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Mistletoes

Pathology, Systematics, Ecology, and Management

Mistletoes are familiar to most Europeans and North Americans because of the Christmas folklore associated with these parasitic flowering plants (33,116). Some may also know these plants are parasites of trees but do not realize that mistletoes are widespread, ecologically important components of forests worldwide. Although some mistletoe species are damaging pathogens, most do not impact economically valuable crops and forest products but actually play key roles in forest ecosystems. Particularly in Loranthaceae, coevolutionary relationships with birds (involving pollination and seed dispersal) have fueled several adaptive radiations, thus producing one of the most diverse and fascinating life forms on our planet. Here we summarize mistletoe biology, pathology, and management as well as current ecological concepts and their evolution as revealed by molecular phylogenetics.

What Is a Mistletoe?

We define a mistletoe as a parasitic flowering plant found in the sandalwood order (Santalales) that attaches to the stem of another plant (primarily gymnosperms and angiosperms). Other angiosperms, such as *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae), also attach to host stems, but these are not considered mistletoes. Thus, the term mistletoe describes a particular plant habit (an aerial parasite) as well as a member of a specific taxonomic group. Although all mistletoes are in Santalales, this habit evolved five times independently therein, thus they are not monophyletic. Even within the Loranthaceae, the family with the most genera of mistletoes, three genera attach only to roots and therefore by our definition cannot be called mistletoes. And finally, genera such as *Tripodanthus* that attach to both stems and roots stretch the definition yet further and demonstrate nature's abhorrence of human categorization. Recent molecular phylogenetic work has greatly clarified our concepts of which members of Santalales are mistletoes and how they are related to one another.

Mistletoe Biology

Infection. The basic biology of mistletoes is remarkable. Host infection has been described in detail for some groups and not others, but is considered to be similar for all mistletoes (33,74,92,112,116,122). Upon germination, seeds form a hypocotyl that elongates until it forms a holdfast that attaches firmly to the host branch. As for other flowering plants, seed germination is influenced by temperature, moisture, and light (122). The seeds of mistletoes in the Viscaceae have a chlorophyllous endosperm and embryo and so are capable of producing simple sugars as an energy source after germination (122). A penetration peg develops on the lower surface of the holdfast that mechanically penetrates the epidermis or bark, eventually contacting the host's phloem and/or xylem. Penetration of host tissue is evidently purely by mechanical means, as no chemical breakdown of host tissue has been identified thus far. Once the mistletoe has entered host tissue, it develops its haustorium and then aerial shoots. Many tropical mistletoes begin forming shoots soon after they establish their connection to their host, while the dwarf mistletoes may take 2 to 6 years to form aerial shoots.

Pollination. Mistletoes are pollinated by biotic agents (primarily birds and insects) as well as wind. Many tropical and subtropical mistletoes in Loranthaceae have large, colorful flowers borne in groups that produce large amounts of sugar-rich nectar that attract avian pollinators (Fig. 1A and B). Elaborate pollination and seed dispersal mechanisms involving birds have evolved in some of these loranth species (69,79,104,109,121,144,176). For example, birds pry open the fused corollas to reach their nectar reward, upon which the pollen "explodes" onto the bird's head (109,121). These mistletoes are often dichogamous (protandrous), and after the birds have visited flowers in the male phase, they eventually visit flowers in the female phase, thereby effecting pollination. The coevolutionary relationship between mistletoes and their bird pollinators is so closely linked that disruption of this association could have long-term negative consequences for both interacting organisms and possibly the entire ecosystem (179,219). However, many bird-pollinated mistletoes are serviced by a broad range of species, and no bird can be considered a mistletoe pollen specialist (219). In Mexico, Central America, and South America, hummingbirds are key pollinators of mistletoes with large, showy red or yellow flowers (15,111,204). A variety of insects are the key pollinators of mistletoes in the Viscaceae and Loranthaceae (74,116). While mammals are known to visit flowers, they have not yet been positively implicated as mistletoe pollinators. Bats are the most likely mammal pollinators of

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doi:10.1094/PDIS-92-7-0988

mistletoes, but studies have not yet confirmed their role in this process (138).

Dispersal. The coevolution of mistletoes with their avian vectors has resulted in attractive and nutritious fruits that provide valuable food for many bird species throughout the world (49,120,134,178, 179,201,220). The mature fruits of mistletoes are brightly colored (usually white, yellow, red, blue, or purple) (Fig. 1C), and their seeds are coated with a natural "glue," termed viscin (116,178). Birds either swallow mistletoe fruits whole, peel off the outer exocarp and ingest the seed and viscin, or eat only the viscin coating around the seed (116,178,199,200,220). Once the bird has eaten the seed, it is either regurgitated or defecated, but the seed is still covered with some of its viscin coat, which allows it to adhere to potential hosts. In many instances, seeds adhering to a bird's beak, legs, or feathers are rubbed off onto a branch of a potential host. Approximately 90 bird species from 10 families are considered mistletoe fruit specialists, exhibiting a range of behavioral and morphological adaptations to their narrow diet. Most of these groups are represented by four or fewer species, except the flowerpeckers (Dicaeidae) of Asia (44 species) (Fig. 2A) and the euphonias (Carduelinae) of Latin America (33 species). While most discussion of mistletoe dispersal is typically restricted to these dietary specialists, a wide range of other avian species disperse their seeds (219,220), accounting for all dispersal in Europe and most regions of North America. Within the United States, vectors of *Phoradendron* spp. (Viscaceae) are fairly well known (74,89,189), but only a few studies have examined in any detail the relationships between birds and *Phoradendron* (12,14). For many mistletoes, particularly those in Central and South America, the key vectors have not been investigated to any large extent (but see 52,139,180). The control of economically damaging mistletoes in managed areas is often confounded by their reintroduction by birds (74). In South and North America, animals other than birds have also been implicated in the dispersal of mistletoe seeds. In South America, a marsupial disperses seeds (4), and in North America, squirrels and other mammals have been shown to rarely disperse dwarf mistletoe seeds adhering to their fur (92,136,198).

Host distribution, size, or sex may influence mistletoe distribution and abundance (11,12). For example, when hosts are widely scattered, their mistletoe parasites may be less common and widely distributed as well. Birds that disseminate mistletoes often perch at the tops of the larger trees, thus depositing mistletoe seeds high in the canopy. For dioecious tree species, bird visitation may be biased in favor of fruiting plants, thereby influencing overall mistletoe distribution (39). Furthermore, the consistent availability of mistletoe fruits can attract birds which also feed on the host's fruits (213). This favors the spread of seeds from infected hosts over noninfected hosts during years when susceptible trees have not produced an abundance of fruits. It has been suggested that when the seeds of infected trees are also spread by mistletoe vectors and this is correlated with greater tree regeneration, the relationship between the mistletoe and host tree approaches mutualism (213). Recent studies have also suggested other intriguing hypotheses regarding the interactions among host morphology, bird behavior, and mistletoe dispersal in South America (133,139). This work suggests

Fig. 1. The colorful flowers and fruits of mistletoes attract birds. A, Many tropical and subtropical mistletoes have large, colorful flowers that are arranged in groups and produce large amounts of sugar-rich nectar that attract pollinating birds. B, Bright red flowers of *Amyema miquelli*, a common mistletoe throughout the arid regions of inland Australia. C, Fruits of *Psittacanthus cucularis* are bright blue, which attracts birds that disperse its seeds.

that spine length of columnar cacti acts as a deterrent to infection by *Tristerix aphyllus* because the bird-disperser of this mistletoe avoids cacti with very long spines.

In contrast to most mistletoes, the dwarf mistletoes are primarily disseminated by an "explosive fruit" system involving both hydrostatic and mechanical mechanisms (92,94). Dwarf mistletoe seeds are expelled from fruits at initial velocities of about 24 m/s and may fly 10 m or more (Fig. 2B). These seeds are also coated with viscin, which allows them to adhere to potential host surfaces. Factors affecting the spread and intensification of dwarf mistletoes associated with both the explosively disseminated seed mechanism and random spread by seeds sticking to animal vectors have been summarized by several investigators (92,136,167). These two mechanisms contribute differently to the spread of dwarf mistletoes, the former producing primarily localized intensification and the latter contributing to occasional establishment of new infection centers (136).

The epidemiology of bird-dispersed mistletoes has been more intensively studied in the last 10 years than previously (13), and much of this work has been summarized by Aukema (11). Aukema (12) and Aukema and Martinez del Rio (14) conducted detailed experimental research on the spread and intensification of a bird-disseminated mistletoe (*Phoradendron californicum*) in Arizona. She found that seed-dispersing birds favored larger infected trees as perching and feeding sites and deposited seeds disproportionately on them. This contributed to the distribution of the mistletoe being significantly aggregated within its host population (14). One area of mistletoe epidemiology that warrants further attention is the contribution of "seed rain" from mistletoe plants occurring high in host canopies on intensification of mistletoe populations within individual hosts (13).

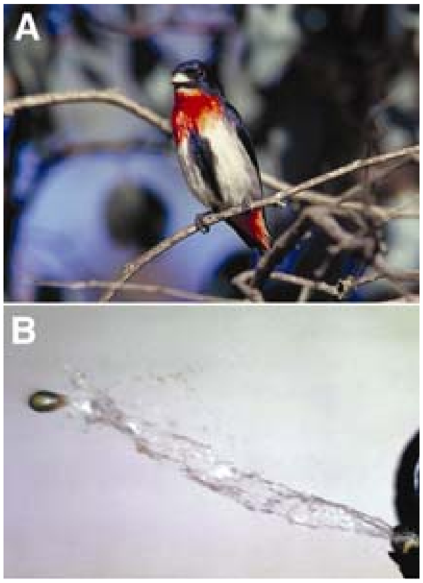

Fig. 2. Mistletoe seed dispersal: A, As the primary seed dispersers in Australia, mistletoebirds (*Dicaeum hirundinaceum*) have specialized digestive tracts through which seeds pass in just a few minutes. (Photo by G. Dabb) B, Dwarf mistletoe seeds are expelled from fruits at initial velocities of about 24 m/s and may fly as far as 10 m or more. (Photo courtesy of USDA Forest Service)

The haustorium. All mistletoes produce a morphologically diverse structure that allows them to interface with their hosts: the haustorium (34,35,36,37,66,67, 80,110,116,117,206,225). Calvin and Wilson (37) described four basic haustorial system types that are found in aerial parasitic mistletoes: (i) epicortical roots that grow along a host branch surface and at intervals form haustoria; (ii) clasping unions where the mistletoe haustorium enlarges, partly encircling a branch; (iii) wood roses where host tissue enlarges forming a placenta to which the mistletoe's haustorium attaches; and (iv) bark strands that spread within the host bark and connect to host xylem and phloem (see also 228). Plants with wood roses, clasping unions, and bark strands are often described as having "solitary unions" with their hosts (66). In contrast, plants with epicortical roots have multiple, visible haustorial connections to their hosts (36,37,66). Because of the diversity and possible phylogenetic implications of the morphology of the mistletoe haustorium, investigators have continued study of these diverse and intricate connections between mistletoes and their hosts (37,119,224).

Mistletoes as Pathogens

The physiology of infection. Competition for water and nutrients is the most obvious explanation for the deleterious effects mistletoes have on their hosts. High transpiration rates by mistletoes cause reduced xylem water potentials in host branches, which reduces net photosynthetic rates of the host (110,112,202,211). Mistletoes generally have higher leaf transpiration and stomatal conductance than their hosts (112,202). Accumulation of osmotically active solutes in mistletoe tissue also promotes lower xylem water potential in their tissue compared with the host, further facilitating absorption of water and solutes. These parasites can decrease xylem hydraulic conductivity of host branches distal to the point of infection. This can cause the end of the branch to die, but the mistletoe remains living, drawing water and nutrients from the infected branch (205). High concentrations of minerals in mistletoes demonstrate that they are also efficient parasites of these nutrients (60,123).

Traditionally, mistletoes were regarded as water parasites: they were thought to absorb only water and minerals from their hosts. Under this paradigm, the host was characterized as functioning as the root system for the mistletoe, whose own root system had been modified into a haustorium. Furthermore, traditional wisdom taught that mistletoes were not damaging because of their autotrophic capabilities. Only those mistletoes that were almost completely dependent on their hosts for all of their nutritional requirements, such as the dwarf mistletoes (97), were considered damaging pathogens. However, several studies have now clearly demonstrated that many mistletoes thought to be only water parasites actually derive some or most of their carbon requirements from their hosts as dissolved compounds in host xylem sap (59,61,62,131,132,168,174,181,182,192,193,202). It has now been estimated that some mistletoes absorb low amounts of carbon (5 to 20% of their requirements) and others absorb as much as 80% of their carbon requirements from their hosts (112). Mistletoes that were once thought to cause little damage to their hosts are actually associated with significant reductions in host growth and potential productivity (96). Furthermore, recent experimental evidence suggests mistletoes are most robust on the most vigorous host trees (23), a concept that has long been assumed (221) but lacked substantiating data.

The mechanism of water and mineral movement from host to mistletoe xylem is still not fully understood. One hypothesis maintains there are direct connections between mistletoe xylem elements and those of their hosts (68,75). Another hypothesis is that no direct connections to xylem exist but that water and minerals are first translocated through the symplast of parenchyma cells prior to entering mistletoe xylem (115,123,202). Evidently mistletoes parasitize their hosts using different anatomical links to their host's xylem and phloem, and this remains an area where additional research is needed.

Pathogenic effects. Around A.D. 1200, Albertus Magnus recognized that mistletoes were plant pathogens, evidently the first organisms to be identified as such (1). Since then, mistletoes have been reported to be associated with losses in food production (Fig. 3A), rubber production, and fiber production (Table 1). However, quantitative data for the amount of economic losses are lacking for most mistletoe–host associations (74,86,110) except for the dwarf mistletoes, which are common and widespread pathogens of commercially valuable conifers (72,92,93). The effects of mistletoes on their hosts include reductions in growth, vigor, fruiting, and seed production. Severe infection by mistletoes is often associated with premature mortality of host trees, particularly trees infected by dwarf mistletoes (Fig. 3B). In addition, severely infected trees are often predisposed to infection by other pathogenic agents and/or attack by insects, which often contribute to the death of the mistletoe-infected plant (65,74,92,110,112). The pathological effects of mistletoes vary considerably depending on their ability to obtain water, minerals, and carbon from their hosts. As with other pathogenic agents, the effects of mistletoes are also compounded by the environmental conditions under which the hosts are growing and the sizes, ages, and densities of the infected plants (110).

Because mistletoes reduce the growth of commercially valuable timber species, pathological effects are usually evaluated by quantifying the reduction in height, diameter, and/or volume of infected trees with varying levels of mistletoe infection. For example, the effects of dwarf mistletoes on the growth of their conifer hosts have been estimated by investigators reporting reductions in radial diameter growth or reduced volume growth for individual trees, stands of trees, or large geographic regions (88,136,198). Economic losses from dwarf mistletoes amount to billions of dollars annually, but no detailed economic analysis has been published recently (72,92).

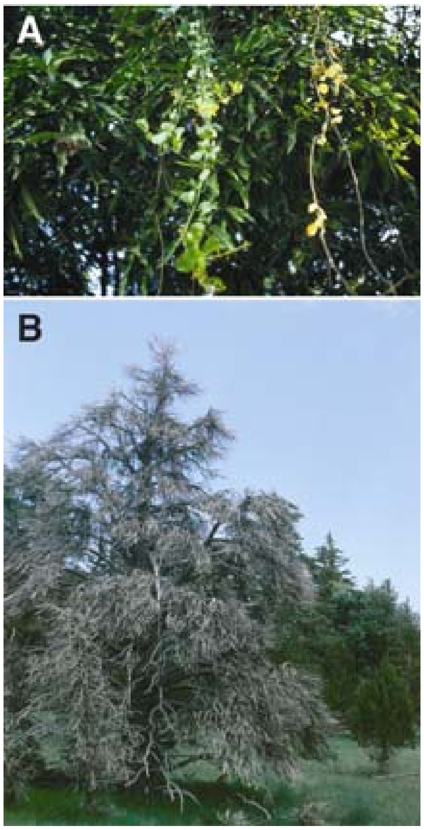

Fig. 3. Mistletoes impact food and fiber production: A, Mango infected with *Sruthanthus orbicularis* in Honduras. This mistletoe is common on mango and citrus in Central America, but no studies have quantified the losses associated with different levels of infection. B, Mortality of bristlecone pine associated with severe infection by dwarf mistletoe on the San Francisco Peaks, AZ. Note the many witches'-brooms on the dead tree, demonstrating that the tree was severely infected before it died.

Estimates of losses associated with mistletoes have more commonly been expressed as percentages of potential or anticipated production of food or fiber (74,86,110). These figures have seldom been based on stringently designed experiments comparing productivity of mistletoe-free plants with plants that have carefully quantified levels of mistletoe infection (86). Because of the time and expense involved in quantifying the pathological effects of mistletoes on their hosts, this aspect of mistletoe pathology has not been adequately addressed. Infection severity often takes several years to increase to the point where host growth and reproduction are adversely affected from an economic perspective. This difficult area of research is clearly in need of controlled, long-term experiments.

Although the damaging effect of mistletoes, like other plant pathogens, is directly related to the severity of infection on individuals and within stands/forests/orchards, infection severity has not been easy to quantify (74). Reports of mistletoe damage often use only a qualitative ranking system of low, moderate, or severe infection levels; exceptions are the severity rating systems developed for the dwarf mistletoes (55,84). While many have been published (55,163), the Hawksworth 6-class system (84) remains the standard disease severity rating system used for dwarf mistletoes throughout North America and has been adapted for use when rating the severity of infection for other mistletoes (48,96). Methods for efficiently and accurately quantifying infection severity and correlating this with host damage are needed for other mistletoes as well.

Host specificity. Some mistletoes parasitize a very large number of hosts in different families. Two notable examples are *Viscum album* subsp. *album* with over 450 host species (21) and *Amyema miquelli,* which parasitizes hosts in 17 plant families (56). In contrast, a few mistletoes only parasitize one host species, for example some dwarf mistletoes (93). Some dwarf mistletoes are so host specific that it has been suggested that their host specificity may be a useful taxonomic character for distinguishing between host populations (87,137). Although host specificity is commonly mentioned in the mistletoe literature, and many authors have pointed to its importance to pathology, few investigations have examined the mechanisms that control mistletoe–host compatibility (7,50, 100,157,188,208,227,228,229). A better understanding of the mechanisms related to host specificity would have applications to mistletoe control, particularly in developing greater host resistance (196). How the mechanisms of host–mistletoe compatibility or incompatibility function remains one of the most fascinating and challenging areas of mistletoe biology and pathology yet to be understood (157).

Another fascinating aspect of mistletoe host specificity is the propensity of mistletoes to parasitize other mistletoes. Host choice may involve another mistletoe, and in this case the facultative association is termed hyperparasitism (Fig. 4A) (217,223). Hyperparasitic mistletoes are known from Loranthaceae, Viscaceae, and Santalaceae (149). A number of species of *Phoradendron* (118) and *Viscum* (169) have been documented as hyperparasites. Even more amazing are the rare tripartite

Table 1. Pathogenic genera of mistletoes, the host groups seriously affected, and the regions where economic losses are associated with mistletoe parasitism (modified from Knutson [110])

Family genus	Hosts affected	Region
Loranthaceae		
Amyema	Eucalyptus, acacia	Australia
Dendropemon	Citrus	Caribbean
Dendrophthoe	Citrus, fig, guava, mulberry	India
Macrosolen	Citrus	India
Oryctanthus	Cocoa	Central America
Phthirusa	Rubber, cocoa, erythrina, citrus, mango, coffee, avocado	Central and South America
Psittacanthus	Pine, citrus	Mexico and Central America
Scurrula	Citrus	Philippines, Indonesia
Struthanthus	Citrus, mango, pine	Central America
Tapinanthus	Cocoa	Africa
Tolypanthus	Citrus	India
Viscaceae		
Arceuthobium	Conifers in the Pinaceae	North America and Asia
Dendrophthora	Rubber, mango, avocado, cocoa	South America
Korthalsella	Eucalyptus, acacia	Australia, Hawaii
Phoradendron	Avocado, citrus, cocoa, coffee, erythrina, fir, oak, pecan, walnut	North, Central, and South America
Viscum	Almond, apple, fig, fir, olive, peach, pear, persimmon, pine, prune, rubber, walnut	Asia, Europe, and Africa (introduced into California)

associations where a mistletoe parasitizes a mistletoe that is parasitizing another mistletoe on a host tree (149,217). When mistletoe upon mistletoe parasitism becomes an obligate association, this is termed epiparasitism. All species in the genus *Phacellaria* (Santalaceae) are obligate epiparasites of Loranthaceae and other Santalaceae (46). Apparently some species of *Phoradendron* are also epiparasites (118) and may become (mistletoe) host specific. Parasitism by an individual of the same species is called autoparasitism (a form of cannibalism!). Given that seed germination in mistletoes does not depend upon substrate, seeds deposited on the mother plant may reach various stages of attachment and development. Autoparasitism occurs frequently in Loranthaceae as well as in Viscaceae, such as *Phoradendron juniperinum* of the southwestern United States (Fig. 4B). Although reports of hyperparasitism, epiparasitism, and autoparasitism by mistletoes are well documented, few anatomical or physiological studies of these relationships have been undertaken. Kuijt and Lye (119) studied the anatomical connection between *Phoradendron tonduzii* parasitizing *Psittacanthus ramiflorus*. Visser (217) reported that the water potential for an epiparasitic mistletoe was 1,000 kPa less than its mistletoe host. Water potential measurements have not been conducted for a tripartite mistletoe association, and it would be interesting to determine how large the water potential difference can become between the parasites involved (149).

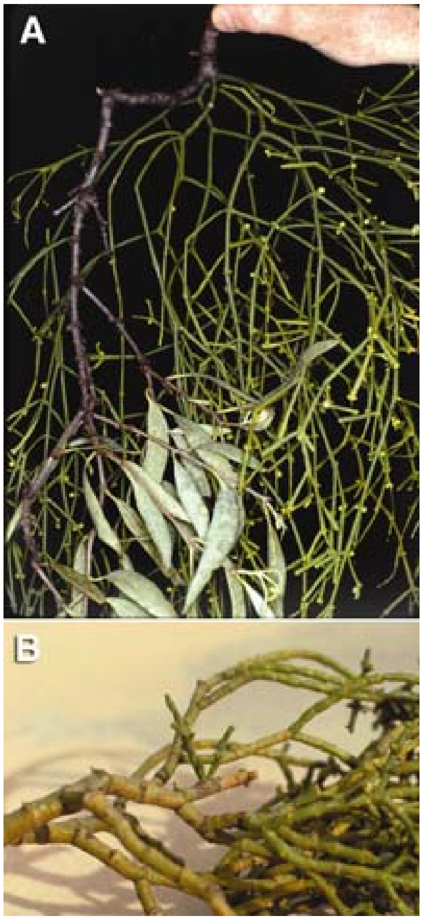

Fig. 4. Some mistletoes parasitize other mistletoes. A, *Viscum articulatum* (Viscaceae) hyperparasitic on *Dendrophthoe glabrata* (Loranthaceae). B, Autoparasitism by *Phoradendron juniperinum*. The small plant protruding upward near the center of the figure is a male plant parasitizing a female plant.

Symptomatology. *Hypertrophy.* Many mistletoes cause localized hypertrophy of host tissues at the site of infection (116) (Fig. 5A), caused primarily by the disruption of normal tissue development (110). Swelling of host tissue may be associated with either an increase in host cambial activity resulting in the formation of secondary xylem cells or displacement of host xylem and phloem tissue (116). It has been hypothesized that extensive hypertrophy of host tissue was indicative of a mistletoe–host incompatibility (91,115). Large swellings on a host branch are also associated with profusely branched extraxylary absorptive structures produced by the mistletoe, such as with some species of *Phoradendron* (207) (Fig. 5B).

A few mistletoes, most notably dwarf mistletoes (Fig. 5C), alter host phytohormone balance, resulting in the formation of dense masses of branches called witches'-brooms (126,159,187). Branches from witches'-brooms exhibit features atypical of uninfected host tissue such as: increased longevity (222); elimination or reduction of seed and cone production (24,116); increased branch elongation on some hosts (83,209); increased biomass compared with uninfected branches of the same age (209); and decreased number, length, and mass of needles (28,29,175). While witches'-brooms are the most easily observed symptom of dwarf mistletoe infection and serve as large nutrient sinks that contribute to the decline of host vigor and growth (136), they also appear to have positive effects in an ecological context (see below).

Branch dieback. A common symptom of mistletoe infection is branch dieback (Fig. 5D). Over a period of time, the branch distal to the mistletoe connection dies; whereas the branch segment proximal to the trunk remains alive and continues to supply water and nutrients to the parasite. In many cases, the distal end of the branch eventually falls away, leaving a live branch supporting a large mistletoe plant at its end (96,116) (Fig. 5E). Branch dieback has been reported for many mistletoe–host combinations, but the pathological effects of branch dieback on hosts have not been adequately investigated. Branch dieback is particularly prevalent during droughts when the host is taxed by lack of water, but the mistletoe continues its demand for the scarce resource (124). During droughts, mistletoe plants distal to other plants often die as well (Fig. 5D).

Dead tops are commonly observed on conifers severely infected with species of *Arceuthobium*, *Phoradendron*, and *Viscum* (92,110). Nutrients and water absorbed by the host's roots are diverted to supply the mistletoe infections occurring between the roots and tree top, thereby depriving the topmost branches of needed resources. Eventually, as the number of mistletoe infections increases, a point is reached where the top of the tree can no longer survive, and a dead top develops as a symptom of severe mistletoe infection (Fig. 5F).

Signs. Signs of mistletoe infection are obviously the aerial shoots mistletoes produce on infected branches and trunks of their host plants. Most mistletoes produce relatively large aerial shoots, sometimes with large leaves which are readily observed, but some produce small shoots that may be overlooked without careful observation. Mistletoe plants are morphologically diverse, as are their flowers. Mistletoes may have large, showy flowers that attract their bird pollinators (Figs. 1A and B, and 6A), while others have undergone extreme reduction in floral morphology, as in all Viscaceae (Fig. 6B), Misodendraceae, and some Loranthaceae (74,116). Leaf size also varies greatly among mistletoes, some species having very large leaves many centimeters in length and width (Figs. 1A and 6A), while others may be squamate, i.e., with leaves reduced to very small scales (Fig. 6C) (116). Because mistletoes are distributed worldwide, their identification requires the use of a wide array of literature (taxonomic monographs, regional floras, agriculture handbooks, and refereed papers) (e.g., 89,92,118,169,189). Typically, individuals interested in their classification are specialists working on one or a few groups of these parasitic plants. As with other plant pathogens, some genera of mistletoes have been studied intensively, particularly if they are economically important such as the dwarf mistletoes (92), while other genera have received relatively little attention (116). The phylogenetic relationships and taxonomic classification of many mistletoes are still under study (or nearly neglected), so their identification is problematic and usually requires the assistance of specialists familiar with specific genera.

In temperate regions where host plants are often deciduous, mistletoe plants are easily observed during the winter because they are perennial evergreens. In tropical regions, mistletoe plants are much more difficult to observe, particularly because their bird dispersers tend to deposit seeds high in the canopy. A few mistletoes successfully mimic the leaves of their hosts, making them very difficult to observe by humans as well as potential herbivores that may prefer parasite leaves to host leaves (Fig. 7A and B). Mimicry of host morphology is particularly common in Australian mistletoes, where many marsupials feed on mistletoe plants, this relationship being the suggested selection pressure contributing to the evolutionary development of mistletoe mimics there (20). However, other hypotheses explaining the relatively high occurrence of host mimicry by mistletoes in Australia have been suggested (10,38,62).

Phylogeny of the Major Mistletoe Groups

Results from molecular phylogenetic studies of Santalales have previously been published (149,150,151,153), but none had utilized complete (or nearly complete) taxon sampling for all families in the order. Moreover, resolution of the phylogenetic trees was often poor, suggesting that additional gene sequences were needed. Since then, both taxon and gene sampling have improved such that we now have a clearer picture of relationships across the order. Molecular phylogenies are now available for Olacaceae (127), Santalaceae (53), Misodendraceae (214), and Loranthaceae (216). Previous work indicated that the mistletoe habit evolved five times independently (148), and more recent work (215) confirmed this finding and also addressed the relative timings of these diversifications. These studies now allow more precise statements to be made about the evolution of aerial parasitism. The tree shown in Figure 8 represents our current concept of relationships among the various

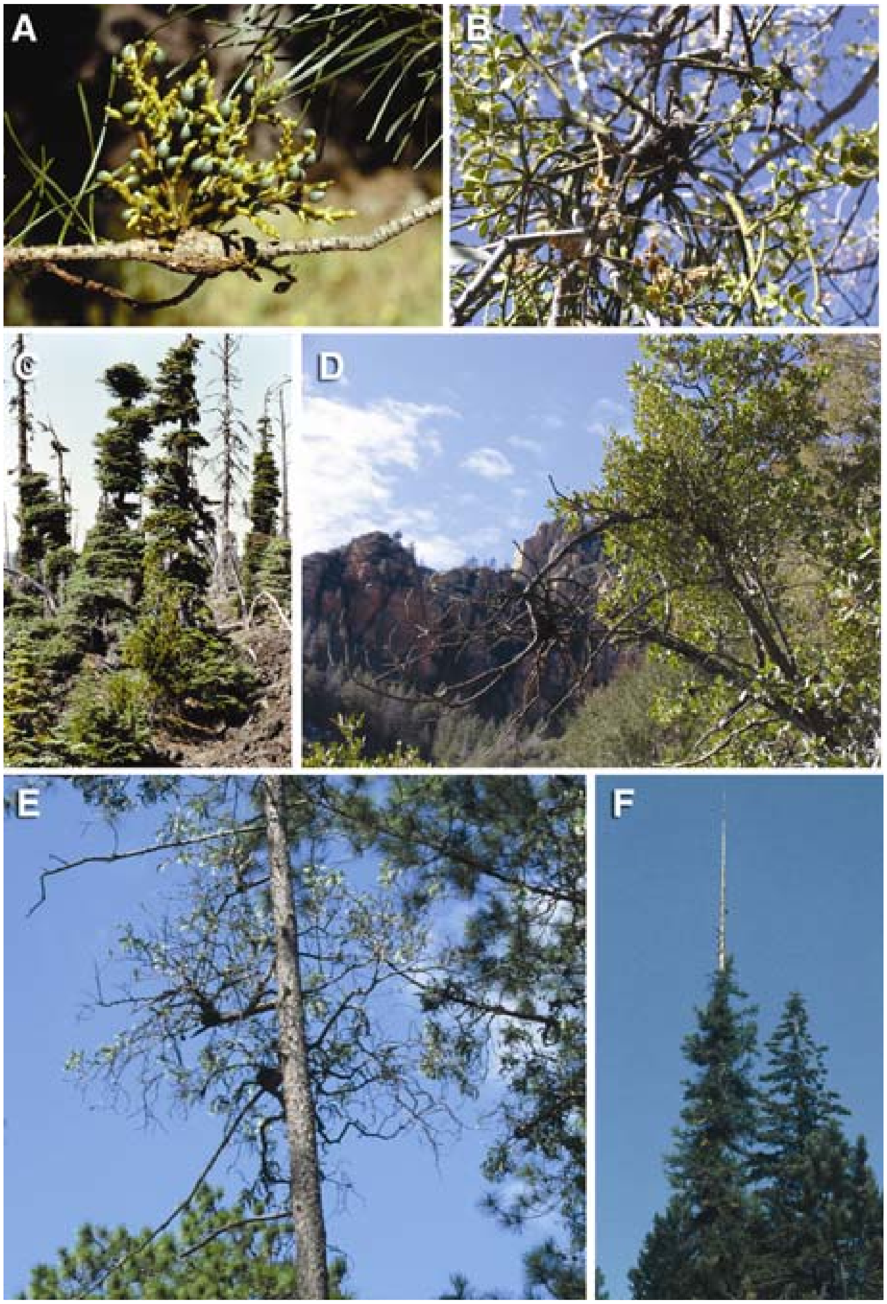

Fig. 5. Symptoms of mistletoe infection. A, One of the common symptoms of infection associated with mistletoes is a hypertrophy of the host branch at the point of infection. Note the large swelling on this pine branch infected by dwarf mistletoe. B, Large swellings on a host branch are associated with profusely branched extraxylary absorptive structures produced by mistletoes, such as with some species of *Phoradendron*. C, The dense masses of branches called witches'-brooms on these western hemlocks are associated with infection by dwarf mistletoe. D, A common symptom of mistletoe infection is branch dieback. This figure illustrates branch dieback associated with infection by southwestern oak mistletoe on Emory oak. Note that the dead branch has a dead mistletoe plant on it and another live mistletoe plant occurs proximal to the dead mistletoe plant. E, The dead end of a branch distal to a mistletoe infection often falls away leaving the mistletoe and live branch proximal to the point of infection. This is common on pines infected by *Psittacanthus angustifolius* in Central America. F, Trees severely infected with mistletoes often develop dead tops. A dead top has developed on this western larch severely infected with dwarf mistletoe.

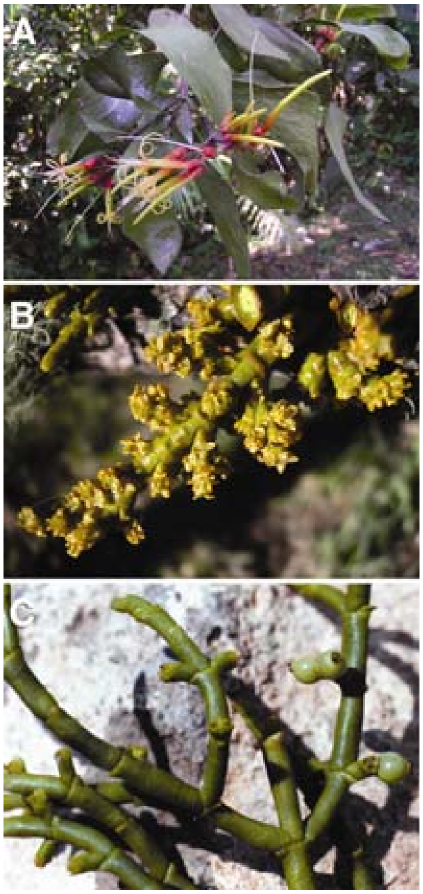

Fig. 6. Mistletoe leaves are morphologically diverse. A, Many mistletoes have very large leaves several centimeters in length and width, particularly tropical loranths, such as *Psittacanthus cucularis*. (Photo by G. Amico) B, In contrast to the large, colorful flowers of many loranthaceous mistletoes, viscaceous mistletoes such as species of *Arceuthobium* have small flowers and are insect or wind pollinated. C, Some species are squamate, i.e., have leaves reduced to very small scales as illustrated here for *Phoradendron juniperinum*.

clades of Santalales, and a brief discussion of these follows in the next section.

Misodendraceae. This southern South American family contains one genus (*Misodendrum*) with eight species (214). It is unique among mistletoes in possessing feathery staminodes on its fruits that aid in wind dispersal and adherence to host branches. Misodendraceae are sister to Schoepfiaceae, and this clade is then sister to Loranthaceae (Fig. 8). Because Schoepfiaceae and some genera of Loranthaceae are root parasites, a single origin of aerial parasitism for Loranthaceae and Misodendraceae must be discounted, as it is less parsimonious than inferring two separate origins. The time-calibrated phylogenetic tree (chronogram) provides evidence that Misodendraceae were the first santalalean lineage to evolve aerial parasitism, ca. 89 million years before present (mybp) (215). This date is near the time of origin of *Nothofagus* (the sole host of *Misodendrum*); thus the possibility exists that the host and mistletoe codiversified during the Cretaceous Period.

Loranthaceae. With 73 genera and over 900 species, Loranthaceae is the largest family of mistletoes. The loranths are always resolved as monophyletic and with strong support from both nuclear and chloroplast genes (215,216). The chronogram indicates that the western Australian root parasite *Nuytsia floribunda* speciated from the main loranth lineage during the Eocene Epoch and is thus sister to the remainder of the family. The eastern Australian root parasite, *Atkinsonia ligustrina*, diverged next followed by the New World tropical root parasite *Gaiadendron punctatum*, although its exact timing and placement on the tree differs among the separate gene partitions. All remaining genera in the family are present in a clade marked by the presence of stem parasitism (Figs. 8 and 9), which appears to have arisen once in the family, not four times as suggested by Wilson and Calvin (224,225). The evolution of this life history trait resulted in a massive adaptive radiation, which was likely fueled by coevolution with pollinating and seed dispersing birds (180). The major loranth clades generally correlate with base chromosome number, and the ancestral (plesiomorphic) state is X = 12 (Fig. 9). Several aneuploid reductions have occurred such as in *Ligaria* (to 10), the small-flowered New World clade (to 8), *Ileostylus* and *Muellerina* (to 11), and the African/Asian clade (to 9, likely via X = 11). The polyploid condition in *Desmaria* is unusual for the family, and the tree topology indicates a more complex situation than might be proposed if this genus evolved from the X = 8 clade.

***Santalum* clade.** The *Santalum* clade, based on studies involving only nuclear small-subunit rDNA sequences (150) and chloroplast genes (153), contains 11 genera (Fig. 8) of root parasites, including the type genus *Santalum*, other Old World genera such as *Osyris* and *Exocarpos,* and New World genera such as *Nestronia* and *Myoschilos*. Three small New World mistletoe genera previously classified as Eremolepidaceae (*Antidaphne* [7 species], *Eubrachion* [2 species], and *Lepidoceras* [2 species]) form a clade within the sandalwood family (Santalaceae). The eremolepidaceous clade is monophyletic with strong support and appears to have arisen in the Late Cretaceous (215).

***Amphorogyne* clade.** With regard to the evolution of trophic modes, one of the most fascinating groups in Santalales is the *Amphorogyne* clade (Fig. 8). As with the *Santalum* clade, these Old World aerial parasites evolved from root-parasitic ancestors. But unlike that clade, where all three aerial parasites can be called true mistletoes, the *Amphorogyne* clade has members exhibiting a much wider diversity of habits. Here one can find not only root parasites (*Choretrum, Leptomeria*) and leafy mistletoes (*Dufrenoya*), but also twining aerial parasites called dendroparasites (*Dendromyza*), squamate mistletoes that are hyperparasitic on Lor-

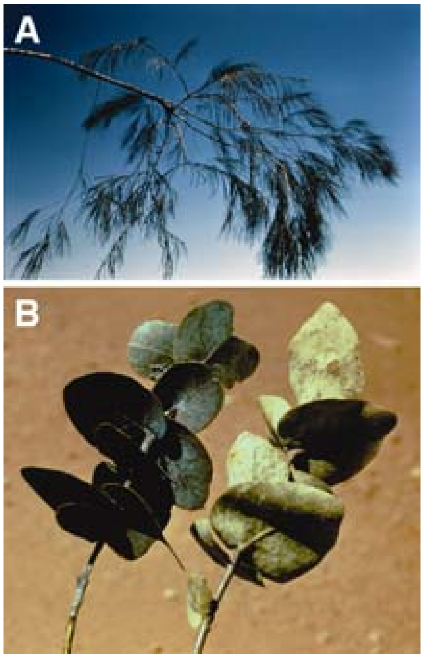

Fig. 7. Several Australian mistletoes mimic the foliage of their hosts. A, An example of mimicry by *Amyema cambadgei* (mistletoe) on *Casuarina torulosa* in Australia. Mistletoe plants extend from the globose swelling near the center of the figure and have reddish fruits. Note how the leaves of the mistletoe clearly mimic the branches of its host. B, Plants of *Dendrophthoe homoplastica* (mistletoe) mimic those of its common host, *Eucalyptus shirleyi* (left). (Photos by D. Wiens)

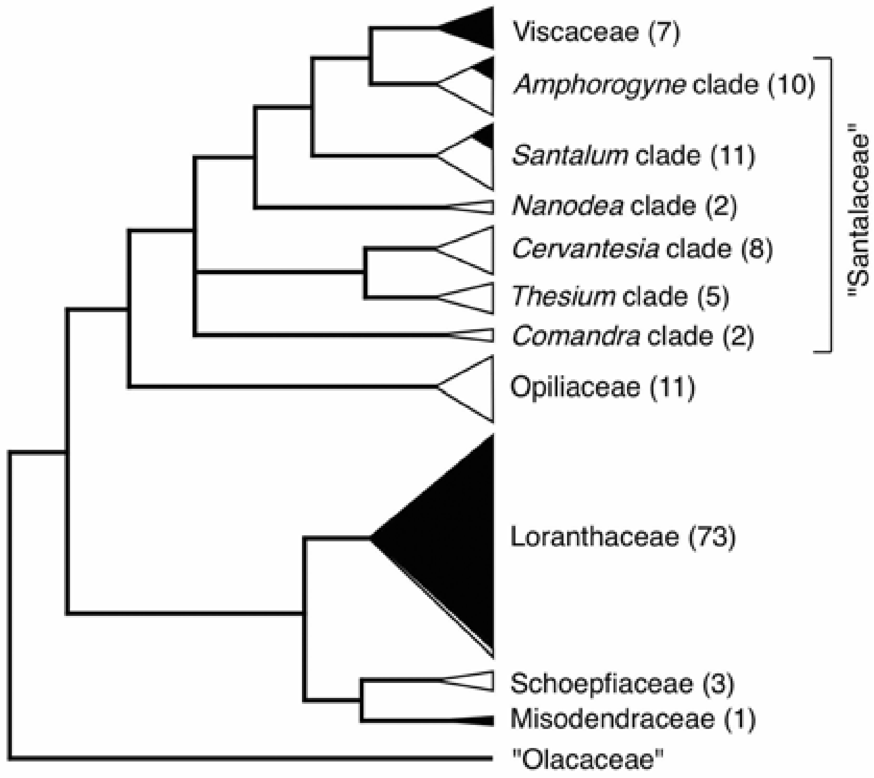

Fig. 8. Current view of relationships among the various clades in the order Santalales. This tree is based upon several multigene molecular phylogenies (53,127,215,216). Areas of the triangles at the branch tips represent the number of genera in the clade; the actual number follows the clade name. Black shading represents aerial parasites (mistletoes, dendroparasites, etc. – see text), and white indicates root parasites. The family names "Olacaceae" and "Santalaceae" are placed in quotes to emphasize their polyphyletic nature.

anthaceae or Santalaceae (*Phacellaria*), and "amphiphagous" parasites that can feed either upon stems, roots, or both simultaneously (*Daenikera*, *Dendrotrophe*). Of the 10 genera in the *Amphorogyne* clade, four are aerial parasites representing ca. 40 species. Although no fossil record exists, the chronogram indicates the clade evolved in the Eocene (215).

In earlier molecular phylogenetic studies where taxon sampling in the *Amphorogyne* clade was incomplete (148), the possibility remained that Viscaceae and the stem parasites of the *Amphorogyne* clade were monophyletic, i.e., shared a common ancestor that was stem parasitic. Recent molecular tree topologies (53), however, indicate that this is not the case. When the various trophic mode characters were optimized on that molecular tree (via MacClade, Sinauer Associates, Inc., Sunderland, MA), the entire backbone of the tree is reconstructed as amphiphagous. This means that the most parsimonious state for the ancestor of the *Amphorogyne* and Viscaceae clades was either a root or stem parasite. This polymorphism suggests that this ancestor may have possessed a high degree of genetic plasticity for trophic mode which may have served as the "raw material" that eventually manifested as the highly successful mistletoe family Viscaceae.

Viscaceae. Viscaceae includes seven genera of Old and New World mistletoes, and with over 540 species is second in size only to Loranthaceae. Although nineteenth century workers considered Viscaceae a part of Loranthaceae, more modern treatments have recognized the distinctiveness of these mistletoe families (17,18,19). Previous molecular phylogenetic work has always resolved Viscaceae as monophyletic with high support. Instead of being most closely related to Loranthaceae, molecular analyses placed this clade among several traditionally classified as Santalaceae. Indeed, the APG (6) classification lumped Viscaceae into a more broadly defined Santalaceae. As shown in Figure 8, an alternate approach is to continue recognizing Viscaceae, but to then split the heterogeneous and paraphyletic group "Santalaceae" into six monophyletic clades. From a practical standpoint, it can be argued that Viscaceae are an important clade because of their impact (both positive and negative) upon humans; thus, subsuming this well-characterized group into a larger, more heterogeneous one is undesirable.

Past attempts to resolve intergeneric relationships within Viscaceae encountered difficulties "breaking" a polytomy that included the four major Viscaceae clades. This is somewhat surprising because these mistletoe sequences contain a large number of variable sites owing to increased evolutionary rates. The major clades are *Viscum* + *Notothixos* (V/N), *Phoradendron* + *Dendrophthora* (P/D), *Korthalsella* + *Ginalloa* (K/G), and *Arceuthobium* (A). The lack of resolution was discussed by Nickrent et al. (151) as a possible example of a "hard polytomy" (i.e., a true rapid radiation). Since then, additional sequences have been obtained and a concatenated matrix involving nuclear 5.8S and SSU rDNA and chloroplast *rbcL* and *matK* was analyzed (Fig. 10). The maximum parsimony tree strongly supports the V/N clade as sister to the remaining taxa; however, the relationship among the other three clades remains unresolved. Given that the three component clades each have high support as monophyletic, there are only three possible topologies for resolving the three clades: (P/D, K/G)A, (P/D, A)K/G, and (A, K/G)P/D. Oddly, any one of these topologies receives support from various different gene partitions (and gene combinations) and even different methods of analysis (maximum parsimony and likelihood) of the same partition. This phenomenon possibly stems from two sources: conflicting signal between the different genes and long-branch attraction, particularly with *Arceuthobium*. It is likely that with additional sequence data the polytomy will be resolved and the source of the conflict between partitions identified.

The stem group date for Viscaceae is 81 mybp (215), competing with Misodendraceae as the earliest mistletoe clade; however, this date is likely inflated due to elevated substitution rates in the family, particularly in *Arceuthobium*.

Infrageneric Studies of Mistletoes

Infrageneric molecular phylogenetic studies have been reported for Misodendraceae, Loranthaceae, and Viscaceae. To date, only in Viscaceae have such studies been conducted on more than one genus. The following gives a brief summary of the results from these studies as well as preliminary information about *Viscum*.

Misodendrum. A previous classification of these Patagonian mistletoes placed the eight species in two subgenera, *Misodendrum* (with two sections) and *Angelopogon* (with three sections). Subgenus *Misodendrum* is characterized by warty stems and two stamens, whereas subgenus *Angelopogon* is characterized by three stamens and foliaceous bracts. This classification was

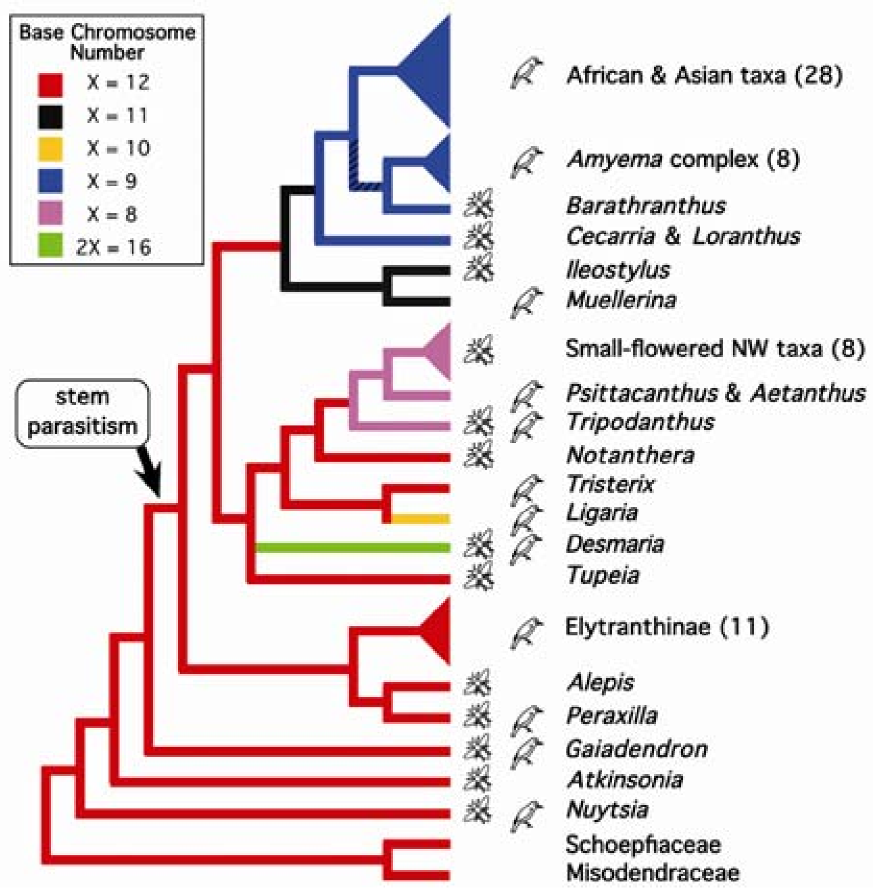

Fig. 9. Stylized tree derived from a multigene molecular phylogeny of Loranthaceae (216). Colors represent the six different base chromosome number types found throughout the various genera. For simplicity, some larger clades have been collapsed and the number of genera in the clade included after the name. According to this reconstruction, stem parasitism arose once in the family (large arrow). Optimization of pollination type (insect versus bird) indicates that exclusively bird pollinated clades arose five times independently. The hatched line indicates an equivocal optimization.

tested by means of two chloroplast genes and 31 morphological characters (214). The molecular tree supported a relationship of *M. quadriflorum* as sister to all other species. *Misodendrum brachystachyum* and *M. oblongifolium* form a well supported clade that is sister to one composed of *M. punctulatum, M. gayanum,* and *M. angulatum*. These phylogenetic relationships show that subgenus *Misodendrum* is monophyletic, whereas subgenus *Angelopogon* is paraphyletic and can be defined only by plesiomorphic characters. If these molecular results are confirmed with nuclear gene sequences, a subgeneric reclassification will be required.

Tristerix. The first generic level molecular phylogenetic study of Loranthaceae was by Amico et al. (5), who examined *Tristerix*, a genus of 11 species with an Andean distribution from Colombia to Chile. The previous classification which divided *Tristerix* into two subgenera, *Tristerix* (*T. aphyllus* and *T. corymbosus*) and *Metastachys* (the remaining nine species), was tested using nuclear internal transcribed spacer (ITS) ribosomal DNA and two chloroplast spacers. Molecular data showed that *Tristerix* was composed of a northern South American clade of six species and a southern clade of four species. *Tristerix verticillatus* and *T. penduliflorus*, originally classified in subgenus *Metastachys*, were strongly supported as members of the (southern) subgenus *Tristerix* clade. One species, *T. corymbosus*, occurs in two distinct habitats: temperate forests and the dry Chilean matorral. Also occurring in the matorral habitat is *Tristerix aphyllus,* an obligate parasite of Cactaceae, whose sister relationship to *T. corymbosus* renders that species paraphyletic. It was proposed that this ecological speciation event occurred in sympatry, likely driven by the behavior of mockingbirds that disperse the seeds. Speciation among the northern *Tristerix* species, many of which occur in the high Andes and in cloud forest biomes, appears to be correlated with interactions with pollinating birds.

Arceuthobium. The first molecular phylogenetic investigation of interspecific relationships in dwarf mistletoes was by Nickrent et al. (154) using ITS sequences. A second more detailed study included all currently recognized species in the genus and added chloroplast (*trnL* region) sequences to the ITS data (152). That study showed that the Old and New World species were genetically distant, so much so that primers for the *trnL* region did not work with the Old World taxa. The tree resulting from concatenating ITS and *trnL* region sequences was well resolved except for four internal nodes. A phylogenetic classification of the genus was proposed that recognized two subgenera: *Arceuthobium* (with three sections) and *Vaginata* (with eight sections). Sequences of both genic regions were nearly identical for 11 species from section *Campylopodum*, thus these were all considered conspecific with *A. campylopodum*. The revised classification reduced the number of species of *Arceuthobium* from 46 to 26. Additional work is needed to examine the genetic structure among populations of wide-ranging taxa. One example is *A. americanum* (101,102), a species that has undergone racial differentiation.

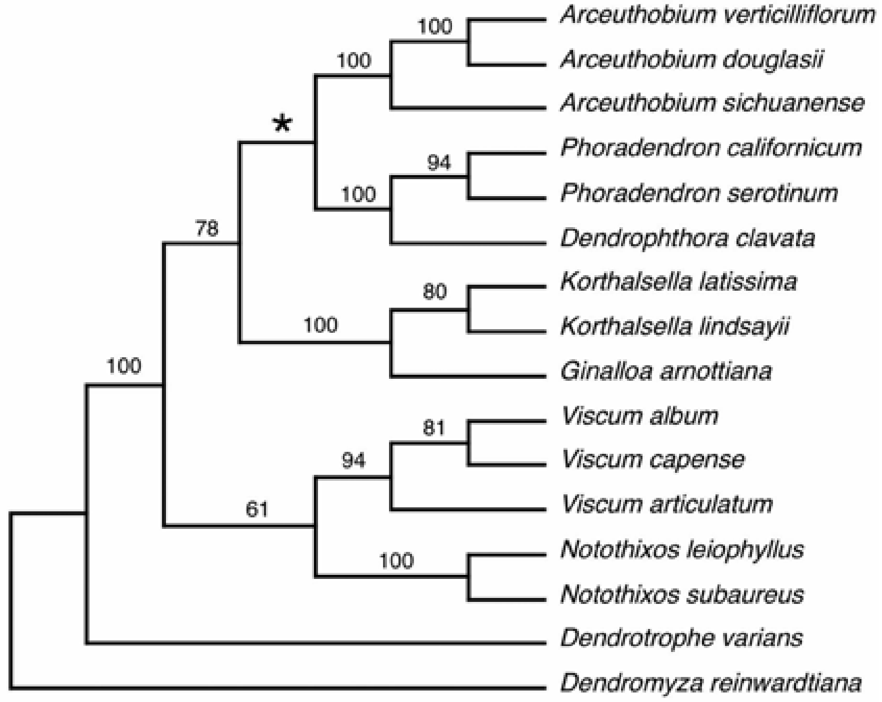

Fig. 10. Tree showing phylogenetic relationships within Viscaceae obtained via maximum parsimony analysis of chloroplast *rbcL* and nuclear 5.8S and SSU rDNA. Numbers above the branches indicate bootstrap percentages (1,000 replications). The node marked by an asterisk received bootstrap support below 50%.

Korthalsella. A molecular phylogenetic study was conducted on nuclear ITS rDNA and chloroplast *trnL-F* sequences collected from populations of *Korthalsella* across its range (143). A species from northern Australia (*K. papuana*) was sister to the remaining taxa, and these were further resolved as two subclades with either differentiated or undifferentiated inflorescence branches. These results did not support a classification based upon morphology (45). Moreover, plants on different hosts that were genetically closely related had markedly different morphologies (measured as internode shapes). This prompted the authors to propose host influence on the morphology of the parasite, an issue visited by workers looking at other viscaceous genera such as *Arceuthobium* (73) and *Viscum* (141).

Phoradendron* and *Dendrophthora. The genus *Phoradendron*, comprising 234 species of New World mistletoes, is closely related to *Dendrophthora* (118). Indeed, a single morphological character defines the two genera: one anther locule for *Dendrophthora* and two for *Phoradendron*. The monophyly of these genera has been questioned based on molecular evidence (150,151). A detailed molecular phylogenetic analysis of these two genera was conducted using nuclear ITS and 26S rDNA sequences (8,9). Five *Dendrophthora* and 35 *Phoradendron* taxa were analyzed with parsimony with santalaceous genera as outgroups. Three major clades were identified: clade A, a morphologically heterogeneous one containing all five *Dendrophthora* species plus *P. crassifolium, P. piperoides*, and *P. sulfuratum*; clade B, containing seven *Phoradendron* species typically with biseriate inflorescences and one pair of basal cataphylls; and clade C, containing the remaining 25 *Phoradendron* taxa (with the exception of *P. californicum*) that have biseriate or triseriate inflorescences and that generally lack basal cataphylls. As with *Arceuthobium* and *Korthalsella*, this study has demonstrated how morphological characters can be unreliable indicators of phylogenetic relationships. Although all five *Dendrophthora* species were resolved in clade A, this clade also contained three *Phoradendron* species, supporting the previous suggestion that neither genus is monophyletic.

Viscum. Despite regional taxonomic works (47,63,169), a monograph for all ca. 150 species of *Viscum* worldwide does not exist. Moreover, there currently exists no phylogenetic information on this genus that could be used to address interspecific relationships. For this reason, a 2.1-kb portion of the nuclear large-subunit ribosomal DNA was used to conduct a preliminary phylogenetic investigation of 12 *Viscum* species. Both scale-leaved (squamate) and leafy mistletoes were sampled representing the subsections *Aspidixia* and *Ploionixia*, respectively, of Engler and Krause (63). The consensus tree (Fig. 10) gave strong support for a monophyletic *Viscum*. Support was also seen for clades containing *V. album* and *V. cruciatum*, *V. obscurum* and *V. triflorum*, *V. articulatum* and *V. orientale*, and a polytomy involving five African species. Less support was obtained for three internal nodes linking the above clades. The phylogenetic analysis provides evidence that the leafless habit has evolved independently in three different clades (*V. minimum*, *V. articulatum*, and *V. capense*). This result is in agreement with Danser (47), who clearly noted that the presence/absence of leaves could not be used to derive a natural classification of the species. Moreover, this molecular phylogenetic analysis does not support the previously proposed sections and subsections of Engler and Krause (63). For example, the diminutive *Viscum minimum*, classified with *V. album* in Section *Euviscum*, is clearly not related to these mistletoes but is a component of a clade of other South African species.

Much work remains to fully resolve interspecific (and in some cases intergeneric) phylogenetic relationships among the various mistletoe clades. This is particularly the case for many of the larger loranth genera such as *Amyema*, *Psittacanthus*, and the small-flowered New World complex (*Cladocolea*, *Phthirusa*, *Struthanthus*, etc.). These studies would not only provide new insights into the phylogeny and taxonomy of these plants but would also generate data critical for evaluating hypotheses stemming from other disciplines such as anatomy, morphology, population biology, and ecology. Molecular phylogenies of mistletoes have revealed numerous examples of what is generally called parallel or convergent evolution. A good example of this involves *Arceuthobium verticilliflorum*, a robust Mexican species that lacks the hallmark of the genus: explosively dehiscent fruits. It was proposed (91,92) that this mistletoe could be primitive (i.e., evolved early in the history of the genus) and was thus the "link" to other members of Viscaceae that have nondehiscent fruits. The topology of the molecular phylogenetic tree clearly showed that this was not the case (152). The ancestor of *A. verticilliflorum* had an explosive fruit, but this feature was lost sometime during the evolution of the modern species. This information immediately suggests numerous additional studies such as: (i) identification of the seed disperser (birds?); (ii) other morphological and anatomical changes that may have accompanied this evolutionary step; (iii) changes in dispersal and colonization dynamics compared with other dwarf mistletoes with explosive fruits; and (iv) how fitness in this species compares with that of others. This example also demonstrates that caution should be exercised when attempting to predict evolutionary directionality based on intuitive "cost-benefit" analyses. In this case, what selection pressures were present in the environment that caused the loss of what many would consider a highly adaptive seed dispersal mechanism? The construction of phylogenetic trees is the first step required to establish a solid footing upon which further research into mistletoe biology can proceed.

Mistletoe Ecology

Ecological research on mistletoes has changed markedly over the last 50 years, in terms of both breadth and depth, reflecting changing priorities and a gradual shift in overall attitudes toward these parasitic plants. A key stimulus for discovering more about mistletoes was the perceived need to control them in commercial forests, orchards, and plantations worldwide (74,86,184). Initial investigations concentrated on host–parasite interactions, quantifying the effects of mistletoes on host growth, and describing the processes of mistletoe dispersal and establishment (74). Subsequent research focused on several components of mistletoe–host interactions: host range, germination and establishment, the anatomical and physiological basis of parasitism, and detailed explorations of the role of frugivorous birds as seed vectors (74,86,112,116,171,172,177). Seed dispersal studies were restricted primarily to the small number of mistletoe fruit specialists consistent with the view that few other species could detect or process the relatively cryptic and sticky fruits (178,199,200). Whereas many researchers viewed mistletoes as botanical anomalies or models for studying plant–animal interactions, the broader perception of these parasitic plants as destructive forest pathogens persisted.

While this targeted research was being conducted, anecdotal and incidental information on mistletoe–animal interactions was accumulating, gathered by biologists working on other components of forests and woodlands throughout the world. This highly dispersed information was synthesized by Watson (219), revealing an unprecedented breadth of interactions. In addition to documenting the wide range of opportunistic consumers of mistletoe fruit (in contrast to the prevailing view), this review also highlighted how many folivores and nectarivores feed on mistletoes. The popularity of mistletoes as a nesting substrate was also revealed, with a wide range of species recorded nesting in mistletoes and in the witches'-brooms associated with dwarf mistletoe infections (43,92,136,198). These interactions were suggested to underpin a generalized positive effect of mistletoe occurrence on diversity, and mistletoes have been proposed to function as a keystone resource in many forest ecosystems (219). Building on these previous advances, current ecological research on mistletoes is dominated by three major themes: mistletoes influence on wildlife habitat; mistletoes as a food source; and mistletoe–ecosystem interactions.

Mistletoes Influence on Wildlife Habitat

Most mistletoe species form dense, evergreen clumps of semisucculent foliage within the canopy of their host—a structural feature that is preferred by many bird species for nesting sites (Fig. 11). Recent

Fig. 11. Birds frequently use mistletoe plants as nesting sites, as illustrated by this bird nest constructed within branches of *Psittacanthus angustifolius* in Honduras.

research has shown that several species actively select mistletoes as nest sites, suggesting a preference for this microhabitat. Painted honeyeaters (16) and diamond firetails (41) nested in mistletoe far more frequently than expected, based on conservative measures of availability. Similar findings have been reported for several other species (regent honeyeaters, noisy friarbirds, Abert's towhees, cactus wrens), with frequency of use greatly exceeding the proportion of mistletoe in the canopy (42). An experimental study comparing predation rates on artificial nests in mistletoe clumps versus host foliage found markedly lower predation rates in mistletoe substrates, despite no difference in estimates of concealment from the side or above (42). Watson (219), in his review of animals known to nest in mistletoes, included species from 43 bird families and seven mammal families, ranging from 3-g hummingbirds to various waterbirds of 2 kg or greater. More recent work by Cooney et al. (43) evaluated the use of mistletoe as a nest site for the entire avifauna of Australia, documenting 245 species or 74% of the 330 species of arboreal nesters that breed on the continent. This boosted the number of bird families known to exhibit this behavior to 60, across 16 orders. Rather than purely an Australian phenomenon, this behavior is widely reported (136) (Fig. 11).

The witches'-brooms induced by many dwarf mistletoes represent a dense clump of foliage in a relatively open canopy, and the base of the infected branch is typically greatly enlarged. Both the swollen branch and the dense clump form favored nesting/roosting sites for a variety of birds (92,136,198). Many mammals also use these structures as resting or hiding sites and sometimes as dens (165,198). Other than descriptive work documenting which species use these structures, there have been no studies specifically examining the attributes of witches'-brooms as nest sites. Microclimate and susceptibility to nest predation are two obvious factors to evaluate (42).

One study in Colorado suggested that ponderosa pine forests with dwarf mistletoe have a greater diversity of bird species as well as higher populations of elk and deer than healthy pine stands (22). However, a similar study conducted in northern Arizona reported a positive correlation for only some birds, primarily secondary cavity nesting species, in ponderosa pine forests with dwarf mistletoe (161). The influence of dwarf mistletoes on species diversity needs to be studied in much more detail and in many regions. However, the consistent use of witches'-brooms as nesting sites by a wide range of birds and other animals is a good example of how mistletoes influence wildlife habitat. Certainly, research on mistletoe–wildlife interactions will continue to be an important area for mistletoe ecology.

Mistletoes as Food Sources

Mistletoe foliage, flowers, and fruits are consumed by wildlife, insects, and fungi (74,92). As indicated above, the breadth of species known to feed on mistletoes is great (and growing), reflecting the high nutritional quality of mistletoe tissues, as well as the almost complete absence of structural defenses (10,62,198,218). Although many members of both Viscaceae and Loranthaceae contain secondary compounds (106,114,125,218), additional research is needed on how these compounds influence herbivory by animals and insects.

Most mistletoes rely solely on frugivorous birds for directed seed dispersal—an interaction that has been studied in detail in a variety of systems. As indicated above, most of this work has concentrated on mistletoe specialists—consistently small bodied birds that forage in pairs or small groups (178,220). Several studies have adopted a broader perspective, and have noted a wide range of opportunistic frugivores taking mistletoe fruit occasionally, regularly, or seasonally (180,186). For many of these species, it is unclear whether these generalists contribute to seed dispersal or whether they are primarily fruit predators. The few studies that have examined this question in detail have found that they can function as dispersers (179), and a key priority for further work is to establish the relative importance of dietary specialists versus generalists, specifically in resolving whether they differ in their capacity as long-distance dispersers that establish new mistletoe populations (180). Preliminary evidence for these differential roles comes from examining distribution patterns of bird dispersed mistletoes. Mistletoe specialist frugivores are wholly restricted to continental areas, suggesting that the large number of mistletoes endemic to oceanic islands were initially established and subsequently dispersed by generalists. Note that, for these long-distance dispersal events (for example, to the Hawaiian and Galapagos island groups), epizoochory (i.e., seeds adhering to the skin or feathers of a bird) may be involved (180), a phenomenon also associated with the dwarf mistletoes (92).

Mistletoes also serve as a food resource for many insects and fungi (74,92,194). A wide variety of insects have been reported to feed on mistletoes (26,27,74), and some insects such as species of butterflies in the genera *Mitoura* and *Hesperocharis* are mistletoe-specific (27,92). Other mistletoe specialists have also been reported, and therefore, some of these mistletoe-specific insects have been considered as possible biocontrol agents (196). Many species of fungi, including several species of rust fungi, have also been reported on mistletoes (74,92), and again several mistletoe-specific fungi have been considered for and some tested as possible biocontrol agents for mistletoes, particularly the dwarf mistletoes (196).

Mistletoe–Ecosystem Interactions

Mistletoes influence forest and woodland plant and animal composition, vertical and horizontal forest structure, ecosystem water use, and forest succession. Most notable, and well studied, in this regard are the dwarf mistletoes in conifers of western North America (198). Severe dwarf mistletoe infestations alter forest stand structure by creating gaps due to mistletoe-associated mortality and branch and tree-top dieback (92), creating patchiness in the stand due to the clumped nature of dwarf mistletoe infection centers (197), and reorganizing vertical canopy structure so that more foliage is concentrated in the lower canopy (76,77). Succession is influenced by mortality of host species and the interaction of dwarf mistletoes, fire, and fire suppression (92,197,203). Ecosystem water use and carbon accumulation is reduced by dwarf mistletoes due to the influence on tree hydraulic architecture, death of branches, and lower leaf nitrogen and photosynthetic capacity of foliage on infected branches (140).

Mistletoes interact with other forest and woodland ecosystem processes in many ways (172). Mistletoes may influence the relationship of mycorrhizal fungi and their hosts by stressing the host to the point that mycorrhizal fungi populations in the roots of severely infected trees are decreased (44,70,145). Mistletoes are patchily distributed and generally most abundant on the largest host trees or shrubs at the local scale, which may have impacts on population structure of host trees in a forest (11,39,167,197,213).

A decade ago, Press (170) asked whether parasitic plants should best be regarded as Robin Hood or Dracula—redistributing nutrients to those in need, or simply taking nutrients from hapless victims. For mistletoes, this remains an open question, but a growing body of evidence is revealing the various pathways used by mistletoes for nutrient transfer. Aside from the well studied one-way flow of water, nutrients, and a variable proportion of photosynthate from host to parasite, recent work has documented the ability of mistletoes to return a range of nutrients back to the host and surrounding organisms via litter-fall (128). As with several root parasites, mistletoe litter contains high proportions of many elements, especially P and K. Coupled with the high turnover of mistletoe leaves, this leads to substantial nutrient enrichment beneath mistletoe plants, altering rates of decomposition and affecting growth rates of annual plants (128). To date, mistletoe litter-fall has been studied only in eucalypt woodlands, characterized by skeletal soils and very low baseline amounts of phosphorous. Whether similar patterns occur in other habitats is unclear, and while it may be less influential in medium to high productivity systems, there are abundant research opportunities to clarify this little-studied aspect of mistletoe influence on ecosystem dynamics.

Many of the ecological interactions among mistletoes, their host plants, and the many organisms that depend on them for food or habitat have not yet been investigated in most of the forest ecosystems of the world. Those studies that have started to examine the ecological roles of mistletoes indicate that they may qualify as keystone species in many forest ecosystems (172,219). Hence, rather than merely curios or destructive pests, mistletoes are now widely regarded as an intriguing group of plants that, through their network of interactions with other forest organisms, can serve as sensitive indicators of overall community integrity and ecosystem health.

Managing Mistletoes

Mistletoes are managed from a variety of perspectives dependent on the nature of the mistletoe and the situation. Whereas the dwarf mistletoes in North America may be managed as destructive forest pests (71), in New Zealand, several loranths are considered endangered species and are managed for preservation (51). *Viscum album* is used in the pharmaceutical industry and is cultivated commercially (32). In Australia and North America, the relationship between mistletoes and wildlife habitat is leading to management practices that use mistletoes to benefit wildlife (198). No longer are mistletoes considered simply tree pests. This has led to a more nuanced and ecological approach to managing them. The classic paper that investigated this potential dichotomy in mistletoe management is Norton and Reid (158), which considered threatened and pest loranths in New Zealand and Australia. They recommended an integrated ecosystem management approach that included consideration of all direct and indirect reasons for the current status of mistletoes, fiend or friend.

Mistletoes as forest, woodland, and orchard pests. The primary control of pest mistletoes remains pruning infected branches and removing infected trees (31,71,86,226). Removal of mistletoe plants from infected branches does not kill the mistletoe, and resprouting from the haustorial system often occurs. This has led to the application of black plastic wraps around the infected portion of the branch to prevent resprouting (160). Although chemical, biological, and genetic controls have been and are still being investigated, particularly for dwarf mistletoes, these techniques have not proved practical or economical thus far (196).

In many parts of western North America, dwarf mistletoes are the primary pests of commercially important conifers, especially in forests managed as wild-lands. Many forests that are intensively managed for fiber production have been clear-felled to eradicate dwarf mistletoes. This practice removes dwarf mistletoes from the site, and silvicultural practices can then prevent their reintroduction. The management of dwarf mistletoes in North America has been summarized (71,92,191). The silvicultural techniques that control dwarf mistletoes are well understood (85,92,146), and the proper implementation of a control program is often the key issue in their management. An excellent set of publications called Forest Insect and Disease Leaflets include management recommendations for several dwarf mistletoes and are available online at: http://na.fs.fed.us/pubs/fidl_hp.shtm.

There is robust evidence that plant breeding could succeed in developing varieties of forest and crop trees that are resistant to loranthaceous and viscaceous mistletoes (81,173,185,196), but the expense of breeding programs apparently has limited its application. Shamoun and Dewald (196) suggested that the low cost and ease with which mistletoes have been controlled silviculturally has prevented investment in developing resistant varieties of commercially valuable trees. Chemical and biological control of mistletoes has been investigated since the 1930s (86,92,160,196). Chemical control has included trunk injection with herbicides (142), application of herbicides to the plant (78), and the use of growth regulators applied to aerial shoots (92,103,196). Biological control with fungi has been discussed for dwarf mistletoes (196), but there have been no reports of leafy mistletoe control with fungi (160).

Fire and mistletoe management. The interaction of mistletoes and fire is currently an important area of fire behavior research, particularly because of the increased frequency and intensity of wildfires in the western United States and in Australia (95,162). Wildfire controls dwarf mistletoes by killing infected trees, reducing stand density, killing infected regeneration, and scorch pruning infected branches (2,3). The historical pattern and intensity of fires on landscapes influenced the current distribution and incidence of dwarf mistletoes in most of North America (3,108,129,203), except in the maritime regions of Alaska where wildfires are rare (147,210). Dwarf mistletoes have increased in abundance partly due to fire suppression over the past 100 years, leading to changes in forest structure and composition that include woody fuels accumulation, increased snag densities, increased crown bulk density, and the lowering of live crowns, all of which can potentially contribute to higher intensity fires and increase the probability that surface fires will transition into crown fires (92,95,136,198) (Fig. 12A). In dry forests dominated by species of *Eucalyptus* in Australia, mistletoes can also influence fire behavior by contributing to canopy density and tree mortality.

As a management tool, prescribed fire can directly control dwarf mistletoes by scorch pruning lower infected branches

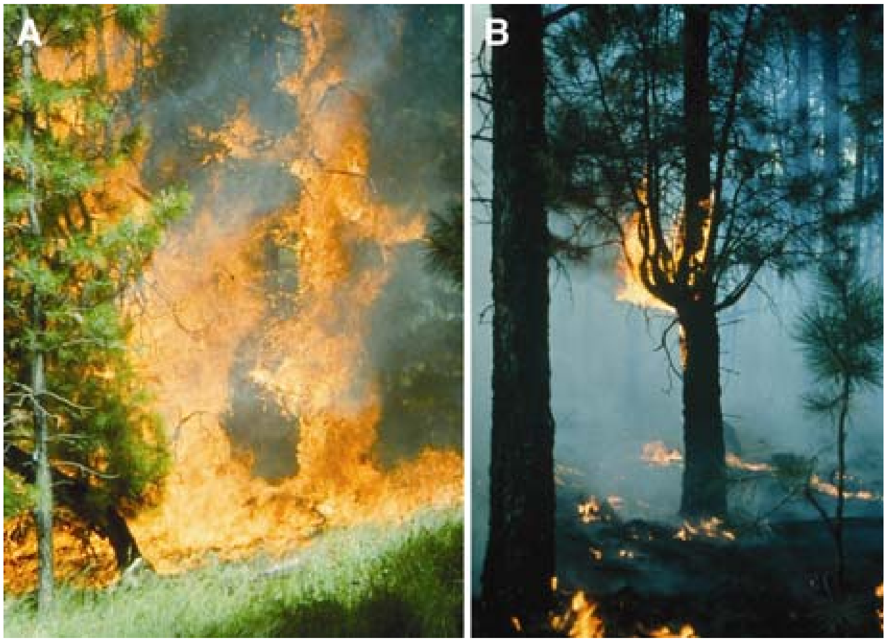

Fig. 12. A, A low intensity surface fire transitioned into a crown fire when flames encountered a ponderosa pine severely infected with southwestern dwarf mistletoe. A witches'-broom that was near the ground ignited initially and then brooms higher in the crown of the tree carried the surface fire into the upper crown. B, A low intensity, prescribed fire ignited this witches'-broom on a ponderosa pine. In this case, the fire did not transition into a crown fire, but killed the mistletoe-infected branches in the broom. (Photo courtesy of USDA Forest Service)

and brooms, killing severely infected trees, and causing dehiscence of mistletoe plants exposed to smoke and heat. Prescribed fire has been shown to reduce dwarf mistletoe populations, but the intensity of fire used is critical to the effectiveness of this management practice (40,82,113). Prescribed fire can also reduce the susceptibility of a forest to spread of dwarf mistletoe, especially if combined with thinning, by killing young regeneration that would become infected from over-story trees, and maintaining wider spacing between trees (2,212) (Fig. 12B).

European mistletoe. The three subspecies of *Viscum album* in Europe (54,229) are the primary mistletoes of concern for forest, orchard, and ornamental trees. Pruning and tree removal are the primary control for *V. album* (31). Because its seeds are spread by birds, it is difficult to prevent reintroductions, and therefore pruning must be continuously practiced. *Viscum album* subsp. *abietis* is an important parasite of *Abies alba*, and is managed by replacing this species with other conifers and selectively thinning infected trees. However, there are now conservation concerns that *A. alba* populations are being reduced to unacceptable levels and that selective thinning is favoring the growth of *V. album* by increasing light levels in thinned forests (155).

Loranthaceae. Much of the information concerning ecology and management of loranthaceous mistletoes is from southern Australia. Reid et al. (179) and Norton and Reid (158) suggest that an ecosystem management approach is the appropriate model for control of over-abundant mistletoes in certain areas of Australia. Direct control by pruning or other techniques does not address the primary reasons for mistletoe problems. In the Northern Tablelands of New South Wales, fire suppression, reduction of natural predators by introduced predators, tree clearance and habitat fragmentation, and grazing-induced suppression of natural tree regeneration all play a role in the current picture. Prescribed fire, grazing management, possum management, and woodland management techniques that take a holistic ecosystem management approach will aid in the maintenance, or when necessary the control, of mistletoe populations there (158).

The use of shading to reduce the impact of mistletoes on crop trees is possible due to the fact that mistletoes do best in high light environments (160). In Africa, control of *Tapinanthus bangwensis* on cocoa with shade has been suggested by Room (184) where cocoa can be grown under canopies of other trees. However, in many situations, the use of shade to control mistletoes may be very difficult, and it is not always possible to experimentally determine the impact of shade on growth of hosts and mistletoe (160). Some trees can outgrow and shade out mistletoes on branches, so that fertilization has been suggested for situations where tree vigor and growth can be improved (160).

Mistletoes managed for wildlife habitat. The management of mistletoes to benefit wildlife is in the early stages of development, but because the positive relationship is so clear, wildlife biologists and ecologists are recommending that mistletoes be ecologically managed rather than eradicated (22,43,158,219). Although the relationship between wildlife and mistletoes is well known, published records of mistletoe management for wildlife are scarce. Bull et al. (30) investigated the effects of thinning to control dwarf mistletoes on arboreal squirrels and found that northern flying squirrel populations declined in thinned stands, while red squirrel populations increased. Both squirrels shifted away from using dwarf mistletoe witches'-brooms as nesting sites to cavity nesting in the thinned forests. Bull et al. (30) recommended that forest managers retain dwarf mistletoe–infected trees with brooms in aggregated clumps to maximize wildlife benefits while controlling damage in the majority of the managed forest. Parks and Bull (164) also noted that aggregating dwarf mistletoe–infected wildlife trees will minimize mistletoe spread and its impact on tree growth.

Dwarf mistletoes present an interesting dichotomy between pest impacts and wildlife benefits in that they can cause growth losses and tree mortality, and their effects on crown structure (witches'-brooms, dead branches, and dead tops) contribute to a complete reorganization of the vertical canopy environment (76,77,92). Yet these same modifications of stand structure can improve habitat for animals by creating complex environments with more dead wood for cavity nesters and foraging animals, while the brooms are used for nesting and other life-history needs (22,136, 165,166,198). One of the most notable relationships between an important wildlife species and dwarf mistletoe is the use by the federally protected northern spotted owl of witches'-brooms associated with Douglas-fir dwarf mistletoe as nesting sites. For example, in southwestern Oregon, 90% of the known northern spotted owl nest sites were located in these brooms (130). Because federal agencies are mandated by law to preserve the owl, management recommendations for preservation of current nesting habitat and for creating future nesting habitat include maintaining dwarf mistletoe populations without detrimentally impacting other resources (130).

Mistletoes managed as endangered species. The management of mistletoes for conservation and preservation has recently become more of an issue in worldwide plant conservation. For example, the International Union for the Conservation of Nature (IUCN) has listed four species of Loranthaceae and 15 species of Viscaceae on the official IUCN Red List of Threatened Species (98,99). Rare parasitic plants in general have emerged as an important and specialized issue for conservation (135). Marvier and Smith (135) noted that parasitic plants require healthy host populations, and these organisms are distinctive from other rare plants in their dependence on their hosts. Therefore, special consideration for host populations is required to manage for healthy parasitic plant populations. As noted by Norton and Reid (158) for New Zealand and Australian mistletoes, an ecosystem management approach is desirable for sustained conservation efforts.

Fig. 13. A woodrose formed on *Pinus oocarpa* by *Psittacanthus angustifolius*. Woodroses are collected and sold as curios (rosarios) throughout Central America and in southern Mexico.

Fig. 14. *Viscum album* was introduced to northern California by Luther Burbank. It is now common on a wide range of host trees in the vicinity of Sebastopol, CA.

Mistletoes in New Zealand are managed primarily for preservation and conservation, with major emphasis on avian pollinators and dispersers as well as the habitat needs of birds and mistletoes (120,158,183,195). The introduced mammalian herbivore, the brushtail possum, is also a major factor in the decline of New Zealand mistletoes, so that control of the possum is fundamental to mistletoe preservation (195). The possum has already contributed to the extinction of *Trilepidea adamsii*, a loranthaceous mistletoe that was endemic to New Zealand (156).

Mistletoe management for commerce. *Pharmaceuticals. Viscum album* has important pharmaceutical properties, and it is used for a wide variety of purposes, including cancer treatments (32,105), but this is not limited to *Viscum* (64). The cultivation and use of *V. album* in Europe is becoming more of an issue as demand for the plant increases. Ramm et al. (173) discussed the cultivation of *V. album*, while Kintzios and Barberaki (107) discussed the biotechnology of *V. album* for application in tissue culture and targeted extracts.

Ornaments and decoration. Viscum album in Europe and some *Phoradendron* species in North America, as well as various leafy mistletoes throughout the world, are collected and sold in the Christmas ornament industry (33). Small twigs of mistletoe with their white berries are packaged and sold before Christmas around the world. The size of this trade is unknown, but it is very common, and is used by many organizations in the United States as a fund-raising activity. Boyce (25) noted that *Phoradendron* control in North America may meet with opposition due to the popularity of mistletoe. For example, *Phoradendron serotinum* is the official floral emblem of Oklahoma, indicating its stature as a valued plant. Additional information on the use of mistletoes as Christmas decorations can be found at http://www.apsnet.org/online/feature/mistletoe/.

In South Africa, mistletoes in the genera *Erianthemum* and *Pedistylis* (Loranthaceae) form the woodrose type of haustorium on their hosts, and the woodroses are detached and polished and sold as curios (57,58). The trade in woodroses is very important in some areas of the African savanna regions in Swaziland, Mozambique, and South Africa, with communal harvest areas and protected areas set up to maintain the mistletoes. Recent studies have sought to understand the impacts of harvesting on woodrose availability and to develop sustainable practices (57,58). It appears that because a significant portion of the total harvest is from dead plants, the present market demand can be met without negative impact on the resource (58). In Central America and Mexico, mistletoes in the genus *Psittacanthus* also form woodroses on infected hosts, and these are also sold as curios (rosarios) (Fig. 13), but the extent of this trade is unknown.

Non-native invasive species. In theory, a mistletoe with a broad host range would be best suited to succeed when transferred to new regions. One example is *Viscum album* in northern California, where the famous horticulturist Luther Burbank intentionally established it on fruit trees for the commercial Christmas ornament industry (190). This is apparently the only known case of a mistletoe species successfully being transferred to a new continent (Fig. 14), completely out of its range (86). By 1984, the mistletoe had spread about 6 km from the original point of introduction in 1900, and it has been reported on over 20 tree species (90). This mistletoe has also been introduced into British Columbia, Canada. Therefore, in some areas, managing mistletoes as non-native invasive species may become important. Again, a potential problem is that the public does not support the eradication of *V. album* from northern California because it is collected for Christmas ornamentation and sold locally.

Final Comments

Humans have known for thousands of years that mistletoes were different organisms than the trees they parasitize. Mistletoes are common throughout the world, and they are included in the mythology of several cultures both ancient and contemporary. The mistletoes associated with Christmas folklore and decorations come to the forefront every December in many regions of the world. They still adorn Christmas cards, and mistletoe is mentioned in popular yuletide songs. They are occasionally used for food or beverage and for a variety of medicinal purposes for humans and animals around the world. They hold a fascination for ecologists because they have coevolved many relationships with animals and other plants in several forest ecosystems. We may find that the relationships between some animals and mistletoes are so intrinsically linked that the removal by natural or human-caused extinction of a mistletoe species may have negative effects on a wide range of other organisms and even an entire ecosystem. While this remains to be shown, the ecological evidence is mounting that mistletoes, while damaging pathogens in some cases from a human perspective, may be keystone species in many forests of the world, and their maintenance may be much more desirable than their elimination. However, the damaging effect of some of these plant pathogens on their hosts has clearly been established, and their management will undoubtedly continue to be a high priority for foresters, arborists, and plant pathologists. Management methodologies now include the cultivation of some mistletoe species for pharmaceuticals or curios, practices aimed at improving endangered wildlife habitat, and conservation of rare species of mistletoe. Molecular phylogenetic work on the aerial parasites in Santalales, additional studies of their physiological relationships with their hosts and their ecological roles in forest ecosystems have now provided a foundation upon which further research can explore this fascinating and important group of parasitic flowering plants we call mistletoes.

Acknowledgments

Many scientists have studied mistletoes over the years, but few were as dedicated to this group of parasitic plants as the late Frank Hawksworth. One of his many contributions to mistletoe research was the collection of literature related to the mistletoes of the world. This collection can be accessed via The Mistletoe Center at http://www.rmrs.nau.edu/mistletoe/. Another excellent source of information on the world's mistletoes is The Parasitic Plant Connection, which can be found at http://www.parasiticplants.siu.edu/. Both of these websites proved invaluable to the authors while preparing this article.

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