; and other occasional or rare hosts include *Picea engelmannii* (doubtful), *P. contorta* var. *latifolia*, and *P. ponderosa* var. *scopulorum*. *Pinus strobus* and *P. strobiformis* are susceptible to infection by artificial inoculation (Hawksworth and Wiens 1972).

Distribution. United States (Idaho, Montana, Oregon, California, Nevada, Utah, Wyoming, and Colorado). This dwarf mistletoe occurs from southern Montana and northern Wyoming south to southern Colorado and west to Oregon and California where it occurs on the east side of the Sierra Nevada, in the Panamint Mountains (Death Valley National Monument), and in the San Bernardino to San Jacinto Mountains (southern California). Distribution maps for *Arceuthobium cyanocarpum* are available for Colorado and Nevada (see Hawksworth and Wiens 1996). Elevational range is 1,600 m in southern Montana to nearly 3,050 m in central Colorado.

Discussion. This dwarf mistletoe, which characteristically infects *Pinus flexilis* and associated high-altitude white pines, is easily recognized by small, densely clustered shoots and common branch flagging. Witches' brooms are typically small and compact, and infection is usually throughout the entire crown. *Arceuthobium cyanocarpum* causes heavy mortality in *Pinus flexilis* in the Rocky Mountains and in *P. albicaulis* on Mount Shasta, California (Mathiasen and Hawksworth 1988).

10. *Arceuthobium divaricatum*
Pinyon Dwarf Mistletoe

Arceuthobium divaricatum Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

=*A. campylopodum* f. *divaricatum*.

Description. Mean shoot height 8 (maximum 3) cm, olive green to brown, branches flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2) mm. Third internode 6 to 15 (mean 9.8 ±2.4) mm long, 1 to 2 (mean 1.6) mm wide, length/width ratio 6.1:1. Staminate flowers 2.5 mm across; perianth three-merous; segments 1.1 mm long, 0.9 mm wide. Mature fruit 3.5 by 2.0 mm; proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Meiosis in July. Peak anthesis usually from early August to late September. Fruits usually mature from early September to late October in the year following pollination; maturation period averages 13 months.

Hosts. *Arceuthobium divaricatum* is restricted to pinyon. The most common principal hosts are *Pinus edulis* (Arizona, Colorado, New Mexico, Texas, and Utah) and *P. monophylla* (California, Nevada). A second set of pinyons including *P. californiarum*, *P. cembroides*, *P. discolor*, and *P. quadrifolia* are also classed as principal hosts even though the mistletoe is not common in their distributions. Infestations occur locally on *P. californiarum* in the Mojave Desert Ranges of New York Mountains, Providence Mountains, Joshua Tree National Monument (subsp. *californiarum*), and Southwest mountains of Zion National Park, Black Hole, and central Arizona (subsp. *fallax*). *Pinus cembroides* is parasitized only in the Davis Mountains, Texas. *Pinus discolor* is parasitized only at Fort Bayard and the Mule Mountains, New Mexico. *Pinus quadrifolia* is parasitized in the Sierra Juárez and Sierra San Pedro Mártir of Baja California and Laguna Mountains, California.

Distribution. United States (California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Baja California Norte). *Arceuthobium divaricatum* occurs in eastern and southern California (the White and Inyo Mountains, the Mount Pinos area, the San Bernardino Mountains, and the Mojave Desert Ranges), the southern three-fourths of Nevada and Utah, western Colorado, Arizona (except far southwest), New Mexico (except far northeast), and south to the Davis Mountains (western Texas). In Mexico, it is known only in northern Baja California. The northernmost population of which we are aware is in the Pilot Range (Box Elder, Utah). Kuijt (1960a) identifies several the scattered populations of this parasite in California; its distribution is probably more common than indicated by collections. *Arceuthobium divaricatum* and *Phoradendron juniperinum* commonly infest the two dominant species respectively of pinyon–juniper woodlands of the Southwestern United States, especially at the Grand Canyon (Hreha and Weber 1979). Distribution maps are published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is from 1,200 m near Sedona, Arizona to 3,000 m in the San Mateo Mountains of New Mexico.

Discussion. The witches' brooms induced by this dwarf mistletoe are often poorly developed and not conspicuous because of the stunted habit of even healthy trees. Our observations suggest that witches' brooms are more consistent in *Pinus edulis* than in *P. monophylla*. Shoots of the mistletoe are often long, slender, and spreading, especially the staminate plants that also tend to have relatively few flowers per shoot. *Arceuthobium divaricatum* is the only dwarf mistletoe of pinyon in the United States. Mathiasen and others (2002a) summarize information on this mistletoe.

11. *Arceuthobium douglasii*
Douglas-fir Dwarf Mistletoe

Arceuthobium douglasii Engelm. in U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:253, 1878.

Description. Mean shoot height 2 (maximum 8) cm, olive green, branches flabellate (fig. 4-3). Basal diameter of dominant shoots 1.0 to 1.5 (mean 1) mm. Third internode 2 to 6 (mean 3.6 ±1.2) mm long, 1.0 mm wide, length/width ratio 3.6:1. Flowers usually axillary in pairs, occasionally borne on pedicel-like segments. Staminate flowers 2.0 mm long, 2.3 mm across; perianth mostly three-merous (occasionally four- or two-merous); segments rounded at the apex, without a keel, inner surface reddish to purple, lower surface same color as shoots, about 1.0 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit olive–green 3.5 to 4.5 (mean 4) mm long, 1.5 to 2.0 mm wide, obovate; proximal portion 2.5 mm long. Seeds 2.4 by 1.1 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in April. Peak anthesis is usually in April or May, but with marked latitudinal variation—March in Mexico, late April to early May in Arizona and New Mexico, late May in Colorado, Utah, and Oregon, and early to mid-June in Washington, northern Idaho, and Montana. Fruit maturity is more uniform throughout the distribution, however, usually from late August to late September; maturation period averages 17 to 18 months. The seeds germinate in March.

Hosts. The principal and only commonly infected host is *Pseudotsuga menziesii*. Both var. *menziesii* (Washington, Oregon, and California) and var. *glauca* (from British Columbia through the Rocky Mountains to Central Mexico) are parasitized, although it is much more common on var. *glauca*. Where associated with infected *Pseudotsuga menziesii*, *Abies amabilis* is occasionally infected. Rare hosts are *Abies concolor*, *A. grandis*, *Picea pungens*, and *P. engelmannii*. Mathiasen (1999) reports that the two taxa *Abies lasiocarpa*, a secondary host (66 percent infected), and *Abies bifolia*, an occasional host (15 percent infected) differed significantly in susceptibility to *Arceuthobium douglasii* on plots where the principal host was over 90 percent infected.

Distribution. Canada (British Columbia), United States (Washington, Idaho, Montana, Oregon, California, Nevada, Utah, Colorado, Arizona, New Mexico, and Texas) and Mexico (Chihuahua, Durango, Coahuila, and Nuevo León). *Arceuthobium douglasii* has the greatest latitudinal range (3,000 km) of any species in the genus. This dwarf mistletoe is common in eastern Washington, eastern Oregon, Idaho, western Montana, Idaho, Utah, Colorado, and New Mexico. It is rare in Nevada (Wheeler Peak), Wyoming (Teton), and Texas (Guadalupe Mountains). Marshall and Filip (1999) relate the occurrence of this mistletoe to stand and ecological relations in Oregon. The distribution of the dwarf mistletoe in Mexico is poorly known, and it is probably more widespread than suggested by a few available records from Chihuahua, Coahuila, Durango, and Nuevo León. Distribution maps of *Arceuthobium douglasii* are published for British Columbia, Montana, Utah, Colorado, New Mexico, and California (see Hawksworth and Wiens 1996). The altitudinal range of this dwarf mistletoe is correlated with latitude; it occurs as low as 300 m near Lytton (British Columbia) and as high as 3,250 m on Cerro Potosí (Nuevo León).

Discussion. This dwarf mistletoe is the smallest in Western North America, but its typically systemic mode of infection produces large witches' brooms and causes severe growth loss and mortality in *Pseudotsuga menziesii* (Tinnin and others 1999). Brooms provide special wildlife habitat for foraging, resting, and nesting (see chapter 5). Hadfield and others (2000) and Schmitt (1997) discuss the biology, ecology, and management of this mistletoe.

12. *Arceuthobium durangense*
Durangan Dwarf Mistletoe

Arceuthobium durangense (Hawksw. & Wiens) Hawksw. & Wiens, Phytologia 66:7, 1989.
=*A. vaginatum* subsp. *durangense*.

Description. Mean shoot height 20 to 30 (50) cm, bright orange; older shoots becoming pendulous. Basal diameter of dominant shoots 4 to 8 (mean 6) mm. Third internode 9 to 22 (mean 17.9 ±4.1) mm long, 3.5 to 6.0 (mean 4.5) mm wide, length/width ratio 3.3:1. Internodes often slightly swollen at base. Staminate flowers 2.5 mm long, 2.5 mm across, segments 1 mm long, 1 mm wide. Mature fruit 7 by 3.5 mm; bluish; proximal portion 4 mm long. Seeds 4 by 1.5 mm.

Phenology. Time of meiosis unknown (probably February). Anthesis usually in April. Fruits mature from mid-July to September of the year following pollination; maturation period averages 15 to 18 months.

Hosts. *Pinus douglasiana*, *P. durangensis*, *P. michoacana*, *P. montezumae*, and *P. pseudostrobus* are the principal hosts. *Pinus herrerai* is occasionally parasitized when it occurs near infected principal hosts. The host status of *Pinus oocarpa* needs confirmation.

Distribution. Mexico (Durango, Sinaloa, and Jalisco). This rather local dwarf mistletoe occurs on the western escarpment of the Sierra Madre Occidental (Durango, Sinaloa, and perhaps Nayarit) and in the Sierra de Quilla (Jalisco). Elevational range is 1,450 to 2,750 m.

Discussion. Although previously referred to as a subspecies of *Arceuthobium vaginatum*, we now recognize this dwarf mistletoe as a distinct species. *Arceuthobium durangense* is not sympatric with *A. vaginatum* and differs by its larger, bright orange shoots, distinct branching pattern, and larger fruit.

13. *Arceuthobium gillii*
Chihuahua Pine Dwarf Mistletoe

Arceuthobium gillii Hawksw, & Wiens, Brittonia 16:22, 1964.
=*A. vaginatum* subsp. *cryptopodum*.

Description. Mean shoot height 8 to 15 (maximum 25) cm, greenish–brown, branches flabellate. Basal diameter of dominant shoots 2.5 to 8.0 (mean 4) mm. Third internode 5 to 18 (mean 10.7 ±3.4) mm long, 2.0 to 4.5 (mean 2.8) mm wide, length/width ratio 3.8:1. Staminate flowers 3.5 mm long, 2.5 to 4.0 (mean 3.2) mm across. Pistillate flowers 1.5 mm long, 1 mm across. Mature fruit 4 to 5 mm long, 2 to 3 mm wide, the proximal portion of fruit conspicuously glaucous. Seeds 3.1 by 1.4 mm.

Phenology. Meiosis in September. Anthesis usually in March and April. Fruits mature in October of the year following pollination; maturation period averages 19 months, the longest in the genus. Seed germination begins in April.

Hosts. The principal and only commonly infected hosts are *Pinus leiophylla* var. *chihuahuana*, *P. lumholtzii*, and *P. herrerai*. Although *Pinus. leiophylla* var. *leiophylla* is a principal host, it is not common within the range of *Arceuthobium gillii*. In western Chihuahua, this dwarf mistletoe rarely parasitizes *Pinus arizonica* var. *arizonica* and *P. cooperi*.

Distribution. United States (Arizona and New Mexico) and Mexico (Chihuahua, Durango, Sinaloa, and Sonora). This dwarf mistletoe occurs in southeastern Arizona (Santa Catalina, Rincon, Santa Rita, Huachuca, and Chiricahua Mountains) and the Animas Mountains in southwestern New Mexico. It is most common in western Chihuahua, but it is also distributed in adjacent northern and eastern Sonora, northern Durango, and northeastern Sinaloa. Elevational range is from 1,700 m in southern Arizona to 2,650 m in southern Chihuahua.

Discussion. This dwarf mistletoe has long been confused with *Arceuthobium vaginatum* subsp. *cryptopodum*, but it differs in host preference, phenology, and its conspicuously glaucous fruits. These two dwarf mistletoes are usually separated by at least 300 m of elevation in Arizona and New Mexico. Where they co-occur in central Chihuahua, there is no evidence of hybridization. A characteristic feature of *Arceuthobium gillii* is its strong sexual dimorphism—staminate plants tall and openly branched and pistillate plants small and densely branched. This dwarf mistletoe causes open, nonsystemic witches' brooms and serious mortality in *Pinus leiophylla* var. *chihuahuana* and *P. lumholtzii*.

14. *Arceuthobium globosum*

Arceuthobium globosum Hawksw. & Wiens, Brittonia 17:223, 1965.

Description. Shoot height 20 to 50 (maximum 70) cm, yellow to greenish, branches flabellate. Basal diameter of dominant shoots 3 to 48 mm. Third internode 4 to 37 mm long, 2 to 24 mm wide. Staminate flowers about 3.5 to 5.0 mm long, 3.0 to 3.5 mm across; perianth three- or four-merous; same color as shoots; segments 1.3 mm long, 1.0 mm wide. Pistillate flowers 1.5 mm long, 1.5 mm across. Mature fruit 5 to 7 mm long, 3 to 4 mm wide; proximal portion 3.5 mm long, with pedicels 4.0 to 5.0 mm long. Seeds 5 by 2 mm.

Hosts. Common on yellow pine.

Discussion. Hawksworth and Wiens (1972) note considerable variation within collections determined as *Arceuthobium globosum*. Subsequent studies by Hawksworth and Wiens (1977) and Wiens and Shaw (1994) have resulted in the segregation of *Arceuthobium globosum* (*sensu lato*) into five taxa:

- *Arceuthobium aureum* subsp. *aureum* (Guatemala)
- *Arceuthobium aureum* subsp. *petersonii* (Southern Mexico)
- *Arceuthobium globosum* subsp. *globosum* (Northwestern Mexico)
- *Arceuthobium globosum* subsp. *grandicaule* (Central Mexico and Central America)
- *Arceuthobium hawksworthii* (Central America)

14a. *Arceuthobium globosum* subsp. *globosum* Rounded Dwarf Mistletoe

Description. Shoots 15 to 20 (maximum 50) cm high, bright yellow, branches flabellate. Basal diameter of dominant shoots 3 to 10 (mean 7) mm. Third internode 19 mm long, 4 mm wide. Staminate flowers 4 mm wide. Mature fruit 5 by 2.5 mm. Seeds 4 by 2 mm.

Phenology. Anthesis usually March and April. Fruits mature June and July; maturation period averages 15 to 16 months.

Hosts. The principal hosts are *Pinus cooperi*, *P. durangensis*, and *P. engelmannii*. *Pinus arizonica* is occasionally parasitized; *Pinus teocote* is a rare host.

Distribution. Mexico (Sonora, Chihuahua, Durango, and Jalisco). This subspecies is widely distributed in the pine forests of the Sierra Madre Occidental from northwestern Chihuahua and adjacent Sonora, through Durango to northern Jalisco. Elevational range is 2,300 to 2,800 m.

Discussion. This dwarf mistletoe is characterized by its bright yellow, globose clusters, and absence of witches' broom formation.

14b. *Arceuthobium globosum* subsp. *grandicaule* Large-Stemmed Dwarf Mistletoe

Arceuthobium globosum Hawksw. & Wiens subsp. grandicaule Hawksw. & Wiens, Brittonia 29:413, 1977.

Description. Shoots 18 to 50 (maximum 70, mean 25) cm tall, yellow green, typically dark at the base of older shoots, branches flabellate. Basal diameter of dominant shoots 10 to 48 (mean 17) mm. Third internode 14 to 37 (mean 27) mm long, 3 to 20 (mean 7) mm wide. Staminate flowers 5 mm wide, four-merous. Mature fruits 6 to 7 mm long, 3.5 mm wide. Seeds 5 by 3 mm.

Phenology. Meiosis in December. Anthesis from January through May, with peak March and April. Fruits maturing July through October; maturation period averages 16 to 18 months. Seed dispersal from early July to early November, with a peak from mid-August to mid-September (Escudero and Cibrián 1985).

Hosts. This subspecies has one of the broadest host ranges of any dwarf mistletoe. It infects at least 12 species of Mexican pines, all of which appear to be about equally susceptible (but see Valdivia 1964): *Pinus douglasiana*, *P. durangensis*, *P. hartwegii*, *P.*

Key to the Subspecies of *Arceuthobium globosum*

1. Plants yellowish; shoots usually 15 to 20 (maximum 50) cm tall, less than 1 cm diameter at the base; witches' brooms not formed; shoots usually only on the host branches; northern Mexico .... 14a. *A. globosum* subsp. *globosum*
1. Plants greenish to yellow–green, typically dark at the base of older shoots; shoots usually 25 to 40 (maximum 70) cm tall, greater than 1 cm diameter at the base; witches' brooms usually induced; shoots on branches, but also frequently on the lower main trunks; central and southern Mexico to the highlands of western Guatemala .... 14b. *A. globosum* subsp. *grandicaule*.

lawsonii, P. maximinoi, P. michoacana, P. montezumae, P. patula, P. pringlei, P. pseudostrobus, P. rudis, and *P. teocote.*

Distribution. Mexico (Jalisco, Michoacán, Mexico, Hidalgo, Distrito Federal, Guerrero, Puebla, Tlaxcala, Veracruz, and Oaxaca), Guatemala, and Honduras. *Arceuthobium globosum* subsp. *grandicaule* is the most abundant dwarf mistletoe in Central Mexico, common in western Guatemala, and recently reported in Honduras (Melgar and others 2001). Elevational range is 2,450 to 4,000 m (Hernandez and others 1992).

Discussion. This subspecies has large shoots reaching a height of 70 cm and with a basal diameter of 5 cm. Valdivia (1964) reports *Arceuthobium globosum* is present on nearly 40 percent of 400,000 ha of pine forest in northeastern Michoacán. Vázquez (1994a) discusses the importance and sampling method for this mistletoe.

15. *Arceuthobium guatemalense*
Guatemalan Dwarf Mistletoe

Arceuthobium guatemalense Hawksw. & Wiens, Brittonia 22:267, 1970.

Description. Mean shoot height 1 to 3 cm on systemic witches' brooms, but shoots on nonsystemic infections up to 7 cm high; living shoots greenish to purple, yellow to brown when dried, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm. Third internode 8 to 15 (mean 11.4 ±2.8) mm long, 1.5 to 2.0 (mean 1.7) mm wide; length/width ratio 6.7:1. Staminate flowers 2 mm across; perianth two- or three-merous, segments 0.9 mm long, 0.7 mm wide. Mature fruit 3.5 to 4.0 mm long, 1.5 to 2.0 mm wide; distal portion 1.2 mm long; dark green, glabrous, with a slightly swollen ring at the base of the fruit where it joins the pedicel. Seeds 2.0 by 0.8 mm.

Phenology. Time of meiosis unknown. Anthesis apparently in August and early September. Fruits mature in September; maturation period about 12 to 13 months. Seed germination in September.

Hosts. Known only on *Pinus ayacahuite* var. *ayacahuite.*

Distribution. Mexico (Oaxaca and Chiapas) and Guatemala. This distinctive species is known only from the high mountains of Western Guatemala and Southern Mexico. Elevational range is poorly known; our collections are from 2,450 to 3,100 m.

Discussion. The consistent formation of systemic witches' brooms is a distinctive characteristic of this species; brooms sometimes measure 3 to 5 m across. An unusual feature of these witches' brooms is that the shoots of the dwarf mistletoe are consistently formed on 1-year-old host shoots and, in some cases, on the current year's growth. This species causes extensive damage and considerable mortality to *Pinus ayacahuite.*

16. *Arceuthobium hondurense*
Honduran Dwarf Mistletoe

Arceuthobium hondurense Hawksworth & Wiens, Brittonia 22: 267, 1970.
=*Arceuthobium nigrum*

Description. Mean shoot height ca. 14 (max. 21) cm, olive brown to grayish green, markedly glaucous; branches flabellate. Basal diameter of dominant shoots 3 to 9 (mean 5) mm; nodes of older shoots swollen; lateral branches of staminate plants at nearly right angles to the axis of the main shoot; third internode 7 to 12 (mean 9.1 ± 1.5) mm long, 2.5 to 4.0 (mean 3.2) mm wide; length/width ratio 6.1:1. Staminate flowers approximately 2.5 mm across; inner surface reddish, lower surface the same color as the shoots; perianth usually three-merous (sometimes two- or four-merous), segments approximately 1.2 mm long, 0.8 mm wide; nectary with two large and one small lobe. Pistillate flowers with stigmas exserted approximately 0.5 mm, with copious stigmatic exudate at anthesis. Mature fruit 5.5 by 3.0 mm, greenish glaucous; proximal portion approximately 4.0 mm long. Seeds approximately 3.1 by 1.5 mm. n = 14.

Phenology. Meiosis in August or early September. Anthesis and fruit maturity in September; maturation period averages ca. 12 months.

Hosts. The only known hosts are *Pinus oocarpa* var. *oocarpa*, var. *ochoterenia*, and *P. tecunumanii* (Mathiasen and others 1998, 2000a).

Distribution. Honduras, Mexico (Chiapas, Oaxaca), and possibly El Salvador. The distribution of this species is poorly known; only four collections are known from Honduras and three from Mexico (Mathiasen and others 2001, 2002b). Elevational range is poorly known, probably between 1,200 and 1,650 m.

Discussion. Collections from Mexico had been previously confused with *Arceuthobium nigrum* (Mathiasen and others 2001, 2002b). *Arceuthobium hondurense* and *A. bicarinatum*, a species endemic to Hispaniola, are both rare species threatened by deforestation and are distributed at the southern limits of dwarf mistletoes and pines in the New World.

17. *Arceuthobium laricis*
Larch Dwarf Mistletoe

Arceuthobium laricis (Piper) St. John, Flora of Southeast Washington and Adjacent Idaho: 115, 1937.
=*A. campylopodum* f. *laricis*.

Description. Mean shoot height 4 (maximum 6) cm, mostly dark purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 14 (mean 8.0 to 2.0) mm long, 1.0 to 2.5 (mean 1.3) mm wide, length/width ratio 6.1:1.

Staminate flowers 2.7 mm across; perianth mostly three-merous (sometimes four-merous); segments 1.4 mm long, 1.1 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 4.5 by 2.5 mm; proximal portion 2.5 mm long.

Phenology. Meiosis in June. Peak anthesis from mid-July to late August, with extremes from early July to early September. Fruits usually mature in September, with extremes from early August to early October; maturation period averages 13 to 14 months.

Hosts. Mathiasen (1998a) revises the host relations of *Arceuthobium laricis* based on field studies and previous reports (Mathiasen and others 1995a). The principal and commonly infected host is *Larix occidentalis*. *Tsuga mertensiana* and *Pinus contorta* var. *latifolia* are secondary hosts. Occasional hosts are *Abies lasiocarpa* and *P. ponderosa* var. *ponderosa*; but *Abies amabilis* and *Pinus albicaulis* are tentatively classified occasional as well. *Abies grandis*, *Picea engelmannii*, *Pinus monticola*, and *Tsuga heterophylla* are rare hosts. Extra-limital hosts and artificially inoculated hosts include *Larix decidua*, *L. leptolepis*, *Picea abies*, *P. glauca*, *Pinus banksiana*, *P. resinosa*, and *P. sylvestris*. (Hawksworth and Wiens 1996). Although natural population of the high-elevation *Larix lyallii* appear not to be infested, this species may become infected if planted in a suitable environment (Mathiasen and others 1995b).

Distribution. Canada (British Columbia) and the United States (Washington, Oregon, Idaho, and Montana). *Arceuthobium laricis* occurs generally throughout the range of its principal host, *Larix occidentalis*, in southern British Columbia, east of the Cascade Mountains in Washington and northern Oregon, northern and central Idaho, and western Montana. Distribution maps of *Arceuthobium laricis* are published for British Columbia and Montana (see Hawksworth and Wiens 1996). Elevational range is 650 to 2,250 m.

Discussion. *Arceuthobium laricis* has long been recognized as a serious pathogen of *Larix occidentalis* (Weir 1916a). Infection usually results in the formation of heavy but compact brooms. Because larch branches are brittle, larger brooms are readily broken off. Surveys in the Inland Empire (eastern Washington, northern Idaho, and western Montana) show that most larch stands are infested and infection rates are commonly high (Hawksworth and Wiens 1996). Mathiasen (1998b) reports that initial infection of *Larix occidentalis* can be when the plants are quite young; Mathiasen recommends that, to avoid spread, removal of the infected overstory should be done before regeneration is 7 years old or 1 m tall. Other publications of interest to managers include those by Beatty and others (1997), Taylor (1995), Wicker and Hawksworth (1991), and Weir (1961a).

18. *Arceuthobium littorum*
Coastal Dwarf Mistletoe

Arceuthobium littorum Hawksw., Wiens & Nickrent, Novon 2:206, 1992.
=*A. campylopodum* f. *typicum*
=*A. occidentale*

Description. Shoots 8 to 20 (mean 12) cm, brown to yellow-brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3.5) mm. Third internode 10 to 20 (mean 15) mm long, 2 to 2.5 (mean 2.2) mm wide, mature fruits 4 to 5 mm long; staminate flowers mostly four-merous.

Phenology. Meiosis occurs in July, flowering begins in August, with peak anthesis probably occurring in September. Seed dispersal probably peaks in September or October.

Hosts. *Pinus radiata* and *P. muricata* are the primary hosts. It occasionally infects Bolander pine (*Pinus contorta*) where this tree is associated with infected *P. muricata*.

Distribution. United States (California: Mendocino, Sonoma, Marin, Monterey, and San Luis Obispo). *Arceuthobium littorum* is restricted to a region within 10 km of the Pacific Ocean from Fort Bragg south to Point Reyes on *Pinus muricata* and along the central coast at Monterey and Cambria on *P. radiata*. It also parasitizes the small population of *P. muricata* associated with infected *P. radiata* at Huckleberry Hill, Monterey, and is established at three locations by transplanting infected *Pinus radiata*—Stanford Arboretum, North Berkeley, and Hillsborough. Elevational range is from sea level to 250 m.

Discussion. Previously, Hawksworth and Wiens (1972) include *Arceuthobium littorum* in *A. occidentale*. A primary feature for distinguishing *A. littorum* from *A. occidentale* is the production of large, nonsystemic witches' brooms.

19. *Arceuthobium microcarpum*
Western Spruce Dwarf Mistletoe

Arceuthobium microcarpum (Engelm.) Hawksw. & Wiens, Brittonia 22:268, 1970.
=*A. campylopodum* f. *microcarpum*.

Description. Mean shoot height 5 (maximum 11) cm, green to purple, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.0 (mean 2) mm. Third internode 5 to 16 (mean 9.3 ±2.2) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.2:1. Staminate flowers 2.3 mm across; perianth mostly three-merous (rarely four-merous); segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3.5 by 2.0 mm; proximal portion 2.5 mm long. Seeds 2.4 by 1.0 mm.

Phenology. Meiosis in July. Anthesis in mid-August to early September, with extremes from late July to late September. Fruits mature in September, with extremes from late August to early October; maturation period averages 12 to 13 months.

Hosts. This dwarf mistletoe is a common and serious pathogen only on *Picea engelmannii* and *P. pungens*. On the San Francisco Peaks of northern Arizona, however, it also parasitizes *Pinus aristata*. *Pinus strobiformis* and *Abies lasiocarpa* var. *arizonica* are rarely infected even where they are associated with infected principal hosts. If populations of a spruce in southern Arizona were determined to be *Picea mexicana* rather than *P. engelmannii* (Taylor and others 1994), this species would be an additional host.

Distribution. United States (Arizona and New Mexico). *Arceuthobium microcarpum* has one of the more restricted distributions in the genus. In Arizona, the parasite occurs on the North Rim of the Grand Canyon, the San Francisco Peaks and nearby Kendrick Peak, White Mountains, and Pinaleno Mountains. In New Mexico, this dwarf mistletoe is present at several locations in the Mogollon Mountains and in the Sacramento Mountains. Elevational range is 2,400 to 3,150 m.

Discussion. This localized species in Arizona and New Mexico is characterized by its near exclusive occurrence on spruce (Hawksworth and Graham 1963a). This species induces small, dense witches' brooms. Heavily infected trees bear hundreds of such witches' brooms. This dwarf mistletoe causes heavy mortality in stands of *Picea pungens* and, to a lesser extent, of *P. engelmannii*.

20. *Arceuthobium monticola*
Western White Pine Dwarf Mistletoe

Arceuthobium monticola Hawksw., Wiens & Nickrent, Novon 2:205, 1992.
=*A. campylopodum* f. *blumeri*
=*A. californicum*

Description. Shoots 5 to 10 (mean 7) cm tall, dark brown, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm; third internode 8 to 15 (mean 12) mm long, 1.5 to 2.0 mm wide. Staminate flowers mostly three-merous. Mature fruits 4.0 to 4.5 mm long, 2.0 to 2.5 mm wide.

Phenology. The period of anthesis is poorly known but apparently occurs late July through August. Fruits mature October and November; maturation period averages 15 months.

Hosts. The principal and only commonly infected host is *Pinus monticola*. *Pinus lambertiana* is a secondary host; *Picea breweriana* an occasional host; and *Pinus jeffreyi* a rare host.

Distribution. United States (Oregon, California). *Arceuthobium monticola* is a local endemic in the Klamath Mountains of southwestern Oregon (Coos, Curry, and Josephine) and the Siskiyou Mountains of adjacent northwestern California (Del Norte and possibly Siskiyou). Elevational range is 700 to 1,900 m.

Discussion. Hawksworth and Wiens (1972) include this taxon under *Arceuthobium californicum*; but subsequent field and laboratory studies demonstrate that it is a distinct species and not apparently sympatric with *A. californicum*. *Arceuthobium monticola* differs from *A. californicum* in its much darker shoot color, later flowering and seed dispersal periods, and host preference for *Pinus monticola* rather than *P. lambertiana*.

21. *Arceuthobium nigrum*
Black Dwarf Mistletoe

Arceuthobium nigrum (Hawksw & Wiens) Hawksw. & Wiens, Phytologia 66:9, 1989.
=*A. gillii* subsp. *nigrum*.

Description. Mean shoot height 15 to 35 (45) cm, dark brown to black. Basal diameter of dominant shoots 3 to 8 (mean 5) mm. Third internode 5 to 19 (mean 10.8 ±3.8) mm long, 2.5 to 6.0 (mean 3.7) mm wide (six collections), length/width ratio 2.9:1. Staminate flowers 3 mm long, 3.5 mm across. Mature fruit 6 to 9 (mean 7) mm long, 3.5 mm wide, proximal portion 2 to 3 mm. Seeds 3.5 by 1.3 mm.

Phenology. This dwarf mistletoe is unusual in *Arceuthobium* by having flowering periods in March and April and September and October. Seed dispersal occurs in September, presumably from flowers pollinated the previous year; when the seeds from the March through April pollinations mature is unknown.

Hosts. This dwarf mistletoe is most common on the principal hosts *Pinus leiophylla* vars. *leiophylla*, var. *chihuahuana*, and *P. lumholtzii*. *Pinus lawsonii*, *P. oaxacana*, *P. patula*, *P. teocote* are also highly susceptible and rated as principal hosts. *Pinus montezumae* and *P. pseudostrobus* are occasional hosts. *Pinus arizonica* var. *arizonica* and *P. cooperi* are rare hosts.

Distribution. Mexico (Durango, Zacatecas, Guanajuato, Querétaro, Hidalgo, Michoacán, Mexico, Tlaxcala, Puebla, Veracruz, Oaxaca, Chiapas) and possibly Western Guatemala. This mistletoe is reported from the northeastern slope of Volcán la Malintzi (Malinche), Tlaxcala (Hernandez and others 1992), and is common on pines in Central and Eastern Mexico. Elevational range is 1,800 to 2,800 m.

Discussion. *Arceuthobium nigrum* resembles *A. gillii*. Both species possess markedly glaucous fruits, strong sexual dimorphism (open, divaricate branching in staminate plants versus densely branched in pistillate plants), and parasitize similar hosts. Although *A. nigrum* was previously classed as a subspecies of *A. gillii*, specific status is warranted (Hawksworth and Wiens 1989). *Arceuthobium nigrum* is a larger plant than *A. gillii* and has dark green to black shoots 15 to 35 (maximum 45) cm high, whereas those of *A. gillii* are only 8 to 15 (maximum 25) cm tall, and colored greenish brown. *Arceuthobium nigrum* also has the two flowering periods (March and April, and September and October) compared to only one for

A. gillii (March and April). To our knowledge, these species are not sympatric.

22. *Arceuthobium oaxacanum* Oaxacan Dwarf Mistletoe

Arceuthobium oaxacanum Hawksw. & Wiens, Phytologia 66:7, 1989.
=*A. rubrum*

Description. Shoots 8 to 20 (mean 12) cm tall, pale brown to reddish, branches flabellate. Basal diameter of dominant shoots 2 to 4 (mean 3) mm. Third internode 10 to 17 (mean 12) mm long and 2 to 3 mm wide.

Phenology. Anthesis in July. Fruits mature in August of the following year; maturation period averages 13 months.

Hosts. *Pinus lawsonii*, *P. michoacana*, and *P. pseudostrobus* are principal hosts; all are about equally susceptible. *Pinus oaxacana* is an occasional host.

Distribution. Mexico (Oaxaca). This species is known from only three localities (two south of Miahuatlán and one near Ixtlán). Elevational range is 2,000 to 2,200 m.

Discussion. Hawksworth and Wiens (1989) recognize *Arceuthobium oaxacanum* as a distinct species previously considered an extreme disjunct (about 1,200 km) of *A. rubrum*. In general, *A. oaxacanum* is a larger, lighter colored, more openly branched plant and causes larger witches' brooms than *A. rubrum*. Furthermore, *Arceuthobium oaxacanum* principally parasitizes *Pinus lawsonii*, *P. michoacana*, *P. pseudostrobus*, and occasionally *P. oaxacana*; none of these pines occurs within the range of *A. rubrum*.

23. *Arceuthobium occidentale* Digger Pine Dwarf Mistletoe

Arceuthobium occidentale Engelm., U.S. Geographical Survey West of 100th Meridian (Wheeler Report) 6:375, 1878.
=*A. campylopodum* f. *typicum*.

Description. Mean shoot height 8 (maximum 17) cm, yellowish, glaucous, branches flabellate. Basal diameter of dominant shoots 1.5 to 5.0 (mean 2) mm. Third internode 7 to 18 (mean 12.7 ±2.0) mm long, 1.5 to 3.5 (mean 1.8) mm wide, length/width ratio 7.1:1. Staminate flowers 3.0 mm across; perianth three- or four-merous; segments 1.5 mm long, 1.0 mm wide. Mature fruit 4.5 by 3.0 mm; proximal portion 3.0 mm long. Seeds 2.6 by 1.0 mm.

Phenology. Meiosis in August. Peak anthesis from late September to late November, extremes from early September to early December. Most fruits mature from mid-October to mid-January, with extremes from late September to early February; maturation period averages 13 months.

Hosts. *Pinus sabiniana* is the most common and only principal host. *Pinus coulteri* and *P. attenuata* are secondary hosts where they occur with infected *P. sabiniana*. Whether the occasional hosts *Pinus ponderosa* and *P. jeffreyi* are infected, however, varies by location and association with their principal dwarf mistletoe, *A. campylopodum*. In the California Coast Range (outside the distribution of *Arceuthobium campylopodum*), these pines are commonly infected where they are occur with infected *P. sabiniana*. In the Sierra Nevada (where *A. campylopodum* occurs), they are seldom infected even under infected *P. sabiniana*. Extralimital and hosts by artificial inoculation are *Pinus banksiana*, *P. bungeana*, *P. caribaea*, *P. halepensis*, *P. palustris*, *P. pinea*, *P. radiata*, *P. sylvestris*, *P. thunbergii*, *P. torreyana*, and *P. virginiana*.

Distribution. United States (California). This dwarf mistletoe is a California endemic and commonly occurs on *Pinus sabiniana* throughout the foothills and low mountains surrounding the Central Valley of California and along the Coast Ranges from Mount Pinos (Ventura) north to Mendocino. Elevational range is about 30 to 1,200 m in the southern Sierra Nevada.

Discussion. Even though *Pinus sabiniana* typically occurs in open, savanna-like forests, *Arceuthobium occidentale* is widely distributed in these stands. Isolated, infected trees more than 100 m away from the closest infected trees are sometimes found, which suggests that bird vectors (possibly phainopepla) are involved in long-distance seed transport of this dwarf mistletoe.

24. *Arceuthobium pendens* Pendent Dwarf Mistletoe

Arceuthobium pendens Hawksw. & Wiens, Brittonia 32:348, 1980.

Description. Mean shoot height 15 (maximum 22) cm, light green, branches flabellate. Basal diameter of dominant shoots 1.5 to 3.5 (mean 2) mm. Third internode 12 to 20 (mean 16) mm long, 1 to 2 (mean 1.5) mm wide. Staminate flowers 2.5 mm across, three-merous.

Phenology. Peak anthesis possibly in September. Fruit maturity from June to September (Cházaro and Oliva 1987a).

Hosts. Known only on *Pinus discolor* (San Luis Potosí) and *P. cembroides* subsp. *orizabensis* (Veracruz and Puebla).

Distribution. Mexico (San Luis Potosí, Veracruz, and Puebla). The distribution of this dwarf mistletoe is poorly known (Cházaro and Oliva 1987a) from only Sierra San Miguelito (San Luis Potosí) and Frijol Colorado (Veracruz), and on the nearby Cerro Pizzaro (Puebla). Elevational range is 2,250 to 2,700 m.

Discussion. The species exhibits striking sexual dimorphism—pistillate plants are densely branched and typically less than 8 cm tall, and mature staminate plants are openly branched and pendant, 15 to 20 cm long. A unique feature of this species, at least in one population, is that only the staminate plants appear to induce systemic witches' brooms. This dwarf mistletoe likely occurs in other areas and on other pinyons.

25. *Arceuthobium pusillum*
Eastern Dwarf Mistletoe

Arceuthobium pusillum Peck, Transactions Albany Institute 7:191, 1872.
=*A. minutum*
=*A. abigenium*.

Description. Mean shoot height 1 (maximum 3) cm, green to brown, usually without secondary branching, but flabellate when occurs. Basal diameter of dominant shoots 1.0 mm. Third internode 1 to 4 (mean 1.9 ±0.8) mm long, 0.5 to 1.5 (mean 1.0) mm wide, length/width ratio 1.9:1, often markedly wider at top than at base. Pistillate shoots often longer than the staminate. Staminate flowers 1.7 to 2.2 (mean 1.8 mm) across; perianth mostly three-merous (sometimes two- or four-merous); segments 0.8 mm long, 0.7 mm wide. Mature fruit 3.0 mm long, 1.25 to 1.75 mm wide (mean 1.5 mm); proximal portion 2.0 mm long. Seeds 2.0 by 0.9 mm.

Phenology. Staminate meiosis in September, pistillate meiosis in May. Anthesis usually in April or May, with extremes from late March to June. Fruits mature in September or early October of the same year as pollination; maturation period averages 5 months, perhaps the shortest in the genus. Seed germination mostly in May and June.

Hosts. *Arceuthobium pusillum* is most common and widely distributed on *Picea mariana*. *Picea glauca* and *P. rubens* appear to be about as susceptible as *P. mariana*, so are also principal hosts, although the dwarf mistletoe is not as common (except in some old-growth stands). *Larix laricina* is an occasional host. *Abies balsamea*, *Pinus banksiana*, *P resinosa*, and *P. strobus* are rare hosts. *Picea pungens* is an extralimital host.

Distribution. Canada (Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland) and the United States (Minnesota, Wisconsin, Michigan, New York, Pennsylvania, New Jersey, Connecticut, Massachusetts, Vermont, New Hampshire, Rhode Island, and Maine). *Arceuthobium pusillum* occurs in Canada from Hudson Bay, the Cumberland areas in eastern Saskatchewan to southern Manitoba, southern Ontario, Québec, and the Maritime Provinces including Newfoundland. Its northern limits in Ontario and Québec are poorly known. In the United States, it occurs in the northern parts of Minnesota, Wisconsin, and Michigan, northeastern Pennsylvania, extreme northwestern New Jersey, and all of New England. It is rare near the limits of its southern distribution. *Arceuthobium pusillum* occurs on several islands isolated 30 km or more from the nearest known populations of the dwarf mistletoe—Mantinicus and Monhegan Islands off the Maine Coast and Beaver Island in Lake Michigan. The numerous distribution maps published for *Arceuthobium pusillum* are identified by Hawksworth and Wiens (1996). Elevational ranges from sea level in Maine and the Maritime Provinces to 800 m on Mount Katahdin, Maine.

Discussion. In spite of having the smallest shoots of any North American mistletoe, *Arceuthobium pusillum* is a damaging pathogen of spruce in many parts of its distribution (Singh and Carew 1989). Mortality is severe in *Picea glauca* along the Maine Coast, and the parasite is considered the most serious disease agent of *P. mariana* in the Great Lakes region. Its biology and management are discussed by Ostry and Nicholls (1979). Witches' brooms appear to be mostly of the systemic type. Shoots usually first appear in late summer or autumn as small eruptions in the bark of host branches 2 years old and mature during the third season. They flower the following spring; fruits mature by autumn. Shoots usually fall after flowering (staminate) or fruiting (pistillate), and only rarely do shoots produce a second crop of flowers. This pattern of reproduction is unique among northern temperate species of the genus. Large swellings on the main trunk are commonly induced by *Arceuthobium pusillum* in old-growth *P. rubens* in New England and New York, but such swellings have not been reported on other spruces. *Arceuthobium pusillum* has an interesting literary and historic past in Thoreau's (1858) description of the witches' broom in spruce at Walden Pond and Lucy Millington's later discovery of the mistletoe itself (Smith 1992). *Arceuthobium pusillum* is common in spruce bogs and generally absent from drier upland sites. In Québec, *A. pusillum* is apparently restricted to within 2 km of lakes or rivers. In Maine, it occurs on *P. glauca* only within 300 to 400 m of the coast. *A. pusillum* may require an uninterrupted period of high atmospheric humidity in the spring for normal growth.

26. *Arceuthobium rubrum*
Ruby Dwarf Mistletoe

Arceuthobium rubrum Hawksw. & Wiens, Brittonia 17:233, 1965.

Description. Mean shoot height 10 (maximum 18) cm, dark red, brown to blackish, branches flabellate. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2 to 3 (mean 2.4) mm. Third internode 4 to 12 (mean 6.9 ±2.7) mm long, 2 to 3 (mean 2.3) mm wide, length/width ratio 3.4:1. Staminate flowers 1.0 to 1.5 mm across; mostly three-merous; segments 0.6 mm long, 0.6 mm wide. Mature fruit 3.5 by 2.0 mm. Seeds 2.0 by 1.0 mm.

Phenology. Meiosis probably in June. Anthesis usually in July. Fruits mature from mid-July to August of the year following pollination; maturation period averages 12 to 13 months.

Hosts. Principal hosts are *P. cooperi*, *P. durangensis*, *P. engelmannii*, *P. herrerai*, and *Pinus teocote*, all of which appear to be highly susceptible.

Distribution. Mexico (Durango and Sinaloa). This species has a localized distribution in the Sierra Madre Occidental of Western Mexico. Elevational range is 2,250 to 2,900 m.

Discussion. This distinctive, slender, reddish dwarf mistletoe is apparently widespread in the mountains of Durango. As the plants dry, the red color turns to dull brown, and the apical portion of each segment becomes golden yellow. This gives dried specimens a characteristic banded appearance. The shiny fruits, a character shared only with *Arceuthobium oaxacanum*, readily distinguish this species. Another distinctive characteristic of *A. rubrum* is the exceptionally small, scarcely opened staminate flowers. The populations in the Pueblo Altares area in northern Durango, about 150 km north of the populations around El Salto, have taller, darker, and stouter shoots that superficially resemble *Arceuthobium vaginatum* subsp. *vaginatum*.

27. *Arceuthobium siskiyouense*
Knobcone Pine Dwarf Mistletoe

Arceuthobium siskiyouense Hawksw., Wiens & Nickrent, Novon 2:204, 1992.
=*A. campylopodum*

Description. Mean shoot height 8 (maximum 10) cm, dark brown, branches flabellate. Basal diameter of dominant shoots 2.0 to 2.5 mm across. Third internode 8 to 15 (mean 9) mm long, 2 mm wide. Mature fruits 3.6 by 2.1 mm.

Phenology. Peak anthesis in August. Fruits at maturation not observed.

Hosts. *Pinus attenuata* is the principal and only common host of *Arceuthobium siskiyouense*. This dwarf mistletoe rarely parasitizes *P. contorta*, *P. jeffreyi*, and *P. ponderosa* where these trees grow in association with infected *P. attenuata*.

Distribution. United States (California and Oregon). The distribution of *Arceuthobium siskiyouense* is restricted to the Klamath Mountains of southwestern Oregon (Curry and Josephine) and the Siskiyou Mountains in adjacent northwestern California (Del Norte and Siskiyou). Elevational range is 400 to 1,200 m.

Discussion. Hawksworth and Wiens (1972) include this taxon in *Arceuthobium campylopodum*, but subsequent studies demonstrate it a distinct species related to *A. campylopodum*. The two species are sympatric in several areas, and their flowering periods partially overlap; but each maintains its own host preferences and distinctive morphologies (for example, *A. siskiyouense* does not induce witches' brooms).

28. *Arceuthobium strictum*
Unbranched Dwarf Mistletoe

Arceuthobium strictum Hawksw. & Wiens, Brittonia 17:234, 1965.

Description. Mean shoot height 7 (maximum 13) cm, pistillate shoots generally greenish yellow brown, branches flabellate. Staminate plants brownish, rarely branching. Staminate plants usually taller than pistillate plants. Basal diameter of dominant shoots 2.5 to 4.0 (mean 3.1) mm. Third internode 1 to 8 (mean 3.6 ±2.0) mm long, 1.5 to 3.5 (mean 2.3) mm wide; length/width ratio 1.6:1. Staminate flowers 3 mm across, perianth three-, four-, or five-merous (rarely six or seven-merous), segments 1.5 mm long, 1 mm wide. Mature fruit 4 by 2.5 mm. Seeds 2.5 by 1.0 mm.

Phenology. Meiosis in July. Anthesis late July through October, with peak in September. Fruits mature from mid-September to October of the year following pollination; maturation period averages 13 months.

Hosts. *Pinus leiophylla* var. *chihuahuana* is the principal host. *Pinus teocote* is an occasional host, and *P. engelmannii* is a rare host.

Distribution. Mexico (Durango). This species is known only in the Sierra Madre Occidental south and west of the city of Durango. Elevational range is 2,200 to 2,500 m.

Discussion. The most distinctive feature of this dwarf mistletoe is the lack of branching by staminate plants. The staminate shoots at anthesis become single spikes 6 to 13 cm long with numerous perianth segments (up to seven, more than any other dwarf mistletoe). The pistillate plants, in contrast, exhibit abundant secondary branching. This dwarf mistletoe causes heavy mortality in its principal host, *Pinus leiophylla* var. *chihuahuana*.

29. *Arceuthobium tsugense*
Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones, University of Washington Publications in Biology 5:139, 1936 (as *A. tsugensis*).
=*A. campylopodum* f. *tsugensis*.

Description. Mean shoot height 5 to 7 (13) (cm), greenish to reddish, darker in winter, branches

Key to the Subspecies

1. Parasitic primarily on *Tsuga heterophylla* or *Pinus contorta* var. *contorta*; shoots 3–13 (mean 7) cm high .... 29a. *A. tsugense* subsp. *tsugense*
1. Parasitic primarily on *Tsuga mertensiana*; shoots 3–9 (mean 5) cm high .... 29b. *A. tsugense* subsp. *mertensianae*

flabellate. Basal diameter of dominant shoots 1.5 to 4.0 (mean 2.0) mm. Third internode 4 to 16 (mean 9.2 ±2.5) mm long, 1 to 2 (mean 1.5) mm wide, length/width ratio 6.1:1. Staminate flowers 2.8 mm across; perianth three- or four-merous, segments 1.2 mm long, 1.0 mm wide. Pistillate flowers 1 mm long, 1 mm across. Mature fruit 3 by 2 mm; proximal portion 2.0 mm long.

Hosts. Mathiasen (1994) reviews the host range of the several taxa included here under *Arceuthobium tsugense* based on natural infection and artificial inoculation. His report provides the basis for hosts and susceptibility used here.

Discussion. Hawksworth and Wiens (1972) comment on the unusually broad host range of *Arceuthobium tsugense,* which encompasses not only both western species of hemlock but also several species of fir, spruce, and pine. *Arceuthobium tsugense* is segregated into subspecies *tsugense* and *mertensianae* and subspecies *tsugense* into two physiologically differentiated host races as western hemlock and shore pine (Hawksworth and others 1992b). Additional field studies on distribution, host preference, and phenology are being conducted to resolve continuing taxonomic uncertainty (see Mathiasen 1994). At this time, however, we retain the taxonomy and host relations presented by Hawksworth and Wiens (1996). Hennon and others (2001) provide a general review and management guide for hemlock dwarf mistletoe. The subspecies are similar morphologically, but the shoots are about 30 percent taller in subsp. *tsugense* than in subsp. *mertensianae* (differences statistically significant at $P<0.01$).

Phenology. Meiosis in July for both subspecies, but the subsequent phenologies of flowering for the subspecies differ. Flowering averages about 1 to 2 weeks earlier in subsp. *tsugense* (peak anthesis in August, extremes from late July to late September) than for subsp. *mertensianae* (peak anthesis from mid-August to mid-September). In contrast to flowering, the seed dispersal for subsp. *tsugense* averages about 2 to 4 weeks later (late September to early November) than for subsp. *mertensianae* (mid-August, rarely to late October).

29a. *Arceuthobium tsugense* subsp. *tsugense* Western Hemlock Dwarf Mistletoe

Description. As the species, but shoots vary from 3 to 13 cm high, mean 7 cm.

Hosts. *Tsuga heterophylla* is the principal and common host; but *A. lasiocarpa* var. *lasiocarpa* is also considered a principal host, as are (tentatively) *Abies amabilis* and *A. procera*. *Abies grandis* and *Pinus contorta* var. *latifolia* are occasional hosts. Rare hosts are *Picea engelmannii*, *P. sitchensis, Pinus monticola, Pseudotsuga menziesii*, and *Tsuga mertensiana*. The status of *Pinus contorta* var. *contorta* (shore pine) as a host is discussed below. Extra-limital and hosts by inoculation (for the western hemlock race) are *Larix decidua* (incompatible), *L. occidentalis* (incompatible), *Picea abies, P. glauca, Pinus contorta* var. *latifolia, Pinus ponderosa, P. radiata, P. sylvestris, Pseudotsuga menziesii,* and *Tsuga canadensis*.

Distribution. Canada (British Columbia) and the United States (Alaska, Washington, Oregon, and California). *Arceuthobium tsugense* subsp. *tsugense* is distributed from Haines, Alaska, to Mendocino, California. *Arceuthobium tsugense* subsp. *tsugense* is common in the *Tsuga heterophylla* forests of coastal Alaska, British Columbia, Washington, and Oregon; but rare in northwestern California; and unlikely in northern Idaho. Elevational range is from sea level in Alaska, British Columbia, and Washington to about 1,250 m in Oregon.

Discussion. Many of the lower infections in *Tsuga heterophylla* produce few shoots of the dwarf mistletoe (Shaw and Weiss 2000). Because dwarf mistletoes are sensitive to light, the absence of dwarf mistletoe shoots from the lower infections may be explained by the dense shade in the lower portions of coastal hemlock forests (Smith 1969). In such situations, vigorous shoots are often found only along margins of stands, on young trees in openings, or in higher branches of older trees. Information on the epidemiology of this mistletoe and management of hemlock is available for Alaska (Shaw and Hennon 1991, Trummer and others 1998, and Wittwer 2002) and Canada (Bloomberg and Smith 1982, Edwards 2001, Muir 1993, Smith 1977).

Discussion on Western Hemlock Compared to Shore Pine. The taxonomic status of the dwarf mistletoe populations on *Pinus contorta* var. *contorta* is the subject of continued debate (Hawksworth and Wiens 1972, 1996, Hunt and Smith 1978, Smith and Wass 1976, 1979). Dwarf mistletoe population on western hemlock (*Tsuga heterophylla*) and shore pine (*P. contorta* var. *contorta*) are similar morphologically, phenologically, and chemically but appear to have consistent differences in host compatibility. Comparing dwarf mistletoe populations on western hemlock to those on shore pine, respectively, maximum shoot height is about 30 percent greater; fruits are slightly but statistically smaller; anthesis and peak dispersal are later. Flavonoid composition and isozyme patterns are similar. Inoculation of shore pine with dwarf mistletoe seeds from western hemlock produce few infections, but those infections that are successful produce abundant aerial shoots. In contrast, inoculations of western hemlock with dwarf mistletoe seeds from shore pine result in more infections but few produce any shoots. *Tsuga heterophylla* and *Pinus monticola* are considered rare hosts. Other species infected by the shore pine race by artificial inoculation include *Abies amabilis, A. grandis, Larix occidentalis*, *Picea glauca*, *P. engelmannii*, *Pinus contorta* var. *latifolia*, *P. ponderosa*, and *Pseudotsuga menziesii*.

Arceuthobium tsugense subsp. *tsugense* parasitizes *Pinus contorta* var. *contorta* in southwestern British Columbia and the San Juan Islands, Washington. Populations of this dwarf mistletoe are distributed on isolated rocky outcrops along the east coast of Vancouver Island, on the Channel Islands, and the mainland of British Columbia north of Vancouver. Two outlying populations occur 250 km north at Port Clements (Queen Charlotte Islands) and at Terrace (British Columbia mainland). In the United States, populations are known from Orcas and San Juan Islands (Washington). The elevational range is from sea level to 800 m.

29b. *Arceuthobium tsugense* subsp. *mertensianae* Mountain Hemlock Dwarf Mistletoe

Arceuthobium tsugense (Rosendahl) G.N. Jones subsp. *mertensianae* Hawksw & Nickrent, Novon 2:209, 1992.

Description. Shoots are typically shorter (5 cm) than in subsp. *tsugense* (7 cm).

Hosts. The common principal host of *Arceuthobium tsugense* subsp. *mertensianae* is *Tsuga mertensiana*; *T. heterophylla* is only rarely infected, even where this species is closely associated with infected *T. mertensiana*. Other principal hosts are *A. amabilis and Abies lasiocarpa*. *Pinus albicaulis* is a secondary host, and *Pinus monticola* is an occasional host. *Picea breweriana* and *Pinus contorta* var. *latifolia*, are rarely infected.

Distribution. Western Canada (southern British Columbia) and Western United States (Washington, Oregon, and California). The distribution of *Arceuthobium tsugense* subsp. *mertensianae* is still poorly known, but it extends from near Vancouver (British Columbia), in the Olympic Mountains, through the Cascade Mountains (Washington and Oregon), and to the central Sierra Nevada (Alpine, California). Hildebrand and others (1997) report on a distribution survey in Washington. Elevational range is 1,200 to 2,500 m.

Discussion. Some populations of *Tsuga mertensiana* such as on Mount Baker and in the Olympic Mountains are exceptionally heavily infected by this dwarf mistletoe.

30. *Arceuthobium vaginatum*

Arceuthobium vaginatum (Willd.) Presl in Berchtold, O PUirozenosti Rostlin aneb Rostinár 2:28, 1825.

Description. Mean shoot height from 20 to 30 (maximum 55 or greater) cm, orange to dark brown, reddish, or black, usually densely branched and erect, but large older plants sometimes become pendulous; branches flabellate; basal diameter of dominant shoots 1 to 3 cm long, 0.2 to 0.4 cm wide. Staminate flower up to 3.5 mm long and up to 3.5 mm across, mostly threemerous (sometimes four-merous), segments up to 2.0 mm long and up to 1.5 mm wide, apex acute to obtuse. Pistillate flower up to 2.5 mm long, up to 1.5 mm across. Fruit 4 to 6 mm long, 2 to 3 mm wide, elliptical to obovate.

Phenology. Anthesis from approximately late March through May.

Hosts. Parasitic on yellow pine.

Discussion. The distributions of the two subspecies overlap in the mountains of central Chihuahua (between latitudes 28° 00' and 28° 30' N) where intermediate characteristics are shown in some populations. Even here, however, there is a tendency to segregate by elevation with subsp. *vaginatum* at lower elevations and subsp. *cryptopodum* at higher elevations. Although the characteristics distinguishing subspecies are greater than those in other species (such as *Arceuthobium tsugense*), this is the only case where we find intermediate populations, therefore we use subspecific rank rather than species rank for this taxon.

30a. *A. vaginatum* subsp. *vaginatum* Mexican Dwarf Mistletoe

Description. Mean shoot height 20 (maximum 55) cm, dark brown to black, rarely reddish. Basal diameter of dominant shoots 4 to 20 (mean 7) mm. Third internode 5 to 30 (mean 17.4 ±6.0) mm long, 2.5 to 8.5 (mean 5.0) mm wide, length/width ratio 2.9: 1. Staminate flower segments 1.6 mm long, 1.1 mm wide. Mature fruit 5.5 by 3.5 mm.

Phenology. Meiosis in February. Anthesis usually March and April. Fruits mature in August of the year following pollination; maturation period averages 16 to 17 months.

Key to the Subspecies

1. Plants dark brown to black, usually over 20 cm tall; staminate flowers usually greater than 3 mm long and wide; anthesis March–April; Sierra Madre Occidental from central Chihuahua southward to the Central Cordillera, and in the Sierra Madre Oriental .... 30a. *A. vaginatum* subsp. *vaginatum*

1. Plants orange, usually less than 20 cm tall; staminate flowers usually less than 3 mm long and wide; anthesis May–June; Sierra Madre Occidental of central Chihuahua and Sonora and mountains of central Coahuila northward to central Utah and northern Colorado .... 30b. *A. vaginatum* subsp. *cryptopodum*

Hosts. *Arceuthobium vaginatum* subsp. *vaginatum* has the broadest known host range of any species in the genus. It is collected on 13 species of Mexican pines and undoubtedly occurs on others. It is common on the principal hosts *Pinus arizonica* vars. *arizonica*, var. *stormiae, P. cooperi, P. durangensis, P. engelmannii, P. hartwegii, P. herrerai, P. lawsonii, P. montezumae, P. patula*, and *P. rudis*. *Pinus teocote* is a secondary host because it was parasitized only when it was associated with an infected principal hosts. It rarely infects *Pinus culminicola* under infested *P. rudis* on Cerro Potosí (Nuevo León).

Distribution. Mexico (Chihuahua, Coahuila, Distrito Federal, Durango, Hidalgo, Jalisco, Mexico, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Sinaloa, Tamaulipas, Tlaxcala, Veracruz, and Zacatecas). This is the most widely distributed dwarf mistletoe in Mexico, extending from the Sierra Madre Occidental in western Chihuahua south through Durango, Jalisco; into the Central Cordillera of Mexico and Puebla; and occurring in the Sierra Madre Oriental from Coahuila and Nuevo León to Oaxaca. Elevational range is from 2,100 m in Nuevo León to 3,900 m on Nevado de Toluca near Mexico City.

Discussion. The shoots of *Arceuthobium vaginatum* subsp. *vaginatum* exceed 55 cm in height in Central Mexico. The plants exhibit considerable sexual dimorphism and variation. The staminate plants tend to be taller than the pistillate plants, but Vázquez (1991) reports on a population near Texcoco, Mexico, where the pistillate plants were short, erect, and dark, and staminate plants were long, pendulous, and reddish. Plants in some areas of the northern Sierra Madre Oriental are often reddish, but plants just 40 km to the south are again typically black (Hawksworth and Cibrián 1985). The hosts and ecological requirements of *Arceuthobium vaginatum* subsp. *vaginatum* and *A. globosum* are similar; and they frequently sympatric and even occur on the same tree.

30b. *Arceuthobium vaginatum* subsp. *cryptopodum* Southwestern Dwarf Mistletoe

Arceuthobium vaginatum (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens, Brittonia 17:230, 1965.
=*A. vaginatum* f. *cryptopodum*.

Description. Mean shoot height 10 cm (maximum 27) cm, usually orange to reddish brown, sometimes dark to near black. Basal diameter of dominant shoots 2 to 10 (mean 4) mm. Third internode 4 to 16 (mean 7.8 ±3.2) mm long, 2.0 to 4.5 (mean 3.1) mm wide, length/width ratio 2.5:1. Staminate flowers 2.5 to 3.0 (mean 2.7) mm across; perianth segments 1.3 mm long, 1.0 mm wide. Mature fruit 4.5 to 5.5 (mean 5.0) mm long, 2.0 to 3.0 (mean 2.5) mm wide; proximal portion 3.5 mm long. Seeds 2.7 by 1.1 mm.

Phenology. Meiosis in March or April. Anthesis usually in May and June, with extremes from late April to early July. Fruits mature in late July or early August, with extremes from early July to early September. Both anthesis and seed dispersal in Colorado occur 1 to 2 weeks later than in Arizona and New Mexico; maturation period averages 14 to 15 months. Seed germination from August to September, immediately following dispersal.

Hosts. *Pinus ponderosa* var. *scopulorum* is the most common host in Arizona, New Mexico, Colorado, Utah, and Texas. The two races of var. *scopulorum* recognized by Conkle and Critchfield (1988) (Rocky Mountain and Southwestern) appear to be about equally susceptible, but most of the distribution of the Rocky Mountain race is primarily north of that of *Arceuthobium vaginatum* subsp. *cryptopodum*. Other principal hosts include *P. arizonica* var. *arizonica* (Arizona, New Mexico, Chihuahua, and Sonora) and var. *stormiae* (Coahuila), *P. engelmannii* (Arizona, Chihuahua, and Sonora), and *P. durangensis* (Chihuahua and Jalisco). *Pinus cooperi* is a secondary host. Occasional hosts are *Pinus aristata* and *P. contorta* var. *latifolia*. Rare hosts are *Pinus flexilis* and *P. strobiformis*. *Pinus sylvestris* is an extra-limital host.

Distribution. Northern Mexico (Sonora, Chihuahua, and Coahuila) and United States (Utah, Arizona, Colorado, New Mexico, and Texas). *Arceuthobium vaginatum* subsp. *cryptopodum* is widely distributed on *Pinus ponderosa* var. *scopulorum* from central Utah (Sevier and Emery) and northern Colorado (Larimer) to Arizona, New Mexico, western Texas (Guadalupe and Davis Mountains), at least as far south as the Sierra de la Madera (Coahuila) and the Sierra Madre Occidental (Sonora and Chihuahua). *Arceuthobium vaginatum* subsp. *cryptopodum* occurs in nearly every mountain range where *P. ponderosa* var. *scopulorum* grows, including isolated ranges such as the Virgin, Trumbull, and Hualapai Mountains (Arizona), the Ladron, Organ, Guadalupe, and San Andreas Mountains (New Mexico), Navajo Mountain (Utah), and Mesa de Maya (Colorado). *Arceuthobium vaginatum* subsp. *cryptopodum* distribution maps have been published for Colorado, Utah, and New Mexico (see Hawksworth and Wiens 1996). Elevational range is 1,700 to 3,000 m, although it is found primarily between 2,000 and 2,600 m in Arizona and New Mexico.

Discussion. *Arceuthobium vaginatum* subsp. *cryptopodum* is characterized by thick, orange-colored shoots. Populations, however, show various color gradations commonly from yellow to red, greenish in deep shade or on *Pinus contorta* var. *latifolia* or rarely from dark purple such as in the Black Forest of Colorado. This dwarf mistletoe is particularly damaging to *Pinus ponderosa* in the Sacramento Mountains in south-central New Mexico (Lincoln National Forest and adjacent Mescalero Apache Indian Reservation; Hawksworth and Lusher 1956), central Arizona, and along the Front Range in Colorado. For reasons yet to be explained, the parasite is common but less damaging in southwestern Colorado and southeastern Utah. The witches' brooms induced by *Arceuthobium vaginatum* subsp. *cryptopodum* are similar on all hosts except for *Pinus contorta* var. *latifolia* with small witches' brooms and large branch swellings. Because of the severe damage caused by this mistletoe and the importance of its principal host, there are numerous reports on its biology and management; the most comprehensive study is by Hawksworth (1961) and a general leaflet by Lightle and Weiss (1974).

31. *Arceuthobium verticilliflorum*
Big-Fruited Dwarf Mistletoe

Arceuthobium verticilliflorum Engelm., Botany of California 2:107, 1880.

Description. Mean shoot height 7 (maximum 11) cm, mostly yellow to yellow-green to purplish, without secondary branching, lightly glaucous when young. Basal diameter of dominant shoots 2.5 to 5.0 (mean 3.6) mm. Third internode 2 to 7 (mean 3.0 ±1.2) mm long, 2.5 to 4.5 (mean 3.2) mm wide, length/width ratio 0.9:1. Staminate flowers 3.5 to 4.5 (mean 4.0) mm across; perianth mostly four-merous (sometimes three-merous); verticillate, with five to 10 flowers per whorl; segments 1.8 mm long, 1.2 mm wide. Mature fruit 15 by 10 mm. Seeds about 11 by 6 mm; embryos 4 by 1 mm.

Phenology. Meiosis September to October. Anthesis usually March and April. Fruits mature in September and October of the year following pollination; maturation period averages 18 to 19 months.

Hosts. This dwarf mistletoe principally parasitizes *Pinus arizonica*, *P. cooperi*, *P. durangensis*, and *P. engelmannii*.

Distribution. Mexico (Durango). Populations occur east of El Salto on the Durango–Mazatlán Highway, in the Sierra Candella, Sierra Huacol, Sierra Guanacevi, and along the road from Santiago Papasquiaro to Altares (Cibrián Tovar and others 1980). Elevational range is 2,000 to 2,750 m.

Discussion. Hawksworth and Wiens (1965) report the rediscovery of this unusual species, first described by Engelmann in 1880, from El Salto, Durango. The species is perhaps the most distinctive and primitive in the genus. The staminate shoots are characterized by thick spikes (4 to 6 mm) with verticillate, four-merous flowers; the entire spikes are deciduous after flowering. This is the only dwarf mistletoe in which the pedicels do not elongate and curve downward when the fruits mature. Typically, the pericarp oozes off the top of the seed, and seeds are released but not explosively discharged. Compared to other dwarf mistletoes, mature fruits are more than twice as large and seeds weight 100 times more (200 to 270 mg). In further contrast, most dwarf mistletoes are found in closed canopy stands as pockets of infested trees with severe infections in the lower crowns; but *Arceuthobium verticilliflorum* is found in open stands with random distributions in trees and crowns. Fruit and seed morphology, ecological distribution, and observation of birds feeding in infected crowns suggest this dwarf mistletoe is dispersed by birds. This dwarf mistletoe causes massive witches' brooms, and the diameter of infected branches is sometimes greater than that of the trunk where the infected branch emerges. Infections on the main trunks of pines sometimes extend up to 3 m in length.

32. *Arceuthobium yecorense*
Yecoran Dwarf Mistletoe

Arceuthobium yecorense Hawksw. & Wiens, Phytologia 66:6, 1989.

Description. Mean shoot height 12 (maximum 17) cm, yellow-green to brown, branches flabellate. Basal diameter of dominant shoots 2 to 5 (mean 3) mm. Third internode 10 to 21 (mean 15) mm long, 2 to 4 (mean 2.4) mm wide.

Phenology. Time of anthesis is unknown but suspected to be June. Time of fruit maturity is unknown, but presumed to be September and October.

Hosts. The principal hosts in the Yecora region are *Pinus leiophylla* var. *chihuahuana* and *P. herrerai*. In the Sierra Madre Occidental, it occurs principally on *Pinus durangensis*, *P. herrerai*, *P. lumholtzii*, and *P. leiophylla* var. *chihuahuana*. *Pinus engelmannii* is a secondary host.

Distribution. Mexico (Sonora, Chihuahua, and Durango). The distribution of this dwarf mistletoe is poorly known and only collected from the Yecora region (Sonora and Chihuahua) and about 100 km west of Santiago Papasquiaro (Durango). Because it is abundant at two locations separated by more than 400 km, the dwarf mistletoe should be expected in the intervening forest areas as well. Elevational range is 1,600 to 2,500 m.

Discussion. *Arceuthobium yecorense* is characterized by its slender, greenish–yellow to brownish shoots and early summer flowering period. The plants are morphologically most similar to *A. aureum* subsp. *aureum* of the lowlands of Guatemala. The two populations are similar except that shoots from western Durango have more yellowish and slightly taller shoots. Yecora is the primary pine-producing area of Sonora; the dwarf mistletoe there is both common and damaging.

B. W. Geils
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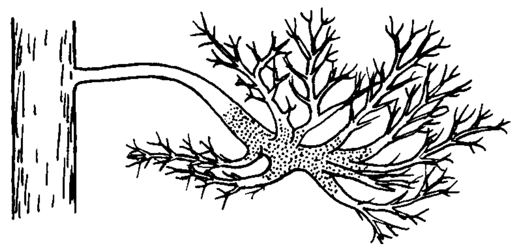
Chapter
5

Damage, Effects, and Importance of Dwarf Mistletoes



All dwarf mistletoes are parasites that extract water, nutrients, and carbohydrates from the infected host; they are also pathogens that alter host physiology and morphology (Gill and Hawksworth 1961, Hawksworth and Wiens 1996). Disease or direct effects are reductions in diameter and height increment, survival, reproduction, and quality; witches' brooms are formed in many pathosystems (Knutson and Tinnin 1980). Where dwarf mistletoe populations develop significant, long-term infestations, cumulative tree damages have various ecological and evolutionary effects. Depending on management objectives and priorities, these effects are interpreted as positive, negative, or usually of mixed consequences. In chapter 4, we discuss in general how the mistletoe's environment affects its growth and development and relate how mistletoe abundance is described by a relative severity index, DMR. In following chapters, the authors present information for quantifying host and mistletoe populations;

they also indicate numerous ways in which managers can influence mistletoe through manipulation of biotic agents, host genetics, and forest stands. In this chapter, we review the physiology of mistletoe parasitism, describe disease effects on infected host trees, identify some of the complex ecological and evolutionary interactions of which mistletoes play a role, and relate these effects and interactions to their consequences for resource management.

Physiology of Dwarf Mistletoe Parasitism

Dwarf mistletoes cause tree disease by affecting host water relations and growth (Knutson 1983, Kolb 2002). The shoot and leaf surface of dwarf mistletoes is small compared to other mistletoes, but they have significant effects on host water relations (Fisher 1983, Sala and others 2001, Wilson and Calvin 1996). Although dwarf mistletoe shoots do transpire, significant transpiration loss is by host foliage, especially those with large witches' brooms. Dwarf mistletoes affect host growth through the interaction of the host with the mistletoe endophytic system (Alosi and Calvin 1985, Calvin and Wilson 1996). The physiological processes involved include: (1) production of growth regulating compounds and (2) expropriation and reallocation of water, minerals, and carbohydrates (Livingston and others 1984, Rey and others 1991, 1992, Snyder and others 1996). The pathological symptoms are retention of infected branches, abnormal growth of infected branches (witches' brooms), crown dieback, and death (Anderson and Kaufert 1959, Broshot and Tinnin 1986, Hawksworth 1961).

Dwarf mistletoe infection affects host foliage, phenology, and respiration. Numerous authors report that needles of severely infected trees are smaller, fewer, and yellowish (Andrade and Cibrián 1981, Hawksworth 1961, Hawksworth and Johnson 1989a, Korstian and Long 1922, Weir 1916b). *Pseudotsuga menziesii* with *Arceuthobium douglasii* initiate bud break earlier and form longer shoots on brooms (Briede and others 1991). Dwarf mistletoe infected trees have lower respiration rates (Ryan 1990, Wanner and Tinnin 1986), perhaps the result of carbohydrate deficiency. Tree vigor as a single "health" index is evaluated in numerous ways; Schaffer and others (1983a) relate mistletoe infection with vigor and electrical resistance of bark tissues. Srivastava and Esau (1961) and Cibrián and others (1980) examine the effects of infection for distorting the host wood anatomy. One difficulty in researching dwarf mistletoe–host physiology is detecting and quantifying the endophytic system especially during incubation and latency. Marler and others (1999) demonstrate a polymerase chain reaction (PCR) method for identifying infected branches based on presence of mistletoe DNA.

Direct Effects to Host Trees

The pathological results of dwarf mistletoe infection are seen as reductions in reproduction, growth, longevity, and quality. The nature and magnitude of these effects are determined by the mistletoe and host species involved, infestation severity (usually measured as DMR, see chapter 4), and vigor of the host. These factors are in turn affected by age, history, and the influences of insects, other disease agents, competition, site quality, and climate (Hawksworth and Scharpf 1978, Hawksworth and Shaw 1984, Hawksworth and others 1992a). From a management perspective of mitigating these effects, the important considerations are time and opportunity. Both mistletoe intensification and damage are progressive and cumulative; they begin at a slow rate, with little effect, but increase exponentially, accumulating to a large effect. Damage first becomes evident when the crown of the host tree is about half infected (moderately infected, DMR class 3) and becomes increasingly severe as the infection intensifies to its culmination when the entire crown is infected and the tree dies. Mistletoe intensification and damage are also interactive with each other and responsive to numerous external factors. Models such as documented by Hawksworth and others (1995) integrate these numerous interactions and factors and portray the development of an infestation with useful management indicators such as numbers of trees, basal area, volume, and ingrowth.

Reproduction

Dwarf mistletoe affects host reproduction through cone production, seed quantity and quality, and seedling survival. Mature trees are large and usually have numerous reserves; a severe mistletoe infection, however, can reduce cone and seed production. Seedlings are especially vulnerable; a single mistletoe infection on the seedling is either lethal or so damaging the host sapling appears more like a bush than a tree.

Cones and seeds—Few studies are available on cone and seed production of dwarf mistletoe-infected trees. Cone production on witches' brooms as measured by numbers and size is usually reduced, but some viable seed may still be produced (Bonga 1964, Kuijt 1960b, Sproule 1996b, Weir 1916b). The reproductive output of infected trees appears to vary by species and severity of infection. Seed germination from parent *Pinus ponderosa* trees infected by mistletoe is reduced (Pearson 1912); germination is only 60 percent for seeds from moderately infected trees and

75 percent for severely infected trees (Korstian and Long 1922). Seed from infected *P. jeffreyi* are smaller, germinate less (80 percent), and produce poor seedlings (Munns 1919). For *P. contorta*, Schaffer and others (1983b) report cone size, seed size, and seed germination are negatively correlated with infection severity. Although Wanner (1986) has similar results for cones and seeds, he observes an initial increase in seedling stocking (at age 1 year) for some in heavily infested stands and attributes this increase to better seedbed conditions, which in these cases offset reduced numbers of seeds produced. Infected *Picea mariana* produce fewer cones, fewer seeds, lighter seeds, and lower germination rates than uninfected trees (Singh 1981, Singh and Carew 1989). In contrast to these reports, Reid and others (1987) did not observe an effect on cone production for infected *Pinus rudis*.

Seedlings—Disease incidence in young stands can be high (see for example Roth 1971, Scharpf and Vogler 1986, Weir 1916b). This is especially serious because seedlings and saplings are severely damaged by infection with even a few mistletoe plants. Reduced height of infected seedlings compared to uninfected seedlings is reported by Knutson and Toevs (1972) and Roth (1971). Seedlings are usually infected on the main stem and quickly killed by the mistletoe. Because of high turnover rates and rapid deterioration after death, mortality rates among seedlings are difficult to determine. Studies such as Roth (1971) in which he observed 50 percent loss of infected seedlings after 12 years, however, support the claim that early mistletoe infection is usually lethal. Those that survive for a few years at least, often develop into little more than a single broom and resemble a bush or bonsai.

Growth

An obvious and important fact about conifer trees is that they grow; they accumulate stem wood on a bole that increases in width, length, and volume. The annual increment for accretion in width varies along the bole and is measured for convenience at a given reference height. The variation in width along the bole is described as form; measures of width, length, and form are used to compute volume. By diverting the tree's resources to other outputs, a mistletoe infestation in a tree affects diameter growth and height growth, and so consequently affects form and volume. Fundamental to forest management is the ability to project expected tree growth under various treatment options. These projections are now often made with simulation models such as the Forest Vegetation Simulator (FVS, Forest Management Service Center 2001) and PrognosisBC (British Columbia Ministry of Forests 2000). Numerous intrinsic and extrinsic factors determine tree growth; these can be categorized as species, site, history, competition, and for infected trees, mistletoe severity. Site covers those long-term, generally fixed factors related to the potential productivity of the area such as soil fertility, water holding capacity, and climatic suitability. History reflects past events (droughts) and conditions (stagnation) that affect a tree's crown, its photosynthetic engine. Competition encompasses factors measured by stand density as basal area. Mistletoe severity is usually quantified as DMR (Hawksworth 1977, chapter 4). Quantitative studies reveal that these factors are usually confounded; that is, they interact so the effect of one factor varies as the level of another factor is changed.

Several techniques exist for study of tree growth. Stem analysis (for example, Baranyay and Safranyik 1970) is the most intensive but provides detailed information on diameter and height increment as well as form and volume. Individual trees can be identified and reexamined after a period of time to obtain information on each tree's change in diameter and height (for example, Hawksworth 1961). Alternatively, trees can be examined once and past diameter growth determined from an increment core (for example, Tinnin and others 1999). Some studies compare the diameters (or heights) for trees of different mistletoe classes; but unless all the trees were the same size and infected at the same time, this method introduces several complications and does not really measure growth response to infection.

Although numerous studies relate mistletoe severity to tree growth, few generalities can be made (Hawksworth and Wiens 1996). Some recent studies use a stem analysis technique (Andrade and Cibrián 1980, Baranyay and Safranyik 1970, Pousette 1991, and Smith 1969). Other studies that examined trees and increment cores include those by Barrett and Roth (1985), Filip and others (1993), Knutson and Tinnin (1986), Mathiasen and others (1990), Tinnin (2001), Tinnin and others (1999), and Vera (1984). Reduction in diameter increment is related to infection severity in nonlinear fashion: with little or no significant reduction for the DMR classes 1 to 3, some reduction for DMR class 4, more for DMR class 5, and much for DMR class 6. The magnitude of these reductions depends on numerous factors (Hawksworth and others 1995, Hawksworth and Shaw 1984, Thomson and others 1997, Wicker and Hawksworth 1988). Reduction in height increment is also related to infection severity; height effects usually appear at a lower severity and are proportionally greater with increase by DMR class. The combined effects of diameter reduction and height reduction on form and volume can vary by species and age (Pousette 1991, Tinnin 2001). Volume reductions, either accounting for stem form or not, are proportionately greater than reductions for diameter or height alone. Because mistletoe infection often occurs earliest on some of the larger trees of a stand, size comparisons of trees in different severity classes do not well reflect effects on growth increment.

Longevity

Mistletoe not only kills small trees but in time, a severe infection can even kill a mature, large tree (Roth 2001). A severe infestation (for example, Wood and others 1979) with many seriously infected trees can generate a high mortality rate. Mortality rates (see Hawksworth and Wiens 1996) are determined from either reexamining a plot after a known period of time (dependable) or estimating which trees had died within the reference period (undependable). The effect of mistletoe on tree survival can also be expressed in terms of tree longevity, the period of time over which a fraction (usually 50 percent) of trees are expected die. Because tree mortality is infrequent and then occasionally synchronous with events such as droughts (Childs 1960, Page 1981, Smith 1983), longevity studies over a long period with frequent observations (Hawksworth and Geils 1990) are especially useful. Like growth effects, mortality is related to a number of interacting factors; the most important are species, size, infection severity, and other mortality agents.

Hawksworth and Wiens (1996) identify 17 mistletoe species that are especially lethal for certain hosts and locations (table 5-1). These hosts include many important forest species such as *Abies magnifica* (Parmeter and Scharpf 1982), *Larix occidentalis* (Weir 1916a), *Picea mariana* (Baker and French 1991), *Pinus contorta* (Baranyay and Safranyik 1970, Hawksworth and Johnson 1989a), *P. ponderosa* (Hawksworth 1961, Roth 2001), and *Pseudotsuga menziesii* (Filip and others 1993, Mathiasen and others 1990). A study reported by Hawksworth and Geils (1990) and Geils and others (1991) demonstrates the interacting (and nonlinear) effects of tree size (diameter) and infection severity (DMR) on the longevity of mistletoe-infected pine. The expected longevity for 50 percent of trees with a severe infection (DMR 6) is less than 10 years for smaller trees (less than 9 inches diameter) and more than 10 years for larger trees. Over 40 years, however, many of the larger, severely infected trees died. During this time, some of the originally moderately infected trees became severely infected and died at a rate greater than that for uninfected trees. Elevated mortality rates due to mistletoe infection are built into the Dwarf Mistletoe Model Impact Model (Forest Health Technology Enterprise Team 2002).

Extremes in temperature and moisture can affect mortality rates of dwarf mistletoe-infected trees. Mortality rates are often highest following periods of drought, but there are few quantitative data. The most comprehensive studies of the interaction of drought and mistletoe are by Page (1981) and Smith (1983) for the California drought of 1975 through 1977. Drought may increase mortality of mistletoe-infected trees more than four times that of uninfected trees. Smith and McMahan (2002) describe an eco-physiology extension for the Forest Vegetation Simulator (Forest Management Service Center 2001). The method they present could be modified and developed for adjusting mistletoe-caused mortality rates to account for climatic variation.

Table 5-1—Combinations of North American taxa of *Arceuthobium* and their hosts in which host mortality rates are particularly high.

Arceuthobium	Host	Location
A. abietinum f. sp. *magnificae*	*Abies magnifica*	CA
A. americanum	*Pinus contorta*; *Pinus banksiana*	Western US and Canada; MB, SK, and AB, Canada
A. blumeri	*Pinus* spp.	Chihuahua and Durango, Mexico
A. campylopodum	*Pinus ponderosa*	Southern CA
A. cyanocarpum	*Pinus flexilis*; *Pinus albicaulis*	ID, UT, WY, CO; northern CA
A. douglasii	*Pseudotsuga menziesii*	Western North America
A. durangense	*Pinus* spp.	Jalisco, Mexico
A. gillii	*Pinus* spp.	Chihuahua and Durango, Mexico
A. guatemalense	*Pinus ayacahuite*	Southern Mexico and Guatemala
A. laricis	*Larix occidentalis*	Northwestern US and BC, Canada
A. microcarpum	*Picea pungens*	AZ, NM
A. nigrum	*Pinus* spp.	Durango and Puebla, Mexico
A. occidentale	*Pinus sabiniana*	CA
A. pusillum	*Picea mariana; Picea glauca*	Eastern North America
A. strictum	*Pinus leiophylla*	Durango, Mexico

Wood Quality, Decay, and Breakage

Although mistletoe infections usually occur on branches, the endophytic system can invade the bole and potentially affect wood quality. Infections and broken branches caused by heavy witches' brooms provide an entry court for decay fungi. Infected branches and brooms are resinous and dense with other flammable materials. These effects of mistletoe infection are important in some situations.

Wood quality of mistletoe-infected trees is affected by production of larger knots, development of abnormal grain, reduced strength, and other altered physical and chemical properties. Infected wood such as found in mistletoe-burls is characterized by shorter, distorted tracheids, increased ray volume, included pitch, frass, and decay (Cibrián and others 1980, Piirto and others 1974, Weir 1916a). The effects on sapwood moisture content and specific gravity are variable: higher, lower, or not different from uninfected wood (Hawksworth 1961, Knutson 1970, Wellwood 1956). Piirto and others (1974) report, however, that infected wood and wood from other parts of infected trees is weaker in strength for modulus of elasticity, modulus of rupture, and work to proportional limit. The effects on pulp quality, however, are negligible (Dobie and Britneff 1975, Hunt 1971, Wilcox and others 1973).

The association of decay and mistletoe varies by species and tree age. In fir, larch, or hemlock trees, mistletoe infections often provide an infection court for decay fungi, especially if the wood is exposed (Aho 1982). Englerth (1942) reports that nearly a third of the decay in hemlock entered through dwarf mistletoe stem infections and adjacent swollen limbs. Several decay fungi are associated; the most frequent is the common brown cubical slash decay fungus *Fomitopsis pinicola* (Etheridge 1973). Decay is usually limited to the area of the swollen bole canker (Aho 1982). Decay is rarely associated with mistletoe infection in the more resinous pines, spruce, and Douglas-fir. Well-managed, young-growth stands of true fir in California should also have little loss from mistletoe-associated decay (Parmeter and Scharpf 1982).

Witches' Brooms

Most dwarf mistletoes and several other disease agents induce abnormal development of host branches into witches' brooms. Mistletoe brooms are infected host branches with excessive branching and shortened (or lengthened) internodes that develop in response to elevated levels of plant growth compounds (Schaffer and others 1983c). Broom form is determined by the mistletoe and may even be a useful taxonomic character. There are a variety of broom forms and classification schemes based on the distribution of the endophytic system, on the host branching pattern, and on the boom position relative to the bole. Systemic or isophasic brooms are those in which the endophytic system of the mistletoe grows with the apical and cambial tissues of the host and produces mistletoe shoots either along the branch or at branch girdles (Hawksworth 1961, Kuijt 1960b). Nonsystemic or anisophasic brooms are those in which the endophytic system remains localized near the original site of infection and only grows with the host cambium (fig. 5-1). *Arceuthobium globosum* subsp. *globosum* and *A. occidentale* do not induce typical broom formation. Most North American mistletoes usually develop nonsystemic brooms and rarely systemic brooms. *Arceuthobium americanum*, *A. douglasii*, *A. guatemalense*, and *A. pusillum* consistently produce systemic brooms (Hawksworth and Wiens 1996). Hawksworth (1961) classifies brooms of *Arceuthobium vaginatum* as typical for nonsystemic brooms where the localized infection is far from the bole, and although branching is prolific, segments are short (fig. 5-1A). He describes the uncommon, volunteer leader

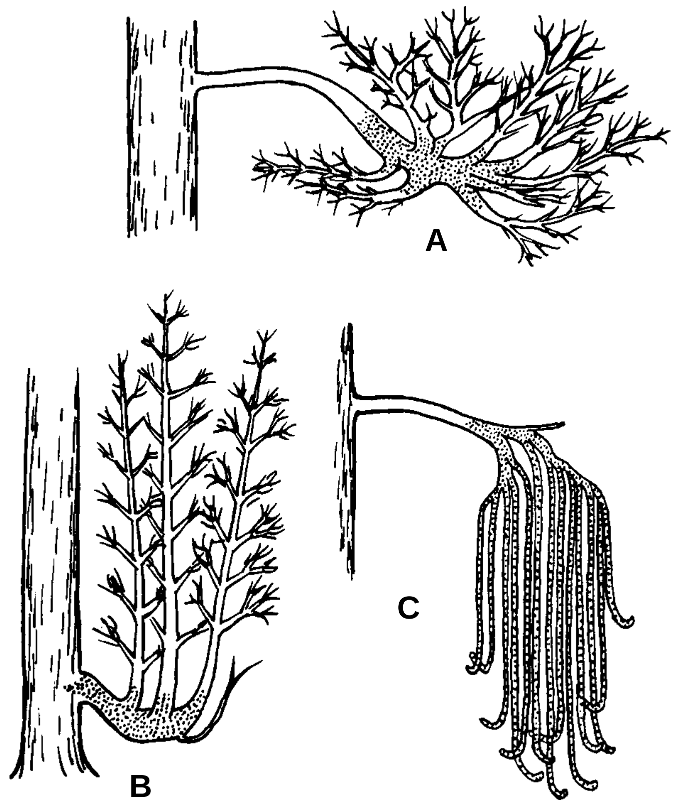


Figure 5-1—Witches' brooms on *Pinus ponderosa* induced by *Arceuthobium vaginatum*; stipple areas indicate region invaded by the mistletoe. **A**, typical broom; **B**, volunteer leader broom; **C**, weeping broom. Adapted from Hawksworth (1961), figure 45.

brooms (fig. 5-1B) as localized infections, near the base of the bole in which one or several leaders develop as long, erect, normally branched forks. Weeping brooms are very rare systemic brooms of numerous, long, pendulous infected branches (fig 5-1C). Tinnin and Knutson (1985) classify the systemic brooms of *A. douglasii* by position. Type I brooms originate away from the bole on long branches and thereby form large brooms on drooping branches. Type II brooms form on branches but near the bole and with a sturdy, upright supporting branch; the supporting branch makes a horizontal platform between the bole and mass of the broom. Type III brooms form at or close to the bole and lack the dominant, platform branch. Witches' brooms can also be produced by rust fungi (broom rusts and gall rusts), other fungi (*Elytroderma deformens*), chromosomal condition (trisomatic cells), and physiological reaction to canopy opening or age (stimulation brooms). Mistletoe brooms can be distinguished by the presence of aerial shoots or their remnant basal cups.

Witches' broom formation by dwarf mistletoes can have a major impact on host growth and crown form. Brooms become quite large on Douglas-fir or numerous on pine and larch. Brooms are a preferred growth-sink; host resources that would have gone to the bole and roots are diverted into broom growth. The importance of this effect is evident from the improved vigor, growth, and survival of broom pruned trees (Lightle and Hawksworth 1973, Scharpf and others 1988). Large brooms, especially on trees with brittle wood, may break off (Hadfield 1999). Brooms differ from normal crown branches for numerous features: needles, twigs, and accumulated detritus (Bonga 1964, Broshot and others 1986, Tinnin and Knutson 1980). These differences are important for their consequences on canopy structure, wildlife habitat, and fuel loading.

Ecological and Evolutionary Effects

The effects of mistletoe infection on trees have numerous consequences for associated species and various natural processes. Mistletoes, especially in significant infestations, act as both keystone species (Watson 2001) and controlling disturbance agents (Holling 1992). From this perspective, we view how dwarf mistletoes affect community dynamics by their interactions with fungi, insects, and fire, effects on vegetation, and use by wildlife. Hawksworth and Wiens (1996) also discuss these topics and providing examples of pathogenic and biotic associates.

Interactions

The forest communities to which dwarf mistletoes belong include large numbers of species of various taxonomic groups and ecological roles. For consideration of the most obvious ecological effects, we focus here on the interactions of mistletoes with other disease, injury, or disturbance agents.

Fungi—Forest fungi are important in nutrient recycling (decay and mycorrhiza) and as pathogens of mistletoes and their hosts. The relation of mistletoes and decay fungi is discussed above, and the pathogens of mistletoes are described in chapter 7 as biological control agents. In many forests, mistletoes are only one of many tree pathogens; the most important are canker fungi (Filip 1984), root disease fungi (Marsden and others 1993), and stem rusts (Hawksworth and others 1983).

Insects and Spiders—Insects and spiders that react to mistletoe infestations can be categorized as those associated with shoots, with brooms and infected branches, and with infested trees (Stevens and Hawksworth 1970, 1984). Insects associated with shoots include pollinators, herbivores, and their predators, parasites, and associates. Some of the important shoot insects are potential biocontrol agents (see chapter 7), others include lepidopterians such as *Mitoura spinetorum* (Grimble and Beckworth 1993) and aphids with their attending ants. Numerous insects and spiders use mistletoe brooms with their accumulation of needles and other detritus as a special habitat for foraging and hunting. The significant insects associated with infected trees are tree defoliators and bark beetles. Defoliators may feed upon mistletoe-infected trees and contribute to tree damage and mortality (Filip and others 1993, Wagner and Mathiasen 1985). Mistletoe may affect tree phenology and shoot development, which has a consequence to defoliator development (Briede and others 1991). The attraction of bark beetles to mistletoe-infected trees depends on the species combination (mistletoe-tree-insect) and severity of infection. Hawksworth and Wiens (1996) review the combinations for which mistletoe infection appears to increase, decrease, or be unrelated to bark beetle attack. For example, Johnson and others (1976), McCambridge and others (1982), and McGregor (1978) discuss mistletoe as a predisposing factor for mountain pine beetle; Wilson and Tkacz (1992) for an outbreak of *Ips* in pinyon. Nebeker and others (1995) and Linhart and others (1994) consider the possible chemical bases for insect attraction to infected trees. An intermediate hypothesis to explain aggressive bark beetle (for example, mountain pine beetle) attraction to infected trees suggests that there would be no difference in beetle attack between similar sized trees that are uninfected or lightly infected (DMR 1 or 2), greater attack for moderately infected trees (DMR 3 or 4), and reduced attack for severely infected trees (DMR5 or 6). This hypothesis requires testing in various situations.

Fire and Fuels—The fire ecology of dwarf mistletoes is reviewed by Alexander and Hawksworth (1975) and updated by Zimmerman and Laven (1984). Several features of mistletoe infection increase the tree's flammability. Infection induces excess resin deposition and increases litter accumulation (including detached brooms). Retained brooms and infected branches form a fuel ladder from the ground into the canopy. Mistletoe severity (DMR) is related to scorching, mortality, and sanitation (Conklin and Armstrong 2001). Although an extreme, stand-replacing fire kills most trees, a few isolated mistletoe-infected trees can escape to not only reseed the stand but also reinfest it. Disturbance regimes and stand structure resulting from mistletoe and fire interactions are discussed by Bradley and others (1992) and Kipfmueller and Baker (1998).

Forest Structure and Composition

Forest insects and pathogens are increasingly being recognized as important agents in shaping the structure and composition of forests (Hessburg and others 1994, Holling 1992, Monning and Byler 1992). Besides their interaction with fire described above, mistletoes affect the forest canopy, landscape pattern, and tree species mix (Baker and French 1991, Mathiasen 1996, Parker and Parker 1994, Reich and others 1991, Wanner and Tinnin 1989). The ecological importance of witches' brooms on community dynamics is examined by Tinnin and others (1982); and the role of mistletoes in forest canopies is reviewed by Mathiasen (1996). The paper on canopy light and mistletoe distribution by Shaw and Weiss (2000) is an example of detailed, canopy ecology studies at the Wind River Canopy Crane. Mistletoe and forest vegetation studies include examinations of plant association (Marshall and Filip 1999) and biotic diversity (Mathiasen and Marshall 1999). Two additional topics that have received special attention are effects and dynamics of mistletoe in old-growth stands and on wildlife habitat.

Old-Growth Forests—Numerous studies have examined mistletoe effects on immature and mature trees in managed stands, but there are few studies for old trees (over 200 years) and old-growth stands. Hawksworth and others (1992a) described a 300-year-old *Pinus contorta* stand infested with *Arceuthobium americanum*. Although infected trees occurred on over half the area, there were no isolated infection centers as were found in nearby 70-year-old stands. Tree mortality was higher among infected trees, but diameter growth was significantly reduced only among the most severely infected trees (DMR 6). These older trees grew slower, and on a percentage basis mistletoe had less effect than seen in younger, faster growing trees. Parker and Parker (1994) examined the spatial pattern of tree density in seven *P. contorta* stands about 120 to 140 years old. They observed dense, closed-canopy stands that appeared to have developed and closed rapidly after initiation (fire) and low density, open-canopy stands with recruitment that is more continuous. They speculated that the open stand might have resulted from low initial stocking and high mortality from mistletoe. Kipfmueller and Baker (1998) describe another set of 43 *P. contorta* stands also in the Central Rocky Mountains and also representative of unmanaged, older stands (some to 500 years). They found that half of the stands were infested, and the average disease severity (DMR) increased with time since stand establishment. At the landscape scale, mistletoe often occurred as severe infestation patches but was absent from other areas of similar age. They concluded that a healthy forest would include a mosaic of infection centers and uninfested stands with periodic stand-replacing fires that vary in intensity.

Wildlife Habitat—Although dwarf mistletoes do not provide large incentives for birds or mammals to visit for pollination or seed dispersal as do other mistletoes, dwarf mistletoes provide forage, foraging sites, protected and special sites, and desirable stand structures for numerous wildlife species. (Bird dispersal is important for *Arceuthobium verticilliflorum* and possibly *A. occidentale*.) Hawksworth and Geils (1996) review the use of mistletoe by birds and mammals for food, nesting, and cover. Numerous studies have since been reported. Allred and Gaud (1994) describe tree selection and bark grazing by Abert squirrels and their high use of mistletoe-infected trees. Brooms in Douglas-fir are frequently used for cover and nesting (Hedwall 2000, Parks and others 1999a, Parks and Bull 1997, Tinnin and Forbes 1999). Brooms in ponderosa pine are also used (Garnett 2002). Brooms and associated mistletoe-infested sites are important for nesting by the northern spotted owl (Everett and others 1997, Marshall and others 2000). Steeger and Hitchcock (1998) describe the effects of several tree diseases, including mistletoe, on stand structure preference for nuthatches. Reich and others (2000) examine the relationship of canopy opening in a mistletoe-infested strand on bird usage. Although Bennetts and others (1996) found a positive association between the stand severity of mistletoe and bird usage in Colorado, Parker (2001) for a similar study in Arizona found a mixture of responses depending on bird species. Mistletoe presence, incidence, and severity may not be good indicators themselves of wildlife habitat value. Wildlife species are probably responding in a complex way to special features such as brooms and snags, to vertical crown structure, to canopy gap pattern, and other factors affected by mistletoes (Reynolds and others 1992).

Consequences to Resources and Other Values

Dwarf mistletoes are important because they are serious pathogens of valuable conifers in many forests of North America. These conifers are valuable economically, primarily for their timber yields and ecologically for their role in forest ecosystems (Hawksworth and Shaw 1984). Importance and worth, however, are only meaningful and relevant within a given value system that is selected by the forest manager, owner, policymaker, stakeholder, or society.

Importance

Species Affected—Conifers that are hosts to dwarf mistletoes can be divided between major species that occur in great numbers over large areas, and rare species with few, sparse populations. In Canada, the major host species are *Larix occidentalis, Picea mariana, Pinus contorta, P. banksiana*, and *Tsuga heterophylla*. In the Eastern United States, the major species are *Picea mariana, P. glauca*, and *P. rubens*; and in the Western United States, they are *Abies magnificae, A. concolor, Larix occidentalis, Pinus ponderosa, P. contorta, Pseudotsuga menziesii*, and *Tsuga heterophylla*. Mexico has a great abundance and diversity of conifers (over 30 taxa) that are mistletoe hosts (Hawksworth 1980, Hawksworth and Cibrián 1985). *Abies religiosa* and *Pseudotsuga menziesii* are infected; but the most common hosts are pines, including yellow pines, white pines, and pinyon pines. One of the more rare conifers that are hosts for *Arceuthobium abietinum* is *Picea breweriana* in Oregon; it is severely infected (Hawksworth and Wiens 1996).

Area Affected—In Canada, Magasi (1984) reports *Arceuthobium pusillum* is common in the Maritime Provinces. Overall, 20 percent of sites are infested and 6 percent of trees infected, but nearly all of the infested sites, infected trees, and mistletoe-caused mortality are in wet areas. Brandt and others (1998) map and summarize the distribution of severe mistletoe infestation (by *A. americanum*) in Manitoba, Saskatchewan, and Alberta. About 5 percent of the forest area or 500,000 ha are specifically identified as severely infested sites, where mistletoe-caused mortality and brooming are visually obvious (also see Baker and others 1992). Moody and Amirault (1992) estimate mistletoe incidence in individual, severely infested stands ranges from 73 to 100 percent. In British Columbia, *A. americanum* and *A. tsugense* are widespread, common, and damaging at many sites (Moody 1992, Thomson and others 1997). Hodge and others (1994) report only 2 percent of managed stands infested and only 3 percent of trees infected (except in a few stands, however, infection reaches 34 percent).

In the United States, *Arceuthobium pusillum* ranges widely across the Northeastern and Lake States; but its occurrence varies from locally common to rare in some States (Hawksworth and Wiens 1996). Drummond (1982) estimates 14 percent of the spruce area in the Lake States is infested. Numbers for dwarf mistletoe-infested area for each of the Western United States, however, are available (Forest Health Protection 2002). Westwide, about 25 percent (Drummond 1982, Bolsinger 1978) or 28.7 million acres of Western forests are infested (Forest Health Protection 2002). In contrast to the report (and accompanying compact disk) by Brandt and others, the United States' summaries (Drummond 1982, Forest Health Protection 2002) and the data on which they are based provide only statistical estimates of area infested and cannot map the specific, infested sites. A number of regional summaries are available. Andrews and Daniels (1960) report on the distribution of dwarf mistletoe in Arizona and Mexico in terms of administrative area (forest), harvest status, and various ecological factors. The most important forest types are ponderosa pine and Douglas-fir; Andrews and Daniels classify 36 percent of the ponderosa pine type as infested and 47 percent of the Douglas-fir type as infested. Maffei and Beatty (1988) report on a resurvey of the ponderosa pine area examined 30 years previously by Andrews and Daniels (1960). Maffei and Beatty (1988) attribute the apparent increase of infested area (8 percent more of the type) to ineffective mistletoe control. Other regional summaries are prepared by Bolsinger (1978) for the Pacific Northwest, Byler (1978) for California, DeNitto (2002) and Stipe and others (1992) for the Northern Region (Montana), and Johnson and others (1981) for the Rocky Mountain Region (Colorado and Wyoming).

Dwarf mistletoe occurs throughout the conifer forests of Mexico. Vázquez (1994a) states that an estimated 1.8 million ha in Mexico are infested. Most the information related to mistletoe damage in Mexico occurs as reports of infested area and infection incidence at various localities (see Hawksworth 1980). Caballero (1968, 1970) indicates the percentage of inventoried forest sites infested for several States: Zacatecas 24 percent, Durango 15 percent, Jalisco 12 percent, Nayarit 10 percent, Sinaloa 10 percent, Sonora 9 percent, Chihuahua 8.5 percent, and Baja California 7 percent. Within stands, the extent of the area infested and the percent of infected trees can be as high as 85 percent (Acosta and Rodriguez 1989, Gutierrez and Salinas 1989).

Growth Loss—Information on reduction of volume increment, mortality, and area infested can be used to estimate mistletoe impact to stand yield on an area basis. The difference between realized volume in an infested stand (reduced by loss of increment and mortality) and potential yield for the site (if mistletoe were not present) is described as *growth loss*. The growth loss concept can be applied nationally, regionally, forestwide, and to individual stands (Baker and Durham 1997 describe a method for computing growth loss). Drummond (1982) estimates a total annual growth loss from mistletoe in the United States at 418 million cubic feet per year; Vázquez (1994a) for Mexico reports a loss of 2 million cubic m per year. Estimates for Canada are available for Newfoundland at 1 cubic m per year per ha (Singh and Carew (1989); for Manitoba, Saskatchewan, and Alberta at 2.4 cubic m per year (Brandt and others 1998); and for British Columbia at 1.8 million cubic m per year (Forest Insect and Disease Survey 1994). DeNitto (2002) provides a growth loss estimate of 33 million cubic feet per for Montana (broken down by host species). Johnson and others (1981) describe growth loss for forests of Colorado and Wyoming. Marsden and others (1993) illustrate use of a forest growth and yield program to compare expected yield for a mistletoe-infested stand to what might be had were the stand not infested. Growth loss can be so significant in severely infested stands (especially immature and infected at an early age) that commercial yield cannot be obtained (Hawksworth and Hinds 1964).

Amenity Values

Dwarf mistletoes are sufficiently unusual and influential that they are important to a number of resource and amenity values besides commercial timber yield. Other forest products have traditionally included watershed protection, recreation opportunity, and wildlife habitat. Over a half century ago, concern over the effects of dwarf mistletoe to old-growth ponderosa pine at the Grand Canyon National Park lead managers to an intensive control project (Lightle and Hawksworth 1973). The effects of dwarf mistletoe on fuel loading and fire behavior are still a serious interest to managers (Zimmerman and Leven 1984). We have already discussed how witches' brooms and forest structure affect wildlife abundance and diversity (Bennetts and others 1996, Parker 2001, Reich and others 2000). Mistletoes are also valuable as mistletoes themselves and as members of a biotic community.

Mistletoes possess aesthetic, scientific, and intrinsic values. Although the mistletoe plant and diseased trees are not usually considered attractive (exceptive by some forest pathologists), a distinctively broomed, dead tree against the backdrop of the Grand Canyon does make a strong and interesting picture. Mistletoes can provide chemical analogs that may be developed into useful drugs. They serve as models for understanding the evolution of parasitism (Atsatt 1983a) and phylogeny of their hosts (Hawksworth 1991). Rolston (1994) describes the value of living entities beyond their worth to humans as achievement and part of the system of life.

Forests are not only managed for the resources they produce but also to sustain and protect forest health (Monning and Byler 1992) and ecosystem values (Taylor 1995). Dwarf mistletoes are important disturbance agents (Holling 1992) with distinct ecological functions (Hessburg and others 1994). They contribute to natural diversity structurally (Mathiasen 1996) and biologically (Mathiasen and Marshall 1999). Some mistletoes are considered species of special concern (Hildebrand 1995), and truly rare species such as *Arceuthobium hondurense* probably deserve protection. A balanced view of mistletoes as the cause of losses of valuable resources, but also as natural agents that shape forests, is emerging (Wittwer 2002).

Coevolution

Information from biogeography, paleobotany, host relations, and molecular systematics indicates the dwarf mistletoes have a long evolutionary history of parasitism with their conifer hosts (Hawksworth and Wiens 1996). Mistletoes are physiologically dependent on their hosts but cause symptoms that eventually result in death for both. What really matters, however, from an evolutionary perspective is their success at leaving descendents. To the present, host and parasite have lived, reproduced, and died in natural ecosystems. These natural ecosystems, even wildlands, are increasingly controlled and affected by managers and human society. We have a fair understanding of the physiology of mistletoe–host parasitism and a good ability to predict the effects of infection on tree growth and survival. We are beginning to appreciate the complex ecological interactions in which mistletoes participate. By management with biological agents, chemicals, genetic manipulation, and silviculture, we attempt to influence how mistletoe affects resources and our environment. For that management to have a beneficial outcome, which is sustaining to the biotic system on which we depend, it is advisable to consider not only immediate results but also ecological and eventually evolutionary consequences.

J.A. Muir
B. Moody

Chapter

6

Dwarf Mistletoe Surveys

Dwarf mistletoe surveys are conducted for a variety of vegetation management objectives. Various survey and sampling techniques are used either at a broad, landscape scale in forest planning or program review, or at an individual, stand, site level for specific project implementation. Standard and special surveys provide data to map mistletoe distributions and quantify disease severity. At a landscape scale, extensive surveys assess regional impacts, estimate mistletoe occurrence, intensity, and effects, and estimate future growth and yield. Intensive surveys evaluate stands, campgrounds, and other sites to design projects and monitor treatments.

Numerous variations and combinations of techniques such as aerial survey and photography, forest inventory, road and plot survey, transects and grid survey, and permanent plots are used to obtain dwarf mistletoe information for program and project management (table 6-1). Only a few studies compare alternative survey and sampling methods (Drummond 1978, Hildebrand and others 1997, Mathiasen

Table 6-1—Surveys for mapping the distribution and quantifying the effects of dwarf mistletoes.

Technique	Objective(s)	Reference Example
Aerial survey	Landscape assessments	Brandt and others 1998
Aerial photography	Landscape assessments	Baker and French 1991
Forest inventory plots	Landscape assessments	Hildebrand and others 1997
Road and plot surveys	Landscape assessments	Thomson and others 1997
Transects and grids	Landscape assessments	Maffei and Arena 1993
Permanent plots	Detailed assessments Project monitoring	Hawksworth and Marsden 1990 Lightle and Hawksworth 1973
Project area assessment	Management prescription Stand or Land Unit examination Recreation management Wildlife habitat	Tkacz 1989 Vásquez 1994 Scharpf and others 1988 Parks and others 1999

and others 1996b, Vázquez 1993b, 1994a). Effective and efficient sampling benefits from use of explicit objectives recognizing the resources of interest (such as timber, recreation, wildlife), specification of statistical standards, and consideration of cost and safety issues (Tkacz 1989, and see assistance provided at Forest Service 2002). In this chapter, we identify the major types of dwarf mistletoe surveys, uses of that data, and subjects for research and development.

General Requirements and Procedures

Before selecting or adapting one or more methods, a user should carefully consider and articulate the purpose and scope of the proposed survey. Almost all the available methods for estimating mistletoe occurrence and effects can be adapted to a variety of purposes including timber management, vegetation inventory, recreation, and wildlife management. Many techniques can be adapted to a range of scales from regional or forest landscapes to individual stands or sites. For any management decision, a wide variety of information from numerous sources on various subjects is needed. In areas with significant dwarf mistletoe infestations, data on mistletoe extent, severity, and potential make an important contribution to the decision process (Stage and others 1986, Tkacz 1989). Given the variety of objectives and constraints encountered by managers, only general guidelines can be stated here. The benefits of proposed treatment in each particular case should be evaluated for expected costs and benefits, impacts to other resources, and conflicts with other objectives. Assessments for landscape-scale management usually require only extensive, relatively broad information on dwarf mistletoe occurrence and effects. A general strategy for dwarf mistletoe management in areas of significant occurrence may be sufficient. At the level of particular stands and sites, however, management prescription may require detailed information on resource and ecological conditions and specific data for mistletoe distribution and abundance. Site prescriptions also require consideration of the general principles for managing infested stands (see chapters 7 and 8) as well as local issues and forest-level management objectives.

Several Provinces and States require a professionally certified evaluation of young forests to ensure that damages from insects and diseases are less than specified levels. This is especially important where the previous stand had been infested by dwarf mistletoe because the regeneration process may have left an infected, residual overstory that allowed spread to the seedlings (Alfaro 1985). In British Columbia, evaluations assess whether the young stand is free-growing and contractor obligations satisfied (British Columbia Ministry of Forests 1995); in other regions, this standard is described as producing adequate stocking of healthy seedlings.

Several existing data sources are available for general information on regional occurrence and potential impacts of dwarf mistletoes. These include Forest Inventory and Analysis (2002), Forest Health Monitoring Program (1994), Current Vegetation Survey (2002, Gregg and Michaels Goheen 1997), and the Canadian Forest Insect and Disease Survey (Cerezke and Emond 1989, Moody 1992, Myren and Gross 1977, Wood 1986). Use of these kinds of data is reviewed by Bolsinger (1978), Drummond (1982); limitations are described by Drummond (1978), Hildebrand and others (1997), and Marsden and others (1990).

If archive, large-scale data are either lacking or not sufficient, other established forest management plots are available from standard resource inventories. Data for dwarf mistletoes are relatively easily determined, as described below (see Forest Inventory Plots). For landscape-level surveys, several techniques such as road surveys or aerial photography can be used separately or in conjunction with inventory plots.

Surveys of dwarf mistletoes on a landscape or large geographic area are undertaken to determine the overall returns from a national or regional program or to compare returns from standard operational treatments applied to a large forest area. More frequently, landscape surveys are used to substantiate the general extent and effects of mistletoes and rank areas for treatment priority. Exercises range from botanical surveys for detection and identification of dwarf mistletoe species (for example, Hernandez 1991) to large-scale, annual programs for tracking broad forest health conditions and trends (Forest Health Monitoring Program 1994). Large-scale surveys have been conducted for Canada (Moody 1992, Myren and Gross 1977), the Southwestern States (Andrews and Daniels 1960, Maffei and Beatty 1988), and California (Byler 1978).

Occasionally, there is a need for a detailed dwarf mistletoe survey on a land unit for a specific purpose such as determining disease impacts to forest ecology, stand structure, productivity, or treatment effectiveness. Generally, detailed analyses are feasible only if foresters or specialists have access to agency-endorsed methods or models for analysis of forest growth and dwarf mistletoe effects (for example, British Columbia Ministry of Forests 2000, Forest Management Service Center 2001). These models are useful in developing detailed prescriptions for harvesting, silvicultural treatment, and other management objectives such as visual quality, wildlife, and recreation management. Use of models to predict the effects of dwarf mistletoe damage and analyze benefits from silvicultural treatments is described in chapter 8.

For intensive surveys such as silvicultural inspections and timber cruising, several tree stand attributes related to dwarf mistletoe status are useful. These include dwarf mistletoe species (see chapter 4), extent of infested area, mistletoe incidence as percent of host trees that are infected, and a measure or rating of disease severity such as DMR (fig. 6-1) or other rating for intensity of infection within trees.

Dwarf Mistletoe Surveys

Dooling (1978) summarizes several methods suitable for dwarf mistletoe surveys. The most commonly used methods and recent examples (table 6-1) are briefly described in the following sections.

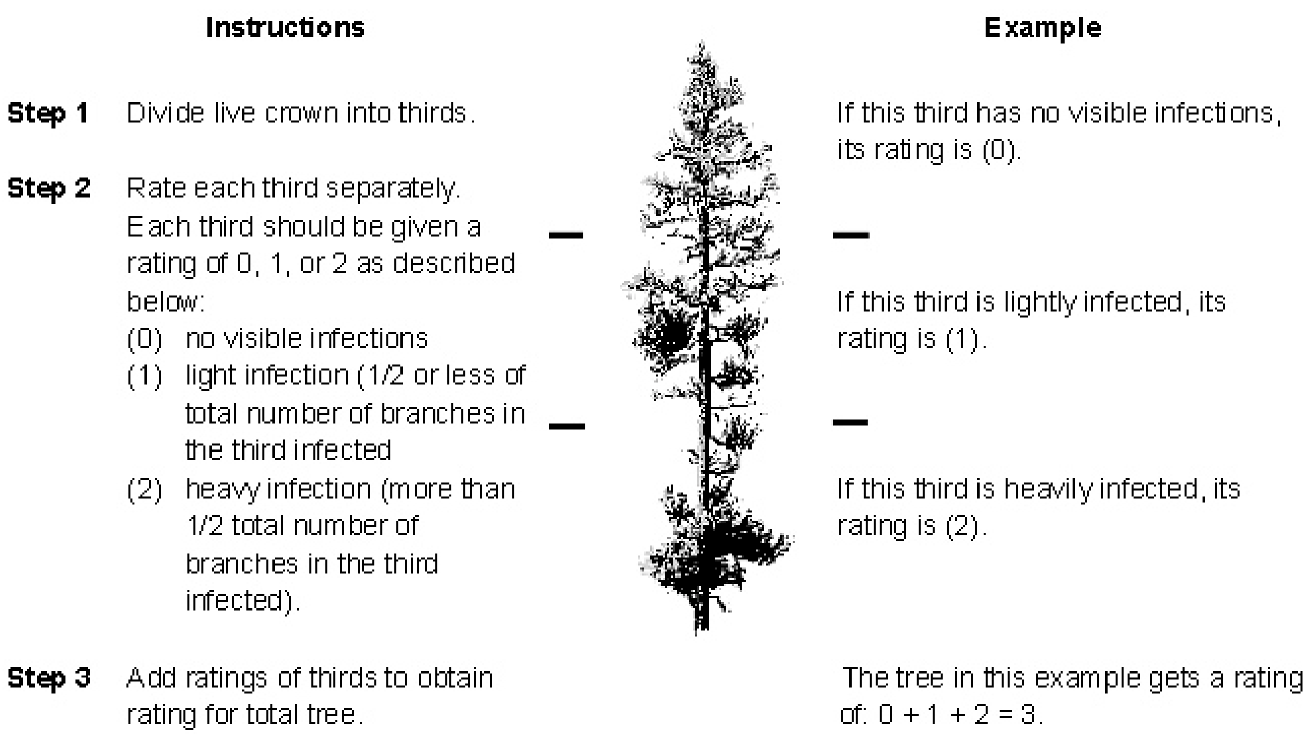


Figure 6-1—Dwarf mistletoe rating system (DMR).

Aerial Surveys

A major technique or approach used for extensive examinations is aerial survey. This technique is described for dwarf mistletoe (*A. americanum*) on jack pine (Robins 1972) and lodgepole pine (Brandt and others 1998), and Eastern spruce dwarf mistletoe (*A. pusillum*) on black spruce (Baker and others 1992). Aerial survey observers can best detect severe infestations by the distinct infection centers associated with heavy mortality and brooming. Total extent and incidence are under estimated. Aerial survey is most practical over low-relief terrain, but rotary-wing aircraft have been used successfully over mountainous areas (Brandt and others 1998, Schwandt and Page 1978). Flight lines are run parallel at intervals of 5 to 10 km (or wider) through areas of susceptible forest types. Fixed, overhead-wing aircraft can be used on clear, bright days at ground speeds of 150 km per hour. One observer alone or one observer on each side of the aircraft draws or sketches the extent of each mistletoe-infested area on an appropriate map (which may be a topographic, forest type, or inventory base map). In some surveys, a lap-top computer with a digital map display of topographic and forest-type features is used with a global positioning system (GPS) to sketch-map directly on the computer screen; this method is in development (L. Rankin, 1999 personal communication). Geographic positions of infested stands can also be located with a GPS-receiver (Brandt and others 1998, Zavala and Zavala 1993). Information is eventually incorporated into a GIS-database. Brandt and others (1998) demonstrate the capability of this technique for mapping the severe damage caused by dwarf mistletoe to jack pine and lodgepole pine for an area of over 28 million ha in Central Canada (Alberta, Saskatchewan, Manitoba).

Aerial Photography

Aerial photography is routinely used for vegetation and forest inventory typing, classification, and sampling. Aerial photography is feasible, however, for landscape dwarf mistletoe surveys only where there are highly distinctive features such as mortality or infection centers. These occur in Central to Eastern, North American forests of black spruce (Baker and French 1991) and jack pine (Muir and Robins 1973). Especially in young infestations, mistletoe infections are often most common in the lower crown and obscure to aerial view. Large-scale aerial photography can be used for individual stands to detect infected trees with large witches' brooms or to identify susceptible tree species and suspect individuals based on various crown attributes.

Forest Inventory Plots

Vegetation or forest inventory sampling is the commonly accepted means of describing and quantifying the forest resource, and it is often the only acceptable data source for projecting dwarf mistletoe impacts on forest growth. Established inventory plots ensure an acceptable sampling scheme and avoid the expense of recollecting associated tree data. Dwarf mistletoe data from routine inventories, however, may have low or uncertain reliability because inventory crews may lack the experience to recognize mistletoe presence and damage (Drummond 1978, Marsden and others 1990). Where inventory plots are reexamined to obtain mistletoe specific data, trained personnel and check cruises are appropriate (Hildebrand and others 1997). Forest inventory plots are often situated by a stratification scheme that if not properly accounted may lead to biased estimates. Nonetheless, this is described and used by several authors including Caballero (1970), Filip and others (1993), DeMars (1980), Gregg and Michaels Goheen (1997), Hildebrand and others (1997).

Surveys for dwarf mistletoes using an existing inventory plot system can be relatively simple and easy to conduct. Each sample tree on the inventory plot is examined and a rating (such as DMR) is recorded. Wide-field, high-quality binoculars (for example, 8x40) are useful; yellow-tinted eyeglasses are not used because they obscure dwarf mistletoe shoots (B. Geils 1999, personal communication). Training and quality checks are appropriate to maintain quality and consistency (Shaw and others 2000).

Growth impacts are calculated from tree data and information for mistletoe severity using the sample design of the inventory (Marsden and others 1990). In many situations, covariate factors are useful. For example, Thomson and others (1997) point out that for lodgepole pine, stand density (number of stems per hectare) has a major effect on tree volume and should be used to adjust estimates. Supplemental data can determine the correlations between radial growth, DMR, tree age, and stand density.

Road and Plot Surveys

Roadside surveys for dwarf mistletoes are popular and suitable for many forests in Western North America with reasonably extensive road access (Andrews and Daniels 1960, Johnson and others 1981, Maffei and Beatty 1988, Merrill and others 1985, Mathiasen and others 1996b, Thomson and others 1997). Good results are obtained in forests of almost pure, even-aged stands of trees at least 20 years old. A vehicle driver and an observer traverse roads through susceptible forest stands at a low speed (say, 30 to 40 km per hour) and rate levels of infestation in segments or fixed intervals (such as 100 to 200 m) along the roads. Data are recorded on inventory maps with cover type information.

Tree infection along roads is usually rated using percentage incidence categories: nil or 0, no infection visible; low, 1 to 33 percent of trees infected; medium, 34 to 66 percent infected; and severe, 67 to 100 percent infected. These data are converted to DMR by correlating roadside incidence ratings with plot DMR. A more direct and probably more efficient method is to directly estimate average DMR along roadsides rather than estimating percentage incidence.

To obtain inventory tree data, fixed-radius or prism plots are established at intervals of 5 to 10 km along roads at a distance 50 m back from the road. On each plot the usual inventory tree measurements are taken for each tree, including DMR (fig. 6-1). Although it is suspected that road development or some forest practices might have increased incidence of dwarf mistletoe at roadside units, Merrill and others (1985) found that incidence at roadsides was similar to that in the adjacent stand (also see Maffei and Beatty 1988).

Although a roadside survey is relatively easy to conduct and produces estimates of growth impacts, it is often difficult to reconcile these results with forest inventory data. Locating plots along roads introduces a sampling bias that may result in substantial discrepancies of tree species volumes and growth estimates between roadside plots and standard inventory plots. Data from a roadside survey as area infested or percent of trees infected cannot be readily incorporated into forest inventory record systems. A potentially more accurate and cost-effective alternative is to move directly to resampling already established forest inventory plots that also have a history of tree growth and mortality.

Transects and Grids

Sample plots systematically distributed as either strip transects or on a gird are another approach for surveying dwarf mistletoe. Transects and grid sampling have been used for landscape-scale surveys (Hawksworth and Lusher 1956, Maffei and Arena 1993), but they are more frequently applied to individual stands. Their use has been largely superseded by vegetation or inventory plots (for example, Current Vegetation Survey 2002).

Permanent Plots

Another type of dwarf mistletoe survey technique is the permanent sample plot system. Hawksworth and Marsden (1990) catalogue a number of these installations. Permanent sample plots are also established to monitor efficacy of management projects (Lightle and Hawksworth 1973). These plots typically are much larger than routine forest inventory plots, have fixed boundaries, and include a map of the position of all plot trees. Given the relatively high costs of establishment and remeasurements, relatively few permanent sample plots have been established recently or are currently being maintained. They are, however, extremely valuable for measuring spatial aspects of dwarf mistletoe spread and intensification and as benchmark stands used to validate simulation models (Taylor and Marsden 1997).

Project Area Assessments

Several methods or techniques for dwarf mistletoe surveys are used primarily to assess stands or sites for a variety of objectives including developing management prescriptions and management of recreation areas and wildlife habitat.

Developing Management Prescriptions—Detailed surveys of stands are used to develop management prescriptions (Tkacz 1989) and for general stand examinations (Mathiasen 1984, Vázquez 1994a).

For dwarf mistletoe infested sites, distribution and severity data are used to assess management options (Hawksworth 1978a, Parmeter 1978, van der Kamp and Hawksworth 1985). The expected effects of a treatment, for example, such as leaving dwarf mistletoe-infected trees on partially or selectively cutover areas, can be evaluated in the specific context in which it is to be applied. These effects can be projected with data representing the actual stand of interest and using the agency-supported growth model or simulation program (for example, PrognosisBC or Forest Vegetation Simulator). The data required from the survey are determined by the requirements of the selected model. Generally these include tree data, DMR (see fig. 6-1), and some ecological classification describing site productivity. Data are usually collected using a grid or series of prism plots or fixed-radius plots according to prescribe methods of the agency (DeMars 1980). Baker and Durham (1997) describe a transect survey for mistletoe in young jack pine and a model to simulate expansion of infection or mortality centers. Marsden and others (1993) evaluate management options for Southwestern ponderosa pine stands with Armillaria root disease and dwarf mistletoe with data from a systematic grid of inventory plots and the Forest Vegetation Simulator. Chapter 8 provides further information on use of models to evaluate silvicultural treatments.

When dwarf mistletoe sanitation practices are planned or have been undertaken, an important consideration is to determine both the potential and realized benefits. In many regions of Western North America, sanitation treatments after harvesting have been a common practice for several years or even decades. Postcontrol or postsuppression surveys and evaluations have been undertaken in several regions (Hawksworth and Johnson 1989b, Knutson and Tinnin 1986, Van Sickle and Wegwitz 1978).

The spatial pattern of infected trees and spatial autocorrelation of mistletoe are important in some situations (Robinson and others 2002). Infected young trees may be clustered around residual infected trees left as blocks, strips, or groups trees. Patterns that deviate greatly from random or uniform toward clusters have significant consequences for sampling design and model projections. The spatial pattern of infected trees and the spatial autocorrelation of mistletoe can be computed from a stem map of the stand of interest or selected from another stand with a similar appearance.

Assessing complex stands—that is, those consisting of two or more tree species, age classes, and height classes — often involves making a compromise between number of locations visited and the detail recorded at each location. Because the dynamics and effects of dwarf mistletoes vary by tree size, it is important that surveys provide data on incidence and severity by tree size class. This can be accomplished by recording DMR and either tree diameter or height for each sample tree and later computing class averages. Alternatively, trees can be grouped into classes and assigned average incidence and severity ratings while the observer is at the plot. With training and experience, observers are able to retain data quality and increase productivity. Vegetation structural stages such as described in table 6-2 or other classification schemes can be used to group trees into size classes. The criteria for determining classes vary by situation but represent canopy structure classes meaningful to the manager. Where there are several mistletoe species with different host tree species, mistletoe incidence and severity should be estimated by structure class for each susceptible tree species.

Assessments of Recreation Areas and Wildlife Habitat—Dwarf mistletoe effects on trees (chapter 5)—including suppression of tree growth, formation of large witches' brooms, and increased mortality—can be important considerations for management of recreation sites and for wildlife habitat. Occasionally, dwarf mistletoe surveys are required for evaluating the need for, or efficacy of, silvicultural treatments (see chapter 8) for these types of management.

Trees in recreation sites are regularly inspected for defects and evaluated for potential hazard to users and facilities (Hadfield 1999, Lightle and Hawksworth 1973, Scharpf and others 1988). Dwarf mistletoe infection is usually included in the inspections. In some areas, as described in chapter 8, infected trees are replaced with other less susceptible tree species. Severely infected trees are pruned to maintain tree vigor. Tree data generally recorded are DMR and an estimate of broom size if these are to be pruned. Infected trees are usually inspected annually or more frequently.

Surveys for dwarf mistletoe in conjunction with wildlife habitat are used for management (Marshall and others 2000) and research (Bennetts and others 1996, Parker 2001, Parks and others 1999a, Reich and others 2000). Information collected about mistletoe includes DMR and usually additional information on broom type, size, and location (Garnett 2002, Hedwall 2000, Tinnin 1998, Tinnin and Knutson 1985).

Table 6-2—Vegetation Structural Stages (VSS), an example of a classification system for describing dwarf mistletoe incidence and severity. (Table excludes VSS class 1, nonforested.)

VSS class	Size class (cm of d.b.h.)	Description
2	2–12.5	Seedlings/saplings
3	12.5–30	Young trees
4	30–45	Mid-age trees
5	45–60	Mature trees
6	60+	Old trees

Evaluations Using Dwarf Mistletoe Survey Data

After a survey is conducted to determine forest-level damage caused by dwarf mistletoe, one or more of several methods are used to project forest growth under different management regimes and evaluate impacts and potential benefits of management programs for dwarf mistletoes (see Power and D'Eon 1991).

One example of this type of evaluation is use of a whole-forest model such as FORPLAN or MUSYC. These models predict timber supplies and possibly other outputs such as wildlife habitat in infested stands under various management regimes. They determine potential returns and benefits of dwarf mistletoe control programs. Landscape or forest-level yield models require both extensive data on dwarf mistletoe occurrence and severity, and response curves based on individual land units or stands, similar to those proposed by Stage and others (1986) for root diseases.

To our knowledge, forest-level evaluations of dwarf mistletoe effects have not yet been reported but they should, however, be relatively simple to develop. Average curves can be developed for average stand conditions, using stand-level models with dwarf mistletoe effects. Growth curves for lodgepole pine infected by dwarf mistletoe are reported by Hawksworth and

Johnson (1989a) and van der Kamp and Hawksworth (1985) and are included in a review of forest growth models by Eav and Marsden (1988).

In evaluating effects of dwarf mistletoe, data used to construct the baseline or "healthy" stand growth curves should be examined. If temporary plot data were used, and plots were located without bias, then empirical growth curves may already include mistletoe effects. Stands that have been treated for dwarf mistletoe, therefore, should grow more than the baseline stands. Growth and yield data for landscape-level analyses, however, are often derived from remeasured plots selected to avoid dwarf mistletoe and other disturbances. If growth curves from these stands were used to represent operational conditions, they represent the growth of "healthy" stands or what is expected when dwarf mistletoe infestations are suppressed. In most analyses, these types of growth curves are usually reduced using one or more "operational adjustment factors" to account for unstocked or unproductive areas (such as swamps or rocky knolls). Tree volumes are also reduced using factors for waste and breakage during harvesting and internal wood decay in live trees. All of these factors and assumptions should be checked and verified as to the manner by which mistletoe effects were incorporated.

Another potentially important use of dwarf mistletoe survey data is to evaluate potential benefits of controlling or preventing effects of dwarf mistletoe on site productivity. Site productivity is one of the major factors affecting sustainability of the forest resource. For an example with lodgepole pine, mistletoe infection at moderate to severe intensities generally reduces growth to such an extent that a forest inventory based on mature trees would underestimate the site index or productivity. Foresters might not be particularly interested in dwarf mistletoe as such. If it were shown, however, that the productivity of the forest land base were substantially underestimated and underutilized and that it could be increased with sanitation, interest may rise.

Further Needs for Surveys and Evaluations

Large-scale, forest-growth projection methods need to be used and modified to accommodate analyses of the actual or potential benefits of dwarf mistletoe control programs. In many regions, more or supplementary data will have to be collected by well-trained personnel in conjunction with forest inventory sampling to provide a more credible basis for determining dwarf mistletoe effects and defining treatment opportunities.

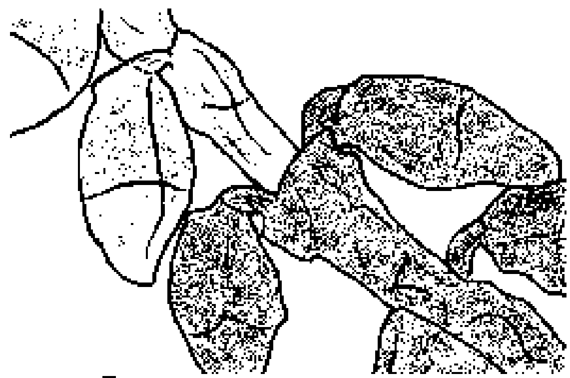
On an individual stand basis, information on spatial patterns of trees and autocorrelation of mistletoe need to be employed in more assessments (Robinson and others 2002). For many stands with complex structures and heterogeneity (see Reich and others 2000), an average DMR does not properly represent conditions where wildfire, windthrow, bark beetles, and mistletoe infestation have created a mosaic of canopy and gaps. Infected trees often occur in or at the edges of residual stands, strips, or patches, or as scattered individual trees; and spread of dwarf mistletoe from these sources is unlike that across a uniform stand (Muir 2002, Edwards 2002).

Detailed dwarf mistletoe surveys of land units are essential for determining effects on forest ecology, stand structure, and productivity or analyzing effectiveness and benefits of silvicultural treatment. These surveys and evaluations, however, are feasible only if foresters or specialists have access to methods or models endorsed by their agencies. Given the increasing complexity of forest management issues, comprehensive and detailed stand-level models are now essential to develop detailed prescriptions for harvesting and silvicultural treatments. These models are needed to ensure that forest ecosystems are managed sustainably and that these treatments do not detrimentally affect other management objectives such as visual quality, wildlife habitat, and recreation management. Although there have been considerable improvements in models in recent years, there is a continuing need for model development for new management scenarios. Access to several models is available from the British Columbia Ministry of Forests (2000) and Forest Health Technology Enterprise Team (2002); other vegetation management tools are at Forest Service (2002). Access to and support for various models are still needed for field foresters to conduct surveys and analyze potential benefits of treatment programs. This is particularly urgent with the increasing need to consider a wide array of effects and objectives such as wildlife and fuel reduction.

Finally, the increasing imperative to manage uneven-aged forest stands infested by dwarf mistletoe necessitates development of indices or measures of tree-to-tree variation of incidence and infection severity of dwarf mistletoe. New or drastically improved models are required to analyze the effects of dwarf mistletoes on trees and the efficacy of silvicultural treatments (including deployment of biological control agents) in these complex situations. Measurements of dwarf mistletoe occurrences and quantitative projections of effects of various forest and stand-level management regimes are essential to guide and help resolve the various, often-conflicting views of desirable forest-resource management strategies.

S. F. Shamoun
L .E. DeWald

Chapter 7



Management Strategies for Dwarf Mistletoes: Biological, Chemical, and Genetic Approaches

The opportunity and need for management of mistletoe populations with biological, chemical, and genetic approaches are greatest for application to the dwarf mistletoes. Although much information is available on these management strategies (see reviews by Hawksworth 1972, Knutson 1978), significant research and development are still required for these to become operational tools. In this chapter, we describe the potential for these tools and status of their research and development. Resource managers and practitioners interested in using these approaches can consult with forest pathologists and geneticists for specific applications.

Biological Control

Many fungi and insects are pathogens or herbivores, respectively, of dwarf mistletoes (Hawksworth and Geils 1996, Hawksworth and others 1977b, Kuijt 1963, Stevens and Hawksworth 1970, 1984). None, however, are sufficiently studied and developed for operational use as biological control agents (Anonymous 1982, Hawksworth 1972). Some fungal pathogens and insect herbivores (particularly lepidopteran larvae) are highly destructive to dwarf mistletoes in some areas and years. The factors that induce or regulate these outbreaks result from complex and often indirect interactions of weather and a multitrophic community of organisms. Dwarf mistletoe pathogens and herbivores are indigenous organisms that have coevolved with their hosts into relationships that are not readily amenable to human control. Nonetheless, given the potential number of agents and the advantages of the approach, development of biological control as a management option appears promising for the near future (Hawksworth 1972, Shamoun 1998).

Integrating Biological Control with Silviculture

Development of an effective biocontrol program requires technologies for mass production of the agent, an efficient delivery system, and a deployment strategy. The biocontrol agent does not have to eradicate all the dwarf mistletoe from the entire stand. A satisfactory strategy is to reduce mistletoe spread from residual trees in a regeneration area by timely introduction of biocontrol agents that kill or deflower the parasite. The selection of a treatment area and schedule is a silvicultural decision based an understanding of the epidemiology of the agent, the population dynamics of the mistletoe, and silvics of the host. The spatial-statistical model described by Robinson and others (2002) simulates mistletoe life cycles under various treatments and schedules and aids the selection of a preferred strategy. The objective is to protect new plantations from early mistletoe infestation where a significant number of infected residual trees are to be retained for various legacy values.

Insects

Initial research identifies several destructive insect predators that are apparently endemic to Pakistan (Baloch and Ghani 1980, Mushtaque and Baloch 1979), but no steps have been taken to test their applicability for introduction into North America. Other Asian dwarf mistletoes also harbor candidates for biological control of New World dwarf mistletoes (Tong and Ren 1980).

Fungi

The extensive literature on biological control of unwanted higher plants (weeds) is reviewed by DeBach (1964), TeBeest and Templeton (1985), Shamoun (2000), Wall and others (1992), and Wilson (1969). Mycoherbicides are developed practical tools in agriculture. Example mycoherbicides include: *Phytophthora palmivora* (DeVine,) for control of strangler vine in citrus (Ridings 1986), *Colletotrichum gloeosporioides* f. sp. *aeschynomene* (Collego,) for control of northern jointvetch in rice and soybean (Daniel and others 1973), and *Colletotrichum gloeosporioides* f. sp. *malvae* (BioMal, and Mallet WP™) for round-leaved mallow in field crops (Jensen 2000, Makowski and Mortensen 1992). *Chondrostereum purpureum*, a well-known primary wood invader, is being developed for biological control of woody vegetation in forests and rights-of-way (de Jong and others 1990, Shamoun and others 1996, Wall 1994). *Chondrostereum purpureum* (Chontrol™) may become the first biological control agent in North America used for integrated forest vegetation management (Shamoun and Hintz 1998). In South Africa, *Cylindrobasidium laeve* (Stumpout,) is used to clear Australian wattle tree (Morris and others 1998). Mortensen (1998) reviews a number of other products in development.

A particular challenge for application of mycoherbicides in controlling mistletoes is that death of the plant is not assured by destruction of the aerial shoots. The endophytic system of mistletoes within the host survives even when the shoots are killed back repeatedly; the endophytic system may persist for a century (Gill and Hawksworth 1961).

For a fungal parasite to be an effective biological control agent, it must possess a number of attributes (Mark and others 1976, Wicker and Shaw 1968):

1. It parasitizes only the target mistletoe, not the host or other vegetation.
2. Its activity seriously interferes with the life cycle of the mistletoe.
3. It produces abundant inoculum and significant infestations on the target mistletoe.
4. It has sufficient ecological amplitude to persistence throughout the range of the target mistletoe.
5. Its distribution coincides with that of the target mistletoe.
6. It exhibits high infectivity.
7. It shows high virulence.
8. It has an efficient mode of action for curtailing development of the target mistletoe.

Fungal parasites of dwarf mistletoe are of two general groups—those that attack aerial shoots and those that attack the endophytic system (canker fungi).

Although a large number of fungal parasites are associated with dwarf mistletoes (see Hawksworth and Geils 1996), there are no complete and comprehensive evaluations for most of these fungi, their hosts, and their interactions (Hawksworth and others 1977b).

Aerial Shoot Fungi—These fungi usually parasitize pistillate flowers, shoots, and fruits of certain spring-flowering species of mistletoe. Three of these fungi—*Colletotrichum gloeosporioides*, *Cylindrocarpon* (*Septogloeum*) *gillii*, and *Caliciopsis* (*Wallrothiella*) *arceuthobii*—are common and widespread in Western North America (Hawksworth and Geils 1996).

Colletotrichum gloeosporioides is commonly isolated from dwarf mistletoes in the United States and the Western Provinces of Canada (Kope and others 1997, Muir 1967, Wicker and Shaw 1968). Although different isolates of the fungus are distinct in mycelial growth, colony color, and sporulation, cross-inoculation experiments demonstrate that isolates are not host-specific (Scharpf 1964). *C. gloeosporioides* infections first appear as small, brown to black, necrotic lesions on the nodes of fruits and shoots (fig. 7-1 and 7-2). Lesions enlarge, coalesce, and cause dieback of the shoots (Parmeter and others 1959, Wicker and Shaw 1968). Parmeter and others (1959) observe that the fungus invades the endophytic system of *Arceuthobium abietinum*. Ramsfield (2002) did not detect the presence of the fungus in the endophytic system of *A. americanum*. Wicker (1967b) states that both sexes of *A. campylopodum* are attacked, and that from 35 to 67 percent of the plants or 24 percent of the shoots may be destroyed. Although the fungus may persist for years (Wicker and Shaw 1968), its occurrence is generally sporadic (Hawksworth and others 1977b). It can be destructive to *A. americanum* and *A. tsugense* subsp. *tsugense* in Western Canada (Muir 1967, 1977, Ramsfield 2002, Kope and others 1997). Muir (1977) concludes that it can exert significant natural control of *A. americanum*.

Figure 7-1—*Colletotrichum gloeosporioides* infecting shoots and fruits of *Arceuthobium tsugense*.

Figure 7-2—*Colletotrichum gloeosporioides* infecting shoots of *Arceuthobium americanum*.

Colletotrichum gloeosporioides is being developed as biocontrol agent of *Arceuthobium tsugense* and *A. americanum*. Successful projects to date include an *in vitro* bioassay system (Deeks and others 2001, 2002) and several laboratory and greenhouse experiments and field trials (Ramsfield 2002). The fungus is easily, inexpensively cultured and germinates over a wide temperature range (Parmeter and others 1959, Shamoun 1998). Its mode of action disrupts development of mistletoe shoots, thereby preventing reproduction. Because it attacks anytime after shoot emergence (Parmeter and others 1959), there is a broad window when the agent can be applied.

Cylindrocarpon gillii (formerly *Septogloeum gillii*) is a fungal parasite that causes anthracnose to staminate and pistillate shoots of dwarf mistletoes (Ellis 1946, Gill 1935, Muir 1973). The fungus and disease is recognized (fig. 7-3) by white eruptions at shoot nodes and conspicuous masses of hyaline, cylindrical to fusiform spores. The fungus parasitizes most dwarf mistletoes of Western North America (Hawksworth and others 1977b), including *A. americanum*, *A. douglasii*, and *A. tsugense* subsp. *tsugense* in Western Canada (Kope and Shamoun 2000, Shamoun 1998, Wood 1986). Mielke's (1959) inconclusive results from inoculating an isolate of a warm, dry climate to a cool, moist one suggest the need for proper climate matching when evaluating or using this fungus (Hawksworth and others 1977b).

Caliciopsis arceuthobii (formerly *Wallrothiella arceuthobii*) is the oldest known, fungal parasite of dwarf mistletoes. It attacks the spring-flowering mistletoes *Arceuthobium pusillum*, *A. americanum*,

Figure 7-3—*Cylindrocarpon gillii* infecting shoots and fruits of *Arceuthobium tsugense*.

A. douglasii, and *A. vaginatum* (Dowding 1931, Kuijt 1969b, Knutson and Hutchins 1979). Infection occurs at anthesis; stigmas are inoculated with ascospores carried by insects, wind, or rain. Within 2 months, hyphae penetrate the fruits to the ovary wall. Host cells deteriorate and are replaced by a black stromatic mass of hyphae (fig. 7-4). Normal fruit development and seed production are destroyed (Wicker and Shaw 1968). The fungus is widely distributed from Western Canada, United States, and Mexico (Hawksworth and others 1977b, Kuijt 1963). Parker (1970) demonstrates the fungus germinates and grows on artificial media. Its potential as a biocontrol agent, however, is limited by large, annual variations of infection. In a given location, natural infection will be high one year (80 percent of flowers infected) and fail (almost no infection) the next (Dowding 1931, Hawksworth and others 1977b, Weir 1915, Wicker and Shaw 1968).

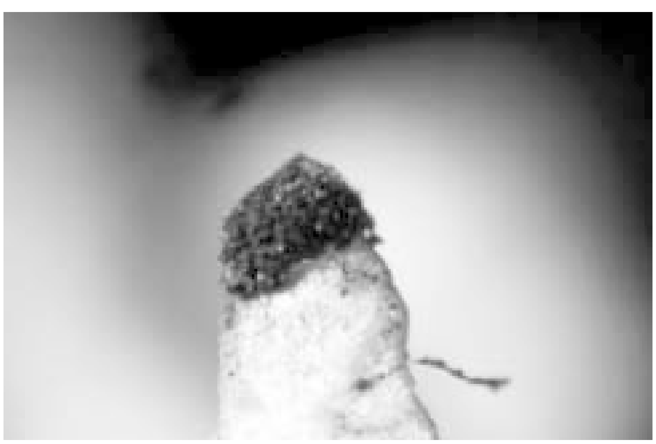


Figure 7-4—*Caliciopsis arceuthobii* infecting the pistillate flowers of *Arceuthobium americanum*.

Other fungal parasites associated with aerial shoots of dwarf mistletoes are: *Alternaria alternata*, *Aureobasidium pullulans*, *Coniothyrium* sp., *Metasphaeria wheeleri*, *Pestalotia maculiformans*, *Pestalotia heteroercornis,* and *Phoma* sp. (Gilbert 1984, Hawksworth and others 1977b, Hawksworth and Wiens 1996, Kope and Shamoun 2000, Shamoun 1998). The potential use of these species as biocontrol agents requires additional evaluation.

Canker Fungi Associated with Endophytic System—The canker fungi of dwarf mistletoe attack both the cortex and endophytic system (Hawksworth and Geils 1996). More than 20 species of canker fungi are identified for *Arceuthobium tsugense* in British Columbia (Baranyay 1966, Funk and Baranyay 1973, Funk and others 1973, Funk and Smith 1981, Kope and Shamoun 2000, Shamoun 1998). Their potential as biological control agents includes both advantages and disadvantages. Because they attack the endophytic system, effects are immediate, pronounced, and likely to kill the mistletoe. Because the host tree may be damaged as well, additional laboratory study is required before field inoculations are attempted. Three canker fungi are good candidates for biological control.

Neonectria neomacrospora (formerly *Nectria macrospora*, *Nectria neomacrospora*) is characterized by a stroma with dark red perithecia containing eight-spored asci (Booth and Samuels 1981, Mantiri and others 2001). The conidial sporodochia (*Cylindrocarpon*) appear white and are found most commonly on freshly cankered swellings (fig. 7-5 and 7-6) caused by *Arceuthobium tsugense* (Funk and others 1973, Kope and Shamoun 2000, Shamoun 1998). Byler and Cobb (1972) report *N. neomacrospora* (as *N. fuckeliana*) is a virulent pathogen of *A. occidentalis* on *Pinus muricata*. The fungus is only weakly parasitic on pine and is secondarily parasitic on western gall rust cankers caused by *Peridermium harknessii*. *Cylindrocarpon cylindroides* is more virulent than *Colletotrichum gloeosporioides* on germinating seeds and callus of *Arceuthobium tsugense* (Deeks and others 2002).

The characteristics that recommend *Neonectria neomacrospora* as a biocontrol agent are its selectivity for dwarf mistletoe-infected host tissue, pathogenicity, ability to invade, rapid canker production, abundant spore production, reduction of shoot growth, girdling, and branch mortality. Further development involves improvements of formulation and delivery technologies (Funk and others 1973, Shamoun 1998, Smith and Funk 1980).

Cytospora abietis is the best known fungus associated with dwarf mistletoe cankers and is common (20 percent) on *Abies magnifica* and *A. concolor* parasit-

Figure 7-5—*Neonectria* canker of *Arceuthobium tsugense*. Note: symptoms of the disease are resinosis and necrosis of mistletoe shoots.

ized by *Arceuthobium abietinum* (Scharpf 1969a, Scharpf and Bynum 1975, Wright 1942). The fungus occasionally parasitizes nonmistletoe-infected branches. The overall interactions of the fungus, the mistletoe, and the host tree need to be evaluated. Although the fungus kills mistletoe-infected branches, it is not known how much the mistletoe population is reduced (Hawksworth 1972).

Resin Disease Syndrome—Resin disease syndrome is common on *Arceuthobium americanum* infecting *Pinus contorta* in the Rocky Mountains (Mark and others 1976). The symptoms include excessive resinosis of the mistletoe canker, necrotic lesions and discoloration of the host bark, and retention of dead needles, necrophylactic periderms, and dead mistletoe shoots. Numerous fungi are isolated from resin disease cankers. *Alternaria alternata* is the most consistent (recovered from 89 percent of cankers), but the syndrome appears to be a disease complex caused by *Alternaria alternata*, *Aureobasidium pullulans*, and *Epicoccum nigrum* (Mark and others 1976). However, Gilbert (1984) isolated these fungi from nonsymptomic mistletoe cankers and host wood; these fungi alone may not be the sole cause of the syndrome. Additional studies needed include: effects on reproductive potential of the mistletoe, comparisons for systematic and nonsytematic mistletoe infections, and assessments of environmental factors and each fungal component in disease development (Mark and others 1976).

Figure 7-6—*Neonectria neomacrospora* (anamorph: *Cylindrocarpon cylindroides*) infecting the basal cup and the swelling (endophytic system) of *Arceuthobium tsugense*.

Summary—Numerous studies of the mycobiotic associates of dwarf mistletoes are complete. The fungal parasites *Colletotrichum gloeosporioides*, *Cylindrocarpon gillii*, *Caliciopsis arceuthobii*, and *Neonectria neomacrospora* are effective in destroying aerial shoots or the endophytic system. They can disrupt the mistletoe life cycle and reduce dwarf mistletoe spread, intensification, and damage. Canker fungi are attractive biological control agents because they attack the mistletoe over a long period and infect the endophytic system. These canker fungi have the potential of killing the mistletoe in addition to reducing reproduction. The most promising biocontrol agents are *Colletotrichum gloeosporioides* and *Neonectria neomacrospora*.

Chemical Control

The development of a selective herbicide to control dwarf mistletoes has been a primary but elusive goal for decades. The fundamental challenge is to find a chemical that is easy to apply and kills the mistletoe without toxic effects to the host or other nontarget species. If the mistletoe cannot be killed, a second strategy is to cause abscission of shoots, thereby reducing and delaying spread and intensification.

Numerous lethal herbicides have been tested for control of dwarf mistletoes (Gill 1956, Quick 1963, 1964, Scharpf 1972). The most common chemicals investigated in early studies are various formulations of 2,4-D and 2,4,5-T. Typically, these chemicals are not effective at killing the mistletoe without also injuring the host. At low rates that do not damage the host, the endophytic system is not killed, and resprouting occurs. The most promising herbicide from a large study by Quick (1964) is an isooctyl ester of 2,4,5-T; but it is now banned for concerns over adverse, nontarget effects.

Hawksworth and Wiens (1996) review a series of tests from 1970 to the early 1990s with a number of herbicides and growth regulators including Dacamine, MCPA, Butyrac, Goal, Thistrol, D-40, Weedone, Emulsamine, DPX, Prime, and Florel. Although these chemicals cause high shoot mortality with minimal host injury, they also do not kill the endophytic system. Experiments to date with systemic chemical are inconclusive.

The most promising chemical for inducing shoot abscission is ethephon (Florel, active ingredient 2-chloroethyl phosphoric acid). The mode of action of ethephon releases ethylene, a natural growth-regulating chemical that causes early abscission of flowers, fruits, and shoots (Hawksworth and Johnson 1989b). Ethylene is a natural substance that dissipates quickly and shows few nontarget effects. It has been evaluated for numerous mistletoe–host combinations (Frankel and Adams 1989, Hawksworth and Johnson 1989b, Livingston and Brenner 1983, Livingston and others 1985):

- *Arceuthobium americanum* on *Pinus banksiana* in Manitoba
- *Arceuthobium americanum* on *Pinus contorta* in Colorado and California
- *Arceuthobium campylopodum* on *Pinus ponderosa* in California and Idaho
- *Arceuthobium campylopodum on Pinus jeffreyi* in California
- *Arceuthobium divaricatum* on *Pinus edulis* in New Mexico
- *Arceuthobium douglasii* on *Pseudotsuga menziesii* in Oregon
- *Arceuthobium laricis* on *Larix occidentalis* in Oregon
- *Arceuthobium pusillum* on *Picea mariana* in Minnesota
- *Arceuthobium vaginatum* on *Pinus ponderosa* in Colorado and New Mexico

An important consideration is achieving adequate coverage. Ground application can be effective (Johnson 1992, Johnson and others 1989, Nicholls and others 1987a, 1987b). Robbins and others (1989) and Baker and others (1989), however, report aerial applications by helicopter are not effective due to poor penetration. Most mistletoe infections are in the lower crown and protected from the spray by overhead host foliage.

With good coverage, shoot abscission rates of 90 to 100 percent are achieved (Johnson 1992). Limited, premature browning of older host needles may occur, but serious side effects on the nontarget host are few (Nicholls and others 1987a). Resprouting from the endophytic system, however, limits effectiveness (Parks and Hoffman 1991). When resprouting is rapid and extensive, long-term protection from mistletoe spread and intensification is not provided. With good control, mistletoe seed production is delayed 2 to 4 years; but it is not a permanent cure. Ethephon may be used to protect understory trees beneath an infested overstory in high-value areas (Adams and others 1993).

Summary

Investigations for chemical control of dwarf mistletoes have considered numerous herbicides intended to selectively kill the parasite or cause shoot abscission. No material tested warrants widespread application. Although the growth-regulating chemical ethephon is approved by the U.S. Environmental Protection Agency for control of dwarf mistletoes, it has limited use. Because the chemical does not affect the endophytic system, new shoots and fruits develop 3 to 5 years after application (or sooner). This chemical is most useful for high value trees at homes, offices, and parks, where frequent applications are possible, but pruning is not acceptable. A chemical treatment regime can be supplemented with various other cultural techniques such as underplanting immune species.

Management Through Selection for Genetic Resistance

Hanover (1966) describes the need for identification of heritable resistance and development of a controlled breeding program for genetic resistance to mistletoes. In the past, the relative low cost and ease with which mistletoes were controlled silviculturally delayed the development of these programs (Hawksworth and Wiens 1996). In general, trees suspected to be resistant to mistletoe are identified in the process of other management activities rather than through a deliberate search (Roth 1974a). A few scientists such as Frank G. Hawksworth, Lewis F. Roth, and Robert F. Scharpf have made consistent efforts to identify genetically resistance trees.

Native mistletoes can be relatively destructive in natural forests, and because tree species have been coevolving with mistletoes for 25 million years (Hawksworth 1978a), we can expect trees to have developed genetic resistance (Roth 1978). The existence of host-specific mistletoes and variation in host preference suggests a genetic basis of resistance, at least at the species level. *Arceuthobium douglasii* does not infect *Pinus ponderosa* (Hawksworth and Wiens 1996). Scharpf (1984) notes that two-thirds of dwarf mistletoes parasitize hosts in addition to a principal species; the levels of infection in these hosts are highly variable from secondary to rare for factors other than escape. *Arceuthobium pusillum* exhibits variation in ability to infect *Larix laricina*, *Picea glauca*, *Picea rubens*, *Pinus resinosa*, and *Pinus strobus* — all species naturally exposed to the mistletoe (Tainter and French 1971).

In contrast to our knowledge of species-specific susceptibility, within-species susceptibility to mistletoe has been less rigorously examined. Field observations of mistletoe-free trees in areas with high levels of mistletoe infection are reported for several host–mistletoe combinations. In Western North America, these reports include healthy *P. ponderosa* in areas heavily infected with *A. vaginatum* subsp. *cryptopodum* (Arizona and New Mexico, Hawksworth 1961); *P. ponderosa* and *P. jeffreyi* free of *A. campylopodum* (Oregon, Roth 1953; California, Scharpf 1984, 1987, Scharpf and Parameter 1967, Wagener 1965); *Pseudotsuga menziesii* var. *glauca* free of *A. douglasii* (Arizona, Nowicki and others, unpublished research); *A. americanum*-free *P. contorta* (Colorado, Hawksworth and Wiens 1996); healthy *Tsuga heterophylla* in areas heavily infected with *A. tsugense* (Vancouver Island, Smith and others 1993); and *Pinus hartwegii* free of mistletoe in heavily infected areas of Mexico (De la Puente 1966). Although the progeny of these "resistant" trees have not generally been tested for resistance, these field observations suggest variation of genetic resistance within host populations exists.

When trees suspected to be resistant to mistletoe are identified in the field, they may be tested by artificially inoculating grafts and out-planting grafted scions in a mistletoe-infested area. Scharpf and Roth (1992) report high correlation between resistant *Pinus ponderosa* parents and their scions grafted and out-planted in areas with heavy mistletoe infection. Artificially inoculated grafted *Tsuga heterophylla* trees from resistant and susceptible parents also show resistance correlations (Smith and others 1993). Although results of these studies using grafted material do not prove heritable resistance, they do verify resistance is being controlled genetically rather than environmentally. These sources represent good candidate trees for progeny tests of heritable resistance.

Progeny tests for inherited genetic resistance to mistletoes show mixed results. Some cases of field resistance represent escapes or other nonheritable mechanisms of resistance. The work of Roeser (1926) and Bates (1927) represents one of the first attempts to breed forest trees for disease resistance in the United States. Regrettably, there are no differences after 50 years in the incidence of infection between slow-growing, susceptible and fast-growing, resistant selections (Hawksworth and Edminster 1981). These results suggest that growth rate is not a reliable indicator of mistletoe resistance. Hawksworth and Wiens (1996) discuss the early results of an unpublished study by G. Fechner examining putative resistance of selected *P. contorta* seedlings. The infection rates 10 years after inoculation for putatively resistant families and susceptible families are similar (Geils, personal communication). Other progeny tests for mistletoe resistance show more positive results. Roth (1971, 1974a, 1974b) demonstrates that *Pinus ponderosa* seedlings from resistant parents have fewer infections and faster growth rates than those from more susceptible parents. Examination of these progeny tests 20 years later shows the same result (Scharpf and Roth 1992). Scharpf (1987) identifies *P. jeffreyi* trees with variation in field resistance; artificial inoculations on 7-year-old progeny from these parents indicate the resistance is heritable (Scharpf and others 1992). Finally, *Pseudotsuga menziesii* var. *glauca* progeny from healthy parents in heavily infested areas had fewer infections than progeny from infected parents. Subsequent genetic laboratory analysis using allozymes support a heritable basis for this apparent resistance (Nowicki and others, unpublished research).

Attempts to identify inherited mechanisms controlling resistance to mistletoe are few. Genetic resistance to pathogens and insects in general is classified as "vertical," where specific resistant genes have developed, or as "horizontal," where aggregate combinations of genes have developed to create a phenotypic response. Roth (1974a and 1974b) suggests that horizontal resistance is more likely controlling resistance to mistletoe in Western conifers. Age-related changes may confer some resistance to mistletoe in pines (Roth 1974b, Scharpf and Roth 1992), but younger true fir trees appear to be more resistant to mistletoe than older individuals (Scharpf 1984). Anatomical changes associated with age are under a high degree of genetic control and may serve as a clue for locating genetically controlled resistance mechanisms. In *Larix laricina*, the formation of a wound periderm that restricts endophytic growth of *Arceuthobium pusillum* is identified as a resistance mechanism (Tainter and French 1971); however, inheritance of the wound periderm response has not been demonstrated. Atsatt (1983a) suggests resistant hosts may produce chemicals that inhibit mistletoe or lack chemicals needed by the mistletoe to initiate and/or develop haustoria formation. In general, production of secondary chemicals is a common, genetically controlled, defense strategy used by plants; secondary chemicals may play a role in genetic resistance to mistletoe.

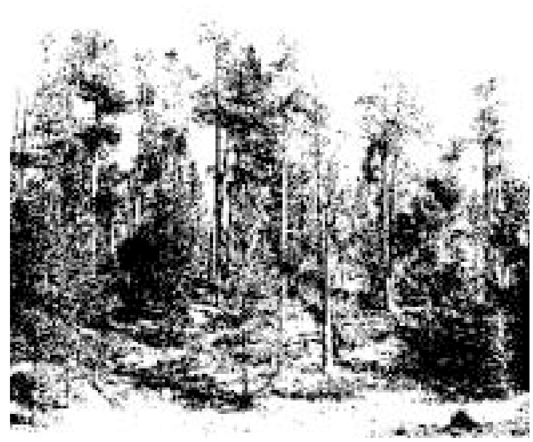
Summary

Despite the relatively limited investigation, there are field observations, progeny tests, and graft studies that all point to the presence of some degree of resistance to mistletoe in North American conifers. The recent need to develop options to traditional, even-aged silvicultural treatments has led to the renewed interest in developing genetic and breeding programs for resistance to dwarf mistletoe. Field identification of resistant sources, progeny testing to confirm heritably, plus screening and breeding programs such as exists for blister rust (*Cronartium ribicola*) are critically needed for a genetic strategy to become a viable. A screening program is being developed by Ringnes and others (1996). The objectives of this program are to identify trees exhibiting resistance to dwarf mistletoe, to evaluate testing methods for screening candidates, to identify resistance levels of candidates and their progeny, and to determine the mode and strength of inheritance for resistance mechanisms. Additional mistletoe resistance screening programs for *Pseudotsuga menziesii* var. *glauca* (DeWald and Nowicki Northern Arizona University, Flagstaff, AZ), and *Tsuga heterophylla* (Shamoun, Canadian Forest Service, Pacific Forestry Centre, Victoria BC, Canada) have been initiated. Finally, biotechnology approaches (including tissue culture, see Deeks and others 2001, Marler and others 1999) can be used to supplement traditional resistance screening and breeding programs. Trees whose resistance to mistletoe has been confirmed can be searched for molecular DNA markers. These markers can then be used in marker-aided selection for mistletoe resistance to eliminate the long generation times currently needed to confirm genetic resistance.

J. A. Muir
B. W. Geils

Chapter 8

Management Strategies for Dwarf Mistletoe: Silviculture



Although there are numerous sources for information on the practice of silviculture (Forest Service 2002), special considerations are required for control of dwarf mistletoe (Scharpf and Parmeter 1978). Mistletoe-infested forests, stands, and trees develop and respond to treatment differently than their uninfested counterparts (chapter 5). The spread, intensification, damage, and impacts of dwarf mistletoe can be reduced, maintained, or enhanced by silvicultural treatments alone or in combination with other control techniques (chapter 7). Silvicultural treatments discussed here include:

- Harvest, retention, and regeneration by clear-felling (even-aged silviculture), or selection harvesting to establish and maintain uneven or all-aged stand structures.

- Design and layout of harvest and treatment blocks.
- Site preparation and vegetation management by brushing, prescribed burning, and other methods.
- Planting or retaining residual and advanced regeneration.
- Thinning and sanitation.
- Pruning brooms and infected branches.

General guidelines for silvicultural treatment that integrate dwarf mistletoe information are presented in symposium proceedings (Scharpf and Parmeter 1978), regional directives (British Columbia Ministry of Forests 1995), and compendia (Alexander 1986). New strategies may be suggested and examined with simulation models (Robinson and others 2002), then tested and evaluated in practice at demonstration forests (Besse and others 2001, Edwards 2002, Nevill and Wood 1995).

The choice to initiate a silvicultural action, and the subsequent selection of techniques, timing, and location, are dictated by considerations in three major areas. First, each dwarf mistletoe species, forest type, and region present different situations. Some mistletoes have a wide distribution and cause serious damage; others are rare curiosities, spread slowly, cause little damage, or even enhance some aspect of the environment (chapter 5). Second, management objectives and constraints for individual stands (or sites), compartments (planning units), and whole forests determine the intended purpose of the treatment. Different objectives require different approaches. Objectives may be to produce timber and fiber (British Columbia Ministry of Forests 1995), enhance wildlife habitat (Reynolds and others 1992), or even promote wild mushroom production (Amaranthus and others 1998). Finally, any action must be consistent with an overall plan of forest regulation and a silvicultural system for regeneration. With even-aged silviculture, clear-felling, shelterwood, and seed tree harvests, planting, sanitation, and intermediate thinning all provide opportunities to direct stand and mistletoe development. With uneven-aged silviculture, tree and group selection determine forest character. Fuel management and prescribed burning may be used in both systems. Aesthetic values and economics may allow special cultural practices such as pruning to be used on high value trees such as found in recreation areas.

In this chapter, we describe silvicultural treatments that have been recommended or are used to prevent, mitigate, or encourage dwarf mistletoe development and effects. We provide examples of frequently encountered management situations. The discussion is organized into six topics. In *Designing Silvicultural Treatments*, we describe biological and ecological factors that apply to silvicultural decisions, especially the features that make mistletoes amenable to treatment. We also identify sources for species-specific guidelines. For *Management of Even-aged Stands*, we describe the strategies used primarily to prevent or reduce detrimental effects of dwarf mistletoes on timber and fiber production. The first and best opportunity is to prevent mistletoe spread into a clean, regenerated stand. Established stands with mistletoe present can still be treated with sanitation, thinning, harvesting, or be reestablished. In the discussion of *Uneven-aged Silviculture and Selection Cutting*, we recognize a shift in forestry to management for ecosystem structure and functions, retention of old-growth forest character, wildlife habitat, recreation, and other amenity values. Although we have less research and management experience for this kind of management, mistletoe can play a large role in determining whether those objectives are met. Techniques and tools are available for influencing the patterns and rates of mistletoe spread and intensification. *Prescribed Burning* is an especially useful tool for either even-aged or uneven-aged silvicultural systems. Regardless of the treatment considered, a manager needs to be aware of the likely responses to a proposed action. Because mistletoes add complexity and because the consequences of specific decisions may not be apparent for decades, managers can use *Models to Assess Treatment Opportunities*. Finally, in *Management for Recreation, Wildlife, and Ecosystem Values*, we describe some of the special requirements and techniques applicable to infested stands and trees managed with these objectives.

Designing Silvicultural Treatments

Dwarf mistletoes markedly affect the growth, form, and survival of infected trees and therefore how these trees and their stands develop and respond to silvicultural treatment (chapter 5). Effects to trees include: distorted growth from branch and stem infections, changes in wood quality, reduced overall tree growth, increased susceptibility to attack by secondary insects and fungi, and increased mortality. These damages aggregate over time, affecting forest health, sustainability, and productivity (DeNitto 2002, Hawksworth and Shaw 1984, Monning and Byler 1992). Consequently, mistletoes affect the basic ecological processes of primary productivity, biomass allocation, mortality, mineral recycling, and succession (Kipfmueller and Baker 1998, Mathiasen 1996, Tinnin and others 1982, Wanner and Tinnin 1989, Zimmermann and Laven 1984). Because significant infestations of dwarf mistletoe have profound, fundamental, and particular effects on stands, mistletoes need to be specifically considered in designing silvicultural treatments on infested sites (fig. 8-1).

Figure 8-1—A portion of lodgepole pine stand in the Bighorn Mountains, Wyoming. As evidenced by the numerous, large witches' brooms, most trees are severely infected with *Arceuthobium americanum.* If the management objective were timber-oriented, this stand is a good candidate for regeneration and a poor candidate for commercial thinning. Fuel distribution and canopy structure depart greatly from what would be expected in an uninfested stand with significant consequences to fire and wildlife objectives.

Dwarf mistletoes and the forest stands at risk of infestation develop at a pace that appears slow from a human perspective but not from that of the host trees. For example, a rule of thumb for spread of a mistletoe infestation is 10 m per decade (Dixon and Hawksworth 1979); intensification in trees is one DMR class per decade (Geils and Mathiasen 1990); half-life of DMR class-6 trees is one decade (Hawksworth and Geils 1990). [Note: many factors influence rates of spread, intensification, and mortality. These rules of thumb are meant only to suggest the magnitude of the rate of change and are not intended as specific management guidelines.] With stand replacement times of one to two centuries, mistletoes are able to produce tens of generations and increase unchecked at a low exponential rate. Noticeable effects are delayed until infection reaches a moderate level, but damage accumulates at an increasing rate after that point (Hawksworth 1961, Tinnin and others 1999).

The potential impacts of dwarf mistletoe infestation and their dynamics have several implications for designing silviculture treatments. First, over time a treated stand that remains infested will develop differently than an uninfested stand. Second, early and frequent interventions provide greater opportunities to affect stand and infestation dynamics and impacts than later or infrequent entries. The timing and number of entries are, of course, determined by other factors as well. Therefore, an early treatment assessment (such as immediately after completion) may not provide a satisfactory indication of its long-term consequences without an adequate model.

Several biological and ecological features make dwarf mistletoes especially amenable to silvicultural treatment (Hawksworth 1978a, Parmeter 1978). The epidemiological bases of these features are discussed in chapters 4 and 5; here we suggest their silvicultural implications:

- *Obligate parasitism*. Dwarf mistletoes require a living host to survive and reproduce. When an infested tree or branch dies (or is cut), the attached mistletoe plants die as well. There is no need to burn or destroy slash or pruned branches to kill and sterilize the pathogen.
- *Host specificity*. Dwarf mistletoes generally infect only a single, susceptible host species or group of related species. Retained immune and less susceptible hosts reduce spread and severity of damage.
- *Extended life cycles*. Life cycles of dwarf mistletoes are relatively long compared to other tree disease agents; a generation ranges from 2 to 10 or more years. Dwarf mistletoe spread from tree to tree, and increase within tree crowns is relatively slow. Because numerous infections are required to cause serious damage, the effects accumulate slowly. Time is available to plan and implement a treatment regime.
- *Limited seed dispersal*. Dwarf mistletoe seeds are dispersed a maximum horizontal distance of only 10 to 15 m; gravity and foliage limit effective spread in the vertical and horizontal planes; animal vectoring of dwarf mistletoe (with one or two exceptions) is rare enough to be ignored other than from ecological and evolutionary perspectives. Consequently, mistletoe tends to occur as pockets of infestation. Spatial variation in mistletoe abundance provides numerous patches in which different, appropriate treatments can be applied. Even with severe infestations, the amount of mistletoe seed produced is limited; small, young understory trees present a minimum target. There is an opportunity to regenerate a stand under an infected overstory before the young trees are infected.
- *Slow intensification within tree crowns*. Dwarf mistletoe infection typically begins in the lower tree crown, and vertical spread is slow enough that trees with rapid height growth can outgrow or at least keep pace with mistletoe intensifica-

tion (Hawksworth and Geils 1985, Roth 1971). Good sites for tree growth allow rapid height growth at higher stand densities, which has several effects on mistletoe. Greater crown closure reduces light within the canopy, reducing mistletoe reproduction and increasing the rate of crown lift; the distance of seed dispersal in a dense stand is also reduced (Shaw and Weiss 2000). At some point, however, for each stand, competitive effects impact tree growth, and eventually trees reach their height limit. Density management and pathological rotation allow silviculturalists to influence the balance between growth of the host and the pathogen (Alexander 1986, Barrett and Roth 1985, Muir 1970, Safranyik and others 1998).

The silvicultural guidelines and treatments we discuss here can only be of a general nature. The literature on damage and control is already summarized by Hawksworth and Scharpf (1978) and suggests that different mistletoes in different regions require different approaches. Recent silvicultural guides with recommendations for mistletoe-infected trees and infested stands are available for some of the principal conifers of North America (table 8-1). There are also regional guides: British Columbia Ministry of Forests (1995), Conklin (2000), Hadfield and Russell (1978), Knutson and Tinnin (1980), and Wicker and Hawksworth (1988). Numerous older publications emphasize methods for reducing dwarf mistletoe populations and damage including: Buckland and Marples (1953), French and others (1968), Gill and Hawksworth (1954), Hawksworth and Lusher (1956), Kimmey and Mielke (1959), Korstian and Long (1922), Wagener (1965), and Weir (1916b). Although dwarf mistletoes cause significant growth losses and mortality in Mexico, we know of only a few publications that discuss silvicultural treatment of Mexican conifers in general terms (Hernandez and others 1992, Reid and others 1987).

Where silviculture dwarf mistletoe management is conducted, treatments to mitigate mistletoe impacts can be integrated with other activities to reduce susceptibility to forest insects, other diseases, and fire. The complex interactions between mistletoes and bark beetles are reviewed by Stevens and Hawksworth (1970, 1984) and include situations where reduction of mistletoe also results in reduction of hazard to bark beetles. Thinning stands to reduce bark beetle hazard presents an opportunity for mistletoe sanitation. Although the effect on the mistletoe infestation was minimal, Vandygriff and others (2000) describe an attempt to relocate bark beetle attacks with aggregant baits to mistletoe-infected trees. Marsden and others (1993) explore the options for management in a stand infested with both root disease and mistletoe. This is

Table 8-1—Silviculture guides for management of North American conifers with dwarf mistletoe.

Forest type	Host species	*Arceuthobium* sp.	References
Black spruce	*Picea mariana*	*A. pusillum*	Johnson (1977) Ostry and Nicholls (1979)
California true fir	*Abies concolor* *Abies magnifica*	*A. abietinum*	Filip and others (2000) Scharpf (1969b)
Douglas-fir	*Pseudotsuga menziesii*	*A. douglasii*	Hadfield and others (2000) Schmitt (1997)
Lodgepole pine	*Pinus contorta* var. *latifolia*	*A. americanum*	Hawksworth and Johnson (1989a) van der Kamp and Hawksworth (1985)
Pinyon pine	*Pinus edulis* *P. monophylla*	*A. divaricatum*	Mathiasen and others (2002a)
Sugar pine	*Pinus lambertiana*	*A. californicum*	Scharpf and Hawksworth (1968)
Western hemlock	*Tsuga heterophylla*	*A. tsugense*	Hennon and others (2001) Muir (1993)
Western larch	*Larix occidentalis*	*A. laricis*	Beatty and others (1997) Taylor (1995)
Western pines	*Pinus jeffreyi* *Pinus ponderosa*	*A. campylopodum*	Schmitt (1996) Smith (1983)
Rocky Mountain ponderosa pine	*Pinus ponderosa* var. *scopulorum*	*A. vaginatum* subsp. *cryptopodum*	Conklin (2000) Lightle and Weiss (1974)

an especially complex situation because trees killed by mistletoe or cut for mistletoe reduction provide stumps, which are the food base for root disease; simulation models are especially useful in such cases. We later discuss prescribed burning as a tool for mistletoe management, but it can be noted here that fuel reduction by cutting or burning can also reduce mistletoe. Applications of direct mistletoe control by chemical and biological means and genetic selection (see chapter 7) can be considered an adjunct to traditional silviculture treatments with the chain saw, planting bar, and drip torch.

An important consideration in the design of a silvicultural entry is whether dwarf mistletoe treatment is necessary. In many cases the presence of dwarf mistletoe poses no threat to stand objectives. The mistletoe may be infrequent and have a low potential for increase and damage. Mistletoes may not be a concern at their altitudinal or geographic range limits (Trummer and others 1998) or where conditions permit rapid tree growth (such as with ponderosa pine in southern Colorado). Where wildlife objectives take precedence, retention of some dwarf mistletoe may even be desired to generate snags (Bennetts and others 1996) or mistletoe brooms (Parks and others 1999a).

Management of Even-Aged Stands

Even-aged, single-storied stands composed of one or two tree species are the simplest to treat for mistletoe. Prevention of dwarf mistletoe infestation in a regenerated stand is essentially guaranteed where all susceptible host trees are harvested or killed soon after harvest.

Most early guidelines assume the objective of management is timber production, and the purpose of treatment is the timely and economical eradication of dwarf mistletoe (Korstian and Long 1922, Weir 1916a). The traditional recommendation for dwarf mistletoe has been clear-cut harvesting with relatively large blocks, followed, if necessary, by intermediate thinning and sanitation to create even-aged stands free of mistletoe (Wicker and Hawksworth 1988). This method has been used extensively and successfully for many Western and Northern species (but see Johnson 1994, Stewart 1978). Treatment before or after harvest removes or kills infected and suspect trees to prevent the young stand becoming infested.

Prevention of Spread Into Cut Blocks

One of the primary issues of dwarf mistletoe treatment in even-aged silviculture is the design and layout of cut blocks (treatment units) to prevent or reduce invasion of dwarf mistletoe from adjacent infested areas. Preventative measures recommended by previous authors and some agencies include:

- Wherever possible, locate cutting boundaries in noninfested stands, nonsusceptible timber types, and natural or created openings, and take advantage of natural or constructed barriers such as roads, streams, openings, or meadows.
- Design cut blocks within infested stands to create large ratios of area to perimeter and minimize the length of infested border; avoid long, narrow blocks and units of less than 8 ha, but compromise where required for natural regeneration of heavy-seeded trees (Alexander 1986).
- Unless local, long-term, successful plantings have been demonstrated, do not plant barriers of nonsusceptible tree species around the cut block perimeter. In the majority of cases, this strategy fails because of rapid natural regeneration and fast growth of the susceptible tree species; however, in a few exceptions, a mixture of nonsusceptible tree species has retarded mistletoe spread.
- If infected trees are to be left on the boundary, avoid leaving fringes or narrow strips but rather maintain dense blocks of trees and leave a relatively uniform, abrupt (nonfeathered) margin. In British Columbia and Alberta, mistletoe spread into an adjacent young stand appears retarded from dense stands with abrupt edges (Muir 1970). Where spread and infection of young trees occurs, remove or kill infected trees at the next treatment entry.
- Avoid leaving single trees or small clumps of residual infected trees scattered throughout the harvested area. Scattered overstory trees are a significant inoculum source for young, understory regeneration, because improved light or growing conditions favor production and dispersal of dwarf mistletoe seeds (Muir 1970, 2002). Remove or destroy these trees.
- When regenerating stands with seed tree or shelterwood systems, select residual trees that are mistletoe-free or only lightly infected (DMR 2 or less). If infected trees are left, remove them before regeneration reaches 1 m in height or about 10 years of age, or prune residual seed trees to remove infected branches. Because of its deciduous habit and ability to produce epicormic, adventitious branches, larch can be severely pruned.

Silvicultural Treatments of Young Stands

When an even-aged, immature stand is already infested by dwarf mistletoe, management options are available to reduce mistletoe at one or more stages of early stand development. Factors involved in evaluating the need, kind, and timing of treatment include stocking level, growth rate, and disease level. Although mistletoe may kill some small trees in young stands, infections are usually too recent and too light to cause much growth loss; damage is a poor management indicator. More important is the potential for future, unavoidable damage as indicated by the areal extent of the infestation, the percent of trees infected, and the rate of spread. In general, treatment options for mistletoe control are to remove infected overstories, favor nonsusceptible tree species, sanitation, and thinning.

Recently Harvested and Regenerated Stands—The best opportunity for preventing reinfestation of an area by dwarf mistletoe is through complete harvest, removal, or killing of infected trees of the previous stand. This opportunity may be exercised during or soon after the harvest and regeneration period. Although the length of time and size of seedlings before which they are at serious risk of infection vary by species and site, few are infected before they are 5 to 15 years old or about 1 m tall (Wicker 1967a). The decisions to be made on the basis of management objectives and specific situation are the number of infected residual trees to be retained and the length of time they remain.

The most important means by which a regenerated stand becomes infested is through infected residual trees left on site. In decreasing order of importance, infected advanced regeneration, spread from adjacent stands (see above), and long-distance animal vectoring play lesser roles. Trees are intentionally retained for a number of reasons, even though some of these trees may happen to be infected. For example, visual quality, screening, and wildlife objectives may call for the retention of "legacy" trees. The potential for these trees to survive and fill their role must be weighted against their possible contribution to the infestation of the new stand. Total eradication of mistletoe-infected trees is neither realistic nor necessary; a sufficient goal of sanitation can be to allow for effective mistletoe management. A new stand with some infested legacy trees can still be treated with periodic sanitation thinning (see below) to selectively remove more severely infected trees and by pruning infected branches.

Some residual trees are left not for legacy objectives but because they have no merchantable value. Many timber contracts and silviculture prescriptions stipulate the felling of diseased, nonmerchantable trees for safety and forest health reasons. If undesired residual trees remain after harvest, remedial work may be appropriate. For mistletoe control purposes alone, only residuals over 3 m in height with branch infections need to be felled; shorter trees and those with only bole infections have limited potential for spreading the pathogen (Mark and Hawksworth 1974).

Another option for controlling mistletoe infestation in a new stand is to regenerate with a mixture of species including trees less susceptible to mistletoe. Robinson and others (2002) report on simulations of stands infested by *Arceuthobium tsugense* and regenerated under three different scenarios including a 20 percent mixture of an immune species (cedar). Their simulations suggest that over time, mistletoe incidence (percent infected) and severity (DMR) are less for the 20 percent mixture compared to the other scenarios. Different mixtures may be better in other situations.

Sanitation Thinning—The purpose of sanitation thinning is to reduce mistletoe incidence. As trees increase in size, stands can benefit from silvicultural thinning to select crop trees and distribute growth to those individuals. Sanitation is conducted in young stands; silviculture thinning with sanitation is practiced in precommercial and commercial stands. Sanitation is most practical in young stands after initial infection appears but before subsequent spread occurs. A postregeneration survey is useful to determine stocking and the distribution and incidence of infection (see chapter 6). A decision is required as to whether there is sufficient stocking of noninfected, potential crop trees. The options are for sanitation or for destruction and reestablishment of the stand. A third option is, of course, to redefine management objectives that reset the decision criteria for selecting a treatment. Each situation requires appropriate assessment because of the ecological and economic constraints of different management objectives, different hosts, and mistletoes with different potentials for growth and damage. Numerous sanitation and thinning studies and computer simulations suggest a few general guidelines where the manager wishes to minimize mistletoe damage and maximize tree growth.

Sanitation is most effective in lightly infested stands younger than 15 to 30 years old. At early ages, infection percentages are less; at later ages potential crop trees can be selected. In the past, most timber stands less than 30 years old were sufficiently stocked (over 1,200 stems per ha) and infested at a low enough percentage (10 to 20 percent) that sanitation was feasible. A sanitation treatment that removes all visibly infected trees can significantly reduce an infestation (Hawksworth and Graham 1963b); but due to latent infections, missed trees, and spacing requirements, complete elimination of mistletoe is unlikely (Conklin 2002). A sanitation treatment usually retains the best, apparently mistletoe-free trees and whatever additional lightly infected trees are required to meet stocking and spacing standards. Mistletoe is sometimes found as a light or moderate infection (DMR 2 or 3) in the larger of the young trees. Given the potential for future spread and growth loss, these initially larger trees may not be as desirable for retention as smaller healthy trees. For stands about 40 years old and with few patches of infected trees, approximately 1,200 healthy stems per hectare on good sites are sufficient to retard mistletoe spread.

The effectiveness of sanitation is doubtful in heavily infested young stands. Although stands about 20 years old with half or more of the stems infected may sometimes be encountered, they are poor candidates for sanitation (Scharpf and Vogler 1986). These stands generally do not have a sufficient number of healthy trees to stock the site. Severely infected trees (DMR 3 to 6) do not sufficiently respond to spacing, and reducing stand density may increase mistletoe spread and intensification. Generally, the degree of infestation in the stand, not strictly stand age, is the best criterion to decide whether sanitation is practical. For example, a general rule for lodgepole pine is that stands with more than 40 percent of the trees infected (average stand rating greater than DMR 0.5) are too heavily infested for sanitation. In these stands, removing all infected trees reduces stocking below minimal standards and depresses yields (Hawksworth 1978b). An alternative is stand replacement by clear-cutting, roller chopping, or prescribed burning.

Thinning Precommercial Stands—Whether or not an early sanitation treatment was conducted, the standard practice of precommercial thinning conducted in some forests—even for healthy stands—provides an opportunity to promote tree growth and reduce mistletoe spread and intensification. For infested stands, the usual criteria for scheduling and marking thinning treatments are supplemented with several mistletoe-related considerations. The silvicultural evaluation that precedes the drafting of a prescription can include an assessment of the size and location of patches of infected trees within a stand, approximate number and location of infected residual trees, and number of potential crop trees. An intensive, systematic survey can provide these data (see chapter 6).

Silviculturalists need to balance two results of thinning that work in opposition to one another. First, spacing reduces tree-to-tree competition and over a density range stimulates height growth and crown lift. Second, opening a canopy also stimulates mistletoe shoot growth, seed production, spread, and intensification (Hodge and others 1994). In practice, thinning is most likely to favor the host where trees are no more than moderately infected (less than DMR 3) and growing in height faster than the vertical spread of the mistletoes (Barrett and Roth 1985, Parmeter 1978, Roth and Barrett 1985). In a similar finding, Hawksworth (1978b) found that thinning in stands less than moderately infested (40 percent incidence) and on better quality sites can produce satisfactory volumes, but not on more severely infested stands or on poor quality sites. As with sanitation, replacement and acceptance are options for stands that cannot be satisfactorily thinned. The sale of merchantable timber may be available to help offset cleaning and reforestation of immature, severely infested stands. Simulation models are useful for particular situations (Hawksworth 1978b, Strand and Roth 1976) and help managers to better understand the range of outcomes that are likely to follow from specific activities.

Sanitation—removing as many infected trees as practical—is usually an integral part of precommercial thinning. For stands where average tree diameter exceeds 5 cm, the prethinning evaluation can include an assessment of potential crop trees. The priority for crop trees depends on species but is often set as:

1. Noninfected dominant and codominant trees.
2. Dominant and codominant trees with mistletoe confined to branches in the lower one-third of live crown (DMR 2 or less).
3. Dominant and codominant trees with mistletoe confined to less than one-half of the branches in the lower two-thirds of the live crown (DMR 3 or less).
4. Intermediate trees with no visible infection.

In mixed species stands where immune or less-susceptible species are available, their priority for retention can be determined by their intrinsic value plus their disease-mitigation value. If acceptable stocking cannot be obtained, alternative objectives and treatments can be considered. Thinning crews must be able to recognize mistletoe infections if a sanitation objective is to be realized. Economics may permit a single precommercial treatment but are unlikely to support additional entries until there is a commercial opportunity. Although usually considered in the context of uneven-aged management, forest health and fuel reduction treatments may be justified as well in young or old even-aged stands.

Commercial Thinning Treatments

As trees reach commercial size and the stand approaches harvest (rotation) age, a different set of concerns and opportunities are presented to the manager. As before, information on mistletoe distribution is useful, but as the infestation develops, disease level as average DMR becomes more relevant than percent of trees infected. Trees rated with a DMR of 3 or greater exhibit growth loss, greater mortality, reduced reproductive capability, and increased potential for mistletoe spread. Trees may be harvested at intermediate thinnings, shelterwood cuts, or at rotation. Simulation programs that project final, cumulative yields can be used to assess the number, timing, and severity of thinnings, to select the kinds of trees to harvest at various entries, and to set the regeneration schedule. Mistletoe factors can be integrated into these simulations to address specific situations.

Thinning trials and simulations suggest three general guidelines for management at this stage (Filip and others 1989, Hawksworth 1978b, Hawksworth and others 1977a, Knutson and Tinnin 1986, Tinnin and others 1999). Intermediate thinning in stands with an average DMR rating of 3 or greater is not practical. As most trees are infected, stocking requirements cannot be met with healthy trees; many trees are so severely infected that growth responses are poor. These stands can be considered for early harvest and regeneration. Because severely infected trees of DMR 5 or 6 show little growth and have a high risk of mortality, they can be removed at any opportunity. Within 10 to 20 years of harvest, however, other sanitation and thinning treatments may be deferred. An important consideration is the early selection of potential seed trees for regeneration; uninfected host trees and nonsusceptible species are usually preferred.

Uneven-Aged Silviculture and Selection Cutting

Because the spread and intensification of dwarf mistletoe in uneven-aged, multistory strands can be quite rapid, management of these stands is a serious challenge. But they also present opportunities. Dwarf mistletoe spread is greatest when seeds rain down from an infested overstory to a susceptible understory. With greater crown closure and competition, understory trees do not increase rapidly in height and are less likely to outgrow the mistletoe. Managers, however, do have several factors to work with. Uneven-aged, multistory stands are usually a mosaic of different size and density of trees and mistletoes. These patches can be used to isolate pockets of mistletoe. Such stands are also often composed of several tree species with a range of susceptibility to the prevalent mistletoe. Nonhost species provide not only immune stocking but also screening, which reduces mistletoe spread. Selection for greater species diversity has numerous, ecological benefits.

Management in uneven-aged stands consists of frequent entries for harvest or improvement thinning. If these entries are timely and removals sufficient, sanitation can check mistletoe spread, intensification, and damage. Several cautions are warranted, however. Mistletoe spread can be several times faster than managers expect from their experience in even-aged strands. Overtopped or severely infected trees (DMR 3 or greater) grow at reduced rates and do not outgrow mistletoe. Periodic entries at 10- to 20-year intervals with modest sanitation may be adequate to check mistletoe; but in 30 to 40 years without control, it can spread throughout the stand. Writing a prescription and marking trees in these stands requires a high skill level to detect mistletoe, recognize its potential, and select the proper action.

Guidelines for uneven-aged management are available (Mathiasen 1989, Conklin 2000). In principle, many of the suggestions described in previous sections for even-aged stands are applicable here also. The goals are to maintain individual tree ratings at DMR 3 or less and prevent infection in the top of the crown. Diligence and thoroughness can be major obstacles in applying treatments, and monitoring is important (Merrill and others 1998). One of the key considerations in uneven-aged management is whether silvicultural treatment (cutting trees) maintains the height growth of remaining trees at a rate that exceeds mistletoe vertical spread. Where trees outgrow the mistletoe and infections remain in the lower crown, impacts on tree growth are generally insignificant (Hawksworth 1978b, Parmeter 1978). For coastal hemlock, Richardson and van der Kamp (1972) suggest that trees growing 36 cm per year outgrow the mistletoe. Parmeter (1978) suggests a rate of 20 cm per year for lodgepole pine. For ponderosa pine in the Pacific Northwest, Barrett and Roth (1985) and Roth and Barrett (1985) report that infected ponderosa pine saplings outgrew the effects of dwarf mistletoe for 20 years at 25 cm annual height growth. Similarly, Wicker and Hawksworth (1991) state that after thinning, western larch grew 37 cm per year, while the larch dwarf mistletoe spread upward only 9 cm per year. Because mistletoe spread and effects vary with stand density, site quality, and other factors, these are only approximate rates (Bloomberg and Smith 1982).

Management of mistletoe-infested uneven-aged stands is discussed in detail by Mathiasen (1989) and Conklin (2000). At each entry they recommend that: more severely infected trees (DMR 5 and 6) are cut; healthy trees and those with a DMR of 1 and 2 are retained; moderately infected (DMR 3 and 4) trees are retained only where height growth is expected to exceed 30 cm per year or where the next cutting entry is scheduled within 20 years. Pruning infected branches or large witches' brooms from moderately to severely infected trees reduces spread, intensification, and damage. Pruning, however, is expensive (see section on Management for Recreation Values).

The practice in the Southwestern United States for management of pine stands with dwarf mistletoe is to consider uneven-aged management where 25 percent or fewer of the stems are infected. Individual tree selection is used where fewer than 15 percent of stems are infected; and group selection of trees in patches of less than 1 ha where 15 to 25 percent of stems are infected. Where more than 25 percent of trees are infected, even-aged management is used. Because larger trees tolerate more dwarf mistletoe infection without deleterious effects, Conklin (2000) proposes cutting and selection guidelines based on tree size and infection severity (table 8-2).

One of the major challenges for management of infested uneven-aged stands is the dispersal of dwarf mistletoe seed from infected overstory trees to the understory (Mathiasen 1989, Bloomberg and Smith 1982). Although the predominant opinion has been that dwarf mistletoe intensifies rapidly after a partial cutting or disturbance such as windthrow, there are exceptions. Shaw and Hennon (1991) and Trummer and others (1998) describe the relatively slow spread and intensification of hemlock mistletoe in Alaska. Situations such as these are good candidates for uneven-aged management. Geils and Mathiasen (1990) provide equations for the increase in DMR for Douglas-fir in uneven-aged, multistory stands. Maffei and others (1999) describe an exercise to develop similar equations for other species and incorporate the results in the Dwarf Mistletoe Model (Forest Health Technology Enterprise Team 2002). Because spatial relations are paramount in uneven-aged, multistory stands, the spatial-statistical model (Robinson and others 2002) provides another means for determining expected mistletoe spread.

In view of the uncertainties and potential adverse effects from selection and partial cutting in infected stands, use of the appropriate criteria for selecting and retaining trees is especially important. Overcutting reduces growing stock and possibly accelerates spread of dwarf mistletoe; undercutting and leaving more infected trees allows severe damage and unacceptable impacts. Cutting cycles and intensity of cutting can be adjusted to maintain healthy stands. Monitoring stand and infestation characteristics is especially important, as is the employment of well trained and highly skilled individuals who can recognize and evaluate dwarf mistletoe infection and apply complex marking guides. Although it is a challenge, management of infested, uneven-aged stands is possible (Hawksworth 1978a, Roth and Barrett 1985).

Table 8-2—Dwarf mistletoe ratings for leave trees in selection cuttings in Southwestern ponderosa pine.

Tree dbh (cm)	Maximum DMR per tree
<10	0
10-15	1
16-20	2
>21+	3

Based on Conklin (2000), acceptable rating of leave trees assumes a 20-year cutting cycle; a maximum of rating of 3 is allowed for trees that are intended for timber purposes.

Prescribed Burning

Prescribed burning is a potential silvicultural treatment applicable to even-aged and uneven-aged stands or forests. Historically, wildfire is an important ecological factor in many Western forest ecosystems and a strong determinant of mistletoe distribution and abundance (chapter 5 and Zimmerman and Leven 1984). In recent years, burning has been prescribed to maintain or reestablish desired stand conditions. Prescribed burning for treatment in dwarf mistletoe-infested stands can be used for stand replacement or mistletoe reduction.

Muraro (1978) and Zimmermann and others (1990) describe the use of fire as an economical method for replacing lodgepole pine stands that are overstocked and severely infested. Lodgepole pine, however, has a number of unusual silvicultural and fire ecology characteristics that make this species suitable for such treatment but that are not shared by all forest types.

Prescribed burning is usually a silvicultural tool for reduction of fuels where forest type and condition permit. Moderately to severely infected trees may be more vulnerable to fire because of lower crowns, witches' brooms, and accumulation of debris and resin. A goal of prescribed burning can be the differential killing of infected trees with discrimination of more severely infected trees and consequently a reduction in average stand infestation (Conklin and Armstrong 2001). Fire intensity and distribution can be directed at specific trees or groups of trees using techniques such as removing or piling duff and selecting upslope/upwind or down slope/downwind ignition points. In some stands, dwarf mistletoe infestation generates openings or gaps where infected trees survive fire (Wanner and Tinnin 1989). An approach for infected lodgepole pine or Douglas-fir stands is to replace these with more fire-resistant species such as ponderosa pine by a series of light fires over a period of several years. In any case, prescribed burning requires careful design and execution by experts (Muraro 1978). Numerous variables such as fuel loading and condition, stand structure, objectives for burn, weather, and other factors must be considered. Although prescribed fire will remain primarily a treatment for other forest management purposes, additional research and development (for example, on fire behavior, fuel distribution, and brooms) can enhance its potential as a tool in dwarf mistletoe infested stands.

Models to Assess Treatment Opportunities

When considering more complex or controversial silvicultural treatments such as sanitation and selection cuttings in uneven-aged stands or thinning of immature, even-aged stands, it is helpful to undertake a detailed, site-specific analysis of potential impacts and benefits. Such evaluations typically include a summary of current conditions, potential growth of an infested stand, costs and effects of treatments, and projected outcome with treatment. A variety of factors are important to consider, such as tree age, stand structure, stand density, species composition, site index, and years to next treatment. Useful mistletoe data are incidence (percent of stems infected), severity (DMR), area and pattern of infestation, and length of time the stand has been infested. The most feasible approach for summarizing information, making projections, and displaying results is with a forest growth and yield simulation model that includes the dynamics and effects of dwarf mistletoe infestation.

Numerous computer models are available that simulate various aspects of tree or stand development for dwarf mistletoe infected trees or infested stands. Strand and Roth (1976) describe a population model for young pine with *Arceuthobium campylopodum*. Baker and others (1982) predict stand impacts on spruce from *A. pusillum*. For hemlock forests with *A. tsugense,* Bloomberg and Smith (1982) model second-growth stands and Trummer and others (1998) model old-age stands. Myers and others (1971) introduce a growth and yield program of mistletoe-infested pine that, through many iterations and updates, has become the Dwarf Mistletoe [Impact] Model (DMIM) described by Hawksworth and others (1995). The DMIM is an operational tool supported by the U.S. Department of Agriculture, Forest Service and available on the Internet (Forest Health Technology Enterprise Team 2002). The DMIM functions with the Forest Vegetation Simulator (FVS) to model tree and stand dynamics and provide a number of presimulation and postprocessor features for data preparation, simulation control, and display (Forest Management Service Center 2001). Development currently under way for the DMIM includes improvement of overstory to understory spread (Maffei and others 1999). Robinson and others (2002) describe a process-oriented simulation model derived from the same origin as the DMIM but with additional capabilities to represent features of the mistletoe life cycle and crown canopy. This spatial-statistical model has a potential for examining such integrated mistletoe treatments as the silvicultural deployment of biological control agents.

The conversion of mistletoe control from eradication with large clear-cuts for timber production to sustained, uneven-aged management for ecological services has greatly increased the complexity of silvicultural assessments. Dwarf mistletoe simulation models are most useful to silviculturalists for addressing these complex situations, in which numerous factors interact over a long period. In chapter 5, we identify some of these interacting factors and effects; in chapter 6, we describe some procedures for acquiring data; in chapter 7 and earlier in this chapter, we outline treatments available to silviculturalists for managing infested stands. Simulation models permit planners to evaluate a number of treatment alternatives and to compare the long-term results before committing on the ground to a single, “experiment” in the sense of adaptive management (Holling 1978). Elaborate simulation models such as the DMIM–FVS incorporate a huge volume of research and experience. These models simplify an analysis by conducting the tedious bookkeeping and arithmetic required for such processes as computing statistics and applying growth functions. Because these processes are coded in the program, they are documented and can be reexecuted numerous times. The analyst is able to focus on formulating the problem, generating possible solutions, evaluating results, and documenting the overall activity.

Models are a simplification of a reality that is more or less “correct” and hopefully at least insightful. Although models are especially useful for novel situations, confidence in their predictions is supported by comparisons to the actual performance of benchmark stands. A useful set of benchmark stands represents the range of conditions and treatments silviculturalists are likely to consider (Taylor and Marsden 1997). Models are usually evaluated for sensitivity to a number of factors (Chen and others 1993). Knowledge of which factors a system is sensitive or insensitive to is useful to the planner, as these suggest what data are required to achieve high levels of accuracy or precision, and what treatments may be effective. The DMIM has numerous stochastic functions and is apparently sensitive to mistletoe incidence (percent of infected trees) at low levels (Chen and others 1993). This may well reflect real situations where a small infestation of only several trees could either spread throughout the stand or be isolated in one packet and eventually expire. A single simulation represents one likely outcome. Gregg and Hummel (2002) describes a bootstrapping facility for FVS that simplifies execution of multiple simulations to obtain information on the distribution (mean and dispersion) of outcomes. It is not necessary to simulate every infested stand to be managed. Most stands can be clustered into groups with similar conditions and treatment regimes. An analysis of these typical situations provides local guidelines that can be applied to all similar stands. Special analyses are then conducted for unusual cases and may contribute to the portfolio of guidelines.

Although the scope, availability, and applicability of current models for dwarf mistletoes are limited, their chief value is in the ability to determine quantitative effects and impacts of dwarf mistletoes under various stand conditions and treatment regimes. In so doing, models provide forest managers with a rational framework for decisionmaking.

Management for Recreation, Wildlife Habitat, and Other Ecosystem Values

It is becoming increasingly evident that active forest management by silvicultural treatment is necessary to sustain or enhance desirable stand conditions where trees or stands are infested by dwarf mistletoe. The particular conditions desired for different objectives vary: for recreation sites, live trees that are not a hazard; for some wildlife species, dense tree cover for screening; for other wildlife species, large openings with a few big trees and mistletoe brooms for nesting and roosting. Forests are not static, and trees, especially mistletoe-infected trees, have short lives. Forest management, working with the opportunity and capability provided by a site or stand, can influence vegetation development, including mistletoe, to meet a variety of objectives.

Management of dwarf mistletoe in recreation, administration, and home sites has the fundamental objective to maintain a safe and pleasant environment (Scharpf and others 1988). Although in these areas there is a low tolerance for mistletoe damage, trees are sufficiently valuable to justify repeated, individual treatment such as pruning branches. Methods are outlined as *Treatments in Developed Recreation Sites*.

Where wildlife habitat is an important consideration, it may be desirable to maintain or encourage features resulting from mistletoe infections, such as snags and witches' brooms. The same factors that can be manipulated to reduce mistletoe spread, intensification, and effects can also be used to enhance these processes and produce a continuing supply of dead and diseased trees. Examples are outlined in the section *Treatments for Wildlife Habitat and Other Ecosystem Values*.

Treatments in Developed Recreation Sites

In developed, intensively managed sites, treatments of dwarf mistletoe are needed to protect human life and property, and aesthetic and recreational values. Scharpf and others (1988) outline general principles and strategies for managing infested recreation sites and for maintaining individual trees or stands. They emphasize that specific management objectives and constraints for each site should be carefully considered and incorporated in the action plan.

The primary interests in developed, intensively used sites are to reduce the negative effects of dwarf mistletoe on tree vigor, longevity, and hazard, and to prevent mistletoe spread into healthy trees (Wood and others 1979). The first opportunity to do this is at the time of site selection and establishment. Spread from adjacent infested areas is slow and easy to control. Site planning and layout can achieve eradication by sanitation of light or patchy mistletoe infestations; hardy, immune species can be planted. The value of early control is appreciated when long-term costs of treatment and site replacement are recognized. Recreation sites range in size and level of intensity from campgrounds to National Parks (Hansen 1997, Lightle and Hawksworth 1973, Maffei 1984). Various techniques and concepts of even-aged or uneven-aged silviculture can be adapted for special uses. For example, a site may be laid out to remove an infested block of trees; or a portion of the infected trees may be removed on a periodic schedule to encourage establishment of healthy trees (Johnson 1998, Pronos 1995). A common feature of recreation sites is inspection and treatment of potentially hazardous trees on a relatively frequent schedule. Although branch pruning is rarely done in commercial forests to produce clear bole wood, pruning infected branches and brooms in high value sites is a common practice.

Pruning mistletoe-infected and broomed branches is used to maintain and improve tree vigor and to reduce hazard (Hawksworth and Johnson 1993, Maffei 1992). The most suitable candidates for branch pruning are trees having: infections in the lower half of the crown only; a DMR of 3 or less, and if smaller than 13 cm in diameter, with no bole infections or branch infections closer than 10 cm from the bole. Mark and Hawksworth (1974) have concluded that infections on tree boles larger than 13 cm have little effect on growth and produced few seeds, and they are therefore not a management concern. Aerial shoots on a branch but within 10 cm of the bole probably emerge from an endophytic system that has already reached the bole. Because most trees can tolerate removal of up to half the live crown, general practice is to prune all live branches to two whorls above the highest visibly infected branch. Mistletoe infestations in a tree usually include a number of latent (invisible, incubating infections) and other easily overlooked infections. Most of the missed infections appear in 3 to 5 years; reinspection and repeated pruning are appropriate. Such treated trees often show dramatic recovery in crown vigor. Trees with severe infections, however, such as those with infections throughout the lower crown or in the upper crown, are not likely to respond but likely to soon die. The proper consideration for these trees is whether the value of retaining them for a few more years is greater than the risk they pose for infecting other trees.

Broom pruning can also prolong the life and crown vigor of individual pine trees (Lightle and Hawksworth 1973, Scharpf and others 1988). In this method, the emphasis is on removing branches with witches' brooms rather than removing all visibly infected branches. Hadfield (1999) describes the hazard in high traffic areas from breakage of brooms in species with large or brittle witches' brooms. Pruning these may also be justified.

Treatments for Wildlife Habitat and Other Ecosystem Values

From certain perspectives and in some situations, dwarf mistletoe infestations have beneficial impacts for associated species and communities (Mathiasen 1996, Monning and Byler 1992, Tinnin and others 1982). In old-growth forests, dwarf mistletoes may exert a different set of effects on infected trees and display different dynamics (Hawksworth and others 1992a, Trummer and others 1998). Special management strategies and silvicultural treatments for infested stands are required where the objectives are to maintain and enhance wildlife habitat, old-growth character, and other ecosystem values.

As described in chapter 5, dwarf mistletoe infection produces mistletoe shoots, fruits, diseased branches, brooms, distorted crowns and boles, detritus, diseased and insect-infested trees, snags, and eventually logs. Infestations alter succession, disturbance regimes, and vegetation pattern of the landscape. Within limits, these features favor some species (or groups), inhibit other species, and are essentially neutral to most (Watson 2001). By influencing the spread and intensification of mistletoe and the environment around infected trees, managers are able to affect mistletoe infestations and ecological effects. The specific goals of a treatment depend on specific management objectives such as identification of featured species. For example, Reynolds and others (1992) describe guidelines for the northern goshawk that include consideration of mistletoe and other forest disturbance agents (also see Steeger and Hitchcock 1998).

Most of the recent interest in research and development of management recommendations has focused on snags, brooms, birds, and mammals. Bennetts and others (1996) describe a study of passerine bird diversity in a Colorado Front Range ponderosa pine forest. They suggest greater bird diversity is associated with increased mistletoe infestation (24 of 28 species positively associated); the key limiting resource for the birds in this situation may be snags. Parker (2001) reports a similar study in a northern Arizona ponderosa pine forest. He finds, however, a more complex situation with four species positively associated with mistletoe (cavity-nesting birds), five species with a negative association (avoiding infested areas), and seven with no relation (indifferent). Fairweather (1995) and Parks and others (1999b) describe mistletoe control treatments in which infected trees were killed but left standing for woodpeckers and other cavity-nesting animals. Although these snags are used, they remained standing for only a few years. Studies of broom use by wildlife include work by Parks and others (1999a), Hedwall (2000), and Garnett (2002). These studies identify which birds and mammals use witches' brooms, how they use it (for nesting and roosting), and what kinds of brooms are preferred. This information is useful to determine if retaining certain brooms is a potential benefit for a favored species. Information still lacking is knowledge of how the number and distribution of snags and brooms relates to levels of mistletoe infestation and to wildlife populations and the dynamics (rates of generation and loss) of these features.

Marshall (1996) discusses management lessons, implications, and research needs from a project to manage infested stands for northern spotted owl in southwestern Oregon. Maffei (2002) presents results of an analysis for a similar situation also in Oregon, and for maintaining owl habitat. Although owls use mistletoe brooms for nesting, vegetation changes and disturbance stimulated by the mistletoe (such as fire) lead to loss of critical owl habitat. The analyses demonstrate use of an infection index that represents desired condition (relative to owls and mistletoe) and application of the FVS-DMIM in a landscape planning exercise. These projects illustrate how mistletoe information can be integrated with wildlife criteria to design treatment regimes that benefit long-term survival of a featured species. Complex situations involving numerous ecological relationships are not amenable to simple guidelines defining which trees to cut and which to retain; rather, they require an adaptive management process of analysis, simulation, experimenting, monitoring, and revision (Holling 1978).

Appendices

Appendix A: References

Acosta D.H.; Rodriguez, T.D.A. 1989. Infestacion de *Arceuthobium vaginatum* subsp. *vaginatum* (Willd.) sobre *Pinus hartwegii* (Lindl.) en el Cerro San Miguel, Desierto de Los Leones, Mexico, DF. En: V Simposio sobre Parasitologia Forestal; 1989 Octobre 4–6; Cd. Juarez, Chih: Sociedad Mexicana de Entomologia. 44.

Acosta, P.R.; Delgado, M.J.; Cervantes, S.P. 1992. La vegetation del Estado de Tlaxcala, Mexico. Publ. 6. Tizatlan, Tlaxcala: Hardin Botanico Tizatlan. 31 p.

Adams, D.H.; Frankel, S.J.; Lichter, J.M. 1993. Considerations when using ethephon for suppressing dwarf mistletoe and leafy mistletoe infestations in ornamental landscapes. Journal of Arboriculture. 19(6):351–357.

Aho, P.E. 1982. Indicators of cull in western Oregon conifers. Gen. Tech. Rep. PNW-144. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 17 p.

Alexander, M.E.; Hawksworth, F.G. 1975. Wildland fires and dwarf mistletoes: a literature review of ecology and prescribed burning. Gen. Tech. Rep. RM-14. Fort Collins, CO. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 12 p.

Alexander, R.R. 1986. Silvicultural systems and cutting methods for old-growth lodgepole pine forests in the Central Rocky Mountains. Gen. Tech. Rep. RM-127. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 31 p.

Alfaro, R. 1985. Survey and appraisal of dwarf mistletoe in second-growth western hemlock stands. In: Muir, J.A., ed. Proceedings of a workshop on management of hemlock dwarf mistletoe; 1983 August 15–16; Burnaby, BC. Forest Pest Management Rep. 4. Victoria, BC: British Columbia Ministry of Forests, Forest Protection Branch: 10–21.

Allen, T.F.H.; Hoekstra, T.W. 1992. Toward a unified ecology. New York: Columbia University Press. 384 p.

Allred, W.S.; Gaud, W.S. 1994. Characteristics of ponderosa pines and Abert squirrel herbivory. Southwest Naturalist. 39(1):89–100.

Alosi, M.C.; Calvin, C.L. 1985. The ultrastructure of dwarf mistletoe (*Arceuthobium* spp.) sinker cells in the region of the host secondary vasculature. Canadian Journal of Botany. 63:889–898.

Amaranthus, M.P.; Weigand, J.F.; Abbott, R. 1998. Managing high-elevation forests to produce American matsutake (*Ticholoma magnivelare*), high-quality timber, and non-timber forest products. Western Journal of Applied Forestry. 13:120–128.

Anderson, R.L.; Kaufert, F.H. 1959. Brooming response of black spruce to dwarf mistletoe infection. Forest Science. 5:356–364.

Andrade Escobar, V.; Cibrián Tovar, D. 1980. Evaluación de poblaciones de muérdago enano (*Arceuthobium globosum* Hawks y Wiens y *A. vaginatum* Willd) en bosques de *Pinus hartwegii* Lindl en Zoquiapan, Edo. de México. En: Primer simposio nacional sobre parasitologia forestal; 1980 Febrero 18–19. Uruapan, Michoacán: Sociedad Mexicana de Entomologia: 238–253.

Andrews, S.R.; Daniels, J.P. 1960. A survey of dwarf mistletoes in Arizona and New Mexico. Station Pap. 49. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 17 p.

Anonymous. 1982. Dwarf mistletoe biocontrol. The IPM Practitioner. 4(8):5.

Ashworth, V.E.T.M. 2000. Phylogenic relationships in *Phoradendron* (Viscaceae) inferred from three regions of the nuclear ribosomal cistron. II. The North American species of *Phoradendron*. Aliso. 19(1):41–53.

Atsatt, P.R. 1983a. Host-parasite interactions in higher plants. In: Lange, O.L.; Nobel, P.S.; Osmond, C.B.; Ziegler, H., eds. Physiological plant ecology. III. Encyclopedia of plant physiology, Volume 12C. New York: Springer-Verlag: 519–535.

Atsatt, P.R. 1983b. Mistletoe leaf shape: a host morphogen hypothesis. In: Calder, M.; Berhhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 259–275.

Baker, F.A.; Durham, S. 1997. Dwarf mistletoe impact on jack pine infection, volume loss and mortality curves. Unpublished report submitted to: Weyehauser, Canada; 1997 March 11. Logan: Utah State University, Department of Forest Resources. 10 p.

Baker, F.A.; French, D.W. 1991. Radial enlargement of mortality centers caused by *Arceuthobium pusillum* Peck in black spruce stands. Forest Science. 37:364–367.

Baker, F.A.; French, D.W.; Rose, D.W. 1982. DMLOSS: a simulator of losses in dwarf mistletoe infested black spruce stands. Forest Science. 28:590–598.

Baker, F.A.; Knowles, K.; Meyer, T.R.; French, D.W. 1989. Aerial application of ethylene-releasing chemicals fail to promote abscission of dwarf mistletoe aerial shoots on jack pine. Forestry Chronicle. 65:194–195.

Baker, F.A.; Knowles, K.; Slivitzky. 1992. Impact of dwarf mistletoe on jack pine forests in Manitoba. Plant Disease. 76:1256–1259.

Baloch, G.M.; Ghani, M.A. 1980. Parasitic weed plants and their natural enemies with special reference to Pakistan: a review. Pakistan Journal of Forestry. 30:2–13.

Baranyay, J.A. 1966. Fungi from dwarf mistletoe infection in western hemlock. Canadian Journal of Botany. 44:597–604.

Baranyay, J.A. 1970. Lodgepole pine dwarf mistletoe in Alberta. Publ. 1286. Ottawa, ON: Canada Department of Fisheries and Forestry. 22 p.

Baranyay, J.A.; Hawksworth, F.G.; Smith R.B. 1971. Glossary of dwarf mistletoe terms. BC P-2-71. Victoria, BC: Department of the Environment, Canadian Forestry Service, Pacific Forest Research Centre. 42 p.

Baranyay, J.A.; Safranyik, L. 1970. Effect of dwarf mistletoe on growth and mortality of lodgepole pine in Alberta. Publ. 1285. Canadian Forestry Service, Department of Fisheries and Forestry. 19 p.

Barlow, B.A. 1964. Classification of the Loranthaceae and Viscaceae. Proceedings Linnaean Society of New South Wales II. 89:268–272.

Barlow, B.A. 1983. Biogeography of Loranthaceae and Viscaceae. In: Calder, M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 19–46.

Barney, C.W.; Hawksworth, F.G.; Geils, B.W. 1998. Hosts of *Viscum album*. European Journal of Forest Pathology. 28:187–208.

Barrett, J.W.; Roth, L.F. 1985. Response of dwarf mistletoe-infested ponderosa pine to thinning: 1. Sapling growth. Res. Pap. PNW-330. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 15 p.

Bates, C.G. 1927. Better seeds, better trees. Journal of Forestry. 25:130–144.

Beatty, J.S.; Filip, G.M.; Mathiasen, R.L. 1997. Larch dwarf mistletoe. Forest Insect and Disease Leaflet 169. [revised 1988]. Washington, DC: U.S. Department of Agriculture, Forest Service. 8 p. [Online]. Available: http://www.fs.fed.us/r6/nr/fid/fidls/fidl169.htm. [2002, June 29].

Becker, H.; Schmoll, H. 1986. Mistel: Arzneipfanze, Brauchtum, Kunstmotiv. Stuttgart: Wissenschaftliche Verlagsgesellschaft. 132 p.

Bello Gonzales, M.A. 1984. Estudio de muérdagos (Loranthaceae) en la region Tarasca, Michoacán. Bol. Téch. 102. México, DF: Secretaría de Agricultura y Recursos Hidráulicos, Instituto Nacional de Investigaciones Forestales. 62 p.

Bello Gonzales, M.A.; Gutierrez Garduño, M. 1985. Clave para la identificación de la familia Loranthaceae en la porción del Eje Neovolcánico localizado dentro del Estado de Michoacán. Ciencia Forestal. 10(54):3–33.

Bennetts, R.E.; White, G.C.; Hawksworth, F.G.; Severs, S.E. 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. Ecological Applications. 6:899–909.

Besse, W.J.; Dunsworth, G.; Perry, J. 2001. The forest project: three-year review and update. Ecoforestry. 16(4):10–17.

Bloomberg, W.J.; Smith, R.B. 1982. Measurement and simulation of dwarf mistletoe infection of second-growth western hemlock on southern Vancouver Island. Canadian Journal of Forest Research. 12:280–291.

Bolsinger, C.L. 1978. The extent of dwarf mistletoe in six principal softwoods in California, Oregon and Washington, as determined from forest survey records. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 45–54.

Bonga, J.M. 1964. An unusual witches' broom on black spruce caused by eastern dwarf mistletoe *Arceuthobium pusillum* on *Picea mariana*. Forest Science. 10:77–78.

Booth, C.; Samuels, G.J. 1981. *Nectria neomacrospora* nom. nov.: a new name for *Nectria macrospora* (Wollenw.) Oullette. Transaction British Mycological Society. 77(3): 645.

Bradley, A.F.; Noste, N.V.; Fisher, W.C. 1992. Fire ecology of forests and woodlands in Utah. Gen. Tech. Rep. INT-287. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 128 p.

Brandt, J.P.; Brett, R.D.; Knowles, K.R.; Sproule, A. 1998. Distribution of severe dwarf mistletoe damage in west-central Canada. Special Rep. 13. Edmonton, AB: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre. 27 p.

Briede, J-W.; Mexal, J.G.; Lynch, A.M.; Hawksworth, F.G. 1991. Shoot growth and development of Douglas-fir and white fir in New Mexico. In: Baumgartner, D.M; Lotan, J.E., eds. Interior Douglas-fir: the species and its management; 1990 February 27–March 1; Spokane, WA. Pullman, WA: Washington State University Cooperative Extension: 155–159.

British Columbia Ministry of Forests. 1995. Dwarf mistletoe management guidebook. Forest practices code of British Columbia. Victoria, BC: British Columbia Ministry of Forests. 20 p. [Online]. Available: http://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/dwarf/dwarftoc.htm. [2002, June 30].

British Columbia Ministry of Forests. 2000. Growth and yield stand modelling PrognosisBC. [Homepage of PrognosisBC, British Columbia Ministry of Forests]. [Online]. Available: http://www.fro.gov.bc.ca/research/gymodels/progbc/index.htm. [2002, July 7].

Broshot, N.; Larson, L.; Tinnin, R. 1986. Effects of *Arceuthobium americanum* on twig growth of *Pinus contorta*. Res. Note. PNW-RN-453. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 6 p.

Broshot, N.E.; Tinnin, R.O. 1986. The effect of dwarf mistletoe on starch concentrations in the twigs and needles of lodgepole pine. Canadian Journal of Forest Research. 16:658–660.

Browner, C.H. 1985. Plants used for reproductive health in Oaxaca, Mexico. Economic Botany. 39:482–504.

Buckland, D.C.; Marples, E.G. 1953. Management of western hemlock infested with dwarf mistletoe. British Columbia Lumberman. 36(5):50–51, 136, 140.

Bunderson, E.D.; Weber, D.J.; Nelson, D.L. 1986. Diseases associated with *Juniperus osteosperma* and a model for predicting their occurrence with environment site factors. Great Basin Naturalist. 46:427–440.

Burke, H.R. 1975. A new species of *Smilcraulax* from Mexico, with key to species of the genus (Coleoptera: Curculionidae). Entomological News. 86:167–171.

Byler, J.W. 1978. The pest damage inventory in California. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 162–171.

Byler, J.W.; Cobb, F.W., Jr. 1972. The occurrence and pathogenicity of *Nectria fuckeliana* on dwarf mistletoe in California. Canadian Journal of Botany. 50:1162.

Caballero Deloya, M. 1968. Los principales enemigos del bosque in los estados de Baja California, Chihuahua, Durango, Nayarit y Sonora, Bosques de clima templado y frío. Publ. 5. México, DF: Direccion General del Inventario Nacional Forestal. 20 p.

Caballero Deloya, M. 1970. La frecuencia de los daños al bosque (areas de coníferas en Zacatecas, Sinaloa y Jalisco). Publ. 14. México, DF: Direccion General del Inventario Nacional Forestal. 28 p.

Calder, D.M. 1983. Mistletoes in focus: an introduction. In: Calder, M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 1–17.
Calder, M.; Bernhardt P., eds. 1983. The biology of mistletoes. Sydney: Academic Press. 348 p.
Calvin, C.L.; Wilson, C.A. 1996. Endophytic system. In: Hawksworth, F.G.; Wiens, D. Dwarf mistletoes: biology, pathology, and systematics. Agric. Handb. 709. Washington, DC: U.S. Department of Agriculture, Forest Service: 113–122.
Calvin, C.L.; Wilson, C.A.; Varughese, G. 1991. Growth of longitudinal stands of *Phoradendron juniperinum* (Viscaceae) in shoots of *Juniperus occidentalis*. Annals of Botany. 67:153–161.
Cerezke, H.F.; Emond, F.J. 1989. Forest insect and disease conditions in Alberta, Saskatchewan, Manitoba, and the Northwest Territories in 1987. Inf. Rep. NOR-X-300. Edmonton, AB: Forestry Canada, Northern Forestry Centre. 25 p.
Cházaro B., M. 1989a. Loranthaceae ("muérdagos") del centro y sur del Estado de Veracruz. En: IV simposio nacional sobre parasitologia forestal; 1987 October 28–30; Durango, Drg. Publicación Especial 60. Instituto Nacional de Investigaciones Forestales y Agropecularis: 604–612.
Cházaro B., M. 1989b. Los muérdago (Loranthacease) del Estado de Jalisco. En: IV Simposio sobre parasitologia forestal; 1989 Octobre 4–6; Cd. Juarez, Chih: 45.
Cházaro B., M. 1990. Los muérdago del Estado de Jalisco. Biosphera. 1:3–7.
Cházaro B., M.; Huerta Martínez, F.M.; Patiño Beltrán, R.M.; Sánchez Fornué, R.; Lomelí Mijes, E.; Flores Macías, A. 1992. Los muérdagos (Loranthaceae) de Jalisco, parásitas poco conocidas. Ciencia y Desarrollo. 17(102):70–85.
Cházaro B., M.; Oliva R., H. 1987a. Loranthaceas del centro de Veracruz y zona limítrofe de Puebla. I. Cactaceas y Succulentas Mexicanas. 32:55–60.
Cházaro B., M.; Oliva R., H. 1987b. Loranthaceas del centro de Veracruz y zona limítrofe de Puebla. II. Cactaceas y Succulentas Mexicanas. 32:78–86.
Cházaro B., M.; Oliva R., H. 1988a. Loranthaceas del centro de Veracruz y zona limítrofe de Puebla. IV. Cactaceas y Succulentas Mexicanas. 33:42–48.
Cházaro B., M.; Oliva R., H. 1988b. Loranthaceas del centro de Veracruz y zona limítrofe de Puebla. V. Cactaceas y Succulentas Mexicanas. 33:71–75.
Chen, C.; Marsden, M.; Taylor, J.E. 1993. Sensitivity analysis of the Interim Dwarf Mistletoe Impact Modeling System for the user. Rep. MAG-93-10. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Pest Management Methods Application Group. 13 p.
Childs, T.W. 1960. Drought effects on conifers in the Pacific Northwest, 1958–59. Res. Note 182. Portland, OR: U.S. Department of Agriculture, Pacific Northwest Forest and Range Experiment Station. 5 p.
Cibrián Tovar, D.; Campos Bolanos, R.; Pineda Torres, C.; Guerrero Alarcon, E.; Olvera Olmos, V. 1980. Aspectos biologicos del genero *Arceuthobium*. En: Primer simposio nacional sobre parasitologia forestal; 1980 Febrero 18–19. Uruapan, Michoacán: Sociedad Mexicana de Entomologia: 229–237.
Conkle, M.T.; Critchfield, W.B. 1988. Genetic variation and hybridization of ponderosa pine. In: Baumgartner, D.M.; Lotan, J.E., eds. Ponderosa pine, the species and its management, proceedings of the symposium; 1987 September 29–October 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 27–43.
Conklin, D.A. 2000. Dwarf mistletoe management and forest health in the Southwest. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region. 30 p.
Conklin, D.A. 2002. Emergence of latent dwarf mistletoe infection in young ponderosa pine regeneration: 10-year monitoring of Whitetail A&B Project at Mescalero. R3-02-02. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region, Forestry and Forest Health. 8 p.
Conklin, D.A.; Armstrong, W.A. 2001. Effects of three prescribed fires on dwarf mistletoe infection in southwestern ponderosa pine. Rep. R3-01-02. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region, Forestry and Forest Health. 17 p.
Current Vegetation Survey. 2002. [Homepage of Current Vegetation Survey, Region 6, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://www.fs.fed.us/r6/survey/. [2002, July 8].
Daniel, J.T.; Templeton, G.E.; Smith, R.J.; Fox, W.T. 1973. Biological control of northern jointvetch in rice with endemic fungal disease. Weed Science. 21:303–307.
Daugherty, C.M; Mathiasen, R.L. 1999. Adult sex ratio of *Phoradendron juniperinum* in ten severely infected *Juniperus monosperma* in northern Arizona. Madroño. 46(4):169–176.
Davidson, A.G.; Prentice, R.M. 1967. Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Ottawa, ON: Ministry of Forestry and Rural Development. 248 p.
Dawson, T.E.; Ehleringer, J.R. 1991. Ecological correlates of seed mass variation in *Phoradendron juniperinum*, a xylem-tapping mistletoe. Oecology. 85:332–342.
Dawson, T.E.; Ehleringer, J.R.; Marshall, J.D. 1990a. Sex-ratio and reproductive variation in the mistletoe *Phoradendron juniperinum* (Viscaceae). American Journal of Botany. 77:584–589.
Dawson, T.E.; King, E.J.; Ehleringer, J.R. 1990b. Age structure of *Phoradendron juniperinum* (Viscaceae), a xylem-tapping mistletoe: Inferences from a non-destructive morphological index of age. American Journal of Botany. 77:573–583.
de Jong, M.D.; Scheepens, P.C.; Zadoks, J.C. 1990. Risk analysis for biological control: a Dutch case study in biocontrol of *Prunus serotina* by the fungus *Chondrostereum purpureum*. Plant Disease. 74:189–194.
De la Puente, J.M. 1966. Forest disease and insect resistance in Latin America. In: Gerhold, H.D.; Schreiner, E.J.; McDermott, R.E.; Winieski, J.A., eds. Breeding pest-resistant trees. Oxford: Pergamon Press: 31–34.
DeBach, P., ed. 1964. Biological control of insect pests and weeds. New York: Reinhold Pulishing. 844 p.
Deeks, S.J.; Shamoun, S.F.; Punja, Z.K. 2001. In vitro germination and development of western hemlock dwarf mistletoe. Plant Cell, Tissue, and Organ Culture. 66:97–105.
Deeks, S.J.; Shamoun, S.F.; Punja, Z.K. [In press]. Histopathology of callus and germinating seeds of *Arceuthobium tsugense* subsp. *tsugense* infected by *Cylindrocarpon cylindroides* and *Colletotrichum gloeosporioides*. International Journal of Plant Sciences.
DeMars, D.J. 1980. Estimates of the occurrence of dwarf mistletoe on the Deschutes National Forest. Res. Note PNW–364. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

DeNitto, G., comp. 2002. Montana forest insect and disease conditions and program highlights—2001. Rep. 02-1. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, State and Private Forestry. 42 p.

Dixon, G.E.; Hawksworth, F.G.1979. A spread and intensification model for southwestern dwarf mistletoe in ponderosa pine. Forest Science. 25(1):43–52.

Dobie, J.; Britneff, A.A. 1975. Lumber grades and volumes from lodgepole pine infected with dwarf mistletoe. Wood and Fiber. 7:104–109.

Dooling, O.J. 1978. Survey methods to determine the distribution and intensity of dwarf mistletoes. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 36–44.

Dowding, E.S. 1931. *Wallrothiella arceuthobii*, a parasite of jack-pine mistletoe. Canadian Journal of Research. 5:219–230.

Drummond, D.B. 1978. Approaches to determining volume losses due to dwarf mistletoe on a Westwide basis. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 55–61.

Drummond, D.B. 1982. Timber loss estimates for the coniferous forest of the United States due to dwarf mistletoes. Rep. 83-2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Pest Management, Methods Application Group. 24 p.

Eav, B. B.; Marsden, M. A. 1988. Pest models for the Inland Mountain West. In: Schmidt, W. C., comp. Future forests of the Mountain West: a stand culture symposium; 1986 September 29–October 3; Missoula, MT. Gen. Tech. Rep. INT-243. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 402 p.

Edwards, D. 2001. Hemlock dwarf mistletoe in the Long Beach Model Forest. Long Beach Model Forest. [Online]. Available: http://www.lbmf.bc.ca. [2002, April 20].

Edwards, D.N. 2002. Incidence of hemlock dwarf mistletoe in variable retention cutblocks in the Long Beach Model Forest. Canadian Plant Disease Survey 82: 128–132. [Online]. Available: http://res2.agr.gc.ca/london/pmrc/english/report/disease2002.html. [2002, August 2].

Ehleringer, J.R.; Cook, C.S.; Tieszen, L.L. 1986. Comparative water use and nitrogen relationships in a mistletoe and its host. Oecology. 68:279–284.

Ellis, D.E. 1946. Anthracnose of dwarf mistletoe caused by a new species of *Septogloeum*. Journal Elisha Mitchell Scientific Society. 62:25–50.

Englerth, G.H. 1942. Decay of western hemlock in western Oregon and Washington. Bull. 50. New Haven, CT: Yale University, School of Forestry. 53 p.

Equiluz Peidra, T. 1991. Biosystematics of the Mexican and Central American white pines. In: Proceedings, symposium on white pine provenances and breeding; August 5–11; Montreal, Quebec. Gen. Tech. Rep. NE-155. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeast Forest Experiment Station: 4–10.

Escudero Moreno, M.; Cibrián Tovar, D. 1985. Determinacion del periodo de dispersion de *Arceuthobium globosum grandicaule* en la region Central de Mexico. En: Memoria de los simposia nacional de parasitologia forestal. II y III. Publicacion Especial 46. Mexico, DF: Secretaria de Agricultura y Recursos Hidraulicolis: 342–351.

Etheridge, D.E. 1973. Wound parasites causing tree decay in British Columbia. Forest Pest Leaflet 62. Victoria, BC: Canadian Department of the Environment, Pacific Forest Research Centre. 15 p.

Everett, R.; Schelihaas, D.; Spurbeck, D.; Ohison, P.; Keenum, D.; Anderson, D. 1997. Structure of northern spotted owl nest stands and their historical conditions on the eastern slope of the Pacific Northwest Cascades, USA. Forest Ecology and Management. 94:1–14.

Fairweather, M.L. 1995. Post-treatment biological evaluation of the 1981 Tusayan dwarf mistletoe (DM) control project. Rep. R3-95-1. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwest Region, Forest Pest Management. 6 p.

Felix, L.S. 1970a. The biology of *Phoradendron bolleanum* subspecies *pauciflorum* on *Abies concolor*. Berkeley: University of California. 194 p. Dissertation.

Felix, L.S. 1970b. Hyperparasitism and autoparasitism in true mistletoes. Plant Disease Reporter. 54:15.

Ferrell, G.T. 1974. Moisture stress and fir engraver (Coleoptera: Scolytidae) attack in white fir infected by true mistletoe. Canadian Entomologist. 106:315–318.

Filip, G.M. 1984. Dwarf mistletoe and *Cytospora* canker decrease grand fir growth in central Oregon. Forest Science. 30:1071–1079.

Filip, G.M.; Beatty, J.S.; Mathiasen, R.L. 2000. Fir dwarf mistletoe. Forest Insect and Disease Leaflet 89. [revised]. Washington, DC: U.S. Department of Agriculture, Forest Service. 8 p. [Online]. Available: http://www.fs.fed.us/r6/nr/fid/firdm.pdf. [2002, June 29].

Filip, G.M.; Colbert, J.J.; Parks, C.A.; Seidel, K.W. 1989. Effects of thinning on volume growth of western larch infected with dwarf mistletoe in northeastern Oregon. Western Journal of Applied Forestry. 4:143–145.

Filip, G.M.; Colbert, J.J.; Shaw, C.G., III; Hessburg, P.F.; Hosman, K.E. 1993. Influence of dwarf mistletoe and western spruce budworm on growth and mortality of Douglas-fir in unmanaged stands. Forest Science. 39:465–477.

Fisher, J.T. 1983. Water relations of mistletoes and their hosts. In: Calder, D.M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 161–184.

Flora of North America Editorial Committee. 1993. Volume 2, Pteridophytes and gymnosperms. New York: Oxford University Press. 475 p.

Flora Mesoamericana. 2002. [Homepage of Flora Mesoamericana, Missouri Botanical Garden, Universidad Nacional Autonoma de Mexico and The Natural History Museum of London]. [Online]. Available: http://www.mobot.org/MOBOT/fm/welcome.html. [2002, July 20].

Forest Health Monitoring Program. 1994. Forest health monitoring: a national strategic plan. Research Triangle Park, NC: U.S Department of Agriculture, Forest Service, Forest Health Monitoring Program. 13 p. [Online]. Available: http://www.na.fs.fed.us/spfo/fhm/index.html. [2002, June 30].

Forest Health Protection. 2002. Forest insect and disease conditions in the United States 2000. U.S. Department of Agriculture, Forest Service. 100 p. [Online]. Available: http://www.fs.fed.us/foresthealth/annual_i_d_conditions/index.html. [2002, June 29].

Forest Health Technology Enterprise Team. 2002. Dwarf Mistletoe Model. [Homepage of Forest Health Technology Enterprise Team, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://www.fs.fed.us/foresthealth/technology/dm.html. [2002, June 28].

Forest Insect and Disease Survey. 1994. Forest depletions caused by insects and diseases in Canada 1982–1987. Inf. Rep. ST-X-8. Ottawa, Canada: Canadian Forestry Survey, Forest Insect and Disease Survey. 9 p.

Forest Inventory and Analysis. 2002. [Homepage of Forest Inventory and Analysis, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://wwwfia.fs.fed.us. [2002, July 8].

Forest Management Service Center. 2000. Forest Vegetation Simulator (FVS). [October 12-last update]. [Homepage of Forest Health Management Service Center, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://www.fs.fed.us/fmsc/fvs/. [2002, June 28].

Forest Service. 2002. [Homepage of Tools for Forest Vegetation Management, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://www.fs.fed.us/vegtools/. [2002, July 7].

Frankel, S.; Adams, D. 1989. Reduction of dwarf mistletoe with the plant growth regulator ethephon. Forest Pest Management Rep. 89-1. San Francisco: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region. 5 p.

Frankel, S.; Dale, J.; Hart, D. 1989. A biological evaluation of pest conditions at five southern California ski areas, San Bernardino National Forest. Rep. 89-5. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region. 21 p.

Frazer, J.G. 1930. The golden bough. London: MacMillian and Company. 12 volumes.

Freeman, C.E.; Worthington, R.D.; Corral, R.D. 1985. Some floral nectar—sugar compositions from Durango and Sinaloa, Mexico. Biotropica. 17:309–313.

French, D.W.; Meyer, M.P.; Anderson, R.L. 1968. Control of dwarf mistletoe on black spruce. Journal of Forestry. 66:359–360.

Funk, A.; Baranyay, J.A. 1973. Additional fungi and gall disease of dwarf mistletoe swellings in western hemlock. Canadian Plant Disease Survey. 53:182.

Funk, A.; Smith, R.B. 1981. *Potebniamyces gallicola* n. sp., from dwarf mistletoe infections in western hemlock. Canadian Journal of Botany. 59:1610–1612.

Funk, A.; Smith, R.B.; Baranyay, J.A. 1973. Canker of dwarf mistletoe swellings on western hemlock caused by *Nectrica funkeliana* var. *macrospora*. Canadian Journal of Forest Research. 3:71–74.

Gallina, S. 1988. Importancia del injerto (*Phoradendron* sp.) para el venado. Southwestern Naturalist. 33:21–25.

García, A.M. 1977. Patología vegetal práctica. Ed. Limusa. México. 156 p.

Garnett, G.N. 2002. Wildlife use of witches' brooms induced by dwarf mistletoe in ponderosa pine forests of northern Arizona. Flagstaff: Northern Arizona University. Thesis.

Gehring, C.A.; Whitham, T.G. 1992. Reduced mycorrhhizae on *Juniperus monosperma* with mistletoe: the influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism. Oecologia. 89:298–303.

Geils, B.W. 2001a. Dwarf mistletoe. In: Maloy, O.C.; Murray, T.D., eds. Encyclopedia of plant pathology. New York: John Wiley & Sons, Inc.: 388–389.

Geils, B.W. 2001b. Leafy mistletoe. In: Maloy, O.C.; Murray, T.D., eds. Encyclopedia of plant pathology. New York: John Wiley & Sons, Inc.: 613–616.

Geils, B.W.; Hawksworth, F.G.; Janssen, J.E. 1991. Longevity of ponderosa pine parasitized by southwestern dwarf mistletoe. Supplement to Bulletin of the Ecological Society of America. 72(2):122.

Geils, B.W.; Mathiasen, R.L. 1990. Intensification of dwarf mistletoe on southwestern Douglas-fir. Forest Science. 36:955–969.

Gentry, H.S. 1946. Notes on the vegetation of Sierra Surotato in northern Sinaloa. Bulletin of Torrey Botanical Club. 73:451–462.

Gibson, I.A.S. 1978. Informe sobre una visita a Mexico. Ciencia Forestal. 3(12):40–53.

Gilbert, J.A. 1984. The biology of dwarf mistletoes (*Arceuthobium* spp.) in Manitoba. Winnipeg: University of Manitoba. 138 p. Thesis.

Gilbert, J.A. 1988. Some aspects of the reproductive biology of *Arceuthobium americanum* in Manitoba. Winnipeg: University of Manitoba. Dissertation.

Gill, F.S. 1990. Ornithology. New York: W.H. Freeman and Company. 660 p.

Gill, L.S. 1935. *Arceuthobium* in the United States. Trans. Conn. Acadamy Arts and Science: 32:111–245.

Gill, L.S. 1956. Summary of chemical tested for controlling western species of dwarf mistletoes (*Arceuthobium* spp.). In: Proceedings 3rd annual western international forest disease work conference; 1955 December; Spokane, WA: 18–25.

Gill, L.S.; Hawksworth, F.G 1954. Dwarf mistletoe control in southwestern ponderosa pine forests under management. Journal of Forestry. 1954:347–353.

Gill, L.S.; Hawksworth, F.G. 1961. The mistletoes, a literature review. Tech. Bull. 1242. Washington, DC: U.S. Department of Agriculture. 87 p.

Gleick, J. 1988. Chaos: making a new science. Penguin. 352 p.

Gregg, J.W. 1991. The differential occurrence of the mistletoe, *Phoradendron juniperinum*, on its host *Juniperus osteosperma* in the Western United States. Salt Lake City: University of Utah, Department of Biology. 78 p. Thesis.

Gregg, T.F.; Hummel, S.S. 2002. Assessing sampling uncertainty in FVS projections using a bootstrap resampling method. In: Crookston, Nicholas L.; Havis, Richard N., comps. Second Forest Vegetation Simulator (FVS) conference; 2002 February 12–14; Fort Collins, CO. Proc. RMRS-P-25. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Gregg, T.F.; Michaels Goheen, E. 1997. Current vegetation survey in the Pacific Northwest Region: a direct link to FVS and the insect and disease extensions. In: Teck, R.; Moeur, M.; Adams. J., comps. Proceedings: Forest Vegetation Simulator conference; 1997 February 3–7; Fort Collins, CO. Gen. Tech. Rep. INT-GTR-373. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 182–190.

Grimble, D.G.; Beckworth, R.C. 1993. Temporal changes in presence of late instar *Mitoura spinetorum* (Lycaenidae) in eastern Oregon. Journal of the Lepidopterists' Society. 47(4):329–330.

Gutierrez Vilchis, L.H.; Salinas Quinard, R. 1989. Algunos aspectos fenologicos del muérdago enano *Arceuthobium vaginatum vaginatum* (Viscaceae) en el Desierto del Los Leones, D.F. En: V simposio sobre parasitologia forestal;

1989 Octobre 4–6; Cd. Juarez, Chih: Sociedad Mexicana de Entomologia. 43.
Guyon, J.; Munson, S. 1991. Biological evaluation of insect and disease conditions of the Carson and Bridgeport Ranger Districts, Toiyabe National Forest. Rep. R4-91-02. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region, Forest Pest Management. 45 p.
Hadfield, J.S. 1999. Douglas-fir dwarf mistletoe infection contributes to branch breakage. Western Journal of Applied Forestry. 14(1):5–6.
Hadfield, J.S.; Mathiasen, R.L.; Hawksworth, F.G. 2000. Douglas-fir dwarf mistletoe. Forest Insect and Disease Leaflet 54. [revised 2000]. Washington, DC: U.S. Department of Agriculture, Forest Service. 9 p.
Hadfield, J.S.; Russell, K. 1978. Dwarf mistletoe management in the Pacific Northwest. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on swarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 73–81.
Hanover, J.W. 1966. Tree improvement for disease resistance in Western United States and Canada. In: Gerhold, H.D.; Schreiner, E.J.; McDermott, R.E.; Winieski, J.A., eds. Breeding pest-resistant trees. Oxford: Pergamon Press: 53–56.
Hansen, D. 1997. Insect and disease conditions in Bryce Canyon National Park detected during August 1995. Rep. R4-97-06. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region, Forest Health Protection. 44 p.
Hawksworth, F.G. 1952. Unusual hosts for two southwestern mistletoes. Plant Disease Reporter. 36(6):246.
Hawksworth, F.G. 1961. Dwarf mistletoe of ponderosa pine in the Southwest. Tech. Bull. 1246. Washington, DC: U.S. Department of Agriculture. 112 p.
Hawksworth, F.G. 1965. Life tables for two species of dwarf mistletoe. I. Seed dispersal, interception, and movement. Forest Science. 11:142–151.
Hawksworth, F.G. 1972. Biological control of the mistletoes. In: Nordin, V.J., comp. Biological control of forest diseases. Fifteenth Congress of the International Union of Forestry Research Organizations; 1971 March; Gainesville, FL. Ottawa, ON: Canadian Forestry Service: 83–92.
Hawksworth, F.G. 1977. The 6 class dwarf mistletoe rating system. Gen. Tech. Rep. RM–48. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.
Hawksworth, F.G. 1978a. Biological factors of dwarf mistletoe in relation to control. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 5–15.
Hawksworth, F.G. 1978b. Intermediate cuttings in mistletoe-infested lodgepole pine and southwestern ponderosa pine stands. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 86–92.
Hawksworth, F.G. 1979. *Phoradendron* in the Western United States. In: Drummond, D.B., comp. Proceedings 26th western international forest disease work conference; 1978 October 24–28; Tucson, AZ. Davis, CA: U.S. Department of Agriculture, Forest Service, Forest Insect and Disease Management, Methods Application Group: 21–31.
Hawksworth, F.G. 1980. Los muérdagos enanos (*Arceuthobium*) y su importancia en la silvicultura de México. En: Primer simposio nacional sobre parasitologia forestal; 1980 Febrero 18–19. Uruapan, Michoacán: Sociedad Mexicana de Entomologia: 207-228.
Hawksworth, F.G. 1983. Mistletoes as forest parasites. In: Calder, M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 317–333.
Hawksworth, F.G. 1987. Taxonomia y distribucion de *Arceuthobium* en Mexico y Centro America. En: Simposio nacional sobre parasitiologia forestal y IV Reunion sobre Plagas y enfermedades forestales; Octobre 28–30; Durango, Dgo. Instituto Nacional de Investigaciones Forestales y Agropecuarias: 559–591.
Hawksworth, F.G. 1991. Coevolution of Mexican white pines and their dwarf mistletoe parasites. In: Proceedings, symposium on white pine provenances and breeding; August 5–11; Montreal, Quebec. Gen. Tech. Rep. NE-155. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeast Forest Experiment Station: 23–28.
Hawksworth, F.G.; Cibrián Tovar, D. 1985. Observaciones sobre las enfermedades de árboles forestales en el norte de México y sur de los Estados Unidos. En: Memoria de los simposia nacionales de parasitologia forestal II y III. Publicación Especial 46. México DF: Secretaría de Agricultura y Recursos Hidráulicos, Institito Nacional de Investigaciones Forestales: 57–66.
Hawksworth, F.G.; Dixon, C.S.; Krebill, R.G. 1983. *Peridermium bethelii*: a rust fungus associated with lodgepole pine dwarf mistletoe. Plant Disease. 67:729–733.
Hawksworth, F.G.; Dooling, O.J. 1984. Lodgepole pine dwarf mistletoe. Forest Insect and Disease Leaflet 18. [revised 2001]. Washington, DC: U.S. Department of Agriculture, Forest Service. 11 p. [Online]. Available: http://www.fs.fed.us/r6/rn/fid/fidls/fidl18.htm. [2002, June 29].
Hawksworth, F.G.; Edminster, C.B. 1981. Carlos Bates' dwarf mistletoe resistant ponderosa pines: a postscript after half a century. Res. Note RM-412. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.
Hawksworth, F.G.; Geils, B.W. 1985. Vertical spread of dwarf mistletoe in thinned ponderosa pine in Arizona. Res. Note. RM-460. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 3 p.
Hawksworth, F.G.; Geils, B.W. 1990. How long do mistletoe-infected ponderosa pines live? Western Journal of Applied Forestry. 5:47–48.
Hawksworth, F.G.; Geils, B.W. 1996. Biotic associates. In: Hawksworth, F.G.; Wiens, D. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agric. Handb. 709. Washington, DC: U.S. Department of Agriculture, Forest Service: 73–89.
Hawksworth, F.G.; Graham, D.P. 1963a. Dwarf mistletoe on spruce in the Western United States. Northwest Science. 37:31–38.
Hawksworth, F.G.; Graham, D.P. 1963b. Spread and intensification of dwarf mistletoe in lodgepole pine reproduction. Journal of Forestry. 61:587–591.

Hawksworth, F.G.; Hinds, T.E. 1964. Effects of dwarf mistletoe on immature lodgepole pine stands in Colorado. Journal of Forestry. 62:27–32.

Hawksworth, F.G.; Hinds, T.E.; Johnson, D.W.; Landis, T.D. 1977a. Silvicultural control of dwarf mistletoe in young lodgepole pine stands. Tech Rep. R2-10. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, State and Private Forestry. 13 p.

Hawksworth, F.G.; Johnson, D.W. 1989a. Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. Gen. Tech. Rep. RM-169. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

Hawksworth, F.G.; Johnson, D.W. 1989b. Mistletoe control with ethephon. In: van der Kamp, B.J., comp. Proceedings 36th annual western international forest disease work conference; 1988 September 19–23; Park City, UT. Vancouver, BC: University of British Columbia, Department of Forest Sciences: 29–45.

Hawksworth, F.G.; Johnson, D.W. 1993. Protect your trees from dwarf mistletoe. Gen. Tech. Rep. RM-225. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 8 p.

Hawksworth, F.G.; Lusher, A.A. 1956. Dwarf mistletoe survey and control on the Mescalero Apache Reservation, New Mexico. Journal of Forestry. 54:384–390.

Hawksworth, F.G.; Marsden, M.A. 1990. Permanent plots for quantifying damage caused by western dwarf mistletoes and their spread and intensification. Res. Note RM-498. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 6 p.

Hawksworth, F.G.; Moir, W.H.; Janssen, J.E. 1992a. Effects of dwarf mistletoe in old-growth lodgepole pine stands at Fraser Experimental Forest, Colorado. In: Kaufmann, M.R.; Moir, W.H.; Bassett, R.L., tech. coords. Old-growth forest in the Southwest and Rocky Mountain Regions, proceedings of a workshop; 1992 March 9–13; Portal, AZ. Gen. Tech. Rep. RM-213. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 60–65.

Hawksworth, F.G.; Scharpf, R.F. 1978. Literature on the dwarf mistletoes: damage and control. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 178–179.

Hawksworth, F.G.; Scharpf, R.F., tech coords.1984. Biology of dwarf mistletoes. Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 53–61.

Hawksworth, F.G.; Scharpf, R.G. 1981. *Phoradendron* on conifers. Forest Insect and Disease Leaflet 164. Washington, DC: U.S. Department of Agriculture, Forest Service. 7 p.

Hawksworth, F.G.; Scharpf, R.S.; Marosy, M. 1991. European mistletoe continues to spread in Sonoma County. California Agriculture. 45(6):39–40.

Hawksworth, F.G.; Shaw, C.G., III. 1984. Damage and loss caused by dwarf mistletoes in coniferous forests of Western North America. In: Wood, R.K.S.; Jellis, G.J., eds. Plant diseases: infection, damage and loss. Oxford: Blackwell Scientific Publications. 327 p.

Hawksworth, F.G.; Wicker, E.F.; Scharpf, R.F. 1977b. Fungal parasites of dwarf mistletoes. Gen. Tech. Rep. RM-36. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 14 p.

Hawksworth, F.G.; Wiens, D. 1965. *Arceuthobium* in Mexico. Brittonia. 17:213–238.

Hawksworth, F.G.; Wiens, D. 1966. Observations on witches' broom formation, autoparasitism, and new hosts in *Phoradendron*. Madroño. 18(7):218–224.

Hawksworth, F.G.; Wiens, D. 1972. Biology and classification of dwarf mistletoes (*Arceuthobium*). Agric. Handb. 401. Washington, DC: U.S. Department of Agriculture, Forest Service. 234 p.

Hawksworth, F.G.; Wiens, D. 1977. *Arceuthobium* in Mexico: additions and range extensions. Brittonia. 29:411–418.

Hawksworth, F.G.; Wiens, D. 1989. Two new species, nomenclatural changes, and range extensions in Mexican *Arceuthobium* (Viscaceae). Phytologia. 66:3–11.

Hawksworth, F.G.; Wiens, D. 1993a. Viscaceae—mistletoe family. Journal of Arizona-Nevada Academy of Science. 27(2):241–245.

Hawksworth, F.G.; Wiens, D. 1993b. Viscaceae, mistletoe family. In: Hickman, J.C., ed. Jepson manual, higher plants of California. Berkeley: University of California Press: 1092–1097.

Hawksworth, F.G.; Wiens, D. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agric. Handb. 709. Washington, DC: U.S. Department of Agriculture, Forest Service. 410 p. [Online]. Available: http://www.rms.nau.edu/publications/ah_709/. [2002, May 2].

Hawksworth, F.G.; Wiens, D.; Nickrent, D.L. 1992b. New Western North American taxa of *Arceuthobium* (Viscaceae). Novon. 2:204–211.

Hawksworth, F.G.; Williams-Cipriani, J.C; Eav, B.B.; Geils, B.G.; Johnson, R.R.; Marsden, M.A.; Beatty, J.S.; Schubert, G.D; Robinson, D.C.E. 1995. Dwarf mistletoe impact modeling system: user's guide and reference manual. Rep. MAG-95-2. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Forest Pest Management, Methods Application Group. 120 p. [Online]. Available: http://www.fs.fed.us/foresthealth/technology/d_mod/dm_ug.pdf. [2002, June 28].

Hedwall, S.J. 2000. Bird and mammal use of dwarf mistletoe-induced witches' brooms in Douglas-fir in the Southwest. Flagstaff: Northern Arizona University. 66 p. Thesis.

Hennon, P.E.; Beatty, J.S.; Hildebrand, D. 2001. Hemlock dwarf mistletoe. Forest Insect and Disease Leaflet 135. Washington, DC: U.S. Department of Agriculture, Forest Service. 8 p. [Online]. Available: http://www.fs.fed.us/r6/nr/fid/fidls/hemlock-dm.pdf. [2002, June 29].

Hernandez Cuevas, L.V. 1991. Los muéradagos (Loranthaceae) de la region central del Estado de Tlaxcala. Publ. 4. Tizatlan, Tlaxcala: Jardin Botanico de Tizatlan. 38 p.

Hernandez Cuevas, L.V.; Acosta P., R.; Galinado F., G.L. 1992. Los muérdago enanos (*Arceuthobium* spp.) en los bosques de pino del Volcan la Malintzi, Estados del Tlaxcala y Puebla. Bol. 15. Tizatlan, Tlaxcala, Mexico: Jardin Botanico Tizatlan. 58 p.

Hessburg, P.F.; Mitchell, R.G.; Filip, G.M. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. Gen. Tech. Rep. PNW-GTR-327. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 72 p.

Hildebrand, D.M. 1995. *Arceuthobium tsugense*—hemlock dwarf mistletoe: a species of special concern? Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 54 p.

Hildebrand, D.M; Mathiasen, R.L.; Beatty, J.S. 1997. Mountain hemlock dwarf mistletoe (*Arceuthobium tsugense* subsp. *mertensianae*), 1995 general regional survey in Washington. Rep. R6-97-01. Portland, OR. U.S Department of Agriculture, Forest Service, Pacific Northwest Region, Natural Resources, Forest Insects and Diseases. 5 p.

Hinds, T.E.; Hawksworth, F.G. 1965. Seed dispersal velocity in four dwarf mistletoes. Science. 148:517–519.

Hitchcock, C.; Cronquist, A.; Ownbey, M.; Thompson, J.W. 1964. Vascular plants of the Pacific Northwest. Part 2. Seattle: University of Washington Press.

Hodge, J.; Humphreys, N.; Van Sickle, G.A. 1994. Surveys of forest health in managed stands in British Columbia, 1993. Victoria, BC: Department of Natural Resources Canada, Canadian Forestry Service, Pacific Forestry Centre.

Holling, C.S. 1978. Adaptive environmental assessment and management. London: John Wiley & Sons.

Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs. 62(4):477–502.

Holling, C.S.; Meffe, G.K. 1996. Command and control and the pathology of natural resource management. Conservation Biology. 10(2):328–337.

Horst, R.K. 2002. Westcott's plant disease handbook. 6th ed. Hingham, MA: Kluwer Academic Publishers. +1000 p.

Hreha, A.M.; Weber, D.J. 1979. Distribution of *Arceuthobium divaricatum* and *Phoradendron juniperinum* on the South Rim of Grand Canyon, Arizona. Southwestern Naturalist. 24(4):625–636.

Hunt, K. 1971. A comparison of kraft pulping of sound and dwarf mistletoe-infected western hemlock wood. Inf. Rep. VP-X-78. Vancouver, BC: Canada Department of Fisheries and Forestry, Forest Products Laboratory. 7 p.

Hunt, R.S. 1993. Abies. In: Flora of North America Editorial Committee. Flora of North America north of Mexico, Volume 2. New York: Oxford University Press: 354–362.

Hunt, R.S.; Owens, J.N.; Smith, R.B. 1996. Penetration of western hemlock, *Tsuga heterophylla*, by the dwarf mistletoe *Arceuthobium tsugense*, and development of the parasite cortical system. Canadian Journal of Plant Pathology. 18:342–346.

Hunt, R.S.; Smith, R.B. 1978. Natural infection of two new hosts by hemlock dwarf mistletoe in British Columbia. Canadian Plant Disease Survey. 58:31–32.

Jensen, K. 2000. *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. f. sp. Malvae. Fungal disease of mallow. Agriculture and Agri-Food Canada Web. [Online]. Available: http://res2.agr.ca/lethbridge/weedbio/agents/acolglom.htm. [2002, July 8].

Johnson, D.W. 1992. Effects of application rate and timing of ethephon treatments on abscission of ponderosa pine dwarf mistletoe 4 years following treatment. Tech. Rep. R2-54. Lakewood, CO: U.S. Department of Agriculture, Rocky Mountain Region, Forest Pest Management. 9 p.

Johnson, D.W. 1994. Dwarf mistletoe suppression program activity review. In: Proceedings joint western forest insect work conference and western international forest disease work conference. Albuquerque, NM: 102–107.

Johnson, D.W. 1998. Evaluation of Hidden Lakes dwarf mistletoe pruning study, Routt National Forest, Colorado. Tech. Rep. R2-61. Lakewood, Co: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Renewable Resources. 8 p.

Johnson, D.W.; Hawksworth, F.G.; Drummond. D.B. 1981. Yield loss of lodgepole pine stands to dwarf mistletoe in Colorado and Wyoming National Forests. Plant Disease. 65:437–438.

Johnson, D.W.; Hildebrand, D.M.; Hawksworth, F.G. 1989. Effects of application rate and timing of ethephon treatments on abscission of ponderosa pine dwarf mistletoe. Tech. Rep. R2-44. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Insect and Disease Management. 7 p.

Johnson, D.W.; Yarger, L.C.; Minnemeyer, C.D.; Pace, V.E. 1976. Dwarf mistletoe as a predisposing factor for mountain pine beetle attack of ponderosa pine in the Colorado Front Range. Tech. Rep. R2-4. Lakewood, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Region, Forest Insect and Disease Management. 7 p.

Johnson, W.F. 1977. Manager's handbook for black spruce in the North-Central States. Gen. Tech. Rep. NC-34. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 18 p.

Julien, M.H. 1982. Biological control of weeds: a world catalogue of agents and their target weeds. Farnham Royal Slough, UK: Commonwealth Institute of Biological Control. 108 p.

Kimmey, J.W.; Mielke, J.L. 1959. Western dwarf mistletoe on ponderosa pine. Forest Pest Leaflet 40. Washington, DC: U.S. Department of Agriculture, Forest Service. 7 p.

Kipfmueller, K.F.; Baker, W.L. 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. Forest Ecology and Management. 108:77–84.

Knutson, D.M. 1970. Effects of dwarf mistletoe infection on ponderosa pine xylem. Northwest Science. 44:64.

Knutson, D.M. 1978. Biological and chemical control of dwarf mistletoe. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 151–155.

Knutson, D.M. 1983. Physiology of mistletoe parasitism and disease responses in the host. In: Calder, M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 295–316.

Knutson, D.M.; Hutchins, A.S. 1979. *Wallrothiella arceuthobii* infecting *Arceuthobium douglasii*: culture and field inoculation. Mycologia. 71:821–828.

Knutson, D.M.; Tinnin, R. 1980. Dwarf mistletoe and host tree interactions in managed forests of the Pacific Northwest. Gen. Tech. Rep. PNW-111. Portland, OR: U.S Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 19 p.

Knutson, D.M.; Tinnin, R. 1986. Effects of dwarf mistletoe on the response of young Douglas-fir to thinning. Canadian Journal of Forest Research. 16:30–35.

Kolb, T. E. 2002. Ecofisiologia del parasitismo en el reino vegetal. En: Saez-Lopez, J.A.; Catalan, P.; Saez, L., eds. Plantas parasitias del la Peninsula Iberica e Islas Baleares. Madrid: Mundi-Prensa: 57–85.

Kope, H.H.; Shamoun, S.F. 2000. Mycoflora associates of western hemlock dwarf mistletoe plants and host swellings collected from southern Vancouver Island, British Columbia. Canadian Plant Disease Survey. 80:144–147.

Kope, H.H.; Shamoun, S.F.; Oleskevich, C. 1997. First report of *Colletotrichum gloeosporioides* on *Arceuthobium tsugense* subsp. *tsugense* in Canada. Plant Disease. 81:1095.

Korstian, C.F.; Long, W.H. 1922. The western yellow pine mistletoe: effect on growth and suggestions for control. Bull. 1112. Washington, DC: U.S. Department of Agriculture. 35 p.

Kuijt, J. 1955. Dwarf mistletoes. Botanical Review. 21(10):569–626.

Kuijt, J. 1960a. The distribution of dwarf mistletoes, *Arceuthobium*, in California. Madroño. 15:129–139.

Kuijt, J. 1960b. Morphological aspects of parasitism in the dwarf mistletoes (*Arceuthobium*). Publ. Botany 30. Berkeley, CA: University of California: 337–436.

Kuijt, J. 1963. Distribution of dwarf mistletoes and their fungus hyperparasites in Western Canada. National Museum of Canada Bulletin. 186:134–148.

Kuijt, J. 1964. Critical observations on the parasitism of New World mistletoes. Canadian Journal of Botany. 42:1243–1278.

Kuijt, J. 1967. On the structure and origin of the seedling of *Psittacanthus schiedeanus* (Loranthaceae). Canadian Journal of Botany. 45:1497–1506.

Kuijt, J. 1968. Mutual affinities of Santalalean families. Brittonia. 20(2):136–147.

Kuijt, J. 1969a. The biology of parasitic flowering plants. Berkeley: University of California Press. 246 p.

Kuijt, J. 1969b. Observations on *Wallrothiella arceuthobii*, a fungus parasite of dwarf mistletoes. Canadian Journal of Botany. 47:1359–1365.

Kuijt, J. 1970. Seedling establishment in *Psittacanthus* (Loranthaceae). Canadian Journal of Botany. 48(4):705–711.

Kuijt, J. 1975a. The genus *Cladocolea* (Loranthaceae). Journal Arnold Arboretum. 56(3):265–335.

Kuijt, J. 1975b. The identity of *Struthanthus haenkei* (*Spirostylis haenkei*) (Loranthaceae). Canadian Journal of Botany. 53:249–255.

Kuijt, J. 1983. Status of the genera *Aetanthus* and *Psathyranthus* (Loranthaceae). Candollea. 38:661–672.

Kuijt, J. 1987. Novelties in Mesoamerican mistletoes (Loranthacease and Viscacease). Annuals Missouri Botanical Garden. 74:511-532.

Kuijt, J. 1988. Monograph of the Eremolepidaceae. Systematic Botanical Monographs. 18.

Kuijt, J. 1996. Cataphylls and taxonomy in *Phoradendron* and *Dendrophtthora* (Viscaceae). Acta Bot. Neerl. 45:263–277.

Lamont, B. 1983. Germination of mistletoes. In: Calder, M.; Bernhardt, P., eds. The biology of mistletoes. Sydney: Academic Press: 129–143.

Lei, S.A. 1997. Host-parasite relationship between Utah juniper and juniper mistletoe in the Spring Mountains of southern Nevada. In: Monsen, S.B.; Stevens, R., comps. Proceedings, ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. RMRS-P-9. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 99–104.

Lichter, J.M.; Reid, M.S.; Berry, A.M. 1991. New methods for control of leafy mistletoe (*Phoradendron* spp.) on landscape trees. Journal of Arboriculture. 17(5):127–130.

Lightle, P.C.; Hawksworth, F.G. 1973. Control of dwarf mistletoe in a heavily used ponderosa pine recreation forest: Grand Canyon, Arizona. Res. Pap. RM-106. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 22 p.

Lightle, P.C.; Weiss, M.J. 1974. Dwarf mistletoe of ponderosa pine in the Southwest. Forest Insect and Disease Leaflet 19. [revised 1998]. Washington, DC: U.S. Department of Agriculture, Forest Service. 7 p. [Online]. Available: http://www.fs.fed.us/r6/nr/fid/fidl/fidl19.htm. [2002, June 29].

Linhart, Y.B.; Synder, M.A.; Gibson, P.J. 1994. Differential host utilization by two parasites in a population of ponderosa pine. Oecologia. 98:117–120.

Linnane, J.P. 1987. Fort Bayard National Cemetery. File Rep. 3420, December 7, 1987. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region. 2 p.

Livingston, W.H.; Blanchette, R.A.; Brenner, M.L.; Zuzek, K.J. 1985. Effective use of ethylene-releasing agents to prevent spread of eastern dwarf mistletoe on black spruce. Canadian Journal of Forest Research. 15:872–876.

Livingston, W.H.; Brenner, M.L. 1983. Ethephon stimulates abscission of eastern dwarf mistletoe aerial shoots on black spruce. Plant Disease. 67:909–910.

Livingston, W.H.; Brenner, M.L., Blanchette, R.A. 1984. Altered concentrations of abscisic acid, indole-3-acetic acid, and zeatin riboside associated with eastern dwarf mistletoe infections on black spruce. In: Hawksworth, F.G.; Scharpf, R.F., tech coords. Biology of dwarf mistletoes. Proceedings of the symposium; 1984 August 8; Fort Collins, CO. Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 53–61.

Lopez De Buen, L.; Ornelas, J.F. 1999. Frugivorous birds, host selection and the mistletoe *Psittacanthus schiedeanus*, in central Veracruz, Mexico. Journal Tropical Ecology. 15:329–340.

Madgiral Sanchez, X. 1967. Contribucion al conocimiento del la ecologia del los bosques de oyamel (*Abies religiosa*) en el Valle de Mexico. Bol. Tech. 18. Instituto Nacional de Investigaciones Forestales. 94 p.

Maffei, H. 1984. Control of dwarf mistletoe at the Grand Canyon: results after a third of a century. In: Hunt, R.S., comp. Proceedings 32nd annual western international forest disease work conference; 1984 September 25–28; Taos, NM: 59–60.

Maffei, H. 1992. Pruning guidelines for dwarf mistletoe infected ponderosa pine. Bend, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Deschutes National Forest. 13 p.

Maffei, H. 2002. A methodology for modeling the spatial and temporal effects of vegetation management alternatives on late successional habitat in the Pacific Northwest. In: Crookston, Nicholas L.; Havis, Richard N., comps. Second Forest Vegetation Simulator (FVS) conference; 2002 February 12–14; Fort Collins, CO. Proc. RMRS-P-25. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Maffei, H.; Arena, J.V. 1993. Forest insect and disease risk and occurrence maps in GIS: application to integrated resource analysis. In: Liebhold, A.M.; Barrett, H.R., eds. Proceedings; spatial analysis and forest pest management; 1992 April 27–30; Mountain Lakes, VA. Gen. Tech. Rep. NE-175. Radnor, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station: 8–14.

Maffei, H.; Beatty, J. 1988. Changes in the incidence of dwarf mistletoes over 30 years in the Southwest. In: van der Kamp, B.J., comp. Proceedings 36th annual western international forest disease work conference; 1988 September 19–23; Park City, UT. Vancouver, BC: University of British Columbia, Department of Forest Science: 88–90.

Maffei, H.; Stone, J.; David, L.; Gregg, T.; Adams, J.; Geils, B. 1999. Development of the understory enhancement for the dwarf mistletoe spread and intensification model. In: Trummer, L., comp. Proceedings 46th western international forest disease work conference; 1998 September 28–Ocober 2; Reno, NV. Anchorage, AK: U.S. Department of Agriculture, Forest Service, State and Private Forestry: 37–46.

Magasi, L.P. 1984. Forest conditions in the Maritimes in 1983. Inf. Rep. M-X-19. Canadian Forest Service, Maritimes Forest Research Centre. 49 p.

Makowski, R.M.D.; Mortensen, K.1992. The first mycoherbicide in Canada: *Colletotrichum gloeosporioides* f. sp. *malvae* for round-leaved mallow. In: Delfosse, E.S.; Scottt, R.R., eds. Proceedings of the first international weed control congress; Melbourne, Australia: 298–300.

Mantiri, F.; Samuels, G.J.; Rahe, J.E.; Honda, B. 2001. Phytogenetic relationships in *Neonectria* species having *Cylindrocarpon* anamorphs inferred from mitochondrial ribosomal DNA sequences. Canadian Journal of Botany. 79:334–340.

Mark, W.R.; Hawksworth, F.G. 1974. How important are bole infections in spread of ponderosa pine dwarf mistletoe? Journal of Forestry. 72:146–147.

Mark, W.R.; Hawksworth, F.G.; Oshima, N. 1976. Resin disease: a new disease of lodgepole pine dwarf mistletoe. Canadian Journal of Forest Research. 6:415–424.

Marler, M.; Pedeersen, D.; Michell-Olds, T.; Callaway, R.M. 1999. A polymerase chain reaction method for detecting dwarf mistletoe infection in Douglas-fir and western larch. Canadian Journal of Forest Research. 29:1317–1321.

Marsden, M.A.; Filip, G.M.; Hessburg, P.F. 1990. Using the forest timber inventory for sampling the occurrence of pests on interior Douglas-fir. In: Baumgartner, D.M.; Lotan, J.E., comp. Interior Douglas-fir: the species and its management; 1990 February 27–March 1; Spokane, WA. Pullman, WA: Washington State University, Cooperative Extension: 109–113.

Marsden, M.A.; Shaw, C.G., III; Morrison, M. 1993. Simulation of management options for stands of southwestern ponderosa pine attacked by Armillaria root disease and dwarf mistletoe. Res. Pap. RM-308. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 5 p.

Marshall, J.D.; Dawson, T.E.; Ehleringer, J.R. 1993. Gender-related differences in gas exchange are not related to host quality in the xylem-tapping mistletoe *Phoradendron juniperinum* (Viscaceae). American Journal of Botany. 80(6):641–645.

Marshall, J.D.; Ehleringer, J.R. 1990. Are xylem-tapping mistletoes partially heterotrophic? Oecology. 84:244–248.

Marshall, J.G.; Dawson, T.E.; Ehleringer, J.R. 1994. Integrated nitrogen, carbon, and water relations of a xylem-tapping mistletoe following nitrogen fertilization of the host. Oecologia. 100:430–438.

Marshall, K. 1996. Management implications of maintaining Douglas-fir dwarf mistletoe brooms for wildlife use. In: Beatty, J.S., comp. Proceedings 44th western international forest disease work conference; 1996 September 16–20; Hood River, OR. Sandy, OR: U.S. Department of Agriculture, Forest Service, Westside Forest Insects and Diseases Technical Center: 72–74.

Marshall, K.; Filip, G.M. 1999. The relationship of Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*) to stand conditions and plant associations in the Southern Cascade Mountains, Oregon. Northwest Science. 73(4):301–311.

Marshall, K.; Mamone, M.S.; Barclay, R.B. 2000. A survey of northern spotted owl nests in Douglas-fir dwarf mistletoe brooms in the Siskiyou Zone, Rouge River National Forest and Ashland Resource Area, Medford District, Bureau of Land Management. Rep. SWOFIDSC-00-3. U.S. Department of Agriculture, Forest Service, Southwest Oregon Forest Insect and Disease Service Center. 12 p.

Martínez, M. 1948. Los Pinos Mexicanos. 2d ed. México. 361 p.

Martínez Gonzáles, F. 1983. Las plagas forestales en Mexico. En: Primeras Jornadas Forestales Hispano-Mexicanas. Publicación Especial 41. México DF: Secretaría de Agricultura y Recursos Hidráulicos, Instituto Nacional de Investigaciones Forestales: 123–128.

Mathiasen, R.L. 1978. Seed germination and infection techniques for three southwestern dwarf mistletoes. Plant Disease Reporter. 62:64–67.

Mathiasen, R.L. 1982. Taxonomic studies of dwarf mistletoes (*Arceuthobium* spp.) parasitizing *Pinus strobiformis*. Great Basin Naturalist. 42:120–127.

Mathiasen, R.L. 1984. Improving assessment of dwarf mistletoe infection in southwestern ponderosa pine stands. Arizona Forestry Notes 21. Flagstaff: Northern Arizona University, School of Forestry. 7 p.

Mathiasen, R.L. 1989. Management of dwarf mistletoe using uneven-aged cutting methods. In: Proceedings 9th intermountain regional silviculture workshop; 1989 September 18–21; Jackson Hole, WY. Ogden UT: U.S. Department of Agriculture, Forest Service, Intermountain Region: 186–194.

Mathiasen, R.L. 1994. Natural infection of new hosts by hemlock dwarf mistletoe. Res. Note RM-RN-530. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 6 p.

Mathiasen, R.L. 1996. Dwarf mistletoes in forest canopies. Northwest Science. 70:61–71

Mathiasen, R.L. 1998a. Comparative susceptibility of conifers to larch dwarf mistletoe in the Pacific Northwest. Forest Science. 44(4):559–568.

Mathiasen, R.L. 1998b. Infection of young western larch by larch dwarf mistletoe in northern Idaho and western Montana. Western Journal of Applied Forestry. 13(2):41–46.

Mathiasen, R.L. 1999. Comparative susceptibility of subalpine firs to Douglas-fir dwarf mistletoe. Canadian Journal of Plant Pathology. 21:45–51.

Mathiasen, R.L.; Beatty, J.S.; Hildebrand, D.M. 1995a. First report of larch dwarf mistletoe on Pacific silver fir and on mountain hemlock in the Cascade Mountains, Washington. Plant Disease. 79:1249.

Mathiasen, R.L.; Beatty, J.S.; Hildebrand, D.M. 1996a. First report of lodgepole pine dwarf mistletoe on subalpine fir. Plant Disease. 80:342.

Mathiasen, R.L.; Beatty, J.S.; Melgar, J. 2000a. First report of *Arceuthobium hondurense* on *Pinus tecunumanii*. Plant Disease. 84(3):372–373.

Mathiasen, R.L.; Beatty, J.S.; Pronos, J. 2002a. Pinyon pine dwarf mistletoe. Forest Insect and Disease Leaflet 174. Washington, DC: U.S. Department of Agriculture, Forest Service. 7 p.

Mathiasen, R.L.; Daugherty, C.M. 2001. Susceptibility of foxtail pine and western white pine to limber pine dwarf mistletoe in northern California. Western Journal of Applied Forestry. 16(2):58–60.

Mathiasen, R.L.; Geils, B.W.; Carlson, C.E.; Hawksworth, F.G. 1995b. Larch dwarf mistletoe not found on alpine larch. Res. Note. RM-RN-533. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.

Mathiasen, R.L.; Hawksworth, F.G. 1988. Dwarf mistletoes on western white pine and whitebark pine in northern California and southern Oregon. Forest Science. 34:429–440.

Mathiasen, R.L.; Hawksworth, F.G.; Edminster, C.B. 1990. Effects of dwarf mistletoe on growth and mortality of Douglas-fir in the Southwest. Great Basin Naturalist. 50:173–179.

Mathiasen, R.L.; Hoffman, J.T.; Guyon, J.C.; Wadleigh, L.L. 1996b. Comparison of two roadside survey procedures for dwarf mistletoes on the Sawtooth National Forest, Idaho. Great Basin Naturalist. 56:129–134.

Mathiasen, R.L.; Howell, B. 2002. First report of *Arceuthobium hawksworthii* in Honduras. Plant Disease. 2002(7):815.

Mathiasen, R.L.; Marshall, K. 1999. Dwarf mistletoe diversity in the Siskiyou–Klamath Mountain Region. Natural Areas Journal. 19:379–385.

Mathiasen, R.L.; Melgar, J.; Beatty, J.; Parks, C. 2000b. First report of *Psittacanthus angustifolius* on *Pinus oocarpa* and *Pinus maximinoi*. Plant Disease. 84(2):203.

Mathiasen, R.L.; Nickrent, D.; Daugherty, C. 2002b. First report of *Arceuthobium hondurense* in Oaxaca, Mexico. Plant Disease. 86:72.

Mathiasen, R.L.; Nickrent, D.; Parks, C.; Beatty, J.; Sesnie, S. 2001. First report of *Arceuthobium hondurense* in Mexico. Plant Disease. 85:444.

Mathiasen, R.L.; Parks, C.; Beatty, J.; Sesnie, S. 2000c. First report of *Psittacanthus angustifolius* on pines in Mexico and Guatemala. Plant Disease. 84:808.

Mathiasen, R.L.; Parks, C.G.; Geils, B.W.; Beatty, J.S. 1998. Notes on the distribution, host range, plant size, phenology, and sex ratio of two rare dwarf mistletoes from Central America: *Arceuthobium hawksworthii* and *A. hondurense*. Phytologia. 84(2):154–164.

Mathiasen, R.L.; Shaw, D.C. 1998. Adult sex ratio of *Arceuthobium tsugense* in six severely infected *Tsuga heterophylla*. Madroño. 45(3):210–214.

McCambridge, W.F.; Hawksworth, F.G.; Edminster, C.B.; Laut, J.G. 1982. Ponderosa pine mortality resulting from a mountain pine beetle outbreak. Res. Pap. RM-235. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

McGregor, M.D. 1978. Management of mountain pine beetle in lodgepole pine stands in the Rocky Mountain area. In: theory and practice of mountain pine beetle management in lodgepole pine forests, proceedings of the symposium; 1978 April 25–27; Pullman, WA. Moscow, ID: University of Idaho Press: 129–139.

McHenry, D.E. 1934. Does mistletoe kill trees at Grand Canyon. Grand Canyon Nature Notes. 9:305–309.

McMinn, H.E. 1939. Loranthanthaceae, mistletoe family, 1. *Phoradendron*. In: An illustrated manual of California shrubs. J.W. Stacey, Inc.: 89–92.

Meinecke, E.P. 1912. Parasitism of *Phoradendron juniperinum libocedri* Engelm. Reprinted from: Proceedings of the Society of American Foresters. Vol. VII, No. 1.1912 March. Washington, DC: Judd & Dettweiler, Inc.: 35–41.

Melgar, J.; Berrios, M.; Mathiasen, R.; Howell, B. 2001. First report of *Psittacanthus angustifolius* on *Psidium guineese* and *Pinus tecunumanii* in Honduras. Plant Disease. 85:1120.

Melgar, J.; Mathiasen, R.; Howell, B. 2001. First report of *Arceuthobium globosum* subsp. *grandicaule* in Honduras. Plant Disease. 85:563.

Merrill, L.M.; Byler, J.W.; Corse, T.; Reedy, T.; Hall. L.D. 1988. An evaluation of the effectiveness of dwarf mistletoe suppression in uneven-aged stands on the Flathead Indian Reservation. Forest Pest Management Rep. 89-6. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region. 9 p.

Merrill, L.M.; Hawksworth, F.G.; Johnson, D.W. 1985. Evaluation of a roadside survey procedure for dwarf mistletoe on ponderosa pine in Colorado. Plant Disease. 69:572–573.

Mielke, J.L. 1959. Infection experiments with *Septogloeum gillii*, a fungus parasitic on dwarf mistletoe. Journal of Forestry. 57:925–926.

Missouri Botanical Garden. 2002. VAST nomenclatural database (revision 1.5). [Homepage of Missouri Botanical Garden]. [Online]. Available: http://mobot.mobot.org/W3T/Search/vast.html [2002, May 2].

Mistletoe Center. 2002. [Homepage of The Mistletoe Center, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture]. [Online]. Available: http://www.rms.nau.edu/mistletoe. [2002, July 2].

Monning, E.; Byler, J. 1992. Forest health and ecological integrity in the Northern Rockies. Rep. 92-7. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Forest Pest Management. 19 p.

Moody, B.H., comp. 1992. Forest insect and disease conditions in Canada, 1989. Ottawa, ON: Forestry Canada, Forest Insect and Disease Survey. 117 p.

Moody, B.H.; Amirault, P.A. 1992. Impacts of major pests on forest growth and yield in the Prairie Provinces and Northwest Territories: a literature review. Inf. Rep. NOR-X-324. Edmonton, AB: Forestry Canada, Northern Forestry Centre. 35 p.

Moore, M. 1979. Mistletoe. In: Medicinal plants of the Mountain West. Santa Fe: Museum of New Mexico Press. 107–109.

Morris, M.J.; Wood, A.R.; Den Breeyen, A.D. 1998. Development and registration of a fungal inoculant to prevent regrowth of cut wattle tree stumps in South Africa, and brief overview of other bioherbicide projects currently in progress. In: Main, D.S.; Burge, M.N., eds. IV international bioherbicides workshop, programme and abstracts; 1998 August 6–7; University of Strathclyde, Glasgow, Scotland: 15.

Mortenson, K. 1998. Biological control of weeds using microorganisms. In: Boland, G.J.; Kuykendall, L.D., eds. Plant-microbe interactions and biological control. New York: Marcel Dekker Inc.: 223–248.

Muir, J.A. 1967. Occurrence of *Colletotrichum gloeosporioides* on dwarf mistletoe (*Arceuthobium americanum*) in Western Canada. Plant Disease Reporter. 51:789–799.

Muir, J.A. 1970. Dwarf mistletoe spread in young lodgepole pine stands in relation to density of infection sources. Bi-Mon. Res. Notes. 26:49. Canada Department of Fisheries and Forests.

Muir, J.A. 1973. *Cylindrocarpon gillii*, a new combination for *Septogloeum gillii* on dwarf mistletoe. Canadian Journal of Botany. 51:1997–1998.

Muir, J.A. 1977. Effects of the fungal hyperparasite *Colletotrichum gloeosporioides* of dwarf mistletoe (*Arceuthobium americanum*) on young lodgepole pine. Canadian Journal of Forest Research. 7:579–583.

Muir, J.A. 1989. European leafy mistletoe. In: Pest Management Progress 8. Victoria BC: British Columbia Ministry of Forests and Lands.

Muir, J.A. 2002. Survey of dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.). Canadian Plant Disease Survey 82: 133–135. [Online]. Available: http://res2.agr.gc.ca/london/pmrc/english/report/disease2002.html. [2002, August 2].

Muir, J.A., ed. 1993. Proceedings of a workshop on management of hemlock dwarf mistletoe. BC Pest Management Rep. 4. Victoria, BC: British Columbia Ministry of Forests. 58 p.

Muir, J.A.; Robins, J.K. 1973. Detection of dwarf mistletoe of jack pine on aerial photographs. Plant Disease Reporter. 57:951–954.

Munns, E.N. 1919. Effect of fertilization on the seed of Jeffrey pine. Plant World. 22:138–144.

Muraro, S. J. 1978. Prescribed fire—a tool for the control of dwarf mistletoe in lodgepole pine. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 124–127.

Mushtaque, M.; Baloch, G.M. 1979. Possibilities of biological control of mistletoes, *Loranthus* spp., using oligophagous insects from Pakistan. Entomophaga. 24:73–81.

Myers, C.A.; Hawksworth, F.G.; Stewart, J.L. 1971. Simulating yields of managed, dwarf-mistletoe-infected lodgepole pine stands. Res. Pap. RM-72. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 15 p.

Myren, D.T.; Gross, H.L. 1977. Distribution of organisms causing important forest tree diseases in Ontario based on collections recorded by the Forest Insect and Disease Survey Unit. Rep. O-X-262. Sault Ste. Marie, ON: Department of Fisheries and the Environment, Canadian Forestry Service, Great Lakes Forestry Research Centre. 136 p.

North American Forestry Commission (NAFC). 2002. [Homepage of the North American Forestry Commission]. [Online]. Available: http://www.fs.fed.us/global/nafc/welcome.html. [2002, July 2].

Najera Martinez, F.; Gonzales Gandarilla, J.F.; Cibrian Tovar, J. 1987. Los muérdago enanos en el Estado de Durango en Mexico. En: IV simposio nacional sobre parasitologia forestal y IV reunion sobre enfermedades forestales; 1987 Octobre 28–30; Durango, Dgo. Instituto Nacional de Investigaciones Forestales y Agropecuarias: 592–603.

Nebeker, T.E.; Schmitz, R.F.; Tisdale, R.A.; Hobson, K.R. 1995. Chemical and nutritional status of dwarf mistletoe, Armillaria root rot, and comandra blister rust infected trees which may influence tree susceptibility to bark beetle attack. Canadian Journal Botany. 73:360–369.

Nevill, R.J.; Wood, C. 1995. Hemlock dwarf mistletoe and decay organisms associated with western hemlock and amabilis fir at the Montane Alternative Silvicultural Systems (MASS) research site in British Columbia. In: Arnott, J.T.; Besse, W.J.; Mitchell, A.K.; Peterson, J., eds. Montane Alternative Silvicultural Systems (MASS), proceedings of a workshop; 1995 June 7–8; Courtenay, BC. FRDA Rep. 238. BC: Canada-BC Partnership Agreement of Forest Research Development. 122 p.

Nicholls, T.H.; Egeland, L.; Hawksworth, F.G.; Johnson, D.W.; 1987a. Control of dwarf mistletoe with ethephon. In: Cooley, S.J., comp. Proceedings 34th annual western international forest disease work conference; 1986 September 8–12; Juneau, AK. Portland, OR: U.S. Department of Agriculture, Forest Service, Forest Pest Management: 78–85.

Nicholls, T.H.; Egeland, L.; Hawksworth, F.G.; Johnson, D.W.; Robbins, M.K. 1987b. Control of dwarf mistletoe with a plant growth regulator. In: Proceedings of a technical conference on management of subalpine forests: building on 50 years of research; 1987 July 6–9; Silver Creek, CO. Gen. Tech. Rep. RM-149. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 154–156.

Nicholls, T.H.; Hawksworth, F.G.; Merrill, L.M. 1984. Animal vectors of dwarf mistletoe, with special reference to *Arceuthobium americanum* on lodgepole pine. In: Hawksworth, F.G.; Scharpf, R.F., tech. coords. Biology of dwarf mistletoes: proceedings of the symposium; 1984 August 8; Fort Collins, CO. Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 102–110.

Nickrent, D.L. 2002. [June 8, last update]. Parasitic plant connection. [Homepage of D. L. Nickrent, Department of Plant Biology, Southern Illinois University at Carbondale]. [Online]. Available: http://www.science.siu.edu/parastic-plant/index.html. [2002, July 5].

Ostry, M.E.; Nicholls, T.H. 1979. Eastern dwarf mistletoe on black spruce. Forest Insect and Disease Leaflet 158. Washington, DC: U.S. Department of Agriculture, Forest Service. 7 p.

Page, J.M. 1981. Drought accelerated parasitism of conifers in the mountain ranges of northern California, USA. Environmental Conservation. 8:217–226.

Parker, A.J.; Parker, K.C. 1994. Structural variability of mature lodgepole pine stands on gently sloping terrain in Taylor Park Basin, Colorado. Canadian Journal of Forest Research. 24:2020–2029.

Parker, A.K. 1970. Growth of *Wallrothiella arceuthobii* on artificial media. Canadian Journal of Botany. 48:837–838.

Parker, T.J. 2001. Bird communities in dwarf mistletoe infested ponderosa pine forests. Flagstaff, AZ: Northern Arizona University. 90 p. Thesis.

Parks, C.; Bull, E.; Tinnin, R.O.; Shepherd, J.F.; Blumton, A.K. 1999a. Wildlife use of dwarf mistletoe brooms in Douglas-fir in northeast Oregon. Western Journal of Applied Forestry. 14:100–105.

Parks, C.; Conklin, D.A.; Bednar, L.; Maffei, H. 1999b. Woodpecker use and fall rates of snags created by killing ponderosa pine infected with dwarf mistletoe. Res. Pap. PNW-RP-515. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 11 p.

Parks, C.; Hoffman, J.T. 1991. Control of western dwarf mistletoe with the plant-growth regulator ethephon. Res. Note PNW-RN-506. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 4 p.

Parks, C.G.; Bull, E.L. 1997. American martin use of rust and dwarf mistletoe brooms in northeastern Oregon. Western Journal of Applied Forestry. 12(4):131–133.

Parmeter, J.R., Jr. 1978. Forest stand dynamics and ecological factors in relation to dwarf mistletoe spread, impact, and control. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Proceedings of the symposium on dwarf mistletoe control through forest management; 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 16–30.

Parmeter, J.R., Jr.; Hood, J.R.; Scharpf, R.F. 1959. *Colletotrichum* blight of dwarf mistletoe. Phytopathology. 49:812–815.

Parmeter, J.R., Jr.; Scharpf, R.F. 1963. Dwarf mistletoe or red fir and white fir in California. Journal of Forestry. 61:371–374.

Parmeter, J.R., Jr.; Scharpf, R.F. 1982. Stem infection by dwarf mistletoe in California true firs. Res. Pap. PSW-165. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 7 p.

Pearson, G.A. 1912. The influence of age and condition of the tree upon seed production in western yellow pine. Circ. 196. Washington, DC: U.S. Department of Agriculture, Forest Service. 11 p.

Perry, J.P., Jr. 1991. The Pines of Mexico and Central America. Portland, OR: Timber Press. 231 p.

Piirto, D.D.; Crews, D.L.; Troxell, H.E. 1974. The effects of dwarf mistletoe on the wood properties of lodgepole pine. Wood and Fiber. 6:26–35.

Plant Names Project. 1999. [Homepage of International Plant Names Index]. [Online]. Available: http://www.ipni.org. [2002, May 1].

Pousette, J. 1991. Impact of dwarf mistletoe on growth in lodgepole pine forests. Internal Rep. PM-PB-60. Victoria, BC: British Columbia Ministry of Forests. 12 p.

Power, J.M.; D'Eon, S.P. 1991. Quantifying pest-caused forest depletion using geographic information systems and database technologies. Inf. Rep PI-X-105. Petawawa, ON: Forestry Canada, Petawawa National Forestry Institute. 17 p.

Pronos, J. 1995. Can dwarf mistletoe be eliminated from recreation areas? In: Proceedings 43rd western international forest disease work conference; Whitefish, MT: 88–92.

Quick, C.R. 1963. Chemical control. Unit IX. Leafy mistletoes (*Phoradendron* spp.). In: Proceedings 10th western international forest disease work conference; 1962 October 15–19; Victoria, Alberta (sic): 97–98.

Quick, C.R. 1964. Experimental herbicide control of dwarf mistletoe on some California conifers. Res. Note PSW-47. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 9 p.

Ramsfield, T.D. 2002. Investigations into a biological control strategy for lodgepole pine dwarf mistletoe. Vancouver, BC: University of British Columbia, Graduate Studies, Department of Forest Sciences. 185 p. Ph.D. Thesis.

Ramsfield, T.D.; Shamoun, S.F.; van der Kamp, B.J. 1999. Fungal parasites of lodgepole pine dwarf mistletoe in British Columbia. Canadian Journal of Plant Pathology. 21:204.

Reich, R.M.; Lundquist, J.; Bravo, V.A. 2000. Spatial relationship of resident and migratory birds and canopy openings in disease ponderosa pine forests. Environmental Modeling and Software. 15:189–197.

Reich, R.M.; Mielke, P.W.; Hawksworth, F.G. 1991. Spatial analysis of ponderosa pine trees infected with dwarf mistletoe. Canadian Journal of Forest Research. 21:1808–1815.

Reid, N.; Florentino Caldera, H.; Marmolejo M., J.G. 1987. Intensidad de infeccion de cuatro especies de muérdago enano *Arceuthobium* en El Cerro El Potosi, Nuevo Leon. En: IV simposio nacional sobre parasitologia forestal y IV reunion sobre y enfermedades forestales; 1987 Octobre 28–30; Durango, Dgo. Instituto Nacional de Investigacciones Forestales y Agropecuarias: 613–624.

Reid, N.; Standford Smith, M.; Yan, Z. 1995. Ecology and population biology of mistletoes. In: Lowman, M.D.; Nadcarni, N.M., eds. Forest canopies. San Diego, CA: Academic Press: 285–310.

Reid, N.; Yan, Z. 2000. Mistletoes and other phanerogams parasitic on eucalypts. In: Keane, P.J.; Kile, G.A.; Podger, F.D.; Brown, B.N., eds. Diseases and oathogens of eucalypts: 353–383.

Reséndiz Reséndiz, J.; Martínez Hernández, J.F.; Carbajal Vera, I.J. 1989. Contribucion al conocimientodel la distribucion geografica, altitudinal y hospederos del muérdago verdadero *Psittacanthus* sp. En: V simposio sobre parasitologia forestal; 1989 Octobre 4–6; Juarez, Chihuahua. México, DF: Sociedad Mexicana de Entomogia, AC: 46.

Rey, L.; Sadik, A.; Fer, A.; Renaudin, S. 1991. Trophic relations of the dwarf mistletoe *Arceuthobium oxycedri* with its host *Juniperus oxycedrus*. Journal of Plant Physiology. 138:411–416.

Rey, L.; Sadik, A.; Fer, A.; Renaudin, S. 1992. Etude de quelques aspects du metolisme carbone et azote chez l'*Arceuthobium oxycedri*, gui nain du genevrir. Canadian Journal of Botany. 70:1709–1216.

Reynolds, R.T.; [and others]. 1992. Management recommendations for the northern goshawk in the Southwestern United States. Gen. Tech. Rep. RM-217. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 90 p.

Richardson, K.S.; van der Kamp, B.J. 1972. The rate of upward advance and intensification of dwarf mistletoe on immature western hemlock. Canadian Journal of Forest Research. 2:313–316.

Ridings, W.H. 1986. Biological control of stranglervine in citrus, a researcher's view. Weed Science. Supplement 1: 31-32.

Ringnes, D.B.; Stover, P.; Scharpf, R.F. 1996. Dwarf mistletoe resistance in ponderosa pine: selection and testing protocols. In: Moreno, M.T.; Cubero, J.I.; Berner, D.; Musselman, L.J.; Parker, C., eds. Advances in parasitic plant research. Proceedings 6th parasitic weed symposium. Cordoba, Spain: Junta de Andalucia, Consejeria de Agricultura y Pesca: 690–696.

Robbins, K.; Johnson, D.W.; Hawksworth, F.G.; Nicholls, T.H. 1989. Aerial application of ethephon is ineffective in controlling lodgepole pine dwarf mistletoe. Western Journal of Applied Forestry. 4:27–28.

Robins, J.K. 1972. Dwarf mistletoe aerial surveying method: results of preliminary trials in the Athabasca Forest. Misc. Rep. NOR-Y-10. Edmonton, AB: Department of the Environment, Canadian Forest Service, Northern Forest Research Center. 6 p.

Robinson, D.C.E.; Geils, B.W.; Muir, J. 2002. A spatial statistical model for the spread of dwarf mistletoe within and between stands. In: Crookston, Nicholas L.; Havis, Richard N., comps. Second Forest Vegetation Simulator (FVS) conference; 2002 February 12–14; Fort Collins, CO. Proc. RMRS-P-25. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. [Presentation online]. Available: http://www.essa.com/downloads/FVS_2002_DMSummary.pdf. [2002, September 5].

Rodriguez Angeles, A. 1983. Muérdago enano sobre Abies, Pinus y Pseudotsugae de Mexico. Ciencia Forestal. 8(45):7–45.

Roeser, J. 1926. The importance of seed source and the possibilities of forest tree breeding. Journal of Forestry. 24:38–51.

Rolston, H., III. 1994. Conserving natural value. New York: Columbia University Press. 259 p.

Roth, L.F. 1953. Pine dwarf mistletoe on the Pringle Falls Experimental Forest. Res. Note. 91. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 3 p.

Roth, L.F. 1971. Dwarf mistletoe damage to small ponderosa pines. Forest Science. 17:373–380.

Roth, L.F. 1974a. Resistance of ponderosa pine to dwarf mistletoe. Silvae Genetica. 23:116–120.

Roth, L.F. 1974b. Juvenile susceptibility of ponderosa pine to dwarf mistletoe. Phytopathology. 64:689–692.

Roth, L.F. 1978. Genetic control of dwarf mistletoe. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Symposium proceedings: dwarf mistletoe control through forest management;. 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest Range and Experiment Station: 69–72.

Roth, L.F. 2001. Dwarf mistletoe-induced mortality in northwest ponderosa pine growing stock. Western Journal of Applied Forestry. 16(3):136–141.

Roth, L.F.; Barrett. J.W. 1985. Response of dwarf mistletoe-infested ponderosa pine to thinning: 2. Dwarf mistletoe propagation. Res. Pap. PNW-331. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 20 p.

Ruhland, B.M.; Calvin, C.L. 2001. Morphological aspects of seedling establishment in four temperate region *Phoradendron* (Viscaceae) species. Madroño. 48(2):79-89.

Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. Canadian Journal of Forest Research. 20:48–57.

Safranyik, L; Nevill, R.; Morrison, D. 1998. Effects of stand density management on forest insects and diseases. Tech. Trans. Note 12. Victoria, BC: Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre. 4 p.

Sala, A.; Carey, E.; Callaway, R. 2001. Dwarf mistletoe affects whole-tree water relations of Douglas-fir and western larch primarily through changes in leaf to sapwood ratios. Oecologia. 126:42–52.

Salas, P.M.A. 1988. Aves dispersoras de muérdago. Informe Técnico. Secretaría de Agricultura y Recursos Hidráulicos, Instituto Nacional de Investigaciones Forestales y Agropecularis.

Schaffer, B.; Hawksworth, F.G.; Beemsterboer, P. 1983a. Effects of dwarf mistletoe and vigor classes on electrical resistance in lodgepole pine. Forest Science. 29:124–126.

Schaffer, B.; Hawksworth, F.G.; Jacobi, W.R. 1983b. Effects of comandra blister rust and dwarf mistletoe on cone and seed production of lodgepole pine. Plant Disease. 67:215-217.

Schaffer, B.; Hawksworth, F.G.; Wullscheger, S.D.; Reid, C.P.P. 1983c. Cytokinin-like activity related to host reactions to dwarf mistletoes. Forest Science. 29:66–70.

Scharpf, R.F. 1964. Cultural variation and pathogenicity of the *Colletotrichum* blight fungus of dwarf mistletoe. Phytopathology. 54:905–906.

Scharpf, R.F. 1969a. *Cytospora abietis* associated with dwarf mistletoe on true firs in California. Phytopathology. 59:1657–1658.

Scharpf, R.F. 1969b. Dwarf mistletoe on red fir: infection and control in understory stands. Res. Pap. PSW-50. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 8 p.

Scharpf, R.F. 1970. Seed viability, germination and radicle growth of dwarf mistletoe in California. Res. Pap. PSW-59. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 18 p.

Scharpf, R.F. 1972. Summation of tests for chemical control of dwarf mistletoe. In: Proceedings 19th annual western international forest disease work conference; 1971 September 13–17; Medford, OR: 80–83.

Scharpf, R.F. 1984. Host resistance to dwarf mistletoes. In: Hawksworth, F.G.; Scharpf, R.F., tech. coords. Biology of dwarf mistletoes, symposium proceedings;. 1984 August 8; Fort Collins, CO. Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 70–76.

Scharpf, R.F. 1987. Resistance of Jeffrey pine to dwarf mistletoe. In: Weber, H.C.; Forstreuter, W., eds. Proceedings of the 4th international symposium on parasitic flowering plants; 1987 August 2–7; Philipps Universitat, Marburg, Germany: 745–753.

Scharpf, R.F.; Bynum, H.H. 1975. *Cytospora* canker of true firs. Forest Pest Leaflet 146. Washington, DC: U.S. Department of Agriculture, Forest Service. 5 p.

Scharpf, R.F.; Geils, B.; Wiens, D.; Parker, C.; Forstreuter, W. 1997. Parasitic plants. In: Hansen, E.M.; Lewis, K.J., eds. Compendium of conifer diseases. St. Paul, MN: American Phytopathological Society: 36–40.

Scharpf, R.F.; Hawksworth, F.G. 1966. Hosts and distribution of *Uredo phoradendri*. Mycologia. 58:811–812.

Scharpf, R.F.; Hawksworth, F.G. 1968. Dwarf mistletoe on sugar pine. Forest Pest Leaflet 113. Washington, DC: U.S. Department of Agriculture, Forest Service, 4 p.

Scharpf, R.F.; Hawksworth, F.G. 1993. Mistletoes. In: Scharpf, R.S., tech. coord. Diseases of Pacific Coast conifers. Agric. Handb. 521. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 112–135.

Scharpf, R.F.; Kinlock, B.B.; Jenkinson, J.L. 1992. One seed source of Jeffrey pine shows resistance to dwarf mistletoe. Res. Pap. PSW-RP-207. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest Range and Experiment Station. 8 p.

Scharpf, R.F.; Parameter, J.R., Jr. 1967. The biology and pathology of dwarf mistletoe, *Arceuthobium campylopodum* f. *abietinum*, parasitizing true firs (*Abies* spp.) in California. Tech. Bull. 1362. Washington, DC: U.S. Department of Agriculture. 42 p.

Scharpf, R.F.; Parmeter, J.R., Jr., tech coords. 1978. Proceedings of the symposium on dwarf mistletoe control through forest management. Gen. Tech. Rep. PSW-31. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 190 p.

Scharpf, R.F.; Parmeter, J.R., Jr. 1982. Population dynamics of dwarf mistletoe on young true firs in the Central Sierra Nevada, California. Res. Pap. PSW-161. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 9 p.

Scharpf, R.F.; Roth, L.F. 1992. Resistance of ponderosa pine to western dwarf mistletoe in central Oregon. Res. Pap. PSW-RP-208. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 9 p.

Scharpf, R.F.; Smith, R.S.; Vogler, D. 1988. Management of western dwarf mistletoe in ponderosa and Jeffrey pines in forest recreation areas. Gen. Tech. Rep. PSW-103. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 11 p.

Scharpf, R.F.; Vogler, D. 1986. Western dwarf mistletoe infects understory Jeffrey pine seedlings on Cleveland National Forest, California. Res. Note PSW-386. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 2 p.

Schmitt, C.L. 1996. BMPMZ management guide, management of ponderosa pine infected with western dwarf mistletoe in northeastern Oregon. BMZ-96-07. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Blue Mountains Pest Management Zone.

Schmitt, C.L. 1997. BMPMZ management guide, management of Douglas-fir infected with dwarf mistletoe in the Blue Mountains of northeastern Oregon and southwestern Washington. BMZ-97-02. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Blue Mountains Pest Management Zone.

Schwandt, J.; Page, D. 1978. Surveying Idaho forests for dwarf mistletoe by helicopter. Rep. 78-6. Coeur d'Alene, ID: Idaho Department of Lands, Forest Insect and Disease Control. 7 p.

Shamoun, S.F. 1998. Development of biological control strategy for management of dwarf mistletoes. In: Sturrock, R., comp. Proceedings 45th western international forest disease work conference; 1997 September 15–19; Prince George, BC. Victoria, BC: Canadian Forest Service, Pacific Forestry Centre. 36–42.

Shamoun, S.F. 2000. Application of biological control to vegetation management in forestry. In: Spencer, N.R., ed. Proceedings of the X international symposium on biological control of weeds; 1999 July 4–14; Montana State University, Bozeman, MT: 87–96.

Shamoun, S.F.; Hintz, W.E. 1998. Development and registration of *Chondrostereum purpureum* as a mycoherbicide for hardwood weeds in conifer reforestation sites and utility rights-of-way. In: Main, D.S.; Burge, M.N., eds. IV international bioherbicides workshop, programme and abstracts; 1998 August 6–7; University of Strathclyde, Glasgow, Scotland: 14.

Shamoun, S.F.; Ramsfield, T.D.; Shrimpton, G.; Hintz, W.E. 1996. Development of *Chondrostereum purpureum* as a mycoherbicide for red alder (*Alnus rubra*) in utility rights-of-way. In: Comeau, P.; Harper, G., eds. Proceedings of the 1996 expert committee on weeds. Victoria, BC: British Columbia Ministry of Forests, Research Branch: 9.

Shaw, C.G., III; Hennon, P.H. 1991. Spread, intensification, and upward advance of dwarf mistletoe in thinned young stands of western hemlock in southeast Alaska. Plant Disease. 75:363–367.

Shaw, D.C.; Freeman, E.A.; Mathiasen, R.L. 2000. Evaluating the accuracy of ground-based hemlock dwarf mistletoe rating: a case study using the Wind River canopy crane. Western Journal Applied Forestry. 15(1):8–14.

Shaw, D.C.; Weiss, S.B. 2000. Canopy light and the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones subsp. *tsugense*) aerial shoots in an old-growth Douglas-fir/western hemlock forest. Northwest Science. 74(4):306–315.

Sinclare, W.A.; Lyon, H.H.; Johnson, W.T. 1987. American mistletoes and dwarf mistletoes In: Diseases of trees and shrubs. Ithaca, NY: Comstock Publishing Association: 420–435.

Singh, P. 1981. Eastern dwarf mistletoe on black spruce in Newfoundland. Phytopathology. 71:255.

Singh, P.; Carew, G.C. 1989. Impact of eastern dwarf mistletoe in black spruce forests in Newfoundland. European Journal of Forest Pathology. 19:305–322.

Smith, B.S. 1992. Lucy Bishop Millington, nineteenth-century botanist: her life and letters to Charles Horton Peck, State Botanist of New York. Huntia. 8:111–153.

Smith, E.L.; McMahan, A.J. 2002. Eco-physiology approach to projecting tree stress and vigor in FVS. In: Crookston, Nicholas L.; Havis, Richard N., comps. Second Forest Vegetation Simulator (FVS) conference; 2002 February 12–14; Fort Collins, CO. Proc. RMRS-P-25. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Smith, R.B. 1969. Assessing dwarf mistletoe on western hemlock. Forest Science. 15:277–285.

Smith, R.B. 1985. Hemlock dwarf mistletoe biology and spread. In: Muir, J., ed. Proceedings, workshop on management of hemlock dwarf mistletoe; 1983 August 15–16; Burnaby, BC. Pest Management Rep. 4. Victoria, BC: British Columbia Ministry of Forests: 4–10.

Smith, R.B.; Funk, A. 1980. Assessing *Nectra macrospora* as a biological control agent for hemlock dwarf mistletoe. Bimonthly Progress Report. Ottawa: Canada Department of Forestry. 36(3):11–12.

Smith, R.B.; Wass, E.F. 1976. Field evaluation of ecological differention of dwarf mistletoe on shore pine and western hemlock. Canadian Journal of Forest Research. 6:225–228.

Smith, R.B.; Wass, E.F. 1979. Infection trials with three dwarf mistletoe species within and beyond their known ranges in British Columbia. Canadian Journal of Plant Pathology. 1:47–58.

Smith, R.S. 1977. Overstory spread and intensification of hemlock dwarf mistletoe. Canadian Journal of Forest Research. 7:632–640.

Smith, R.S. 1983. Diseases of eastside pine types. In: Robson, T.F.; Standford, R.B., eds. Management of the eastside pine type in northeastern California; proceedings of a symposium; 1982 June 15–17; Susanville, CA. Publ. SAF 83-06. Northern California Society of American Foresters: 79–81.

Smith, R.S.; Wass, E.F.; Meagher, M.D. 1993. Evidence of resistance to hemlock dwarf mistletoes (*Arceuthobium tsugense*) in western hemlock (*Tsuga heterophylla*) clones. European Journal of Forest Pathology. 23:163–170.

Snyder, M.A.; Fineschi, B.; Linhart, Y.B.; Smith, R.H. 1996. Multivariate discrimination of host use by dwarf mistletoe *Arceuthobium vaginatum* subsp. *cryptopodum*: inter- and intraspecific comparisons. Journal of Chemical Ecology. 22(2):295–305.

Sproule, A. 1996a. Branch age in jack pine at the time of dwarf mistletoe infection. Forestry Chronicle. 72(3):307.

Sproule, A. 1996b. Impact of dwarf mistletoe on some aspects of the reproductive biology of jack pine. Forestry Chronicle. 72(3):303–306.

Srivastava, L.M.; Esau, K. 1961. Relation of dwarf mistletoe (*Arceuthobium*) to the xylem tissues of conifers. II. Effect of the parasite on the xylem anatomy of the host. American Journal of Botany. 48:209–215.

Stage, A.R.; Crookston, N.L.; Wiitala, M.R. 1986. Procedures for including pest management activities in forest planning using present or simplified planning methods. In: Bailey, R.G., tech. coord. Lessons from using FORPLAN: proceeding of a planning and implementation workshop; 1986 April 29–May 1; Denver, CO. Washington, DC: U.S. Department of Agriculture, Forest Service, Land Management Planning Systems: 202–215.

Standley, P.C. 1920. Loranthaceae. In: Trees and shrubs of Mexico. Contributions from the United States National Herbarium, Volume 23. Washington DC: Smithsonian Institution: 222–235.

Steeger, C.; Hitchcock, C.L. 1998. Influence of forest structure and diseases on nest-site selection by red-breasted nuthatches. Journal of Wildlife Management. 62(4):1349–1358.

Stevens, R.E.; Hawksworth, F.G. 1970. Insects and mites associated with dwarf mistletoes. Res. Pap. RM-59. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 12 p.

Stevens, R.E.; Hawksworth, F.G. 1984. Insect-dwarf mistletoe associations: an update. In: Hawksworth, F.G.; Scharpf, R.F., tech. coords. Biology of dwarf mistletoes: proceedings of the symposium; 1984 August 8; Fort Collins, CO. Gen Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 94–101.

Stewart, J.L. 1978. Overview of the dwarf mistletoe problem. In: Scharpf, R.F.; Parmeter, J.R., Jr., tech. coords. Symposium proceedings: dwarf mistletoe control through forest management;. 1978 April 11–13; Berkeley, CA. Gen. Tech. Rep. PSW-31. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest Range and Experiment Station: 2–4.

Stipe, L.E.; Kohler, S.; Hagle, S.; Hastie, L. 1992. Montana forest pest conditions and program highlights, 1991. Rep. 92-2. Missoula, MT: U.S. Department of Agriculture, Forest Service, Northern Region, Forest Pest Management. 27 p.

Strand, M.A.; Roth, L.F. 1976. Simulation model for spread and intensification of western dwarf mistletoe in thinned stands of ponderosa pine saplings. Phytopathology. 66:888–895.

Sutton, G.M. 1951. Dispersal of mistletoes by birds. Wilson Bulletin. 63(4):235–237.

Tainter, F.H.; French, D.W. 1971. The role of wound periderm in the resistance of eastern larch and jack pine to dwarf mistletoe. Canadian Journal of Botany. 49:501–504.

Taylor, J.E. 1995. Western larch dwarf mistletoe and ecosystem management. In: Schmidt, W.C.; McDonald, K.J., comp. Ecology and management of Larix forests: a look ahead, proceedings of an international symposium; 1992 October 5–9; Whitefish, MT. Gen. Tech. Rep. INT-GTR-319. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station: 310–313.

Taylor, J.E.; Marsden, M.A. 1997. Permanent plots for studying the spread and intensification of larch dwarf mistletoe and the effects of the parasite on growth of infected western larch on the Flathead Indian Reservation, Montana. Rep. 97-5. U.S. Department of Agriculture, Forest Service, Northern Region, Forest Health Protection. 5 p.

Taylor, R.J.; Patterson, T.F.; Harrod, R.J. 1994. Systematics of Mexican spruce—revisited. Systematic Botany. 19(1):47–59.

TeBeest, D.O.; Templeton, G.E. 1985. Mycoherbicides: progress in the biological control of weeds. Plant Disease. 69:6–10.

Thomson, A.J.; Muir, J.A.; Lewis, K.J. 1997. Variability in sub-regional impacts of dwarf mistletoe on mature lodgepole pine. Forestry Chronicle. 73:371–375.

Thoreau, H.D. 1858. The journal of Henry David Thoreau, February 12, 1858. Boston: Houghton Mifflin. [1962 Dover reprint, Vol. 2:278–279.]

Tinnin, R.O. 1998. An alternative to the 6-class dwarf mistletoe rating system. Western Journal of Applied Forestry. 13:64–65.

Tinnin, R.O. 2001. Effect of dwarf mistletoe on bole taper and volume in young Douglas-fir. Western Journal of Applied Forestry. 16(1):5–8.

Tinnin, R.O.; Forbes, R.B. 1999. Red squirrel nests in witches' brooms in Douglas-fir trees. Northwest Naturalist. 80:17–21.

Tinnin, R.O.; Hawksworth, F.G.; Knutson, D.M. 1982. Witches' broom formation in conifers infected by *Arceuthobium* spp.: an example of parasitic impact upon community dynamics. American Midland Naturalist. 107:351–359.

Tinnin, R.O.; Knutson, D.M. 1980. Growth characteristics of the brooms on Douglas-fir caused by *Arceuthobium douglasii*. Forest Science. 26:149–158.

Tinnin, R.O.; Knutson, D.M. 1985. How to identify brooms in Douglas-fir caused by dwarf mistletoe. Res. Note PNW-426. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

Tinnin, R.O.; Parks, C.G.; Knutson, D.M. 1999. Effects of Douglas-fir dwarf mistletoe on trees in thinned stands in the Pacific Northwest. Forest Science. 45(3):359–365.

Tkacz, B.M. 1989. Incorporating pest management into land management decisions. In: Tecle, A.; Covington, W.W.; Hamre, R.H., tech. coords. Multiresource management of ponderosa pine forests; 1989 November 14–16; Flagstaff, AZ. Gen. Tech. Rep. RM-185. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 60–64.

Tong Jun; Ren Wei. 1980. Preliminary studies on the disease cycle of *Arceuthobium chinense*. Journal Yunnan Forestry College. 1:19–25.

Trelease, W. 1916. The genus *Phoradendron*, a monographic revision. Urbana: University of Illinois Press. 224 p.

Tropical Agriculture Research and Training Center. 1992. Forest pests in Central America. Tech. Man. 3. Turrialba, Costa Rica: Tropical Agriculture Research and Training Center. 49 p.

Trummer, L.M.: Hennon, P.E.; Hansen, E.M.; Muir, P.S. 1998. Modeling the incidence and severity of hemlock dwarf mistletoe in 110-year-old wind-disturbed forests in southeast Alaska. Canadian Journal of Forest Research. 28:1501–1508.

Turner, N.J.; Szczawinski, A.F. 1991. Common poisonous plants and mushrooms of North America. Portland, OR: Timber Press: 250.

Unger, L. 1992. Dwarf mistletoes. Forest Pest Leaflet 44. Victoria, BC: Canadian Forest Service. [Online]. Available: http://www.pfc.cfs. nrcan.gc.ca/diseases/hforest/Pests/dmistle_e.html. [2002, June 29].

Urness, P.J. 1969. Nutritional analysis and in vitro digestibility of mistletoes browsed by deer in Arizona. Journal of Wildlife Management. 33(3):499–505.

USDA, NRCS. 2001. The PLANTS database, Version 3.1. [Homepage of Natural Resources Conservation Service, U.S. Department of Agriculture]. [Online]. Available: http://plants.usda.gov/. [2002, July 2].

Valdivia Sanchez, J.J. 1964. Pathogia forestal. I. El muérdago enano (*Arceuthobium* spp.) en los bosques de la zona noreste de Michoacán. Bol. 15. Comision Forestal Michoacan: 1–67.

van der Kamp, B.J.; Hawksworth, F.G. 1985. Damage and control of the major diseases of lodgepole pine. In: Baumgartner, D.M.; Krebill, R.G.; Arnott, J.T.; Weetman, G.F. Lodgepole pine the species and its management, symposium proceedings; 1984 May 8–10 and May 14–16; Spokane, WA, and Vancouver, BC. Pullman WA: Office of Conferences and Institutes, Cooperative Extension: 125–131.

Vandygriff, J.C.; Rasmussen, L.A.; Rineholt, J.F. 2000. A novel approach to managing fuel wood harvest using bark beetle pheromones. Western Journal Applied Forestry. 15(4):183–188.

van Ommeren, R.J.; Whitham, T.G. 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. Oecologia. 130:281–288.

Van Sickle, G.A.; Wegwitz, E. 1978. Silvicultural control of dwarf mistletoes in young lodgepole pine stands in Alberta and British Columbia. Rep. BC-X-180. Victoria, BC: Environment Canada, Canadian Forest Service, Pacific Forestry Centre. 11 p.

Vasek, F.C. 1966. The distribution and taxonomy of three western junipers. Brittonia. 18:350–372.

Vázquez Collazo, I. 1986. Sistema de evaluación de 4 clases para muérdago verdadero (*Psittacanthus* spp.). Archivo Téch. México DF: Secretaría de Agricultura y Recursos Hidráulicos, Instituto Nacional de Investigaciones Forestales y Agropecularis.

Vázquez Collazo, I. 1989. Ciclo biologico y fenologia del muérdago verdadero (*Psittacanthus calyculatus* (DC.) Don) en el C.E.F. Barranca de Cupatitzio. En: V simposio sobre parasitologia forestal; 1989 Octobre 4–6; Juarez, Chih. Mexico, DF: Sociedad Mexicana de Entomogia. 42 p.

Vázquez Collazo, I. 1991. Notas sobre polinazcion y dispersion de *Arceuthobium vaginatum* (Willd.) Presl (Viscaceae). La Ciencia y el Hombre [Universidad Veracruzana]. 8:101–109.

Vázquez Collazo, I. 1993a. Contribución al conocimiento del muérdago verdadero (*Psittacanthus* spp.) en México. En: II simposio sobre detección, evaluación y Manejo de Muérdagos en coníferas. México: Secretaría de Agricultura y Recursos Hidráulicos, SFF.

Vázquez Collazo, I. 1993b. Determinacion de "tipo de sitio" para evaluar rodales infectados por muérdago enano (*Arceuthobium globosum* Hawksworth et Wiens). Ciencia Forestal. 18(73):77–103.

Vázquez Collazo, I. 1994a. Intensidad del muestreo para evauar rodales infestados por muérdago enano (*Arceuthobium globosum* Hawksworth & Wiens). Foll. Tech. 17. Uraupan, Michoacán: Secretaria de Agricultura y Recursos Hidraulicos, Instituto Nacional de Investigaciones Forestales y Agropecuaries, Centro Investigaciones del Pacifico Centro. 23 p.

Vázquez Collazo, I. 1994b. Determinacion de la epoca y dosis del Esteron 47M para el control del muérdago verdadedo (*Psittacanthus calyculatus*) en mezquite (*Prosopis laevigata*). Ciencia Forestal. 19(76):27–50.

Vázquez Collazo, I.; Pérez Chávez, R. 1989. Efecto del parasitismo del muérdago verdadero (*Psittacanthus* spp.) en la producción de semilla de tres especies de pino. En: V simposio sobre parasitologia foresta; 1989 Octobre. 4–6; Juarez, Chihuahua. México, DF: Sociedad Mexicana de Entomogia, AC: 64.

Vázquez Collazo, I.; Pérez Chávez, R.; Pérez Chávez, R. 1982. Efecto del parasitismo del muérdago (*Psittacanthus schiedeanus* Cham. and Schlecht Blume) en el desarrollo de tres especies del género *Pinus*. Ciencia Forestal. 40(7):48–64.

Vázquez Collazo, I.; Pérez Chávez, R.; Pérez Chávez, R. 1985. Efecto del parasitismo del muérdago, *Psittacanthus schiedeanus* (Cham. and Schleicht) Blume, en el desarrollo de tres especies del genero *Pinus*. En: Memoria de los simposia nacionales de parasitologia forestal II y III. Publicacion Especial 46. México, DF: Secretaría de Agricultura y Recursos Hidráulicos: 47–56.

Vázquez Collazo, I.; Perez Chavez, R.; Perez Chavez, R. 1986. Control quimico del muérdago verdadero (*Psittacanthus* sp.) en la Sierra Purepecha (Meseta Tarasca). Ciencia Forestal. 59(1):106–126.

Vega Rojas, E.J. 1976. El muérdago, enfermedad en bosques de conferas y hojosas. Bosques y Fauna. 13(1):3–19.

Venkata Rao, C. 1963. On the morphology of the calyculus. Journal of Indian Botanical Society. 42:618–628.

Vera Gaxiola, F. 1984. Observiones dasmetricas en un rodal de *Pinus hartwegii* Lind. atacado por muérdago. En: Memoria de los simposia nacionales de parasitologia forestal II y III. Publicacion Especial 46. Sociedad Mexicana de Entomologia: 39–46.

Wagener, W.W. 1957. The limitation of two leafy mistletoes of the genus *Phoradendron* by low temperatures. Ecology. 38:142–145.

Wagener, W.W. 1965. Dwarf mistletoe removal and reinvasion in Jeffrey and ponderosa pine, northeastern California. Res. Note PNW-73. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 8 p.

Wagner, M.R.; Mathiasen, R.L. 1985. Dwarf mistletoe-pandora moth interaction and its contribution to ponderosa pine mortality in Arizona. Great Basin Naturalist. 45:423–426.

Wall, R.E. 1994. Biological control of red alder using stem treatments with the fungus *Chondrostereum purpureum*. Canadian Journal of Forest Research. 24:1527–1530.

Wall, R.E.; Prasad, R.; Shamoun, S.F. 1992. The development and potential role of mycoherbicides for forestry. Forestry Chronicle. 68:736–741.

Walters, J.W. 1978. A guide to forest diseases of southwestern conifers. Rep. R3 78-9. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwestern Region, Forest Insect and Disease Management. 36 p.

Wanner, J.; Tinnin, R.O. 1986. Respiration in lodgepole pine parasitized by American dwarf mistletoe. Canadian Journal of Forest Research. 16:1375–1378.

Wanner, J.L. 1986. Effects of infection by dwarf mistletoe (*Arceuthobium americanum*) on the population dynamics of lodgepole pine (*Pinus contorta*). Portland, OR: Portland State University. 103 p. Dissertation.

Wanner, J.L.; Tinnin, R.O. 1989. Some effects of infection by *Arceuthobium americanum* on the population dynamics of *Pinus contorta* in Oregon. Canadian Journal of Forest Research. 19:736–742.

Watson, D.M. 2001. Mistletoe—a keystone resource in forests and woodlands worldwide. Annual Reviews of Ecology and Systematics. 32:219–250.

Weir, J.R. 1915. *Wallrothiella arceuthobii*. Journal of Agricultural Research. 4:369–378.

Weir, J.R. 1916a. Larch mistletoe: some economic considerations of its injurious effects. Bull. 317. Washington, DC: U.S. Department of Agriculture. 25 p.

Weir, J.R. 1916b. Mistletoe injury to conifers in the Northwest. Bull. 360. Washington, DC: U.S. Department of Agriculture. 39 p.

Wellwood, R.W. 1956. Some effects of dwarf mistletoe on hemlock. Forestry Chronicle. 32:282–296.

Whiting, A.F. 1950. Ethnobotany of the Hopi. Bull. 15 (revised). Flagstaff, AZ: Museum of Northern Arizona. 120 p.

Wicker, E.F. 1967a. Seed density as a klendusic factor of infection and its impact upon propagation of *Arceuthobium* spp. Phytopathology. 57:1164–1168.

Wicker, E.F. 1967b. Appraisal of biological control of *Arceuthobium campylopodum* f. *campylopodum* by *Colletotrichum gloeosporioides*. Plant Disease Reporter. 51:311–313.

Wicker, E.F. 1974. Ecology of dwarf mistletoe seed. Res. Pap. INT-154. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 28 p.

Wicker, E.F.; Hawksworth, F.G. 1988. Relationships of dwarf mistletoes and intermediate stand cultural practices in the Northern Rockies. In: Schmidt, W.C., comp. Proceedings, future forests of the Mountain West: a stand culture symposium; 1986 September 29–October 3; Missoula, MT. Gen. Tech. Rep. INT-243. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 402 p.

Wicker, E.F.; Hawksworth, F.G. 1991. Upward advance, intensification and spread of dwarf mistletoe in a thinned stand of western larch. Res. Note RM-504. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 4 p.

Wicker, E.F.; Shaw, C.G. 1968. Fungal parasites of dwarf mistletoes. Mycologia. 60:372–383.

Wiens, D. 1964. Revision of the acataphyllous species of *Phoradendron*. Brittonia. 16:1–54.

Wiens, D. 1970. *Phoradendron*. In: Correll, D.S.; Johnston, M.C. Manual of the vascular plants of Texas. Renner: Texas Research Foundation: 504–505.

Wiens, D.; Barlow, B.A. 1971. The cytogeography and relationships of the viscaceous and eremolepidaceous mistletoes. Taxon. 20:313–332.

Wiens, D.; Calvin, C.L. 1987. Epiparasitism in mistletoes. Golden Bough (Royal Botanic Gardens, Kew). 9:3–5.

Wiens, D.; DeDecker, M. 1972. Rare natural hybridization in *Phoradendron* (Viscaceae). Madroño. 21:395–402.

Wiens, D.; Hawksworth, F.G. 1990. *Phoradendron* sect. *Pauciflorae* (Viscaceae): new species and combinations. Unpublished manuscript, October 18. 19 p.

Wiens, D.; Nickrent, D.L.; Shaw, C.G., III.; Hawksworth, F.G.; Hennon, P.E.; King, E.J. 1996. Embryonic and host-associated skewed adult ratios in dwarf mistletoe. Heredity. 77:55–63.

Wiens, D.; Shaw, C.G., III. 1994. *Arceuthobium hawksworthii* (Viscaceae), a new species of dwarf mistletoe from Belize. Journal of Idaho Academy of Science. 30(1):25–32.

Wiggins, I.L. 1980. Flora of Baja California. Stanford, CA: Stanford University Press: 139–141.

Wilcox, W.W.; Pong, W.Y.; Parmeter, J.R. 1973. Effects of mistletoe and other defects on lumber quality in white fir. Wood and Fiber. 4:272–277.

Wilson, C.A.; Calvin, C.L. 1996. Anatomy of the dwarf mistletoe shoot system. In: Hawksworth, F.G.; Wiens, D. Dwarf mistletoes: biology, pathology, and systematics. Agric. Handb. 709. Washington, DC: U.S. Department of Agriculture, Forest Service: 95–111.

Wilson, C.L. 1969. Use of plant pathogens in weed control. Annual Review of Phytopathology. 7:411–434.

Wilson, J.L.; Tkacz, B.M. 1992. Pinyon ips outbreak in pinyon juniper woodlands in northern Arizona: a case study. In: Ffolliott, Peter F.; Gottfried, Gerald J.; Bennett, Duane A.; Hernandez C., Victor Manuel; Ortega-Rubio, Alfredo; Hamre, R. E., tech. cords. Ecology and management of oak and associated woodlands: perspectives in the Southwestern United States and Northern Mexico. Gen. Tech. Rep. RM-218. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 187–190.

Wittwer, D., comp. 2002. Forest insect and disease conditions in Alaska—2001 R10-TP-102. Anchorage, AK: U.S. Department of Agriculture, Forest Service, Alaska Region. 65 p.

Wood, C. 1986. Distribution maps of common tree diseases in British Columbia. Inf. Rep. BC-X-281. Victoria, BC: Canadian Forestry Service, Pacific Forestry Centre. 68 p.

Wood, R.E.; Shuft, M.J.; Schultz, D.E. 1979. An evaluation of tree mortality in Laguna Mountain Recreation Area. Insect and Disease Management Rep. 79-1. San Francisco: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Cleveland National Forest. 22 p.

Wright, E. 1942. *Cytospora abietis*, the cause of a canker of true firs in California and Nevada. Journal Agricultural Research. 65:143–153.

Zavala, I.; Zavala, M.A. 1993. Global positioning system as a tool for ecosystem studies at the landscape level: an application in the Spanish Mediterranean. Landscape and Urban Planning. 24:95–104.

Zimmerman, G.T.; Laven, R.D. 1984. Ecological interrelationships of dwarf mistletoe and fire in lodgepole pine forest. In: Hawksworth, F.G.; Scharpf, R.F., tech. coords. Biology of dwarf mistletoes: proceedings of the symposium; 1984 August 8; Fort Collins, CO. Gen. Tech. Rep. RM-111. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 123–131.

Zimmermann, G.T.; Laven, R.D.; Omi, P.N.; Hawksworth, F.G. 1990. Use of prescribed fire for dwarf mistletoe control in lodgepole pine management. In: Alexander, M.E.; Bisgrove, G.F., tech. coord. The art and science of fire management; 1988 October 24–27; Kananaskis, AB. Info. Rep. NOR-X-309. Edmonton, AB: Forestry Canada, Northern Forestry Centre: 163–174.

Appendix B: Scientific and Common Names of Trees

Abies amabilis Douglas ex J. Forbes[a]	Pacific silver fir
Abies balsamea (Linnaeus) Miller[a]	balsam fir
Abies bifolia A. Murray[a]	Rocky Mountain subalpine fir
= *Abies lasiocarpa* var. *arizonica* (Merriam) Lemmon	corkbark fir
Abies concolor (Gordon & Glendinning) Hildebrand[a]	white fir
Abies durangensis Martinez[c]	Durango fir
Abies grandis (Douglas ex D. Don in Lambert) Lindley[a]	grand fir
Abies lasiocarpa (Hooker) Nuttall[a]	subalpine fir
Abies lowiana (Gordon) A. Murray[a]	Sierra white fir
= *Abies concolor* var. *lowiana* (Gordon) Lemmon	
Abies magnifica A. Murray[a]	California red fir
Abies procera Rehder[a]	noble fir
Abies religiosa Lindley[c]	sacred fir
Abies religiosa var. *emarginata* Loock & Martinez[c]	
Abies vejarii Martinez[c] [as *vejari*]	Vehar fir
Abies vejarii subsp. *mexicana* (Martinez) A. Farjon[c]	Mexican fir
=*Abies mexicana* Martinez	
Calocedrus decurrens (Torrey) Florin[a]	incense-cedar
Cupressus arizonica Greene[a]	Arizona cypress
Cupressus arizonica var. *montana* (Wiggins) Little[c]	cypress
Cupressus bakeri Jepson[a]	Baker cypress
Cupressus benthami Endlicher[c]	cypress
Cupressus goveniana Gordon[a]	Gowen cypress
Cupressus lusitanica Miller[c]	cypress
Cupressus macnabiana A. Murray[a]	MacNab cypress
Cupressus macrocarpa Hartweg[a].	Monterey cypress
Cupressus sargentii Jepson[a]..	Sargent cypress
Juniperus ashei J. Bucholtz[a]	Ashe juniper
Juniperus ashei var. *saltillensis* (H.M. Hall) Silba[c]	
Juniperus californica Carrière[a]	California juniper
Juniperus deppeana Steudel[a]	alligator juniper
Juniperus flaccida Schlechtendal[a]	drooping juniper
Juniperus monosperma (Engelmann) Sargent[a]	one-seed juniper
Juniperus occidentalis Hooker[a]	western juniper
Juniperus osteosperma (Torrey) Little[a]	Utah juniper
Juniperus pinchotii Sudworth[a]	Pinchot juniper
= *Juniperus erythrocarpa* Cory	
Juniperus scopulorum Sargent[a]	Rocky Mountain juniper
Larix decidua Miller[c]	European larch
Larix leptolepis (Sieb. & Zuccarini) Gordon[c]	Japanese larch
=*Larix kaempfer* (Lambert) Sargent[c]	
Larix laricina (Du Roi) K. Koch[a]	tamarack
Larix occidentalis Nuttall[a]	western larch
Picea abies (Linneaus) H. Karsten[a]	Norway spruce
Picea breweriana S. Watson[a]	Brewer spruce
Picea engelmannii Parry ex Engelmann[a]	Engelmann spruce
Picea glauca (Moench) Voss[a]	white spruce
Picea mariana (Miller) Britton, Sterns, & Poggenburg[a]	black spruce
Picea mexicana Martinez[c]	Mexican spruce
Picea pungens Engelmann[a].	blue spruce
Picea rubens Sargent[a]	red spruce
Picea sitchensis (Bongard) Carrière[a]	Sitka spruce
Pinus albicaulis Engelmann[a]	whitebark pine
Pinus aristata Engelmann[a]	Colorado bristlecone pine
Pinus arizonica Engelmann[b]	Arizona pine
= *Pinus ponderosa* var. *arizonica* (Engelmann) Shaw[a]	
Pinus arizonica var. *stormiae* Martinez[b]	pino real
Pinus attenuata Lemmon[a].	knobcone pine
Pinus ayacahuite C. Ehrenberg ex Schlechtendal[b]	Mexican white pine
Pinus ayacahuite var. *brachyptera* Shaw[b]	
Pinus balfouriana Greville & Balfour[a]	foxtail pine
Pinus balfouriana subsp. *australis* Mastoguiseppe & Mastoguiseppe	Sierra foxtail pine
Pinus banksiana Lambert[a]	jack pine
Pinus bungeana Zuccarini[c]	lacebark pine
Pinus californiarum D. K. Bailey[c]	singleleaf pinyon
Pinus californiarum subsp. *fallax* (Little) D. K. Bailey[c]	Arizona singleleaf pinyon
Pinus caribaea Morelet	Caribbean pine
Pinus caribaea var. *hondurensis* (Sénécl) Barr. & Golf.[b]	Honduras Caribbean pine
Pinus cembroides Zuccarini[b]	Mexican pinyon
Pinus cembroides subsp. *orabensis* D. K. Bailey[b]	Orizaba pinyon
=*Pinus orizabensis* (D. K. Bailey) D. K. Bailey & Hawksworth	
Pinus contorta Dougl. ex Loudon[a]	lodgepole pine

Pinus contorta var. *contorta*[a]	shore pine
=*Pinus contorta* subsp. *bolanderi* (Parlatore) Critchfield[a]	Bolander pine
Pinus contorta var. *murrayana* (Grenville & Balfour) Engelmann[a]	Sierra lodgepole pine
Pinus contorta var. *latifolia* Engelmann in S Watson[a]	lodgepole pine
Pinus cooperi Blanco[b]	pine amarillo
Pinus coulteri D. Don[a]	Coulter pine
Pinus culminicola Andresen & Beaman[b]	Potosi pinyon
Pinus discolor Bailey & Hawksworth[b]	border pinyon
Pinus douglasiana Martinez[b]	pino
Pinus durangensis Martinez[b]	ocote
Pinus edulis Engelmann[a]	pinyon
Pinus engelmannii Carrière[a]	Apache pine
Pinus flexilis E. James[a]	limber pine
Pinus halepensis Miller[c]	Aleppo pine
Pinus hartwegii Lindley[b]	Hartweg pine
Pinus herrerai Martinez[b]	ocote
Pinus jaliscana Perez de la Rosa[b]	Jalisco pine
Pinus jeffreyi Greville & Balfour in A. Murray[a]	Jeffrey pine
Pinus lambertiana Douglas[a]	sugar pine
Pinus lawsonii Roezl ex Gordon & Glendinning[cb]	pino
Pinus leiophylla Schiede & Deppe[a]	pine chino
Pinus leiophylla var. *chihuahuana* (Engelmann) G.R. Shaw[a]	Chihuahua pine
Pinus longaeva D. K. Bailey[a]	Intermountain bristlecone pine
Pinus lumholtzii Robins & Fern.[b]	pino triste
Pinus maximinoi H. E. Moore[b]	pino
Pinus michoacana Martinez[b]	pino lacio
Pinus monophylla Torrey & Fremont[a].	singleleaf pinyon
Pinus montezumae Lambert[b]	Montezuma pine
Pinus monticola Douglas ex D. Don[a]	western white pine
Pinus mugo Turra[c]	dwarf mountain pine
Pinus muricata D. Don[a]	Bishop pine
Pinus oaxacana Mirov[b]	pino chalmaite
Pinus occidentalis Swartz[c]	West Indian pine
Pinus oocarpa Schiede[b]	pino prieto
Pinus oocarpa var. *ochoterenia* Martinez [b]	
Pinus oocarpa var. *microphylla* Shaw[b]	
=*Pinus praetermissa* Styles & McVaugh[c]	
Pinus palustris Miller[a]	longleaf pine
Pinus patula Schl. & Chamisso[b]	pino triste
Pinus pinea Linneaus[c].	Italian stone pine
Pinus ponderosa Douglas ex Lawson & C. Lawson[a]	ponderosa pine
Pinus ponderosa var. *scopulorum* Engelmann in S. Watson[a]	Rocky Mountain ponderosa pine
Pinus pringlei Shaw[b]	pino rojo
Pinus pseudostrobus Lindley[b]	pino
Pinus quadrifolia Parlatore[b]	Parry pinyon
Pinus radiata D. Don[a]	Monterey pine
Pinus resinosa Aiton[a]	red pine
Pinus rudis Endlicher[b]	pino
Pinus sabiniana Douglas ex D. Don in Lambert[a]	digger pine
Pinus strobiformis Engelmann[a]	southwestern white pine
Pinus strobiformis var. *potosiensis* Silba[c]	
Pinus strobus Linnaeus[a]	eastern white pine
Pinus sylvestris Linnaeus[a].	Scotch pine
Pinus tecunumanii (Schwertfeger) Equiluz & Perry[b]	pino
Pinus teocote Schl. & Chamisso[b]	ocotl
Pinus thunbergii Parlatore	pine
Pinus torreyana Parry ex Carrière[a]	Torrey pine
Pinus virginiana Miller[a]	Virginia pine
Pinus washoensis H. Mason & Stockwell[a]	Washoe pine
*Pseudotsuga macrocarpa (*Vasey) Mayr[a]	bigcone Douglas-fir
Pseudotsuga menziesii (Mirbel) Franco[a]	Douglas-fir
Pseudotsuga menziesii var. *menziesii*	coast Douglas-fir
Pseudotsuga menziesii var. *glauca* (Mayr) Franco[a]	Rocky Mountain Douglas-fir
Taxodium distichum (L.) Richard var. *mexicanum* Gordon[a]	Mexican bald-cypress
=*Taxodium mucronatum* Tenore	
Tsuga heterophylla (Rafinesque) Sargent[a]	western hemlock
Tsuga mertensiana (Bongard) Carrière[a]	mountain hemlock

[a] Flora of North America Committee (1993)
[b] Perry (1991)
[c] Plant Names Project (1999)

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Appendix D: Glossary

Baranyay and others (1971) provide a complete glossary of terms and special definitions that apply to mistletoes. Although most of our readers ought to be familiar with the concepts and terms of forestry, they may be less comfortable with a number of other terms used here. These are primarily botanical and plant pathology terms or words with a special application in this context.

Abundance. See incidence.

Acuminate apex. Tapering to a point with the sides more or less pinched in before reaching the tip.

Adnate. The union of unlike parts, as an inferior ovary to the calyx tube.

Allozymes. Similar proteins that provide a physiochemical trait for investigating the population genetics of groups of plants (hosts or parasites).

Anamorph. An imperfect stage of a fungus that is taxonomically described and provides a basis for identification and referral.

Anthesis. Period when the flower is open.

Ascospore. A spore of a fungus produced within an ascus, a saclike cell of ascomycetes in which, following meiosis, a specific number (usually eight) of ascospores is produced.

Autocorrelation, spatial. A quantification of a relation between two entities whereby the similarity of a feature depends on the distance between the entities. Because of mistletoe spread and intensification, the severities of mistletoe infection on two neighbor trees tend to be more or less similar, or spatially autocorrelated.

Bark strand. A structure that ramifies throughout the inner bark of the host and from which shoots and sinkers of the mistletoe are derived.

Blight. Rapid discoloration and death of all parts of a plant.

Bootstrapping. A statistical processing method using iteration and repeat calculation to estimate variation.

Branch girdle, segment. Girdle refers to a region on a vegetative branch or main stem of a conifer between two annual growth segments; segment refers to a single year's growth of a vegetative branch or main stem.

Brooming. See witches' broom.

Callus. Undifferentiated plant tissue, usually as grown in a laboratory with artificial media.

Calyculus. A floral structure of the Loranthaceae, a vestigial whorl of bracts of the suppressed flowers of a lateral branch inflorescence that have become adnate to the inferior ovary.

Canker, mistletoe canker. The structure and malformation of a host stem or branch caused by a disruption of the cambium and bark as a result of dwarf mistletoe infection.

Cordate. A shape of a leaf like a stylized heart.

Cortex. Ground-tissue region of a stem or root bounded externally by epidermis and internally by the vascular system; a primary-tissue region.

Decussate. Of leaves or scale-like leaves that are arranged in pairs that alternately cross each other.

Disjunct. Pertaining to a discontinuous range having two or more potentially interbreeding populations separated by a distance that precludes genetic exchange by pollination or dissemination.

Dyads. See monads.

Endemic. The kind of distribution for taxa that is geographically small.

Endophytic system. The root system parts of a dwarf mistletoe within host tissues. The endophytic system consists of bark strands within the inner bark and "sinkers" that are embedded in successively formed layers of xylem, referred to as haustorial root system or haustorium.

Endosperm. A tissue, containing stored food, that develops from the union of a sperm nucleus and the polar nuclei of the central cell; it is digested by the growing sporophyte either before or after the maturation of the seed; found only in angiosperms.

Epigynous. Growing, or appearing to grow, on the summit of the ovary.

Flabellate branching. Fan shaped, a branching pattern produced by the continued development of superposed axillary buds.

Flowering, direct and indirect. Indirect flowering is the result of an intervention of a rest period between initiation of a floral bud and anthesis, whereas direct flowering is the result of uninterrupted development of floral buds from initiation to anthesis.

Frass. Solid larval insect excrement.

Fusiform. Spindle-shaped; broadest at the middle and tapering at both ends.

Glabrous. Smooth, no hairs present.

Glaucous. Covered with a whitish or bluish waxy covering.

Growth loss. An expression of yield reduction that includes both lost annual production on still living trees and lost volume to tree death.

Growth, primary and secondary. The growth of shoots and roots from inception until completion of their expansion is primary growth. This growth is the result of apical meristems and their three primary derivative meristems (protoderm, ground meristem, and procambium). Secondary growth results from divisions of secondary meristems (typically the vascular cambium and phellogen) and adds circumference to the plant body.

Haustorium, primary and secondary. The primary haustorium is a wedge-like projection, arising from the circular attachment disc of the radicle, that penetrates the outer bark extending to the host xylem. Secondary haustoria are "sinkers" produced by bark strands that grow radially to the vascular cambium.

Holdfast. A disc-like swelling at the distal end of the radicle through which infection of the host occurs.

Host susceptibility. A subjective classification system based on the percentage of trees of the host species in question that are infected by dwarf mistletoe within 6 m of a principal host heavily infected with the same species of dwarf mistletoe.

Hyphae. Tubular threads of the mycelium of a fungus or similar organism.

Hypocotyl. Region of an embryo that is between the radicle and the attachment point of the cotyledons.

Incidence, abundance, distribution, severity. Incidence refers to the frequency of which host trees in a given stand are infected by a given species of mistletoe (usually measured as percent of trees infected). Abundance refers to the relative quantity of mistletoe in a stand or on a host (not usually quantified). Distribution describes the spatial extant and pattern of a mistletoe species or population within a given area. Severity is a qualitative term describing the disease situation (see infection class); high incidence along with large abundance would result in a severe disease situation.

Incubation period. That period from infection to production of first shoots. See latency.

Infection class. A measure (generally from 0 to 6) of the relative severity of dwarf mistletoe infection for individual trees, in contrast to host susceptibility class.

Infection, secondary infection, localized and systemic infections. Infection refers to that process in which dwarf mistletoes successfully penetrate host tissue and initiate establishment of the endophytic system; infection also refers to the mistletoe plant and the associated diseased host tissues. Secondary infection is reinfection by dwarf mistletoe of already infected tissue. Localized infections (anisophasic) are those in which the endophytic system is generally restricted to within or near (such as a few centimeters) the swollen portion of the host, whereas systemic infections (isophasic) are those in which the endophytic system occurs within the host terminal bud, and growth keeps pace with that of the host's shoot apices.

Infestation. A condition in which one or more trees of a stand or group are infected.

Intensification. Increase in the number of dwarf mistletoe infections within a tree (see spread).

Internode. See node.

Latency. Phenomenon in which host tissues are infected by dwarf mistletoe but either visible symptoms of swelling or brooming are not apparent or shoots are not present. Infections are latent during the incubation period and when environmental conditions induce a cessation in production of shoots.

Lenticel. A group of loose corky cells formed beneath the epidermis of woody plants; allows gas exchange to occur across the periderm.

Ligulate. A property of a leaf, petal, or similar structure whereby the structure possesses a small membranous appendage.

Meiosis. The chromosome reduction stage in formation of gametes.

-Merous. A suffix indicating division into parts; a five-merous flowers would have five sepals, five petals, five stamens and a five-carpellate pistil (providing all these structures were present).

Monads, dyads, triads. Sets of flowers arising from a common peduncle, in singles (monads), pairs (dyads), or triples (triads).

Mycelial stroma. A mass of vegetative hyphae in or on which spores are produced.

Mycoherbicide. A plant-killing substance based on the action of live fungi that induce disease.

Mycorrhizae. Fungus-root, a symbiotic relation of a fungus and plant root.

Node, internode. A region of the stem where a leaf or leaves diverge; the region in between nodes is an internode.

Obovate. A shape of a leaf like an oval, wider at one end (stylized egg).

Parasite, parasitism. A parasite is an organism, such as a mistletoe, that obtains sustenance from another organism, and also completes all, or at least some, of its life cycle on that host organism. Parasitism is the typical mode of existence or behavior of a parasite.

Pathosystem. A biotic combination consisting of a host and a pathogen; the reference is to the pair of organisms rather than the nature of their relationship.

Pedicel. The stalk of an individual flower.

Peduncle. The stalk of an inflorescence (basal to a pedicel).

Penetration wedge. A structure in dwarf mistletoes that develops from the holdfast and initiates the infection process.

Pericarp. The wall of the ripened ovary (fruit); consists of three layers, the exocarp (outer), mesocarp (middle), and endocarp (inner).

Periderm, necrophylatic. A bark, cortex tissue that reacts to invasion by rapid, localized necrosis (isolating the potential pathogen).

Phloem, primary and secondary. The principal food-conducting tissue of a plant composed mainly of sieve elements, various kinds of parenchyma cells, fibers, and sclereids. Primary and secondary phloem are formed during primary and secondary growth, respectively.

Phyllotaxy. The morphological arrangement of leaves.

Pistillate, stigma. Referring to the female flower, which includes an ovary, pistil, style, and stigma (which receives the pollen).

Primary growth. See growth.

Pubescence, trichomes, puberulent, papillate-hispid, stellate. Hair-like structures on a plant surface are epidermal glands called trichomes. A surface that bears trichomes is pubescent or puberulent if the hairs are thin and sparse or papillate-hispid if it has “hairy bump.” Stellate hairs have a stalk and three or more branches from a common point.

Radicle. See holdfast.

Severity. See incidence.

Sessile. Of a leaf that appears attached directly to the stem, without a petiole.

Sinker. A radially oriented structure, composed of tracheary and parenchymal elements, that originates from a dwarf mistletoe bark strand and grows centripetally to the cambium where it becomes embedded by successive layers of xylem.

Source–sink. In the context of the mistletoe–tree interaction, the tree is the source or supplier of water and nutrients to the mistletoe, and the mistletoe plays the role of sink or depository of water and nutrients taken up by the host tree.

Spike, determinate, indeterminate spike. The unbranched inflorescence of a mistletoe of indeterminate type when flowering proceeds from the base while younger flowers are formed as the spike continues to elongate or of determinate type otherwise.

Sporodochia, conidial. An asexual reproductive structure of a fungus that produces spores by a budding process.

Spread, vertical spread. Increase in the area of mistletoe infestation by infection of additional host trees. Vertical spread refers to the net result of dispersal of mistletoe seeds to higher portions of the host crown.

Staminate. Referring to the male flower, which produces pollen.

Stigma. See pistillate.

Symbiont. A member of a close biotic relation whereby both species benefit, such as in mycorrhizae, and in contrast to a pathogen that benefits to the harm of the host. The terms of these forms of mutualisms — symbiosis and parasitism — are relative and contextual.

Sympatry. The condition in which the distributions of two species overlap and hybridization between taxa would be possible if they were not reproductively isolated by factors other than spatial separation.

Synonymy. See taxonomy.

Systematics. See taxonomy.

Systemic infection (isophasic). Infection in which growth of the endophytic system keeps pace with the growth of the infected host branch. See infection.

Taxon (plural, Taxa). A taxonomic unit of any rank (order, family, genus, species, subspecies, and so forth).

Taxonomy, systematics, synonymy. Taxonomy refers to the valid assignment of names to organisms based on natural relations and rules of convention; systematics refers to the natural relations based on decent from a common ancestor. Several (taxonomic) names may be used for an individual plant or population of plants. One name will be preferred (for reasons dealing with the inferred relations and application of conventions); other names are synonyms.

Terete. Of a stem, approximately cylindrical but tapering at ends.

Trichomes. See pubescence.

Triads. See monads.

Verticillate branching. Whorled, a branch pattern produced by the continued development of superposed axillary buds.

Vertical spread. See intensification.

Viscin. Sticky material contained in the viscin cells of dwarf mistletoe fruit, which acts as the initial means of seed attachment to the host.

Witches' broom. An abnormally profuse, dense mass of host branches. This is a common symptom induced by dwarf mistletoe infection, as well as other parasites and abiotic agents.

Woodrose. An ornamental object composed of the host wood deformed by a mistletoe haustorium and exposed by removing the mistletoe tissue.

Appendix E: Index

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RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

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