

Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia—ecological analogs and reciprocal models for ecosystem management

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Abstract. Whereas the biology, physiology and systematics of mistletoes have been explored in considerable detail, their ecology has received less attention and our understanding is highly fragmentary. A conspicuous exception is the dwarf mistletoes (*Arceuthobium* spp.)—a genus that exclusively parasitises coniferous trees, including many commercially valuable species in the forests of the western United States. Accordingly, these plants have been the subjects of intensive cross-disciplinary research for the past five decades, initially from a control and management perspective but extending into most aspects of their ecology and life history. This review summarises our understanding of dwarf mistletoes, focusing on recent developments in the areas of mistletoe–wildlife interactions, fire, ecosystem ecology and conservation biology. We also compare dwarf mistletoes with Australian mistletoes in the genus *Amyema*, a diverse suite of species found throughout the continent. Despite fundamental differences in their evolutionary origin and most aspects of their autecology and life history, the genera exhibit many similarities in terms of their ecological role in forests and woodlands, and their influence on stand- and forest-scale dynamics. In particular, both groups provide nesting resources for a range of birds and mammals, and nutritional resources for a diverse assemblage of species. Both also interact with fire, potentially leading to changes in successional dynamics at the stand scale. At an applied level, both groups are widely considered as pests but, as our understanding of these keystone species improves, they have the potential to serve as sensitive ecological indicators for their respective ecosystems. Key research priorities are identified for further research on both groups of mistletoes and more explicit comparative research, with *Arceuthobium* serving as a valuable template for future work on *Amyema* and Australian mistletoes in general.

Introduction

Mistletoes are the most speciose parasitic plants, with some 1400 species from five families within the Santalales. Distributed throughout the world, these plants have recently been designated a keystone resource (Watson 2001), having a disproportionately important influence on the distribution of diversity in a broad range of habitats. This ecological prominence contrasts with our emerging understanding of the ecology and life history of these plants, which have only recently been included in discussions of canopy biology and forest ecology.

A notable exception is the dwarf mistletoes (*Arceuthobium* spp., Viscaceae) represented by 34 species in the New World (primarily in North and Central America),

with a further eight species found elsewhere in the Palaearctic (Hawksworth and Wiens 1996). Recently, a new classification has been proposed that reduces the total number of species from 42 to 26 (Nickrent *et al.* 2004). This genus exclusively parasitises coniferous trees, including most species used for commercial timber production in the western United States. Accordingly, they have been the subject of an intensive research program over the past 40 years, spanning most aspects of their ecology and life history (Hawksworth and Wiens 1996; Geils *et al.* 2002).

Another diverse genus of mistletoe is *Amyema* (Loranthaceae), with the greatest richness (36 species) occurring in Australia (Barlow 1992). Despite at least one representative of this genus occurring in almost every

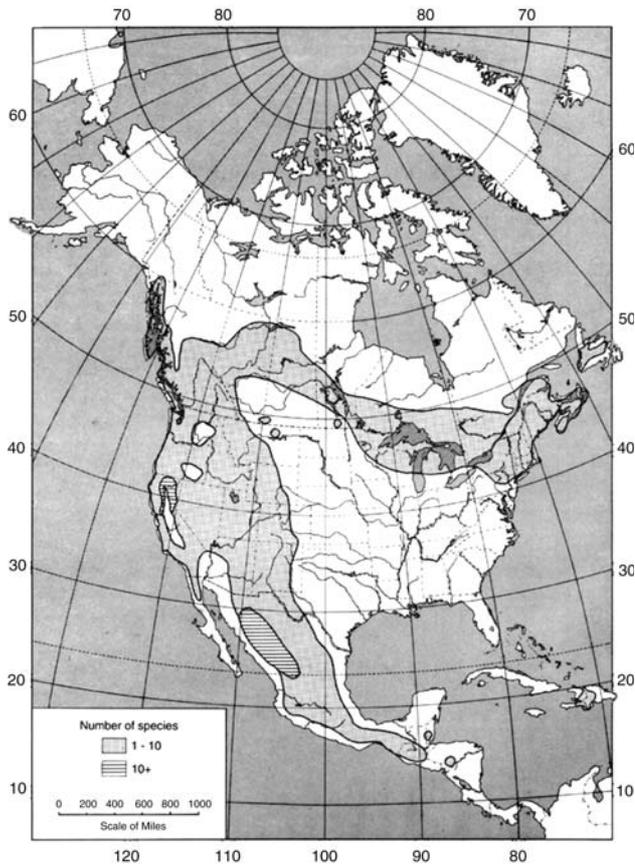


Fig. 1. Distribution of *Arceuthobium* in North America. Note the two regions that contain more than 10 species in northern California, USA, and Sierra Madre Occidental in Chihuahua and Durango, Mexico. Map from Hawksworth and Wiens (1996, p. 29).

woodland and forest type on the continent (from tropical rainforests and mangroves to arid shrublands and coastal heaths), there has been remarkably little research conducted on the group as a whole. Although several species have been the subject of substantial research in south-eastern Australia, this has been on an *ad hoc* basis and there are many gaps in our understanding of the ecology of this genus.

Although being from separate families and having vastly different life histories, there are some striking similarities between the two genera in terms of their ecology and the roles they play in their respective ecosystems. As such, *Arceuthobium* can be considered as a valuable case study, serving as a model for understanding the ecology of mistletoes as a whole. More specifically, given several similarities between western North America and some Australian regions, this comparative exercise can yield useful insight into specific research priorities for *Amyema* and Australasian mistletoes more broadly.

Most of the literature on dwarf mistletoes is contained within forestry reports, theses and proceedings of conferences and workshops and, although there are also



Fig. 2. Female plant of *Arceuthobium tsugense* in western hemlock (*Tsuga heterophylla*). Photograph taken by Ken Bible.

many books, journal articles and synthetic reviews, most of the primary empirical findings are inaccessible to international researchers. Moreover, several emerging themes in recent dwarf-mistletoe research have not been covered by previous reviews. So, our purpose here is 2-fold: first, to provide an up-to-date synthesis of *Arceuthobium* research, emphasising recent work in western North America; and second, to draw comparisons between this system and the *Amyema* mistletoes of Australia.

Arceuthobium ecology and life history

There are 34 species of *Arceuthobium* in the New World, with eight additional species in the Old World (Hawksworth and Wiens 1996). Although Nickrent *et al.* (2004) proposed a revision that reduces the total number of species to 26, based on DNA sequences, for the purposes of this paper, we follow Hawksworth and Wiens (1996). Centres of biological diversity include the Sierra Madre Occidental in north-western Mexico (11 taxa) and northern California (12 taxa) (Fig. 1). The genus is distributed in the Northern Hemisphere from Central America, through western North America and across Canada (Fig. 1), and from Spain and Portugal east through southern Europe, northern Middle East, and into the Himalayas and western China. Disjunct populations occur in the Azores and Africa (Hawksworth and Wiens 1996).

Arceuthobium is dioecious. The seed is produced in a single-seeded berry (Fig. 2) that is explosively discharged from the female plant. The seeds are covered with viscin, a sticky substance, and may adhere to host branches or needles they strike, but successful infections are usually accomplished only on young (<5-year-old) branchlets with thin bark (Hawksworth and Wiens 1972). The dwarf-mistletoe plant develops an endophytic system within the branches of host trees, creating infections that may initially appear as spindle-shaped swellings (Kuijt 1960; Calvin and Wilson 1996). Although the infection generally remains localised, several species characteristically form



Fig. 3. Severely infected western hemlock tree (*Tsuga heterophylla*) in the Cascade Mountains of Washington. Note the 'witches' brooms caused by *Arceuthobium tsugense* as well as several declining branches. Photograph taken by David Shaw.

systemic infections. Aerial shoots bearing reduced scale-like leaves emerge after 1–3 years (Wilson and Calvin 1996) and serve in physiological regulation (i.e. transpiration, photosynthesis), and flower and fruit production. Dwarf-mistletoe plants are perennial, remaining alive as long as the infected branch, and are not dependent on aerial shoots for survival. Most carbohydrates are obtained from the host, as are all water and mineral requirements. The host may respond to infection by forming dense multi-branched structures that are fan-shaped—referred to as 'witches' brooms' (Kuijt 1960; Hawksworth and Wiens 1972). Severely infected trees take on a unique 'broomy' structure (Fig. 3), with dwarf-mistletoe infection having a profound influence on the host-canopy structure and function (Kuijt 1960; Tinnin *et al.* 1982; Mathiasen 1996).

Current knowledge of the pollination ecology of dwarf mistletoes has been summarised by Hawksworth and Wiens (1996). Dwarf mistletoes have flower characteristics

common to both entomophily and anemophily. Some species may use both strategies, whereas others may depend more exclusively on entomophily. However, in all studies, a wide range of insects have been recorded visiting mistletoe flowers in search for pollen and nectar. All these insects may not play an important role in pollination but they do gain resources from the dwarf-mistletoe plant. Dwarf mistletoes often flower when no other entomophilous plants are in flower. For example, Gregor *et al.* (1974) observed that *A. americanum* in both Colorado and Utah flowered from mid-April to mid-May while the ground was still snow-covered. *A. americanum* in Manitoba flowers in early spring, only coming into competition with other entomophilous plants at the end of the flowering season (late May and early June; Gilbert and Punter 1990). In the Wind River region of Washington State, we have observed that the mid-July to late August flowering of *A. tsugense* occurs after all other entomophilous plants have finished flowering. Therefore, dwarf-mistletoe flowers often provide nectar and pollen resources when other sources are limited.

Animal vectors also act as dispersal agents of dwarf-mistletoe seeds. Birds, squirrels and chipmunks have been reported carrying dwarf-mistletoe seeds on surface feathers and fur. They may be hit by sticky seeds and disperse to another site where the seeds are preened, and may stick to host foliage (Nicholls *et al.* 1984). Animal vectors have been implicated in the establishment of dwarf-mistletoe infection centers far removed from all other centres, and not associated with residual trees (Hudler *et al.* 1979; Nicholls *et al.* 1984). In one species (*A. verticilliflorum*, big-fruited dwarf mistletoe), the seed weight is ~100 times that in other species. They are not explosively discharged, but instead appear to rely on animals for dispersal (Hawksworth and Wiens 1996).

There are two primary elements to the population dynamics of dwarf mistletoe: spread into uninfected hosts and intensification within these hosts (Geils and Mathiasen 1990; Shaw and Hennon 1991; Mathiasen 1996; Hawksworth *et al.* 2002). Spread depends on a seed source, usually from adjacent trees within 15 m, but possibly from seed brought in from farther away by birds or mammals. In both cases, intensification will not proceed without male and female plants. Intensification is the horizontal and vertical build-up of mistletoe population numbers in the host trees as numerous infections develop in tree crowns (Hawksworth 1969; Geils and Mathiasen 1990). More seeds, more plants, and the cycle continues until a tree may become so severely infected that it begins to decline, and eventually dies (Roth 2001). Intensification may result in the formation of distinct infection centres in forests where severely infected trees are located and susceptible hosts reproducing in the understorey will become infected as they mature (Mathiasen 1996).

On a local scale, stand composition and structure control the vertical and horizontal spread and intensification of

dwarf mistletoes (Mathiasen 1996; Geils *et al.* 2002). The spatial pattern of hosts and non-hosts (i.e. tree species not infected by dwarf mistletoe), distance between trees, density of tree crowns, and density of foliage and branches have a major effect on the distance that the seeds disperse (Parmeter 1978). Interruptions in the forest stand, such as rock outcrops and rivers, also prevent spread of dwarf mistletoe by the seed-dispersal mechanism. Recently, Robinson *et al.* (2002) developed a spatial statistical model that integrates life history and complex spatial patterns of forest trees and mistletoe plants and predicts spread of dwarf mistletoe within and among forest stands.

Arceuthobium is considered an important pest of coniferous trees in western North America, particularly in the context of large-scale commercial forestry (Geils *et al.* 2002). This view of *Arceuthobium* as a pest has defined management of dwarf mistletoes, which includes biological, genetic, chemical and silvicultural controls (Muir and Geils 2002; Shamoun and DeWald 2002). However, silviculture has been most successful in managing impacts of dwarf mistletoes within intensively managed stands (Scharpf and Parmeter 1978; Muir and Geils 2002). Control of mistletoe is best achieved with clearfelling followed by prescribed burning of the site. This practice attempts to kill all hosts and therefore all of the dwarf mistletoe in an area. The site can then be regenerated with 'clean' stock and management becomes an issue of keeping dwarf mistletoe out of the plantation. However, clearfelling and prescribed fire is not possible or desirable in all situations, and can have negative effects on biodiversity values and particular forest-dependent species.

***Amyema* ecology and life history**

Amyema is the one of the most diverse genera within the Loranthaceae, with a correspondingly high degree of morphological variation. The 92 described species are distributed from the Phillipines and South-east Asia to Australia and Polynesia, with New Guinea and Australia being the two greatest centres of diversity (27 and 32 endemics, respectively; Barlow 1992). The majority of research on this group has been on Australian representatives, especially those 10 species occurring in south-eastern Australia. Although most of the literature we have drawn on is restricted to these species, much of this summary applies to other species in the genus.

Most studies conducted on *Amyema* have been from a systematic viewpoint—describing morphology, establishing generic limits, proposing inter-generic relationships and their relationship with biogeographic patterns (Barlow 1966, 1992). In terms of the ecology of *Amyema* and the influence of these plants on the woodlands and forests in which they occur, there has been little directed research. However, as *Amyema* is by far the most speciose group of Australasian mistletoes (Barlow 1996), most of the mistletoe research

conducted in the region typically involves a representative of the genus, so there are many disparate studies to draw on.

Amyema is typical of most Loranthaceous mistletoes in terms of its ecology and life history. Infection is non-systemic and haustoria range from simple primary haustoria to complex secondary haustoria on runners, sometimes with associated strands penetrating the cortex or cambium of the host (Barlow 1992; Yan and Reid 1995). Once the mistletoe plant has established, the distal portion of the host branch typically reduces in vigour, often dying as vascular flow is directed primarily to the hemiparasite. The site of haustorial connection may also swell; however, otherwise infection by *Amyema* has little effect on the growth form of the host. *Amyema* plants are typically robust and shrubby, clumps ranging in size from less than 0.3 m in an overall diameter to almost 2 m, with most species typically between 0.5 m and 1 m in an overall diameter. Longevity of the plants has not been measured, but they are considered to be short-lived relative to their hosts and dead plants are often seen in woodlands and forests.

Plants are bisexual, with the large hermaphroditic flowers borne in umbellate inflorescences (Calder and Bernhardt 1983; Barlow 1992). Flowers are typically red or orange (rarely green), yielding large volumes of nectar rich in dissolved sugars. Some species or populations are partially self-compatible, with Bernhardt (1983) noting that this strategy was more common for species parasitising a narrow range of hosts. For most *Amyema* species, however, out-crossing is the rule and ornithophily is considered the main pollination mechanism (Paton and Ford 1977; Ford *et al.* 1979; Calder and Bernhardt 1983). The most frequent visitors to mistletoe flowers are generalist honeyeaters (Passeriformes, Meliphagidae), although species from many other families have been recorded (Reid 1986). Reid (1986) summarised the phenology of six *Amyema* species, documenting pronounced complementarity in peak flowering between populations and between species within a region. Moreover, peak flowering periods corresponded to times when few other bird-pollinated flowers were available, i.e. mid-winter in temperate southern Australia and mid-summer in arid central Australia.

Amyema seeds are also bird-dispersed but, in contrast to the wide range of pollen vectors, only three species are considered to be the main dispersal agents, two of them considered mistletoe-fruit specialists (Reid 1986; Yan 1993). The prime disperser of most *Amyema* species is the mistletoebird (*Dicaeum hirundinaceum*), but as this species is a relatively recent arrival to Australasia from Asia, it is considered not to have been the selective force driving flower morphology and phenology (Reid 1987). Rather, the endemic spiny-cheeked honeyeater (*Acanthagenys ruficularis*) and painted honeyeater (*Grantiella picta*), both monotypic genera, are believed to be the extant representatives of the coevolved disperser(s). The ecology of

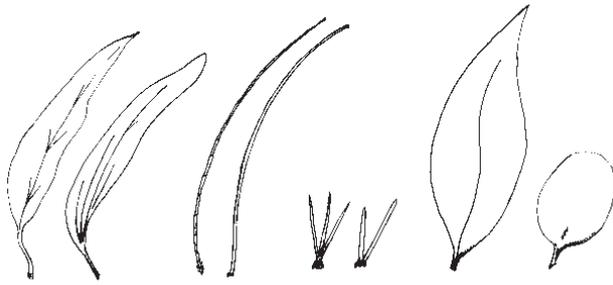


Fig. 4. Diagrams of host (left) and mistletoe (right) leaves in the Australian genus *Amyema* (from left to right): *Eucalyptus meliodora* and *Amyema miquellii*, *Casuarina cunninghamiana* and *Amyema cambagei*, *Acacia tetragonophylla* and *Amyema preissii*, *Avicennia maritima* and *Amyema mackayense*. All display a high degree of mimicry except for the mangrove example—the only system in which there are no mammalian folivores.

all three species is poorly known, especially in relation to their role as mistletoe dispersers, with no estimates of distances moved, microhabitat use, feeding rates or gut-passage times. Other species, including the olive-backed oriole (*Oriolus sagittatus*), striped honeyeater (*Plectorhyncha lanceolata*), grey honeyeater (*Conopophila whitei*), and singing honeyeater (*Lichenostomus virescens*) may also act as occasional seed-dispersers for some *Amyema* species (Reid 1986, 1989); however, they play a lesser role for the group as a whole.

Hosts of *Amyema* are typically trees or large shrubs. Although five species have been recorded parasitising *Callitris* spp. (Cupressaceae), all other host records for *Amyema* (over 6000 summarised by Downey 1998) are from dicotyledonous angiosperms. Main host genera are *Eucalyptus*, *Acacia* and *Casuarina/Allocasuarina*, all common genera of forest and woodland trees. Some *Amyema* species have also been recorded parasitising other hemiparasites—both Loranthaceous mistletoes (nine species) and root parasites in the Santalaceae (six species). Several species are confined to a narrow host range, with seven *Amyema* species known only from hosts in a single genus (Downey 1998). True host specificity is rare and, although several species are specific to a single host within a population, no species of *Amyema* can be considered truly restricted to a single host species. In contrast, several species are notable for their wide host range: *A. congener* has been recorded on 90 species from 31 families, *A. miquellii* from 125 species in 10 families.

One of the notable features of *Amyema* biology is host mimicry, with many species demonstrating remarkably similar morphologies to their main host (Barlow and Wiens 1977; Canyon and Hill 1997). Although this typically has been discussed relative to leaf shape, the resemblance also extends to bark and overall growth habit. Indeed, some species (e.g. *Amyema cambagei*, *A. linophyllum*) are almost



Fig. 5. Mangrove habitat, note the leaf shapes of the mistletoe, *Amyema mackayense* (centre), and the mangrove, *Avicennia maritima* (especially lower left).

impossible to distinguish from their host, only becoming noticeable when flowering. The range of leaf shapes within the genus varies greatly (Fig. 4) from long lanceolate leaves to thin needles, and from broad fleshy leaves to reduced spikes. The origin and maintenance of this pattern has been widely discussed, with mammalian herbivory considered to be one of the key selective forces driving mistletoe host mimicry in leaf shape and growth form (Canyon and Hill 1997; Fig. 4). In the relatively well studied forests of south-eastern Australia, a range of folivorous marsupials are known to favour mistletoe foliage over the secondary compound-rich leaves of their eucalypt hosts (Kavanagh and Lambert 1990). A notable exception to this pattern occurs in mangrove woodlands (Fig. 5), a habitat in which there are two species of *Amyema*, but no mammalian herbivores.

Several studies have examined the effects of *Amyema* infection on host survival and growth. *Amyema* plants do not change the overall growth form of their host, nor necessarily have a deleterious effect on host mortality (Reid *et al.* 1992, 1994). Rather, infected trees have been found to exhibit slower rates of growth (in terms of number of radial branches and trunk diameter). Physiological studies have revealed that *Amyema* mistletoes are primarily water parasites, deriving little, if any, carbohydrates from their host. Transpiration rates are typically higher than their hosts. Although potentially exacerbating water stress to the host, some species are facultatively deciduous, and others die of water stress before the host (D. M. Watson, unpubl. data). In spite of these findings, they are widely considered to be pests and are commonly removed as a part of standard forestry practices.

In terms of other aspects of *Amyema* biology and ecology, little is known. Even though there have been isolated studies on the effect of fire and landscape context, and the influence

of *Amyema* mistletoes on the diversity and distribution of particular species, these findings have generally been restricted to one or two species in a single area. Hence, ecological studies on this group of mistletoes can be considered to be in the early stages. To guide further work and identify key research priorities, it is useful to examine *Arceuthobium* ecology in more detail. The subsequent sections highlight several key areas of dwarf-mistletoe ecology, most of which are yet to be examined for *Amyema*. Following this summary, we will contrast the divergent life histories of these genera with emerging similarities in their ecological roles in forest communities.

Research on dwarf mistletoes and wildlife interactions

Complex interactions exist between dwarf mistletoes and wildlife in western North America. Many species of wildlife benefit directly or indirectly from trees infected with dwarf mistletoes. A number of mammals and birds eat the shoots and/or fruits of dwarf mistletoes (Hawksworth and Wiens 1996; Mathiasen 1996; Bull *et al.* 1997). Insects associated with dwarf-mistletoe shoots and/or witches' brooms provide forage for foliage-gleaning birds (Hudler *et al.* 1979). Reactions of the host tree to dwarf-mistletoe infections can also provide additional forage and structural diversity within tree canopies (Tinnin *et al.* 1982; Tinnin 1984; Mathiasen 1996; Bull *et al.* 1997). Structural diversity associated with severe infestations of dwarf mistletoes may enhance habitat for birds and mammals (Bennetts *et al.* 1996; Parker 2001). The documented uses of dwarf mistletoes by wildlife are presented here, but there are undoubtedly many more interactions between wildlife and dwarf mistletoes that have not yet been studied.

Until recently, the majority of investigations on the relationships between wildlife and dwarf mistletoes has concentrated on animals serving as vectors for long-range dissemination of dwarf-mistletoe seeds. This relationship has been well documented by several investigators (Zilka and Tinnin 1976; Hudler *et al.* 1979; Nicholls *et al.* 1984, 1987, 1989; Punter and Gilbert 1989). Although the frequency and ecological importance of dissemination of dwarf-mistletoe seeds by wildlife is still being debated, it is undoubtedly responsible for establishing new infection centres at much greater distances than could be attained by the explosive seed-dispersal mechanism (Hudler *et al.* 1979; Hawksworth and Wiens 1996). Several species, primarily passerine birds and squirrels, have been identified as vectors of dwarf-mistletoe seeds (Table 1). However, which of these species is most frequently involved in the transport of dwarf-mistletoe seeds is unknown and this most certainly varies among geographic locations and the dwarf-mistletoe species involved.

Another interaction that has been well documented between wildlife and dwarf mistletoes is the use of witches' brooms as nesting sites (Mathiasen 1996; Table 1). However,

whether or not wildlife depends on or preferentially selects dwarf mistletoe-induced witches' brooms as nesting sites is still unknown. Six species of raptors have been documented using dwarf-mistletoe brooms as nesting sites, mostly in witches' brooms formed in Douglas-fir (*Pseudotsuga menziesii*) associated with infection by Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*). The northern spotted owl (*Strix occidentalis caurina*; Forsman 1983; Forsman *et al.* 1984, 1990, Irwin *et al.* 1989; Richards 1989; Martin *et al.* 1992; Buchanan *et al.* 1993; Marshall *et al.* 2000), Mexican spotted owls (*Strix occidentalis lucida*; Pederson 1989; Fletcher 1990; Seamans and Gutiérrez 1995), long-eared owls (*Asio otus*), and great grey owls (*Strix nebulosa*; Bull *et al.* 1989; Bull and Henjum 1990), goshawk (*Accipiter gentilis*) and Cooper's hawk (*Accipiter cooperii*; Moore and Henny 1983), and sharp-shinned hawk (*Accipiter striatus*; Hedwall 2000) have been documented nesting in Douglas-fir witches' brooms.

The marbled murrelet (*Brachyramphus marmoratus*), a seabird, uses witches' brooms associated with hemlock dwarf mistletoe (*Arceuthobium tsugense*) in western hemlock (*Tsuga heterophylla*) trees as nest sites along the west coast of North America (Clint Smith, Oregon Department of Forestry, pers. comm.; Hammer and Nelson 1995). Furthermore, several authors have observed passerine species nesting in witches' brooms induced by dwarf mistletoes (Table 1). For example, in ponderosa pine (*Pinus ponderosa*) forests in the Front Range of Colorado, Bennetts (1991) found 12 (five species) of 47 nests in dwarf mistletoe-induced witches' brooms. Mannan and Siegel (1988) found five hermit thrush (*Catharus guttatus*) nests on limbs deformed by dwarf mistletoe. In northern Arizona, Hedwall (2000) reported four nests of three songbird species in Douglas-fir dwarf mistletoe-induced witches' brooms, whereas Martinka (1972) reported the use of brooms for hiding cover by blue grouse (*Dendragapus obscurus*) in Montana.

Also mammals use witches' brooms, especially squirrels which use dwarf mistletoe-induced witches' brooms for nesting sites. Red squirrels (*Tamiasciurus hudsonicus*) frequently use witches' brooms induced by Douglas-fir dwarf mistletoe for nesting sites in northern Arizona and they use these brooms for caching food as well (Patton and Vahle 1986; Hedwall 2000). Red squirrels have also been reported nesting in witches' brooms in Colorado (Hatt 1943), Washington (Tinnin and Forbes 1999) and Oregon (Lemons 1978). Abert squirrels (*Sciurus aberti*) have commonly been reported to use dwarf mistletoe-induced witches' brooms in ponderosa pine for nesting sites in northern Arizona (Garnett 2001). Farentinos (1972) reported that 10 of 40 Abert squirrel nests were constructed in large witches' brooms in ponderosa pine at a site in Colorado. Pollock (1981) observed similar findings for Abert squirrels in Colorado. Northern flying squirrels (*Glaucomys sabrinus*) and bushy-tailed woodrats (*Neotoma cinerea*) used dwarf

Table 1. Wildlife interactions with dwarf mistletoes in western North America

Vector indicates the bird or mammal has been reported to be a vector of dwarf-mistletoe seeds. Nest indicates the bird or mammal has been reported to nest in dwarf mistletoe-induced witches' brooms. Food indicates the bird or mammal has been reported to use dwarf mistletoe as a food source.

Based on information in Farentinos (1972), Hudler *et al.* (1979), Pinkowski (1981), Tinnin *et al.* (1982), Nicholls *et al.* (1984, 1987, 1989), Crawford *et al.* (1986), Pederson *et al.* (1987), Allred (1989), Punter and Gilbert (1989), Hammer and Nelson (1995), Hawksworth and Wiens (1996), Hedwall (2000) and Garnett (2001). Bird names are based on American Ornithological Union checklist of North American birds (7th edn). Mammal names from the Smithsonian National Museum of Natural History, North American mammals

Common name	Scientific name	Vector	Nest	Food
Birds				
Ruffed grouse	<i>Bonasa umbellus</i>			X
Spruce grouse	<i>Falcapennis canadensis</i>			X
Blue grouse	<i>Dendragapus obscurus</i>			X
Sharp-shinned hawk	<i>Accipiter striatus</i>		X	
Cooper's hawk	<i>Accipiter cooperii</i>		X	
Northern goshawk	<i>Accipiter gentilis</i>		X	
Marbled murrelet	<i>Brachyramphus marmoratus</i>		X	
Band-tailed pigeon	<i>Patagioenas fasciata</i>			X
Mourning dove	<i>Zenaida macroura</i>		X	X
Great horned owl	<i>Bubo virginianus</i>		X	
Northern spotted owl	<i>Strix occidentalis caurina</i>		X	
Mexican spotted owl	<i>Strix occidentalis lucida</i>		X	
Great gray owl	<i>Strix nebulosa</i>		X	
Long-eared owl	<i>Asio otus</i>		X	
Northern saw-whet owl	<i>Aegolius arcadicus</i>	X		
Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>	X		
American three-toed woodpecker	<i>Picoides dorsalis</i>	X		
Gray jay	<i>Perisoreus canadensis</i>		X	X
Steller's jay	<i>Cyanocitta stelleri</i>	X		
Common raven	<i>Corvus corax</i>		X	
Black-capped chickadee	<i>Poecile atricapillus</i>			X
Mountain chickadee	<i>Poecile gambeli</i>	X		
Red-breasted nuthatch	<i>Sitta canadensis</i>	X		
Pygmy nuthatch	<i>Sitta pygmaea</i>	X		
Brown creeper	<i>Certhia americana</i>	X		
House wren	<i>Troglodytes aedon</i>		X	
Western bluebird	<i>Sialia mexicana</i>			X
Mountain bluebird	<i>Sialia currucoides</i>			X
Townsend's solitaire	<i>Myadestes townsendi</i>	X		
Swainson's thrush	<i>Catharus ustulatus</i>	X		
Hermit thrush	<i>Catharus guttatus</i>	X	X	
American robin	<i>Turdus migratorius</i>	X	X	X
Phainopepla	<i>Phainopepla nitens</i>			X
Yellow warbler	<i>Dendroica petechia</i>	X		
Yellow-rumped warbler	<i>Dendroica coronata</i>	X		
Palm warbler	<i>Dendroica palmarum</i>	X		
Western tanager	<i>Pitanga ludoviciana</i>		X	
Chipping sparrow	<i>Spizella passerina</i>		X	
Dark-eyed junco	<i>Junco hyemalis</i>	X		
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>			X
Cassin's finch	<i>Carpodacus cassinii</i>		X	
Red crossbill	<i>Loxia curvirostra</i>	X	X	
Pine siskin	<i>Carduelis pinus</i>		X	
Evening grosbeak	<i>Coccothraustes vespertinus</i>			X
House sparrow	<i>Passer domesticus</i>			X
Mammals				
Mule deer	<i>Odocoileus hemionus</i>			X
White-tailed deer	<i>Odocoileus virginianus</i>			X
Elk	<i>Cervus elaphus</i>			X
American martin	<i>Martes americana</i>	X	X	
Golden-mantled ground squirrel	<i>Spermophilus lateralis</i>		X	
Chipmunk	<i>Tamias spp.</i>			X
Least chipmunk	<i>Tamias minimus</i>	X		
Red squirrel	<i>Tamiasciurus hudsonicus</i>	X	X	X
Abert's Squirrel	<i>Sciurus abert</i>	X	X	X
Northern flying squirrel	<i>Glaucomys sabrinus</i>	X		
North American porcupine	<i>Erethizon dorsatum</i>			X

mistletoe-induced witches' brooms for nesting sites in ponderosa pine in eastern Oregon (Lemons 1978).

Several other mammal species use witches' brooms induced by dwarf-mistletoe infections as resting sites, hiding sites and/or foraging sites. American marten (*Martes americana*), in particular, has been documented using dwarf mistletoe-induced witches' brooms in western larch (*Larix occidentalis*), Douglas-fir, lodgepole pine (*Pinus contorta*) and ponderosa pine as resting sites (Campbell 1979; Hauptman 1979; Burnett 1981; Spencer 1987; Buskirt *et al.* 1987; Parks and Bull 1997; Parks *et al.* 1999). Witches' brooms in lodgepole pine are also frequently used as nest sites by American marten in California (Spencer 1987), Montana (Burnett 1981), Wyoming (Buskirt *et al.* 1987) and Oregon (Bull and Heater 2000), whereas porcupine (*Erethizon dorsatum*; Smith 1982) uses dwarf mistletoe-induced brooms in Douglas-fir as winter shelter.

Wildlife species are known to feed on dwarf mistletoe shoots or on the mistletoe's endophytic system by chewing and eating dwarf mistletoe-infected bark (Table 1). Although the use of dwarf mistletoes as food by wildlife is well documented, the importance of dwarf mistletoes in the diet of these species is uncertain. Much of the use of dwarf mistletoes appears to be during the winter when other food sources are less common or completely unavailable. Dependence by birds, rodents or mammals on dwarf mistletoes as a food source has not been reported. Investigators have demonstrated that dwarf-mistletoe shoots are highly digestible; they are high in carbohydrates but low in mineral and protein content (Urness 1969; Craighead *et al.* 1973). Hawksworth and Wiens (1996) listed 14 species of birds observed feeding on the shoots, fruits or seeds of dwarf mistletoe; however, they considered this behaviour uncommon. Severson (1986) reported that Douglas-fir dwarf-mistletoe shoots comprise only up to 8% of the blue grouse's diet in eastern Arizona.

In ponderosa pine, a small part of the Abert squirrels' total diet comprises dwarf-mistletoe shoots and fruits (Stephenson 1975; Sanford 1986). Trees with dwarf-mistletoe infections represented 34% of a sample of Abert squirrel feed trees in northern Arizona (Allred 1989; Allred and Gaud 1994). In addition, Allred (1989) reported 100% correlation between Abert squirrel bark-grazing and mistletoe infection. Chipmunks (*Tamias* spp.) in Washington, Colorado and Idaho occasionally feed on dwarf-mistletoe seeds and fruits (Nicholls *et al.* 1984). Taylor (1935) observed a substantial amount of winter-feeding on dwarf-mistletoe shoots by porcupines in ponderosa pine forests of the South-west. Mule deer (*Oedocoileus hemionus*) feeds opportunistically on the shoots of dwarf mistletoe (Hawksworth 1961).

Many birds eat the insects associated with dwarf-mistletoe shoots (Holmes *et al.* 1979; Crawford and Jennings 1989). Mountain chickadees (*Poecile gambeli*)

were observed directing 25% of their foraging effort to the shoots of dwarf mistletoes (Hudler *et al.* 1979). This relationship should be investigated in more detail because observations by many investigators have suggested that the use of witches' brooms as foraging sites might be ecologically significant; however, few quantitative data are available.

Effects on diversity

In some areas bird diversity has been reported to be greater in dwarf mistletoe-infested pine forests than in uninfested forests; however, other studies have not supported these findings. Bennetts *et al.* (1996) investigated the indirect effects of dwarf-mistletoe infestations on breeding bird communities in the Front Range of Colorado. They reported a positive correlation between bird abundance and the level of dwarf-mistletoe infestation in eight stands for 24 of 28 bird species. However, in a similar study in northern Arizona, Parker (2001) found a positive correlation between bird abundance and the level of dwarf-mistletoe infestation for only 4 of 16 bird species. Parker (2001) reported a negative correlation for five of the bird species he investigated and no correlation for seven species. Bennetts *et al.* (1996) reported a positive correlation between severity of dwarf mistletoe and numbers of snags and they found three times more cavity-nesting birds in stands severely infested with dwarf mistletoe than in uninfested stands. Parker (2001) also reported a higher density of snags in dwarf mistletoe-infested pine stands than in uninfested stands and three of the four species he reported being positively correlated with dwarf-mistletoe infestations were cavity-nesting birds. This is another example of where additional research is needed to better determine the correlations between bird diversity and the levels of dwarf-mistletoe infection. However, the connection between high levels of dwarf-mistletoe infection, increased snag densities, and therefore, higher densities of cavity-nesting birds is not only intuitive; it has been demonstrated by at least two studies in pine forests of the western United States.

The effects on mammal-population density and use of forests because of dwarf mistletoe-induced changes in horizontal and vertical forest structure are not well documented. These structural changes include increased crown diversity related to witches' brooms, increased number of forest openings, increased snag densities and increased downed woody debris (Mathiasen 1996; Conklin 2000). Dwarf mistletoe-infested ponderosa pine forests in northern Arizona were used significantly more in certain years by mule deer (Clary and Larson 1971). Bennetts *et al.* (1991) reported both mule deer and elk (*Cervus elaphus*) using infested ponderosa pine stands more frequently than uninfested stands in the Front Range of Colorado. Additional research on the interactions of wildlife and direct forest-structure alterations because of dwarf-mistletoe

infestation is needed and would be useful to wildlife managers.

Although more research is clearly needed on the many interactions between dwarf mistletoes and wildlife, it is already well documented that dwarf mistletoes are an important resource that a variety of wildlife species use for many different habitat requirements in forest ecosystems of the western United States. However, although none of the wildlife species appears to be dependent on dwarf mistletoes for survival and/or reproductive success, the complete removal of dwarf mistletoes from these forest ecosystems would undoubtedly have a negative effect on several different wildlife species inhabiting these forests.

Dwarf mistletoes and fire in the western United States

Fire history has been an important factor in determining the distribution and abundance of dwarf mistletoes in western North America (Heinselman 1970; Alexander and Hawksworth 1975; Wicker and Leaphart 1976; Koonce and Roth 1980, 1985; Hawksworth and Johnson 1989; Hawksworth and Wiens 1996; Kipfmüller and Baker 1998; Conklin 2000). All of these studies on wildfire and dwarf-mistletoe interactions have concluded that the natural fire–dwarf mistletoe ecological relationship has largely been disrupted by fire suppression in western North America. Because wildfire is considered the primary natural control agent of dwarf mistletoes, it is generally believed that the effective suppression of wildfires since the early 1900s has greatly contributed to an increase in the distribution and abundance of dwarf mistletoes in forests of the western United States (Hawksworth 1975; Zimmerman and Laven 1984; Hessburg and Beatty 1985; Maffei and Beatty 1988; Hawksworth and Wiens 1996, Conklin 2000).

Fires in dwarf mistletoe-infested western forests have either favoured the spread and intensification of dwarf mistletoes or limited their distribution. Stand-replacing wildfires can completely sanitise an area of dwarf mistletoes when all host and mistletoe biomass is destroyed because dwarf mistletoes will spread into the newly regenerated forest at much slower rates than its hosts. In contrast, incomplete fires that burn in a mosaic pattern can leave behind infected trees that will infect susceptible regeneration following a fire (Jones 1974; Baranyay 1975; Hawksworth 1975; Hreha and Weber 1979; Hawksworth and Johnson 1989).

Suppression of ground fires in the south-western ponderosa pine ecosystems has allowed the establishment of stands that are more dense than the open park-like forests of pre-settlement times (Covington and Moore 1994; Dahms and Geils 1997). Previously, stands may have been too open to allow spread of dwarf-mistletoe seed (Conklin 2000). This concept is supported by the fact that present ponderosa pine stands with low tree densities generally have lower levels of dwarf-mistletoe infestation than denser stands (Koonce and

Roth 1980). Broom development is also reduced in stands with high tree densities (Koonce and Roth 1985), potentially mitigating dwarf mistletoe-related flammability of dense stands.

In limited cases, fire suppression may have decreased dwarf-mistletoe abundance. In stands where frequent wildfires maintained early seral tree species susceptible to dwarf mistletoes, such as lodgepole pine, fire suppression has allowed the establishment of fire-sensitive climax species such as spruce and fir. Because these genera are not principal hosts of lodgepole pine dwarf mistletoe, the abundance of this dwarf mistletoe may be reduced (Hawksworth 1975; Lotan *et al.* 1981).

Infection by dwarf mistletoe increases live-tree consumption during fires because trees infected by dwarf mistletoes may have a greater abundance of highly flammable fuels such as resin-soaked branches, dead witches' brooms and dead needles (Koonce and Roth 1980, 1985; Harrington and Hawksworth 1990; Zimmerman *et al.* 1990), whereas live witches' brooms trap fallen needles adding to aerial fuels (Brown 1975). In addition, dwarf mistletoe-infected trees do not self-prune lower branches as much as uninfected trees do and the live crown extends closer to the ground. This provides a vertical fire ladder, increasing the potential for fires to consume whole trees. Even if the tree does not die, mortality of infected branches is greater than that of uninfected branches during fire (scorch pruning) (Koonce and Roth 1980; Harrington and Hawksworth 1990).

Dwarf mistletoes also cause increased fuel accumulations in severely infested stands (Brown 1975; Koonce and Roth 1985; Conklin and Armstrong 2001). In ponderosa pine forests, Koonce and Roth (1985) reported 73% greater aerial fuels (live and dead witches' brooms) in dwarf mistletoe-infested stands than in uninfested stands. Conklin and Armstrong (2001) reported that much of the higher mortality in dwarf mistletoe-infested plots they studied might have been due to increased ground fuels such as down logs and dead witches' brooms that burn intensely and for a long time. In one plot that was heavily thinned, crown scorch seemed largely determined by the amount of thinning slash on the ground. In other stands with less thinning slash, crown scorch increased with increasing tree-infection ratings. Ground-surface fuel accumulations may generally be greater in dwarf mistletoe-infested stands than in uninfested stands when thinning slash is not considered (Koonce and Roth 1985). Koonce and Roth (1985) speculated that dwarf mistletoe-infected branches persisted in surface fuels because of their increased average diameter and tendency to be resinous.

Prescribed fire (Fig. 6) can be used both for direct reduction of dwarf-mistletoe plants and to make forests less susceptible to spread of dwarf mistletoe (Alexander and Hawksworth 1975). The direct effects of fire on dwarf



Fig. 6. Prescribed fire in ponderosa pine (*Pinus ponderosa*) forest infected with south-western dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*). Note within the fire, there is a broom blazing. Also note the small brooms in foreground developing on ponderosa pine.

mistletoes include scorch pruning of infected branches and witches' brooms, mortality of severely infected trees, and dehiscence of mistletoe plants exposed to smoke and heat and resulting reductions in mistletoe seed crops. Prescribed fire can lower the susceptibility of a forest to dwarf-mistletoe spread, especially after thinning treatments have been applied, because periodic ground fires can deter regeneration and eliminate potentially infected advanced regeneration while maintaining buffers and tree spacing (Alexander and Hawksworth 1975; Van der Kamp and Hawksworth 1985).

Interest in the many interactions among dwarf mistletoes, wildfires and prescribed fires in the western United States has increased dramatically in the last 5 years as more ecologists and forest managers have recommended the re-introduction of natural fire cycles into fire-dependent forest ecosystem as part of west-wide programs to improve forest health and reduce the possibilities of catastrophic wildfires in dense, unhealthy forests. Further research is clearly warranted on the effects dwarf mistletoes have on fire behaviour and on the effects low-intensity prescribed fires have on dwarf-mistletoe populations.

Ecosystem and community ecology

Ecosystem ecology is a synthetic science that utilises a systems approach to understanding the ecology of communities. It has become important in management of forests because of the emergence of 'ecosystem management' (Salwasser *et al.* 1996). Rather than managing single components of the forest, which may lead to unforeseen problems, land managers are managing ecosystems or the whole system. This incorporates concepts of productivity, sustainability, biodiversity and global change (Vogt *et al.* 1997). It has forced a more educated and integrated approach to understanding dwarf mistletoes, which can now be seen as integral components of ecosystems, rather than merely pests to be eradicated (Bennetts *et al.* 1991; Trummer *et al.* 1998; Marshall and Filip 1999). Dwarf mistletoes have ecosystem-level effects on biodiversity, whole-forest water use, carbon balance, mortality rates and processes, and community ecology.

Association with arthropods

Insects that visit dwarf-mistletoe flowers may be important to the wider ecology of forests. Flies in the families Syrphidae and Tachinidae are common dwarf-mistletoe flower visitors and play a role in predation and parasitism of other forest insects. In studies of the pollination ecology of three Rocky Mountain dwarf mistletoes, Penfield *et al.* (1976) found that *Copidosoma bakeri* (Hymenoptera: Encyrtidae), an encyrtid wasp, was the principle pollinator of *A. vaginatum* subsp. *cryptopodum* and *A. cyanocarpum*. *Copidosoma bakeri* is a parasitoid of Lepidoptera, especially cutworms (Penfield *et al.* 1976). This potentially important parasitoid wasp may require the nectar from dwarf-mistletoe flowers for adult energy. Would removal of mistletoes result in an increase of cutworms?

Although many species of generalist herbivore insects have been observed feeding on dwarf mistletoes, there are dwarf-mistletoe specialists known from the orders Lepidoptera, Hemiptera, Coleoptera and Thysanoptera (Hawksworth and Wiens 1996). In general, little is known concerning the ecology of these arthropods. Two species of *Mitoura* (hairstreak) butterflies (Lepidoptera: Lycaenidae), *M. spinetorum* and *M. johnsonii*, specialise on *Arceuthobium* shoots in the caterpillar stage. *Mitoura johnsonii* is a Washington State candidate species for Threatened Status (Larsen *et al.* 1995) and permits are required for collecting. The butterfly is found on several species of dwarf mistletoe, but is most common on *A. tsugense*. However, little is known about these hairstreak butterflies because of the difficulty in studying them. Does herbivory by these species reduce populations of dwarf mistletoe? Would the butterflies go extinct if dwarf-mistletoe populations were reduced?

The complex structure associated with brooms developed by dwarf-mistletoe infections may create habitat structure

that is beneficial to spiders and other arthropods. Although this topic has not been researched and is therefore hypothetical, there is experimental evidence that structural complexity, such as brooms, may increase spider numbers. This has been demonstrated in Douglas-fir forests by Halaj *et al.* (2000) when they compared population numbers of spiders in untreated foliage clusters with those that had been tied together to form clumps. The number and diversity of spiders in the tied-together clumps were significantly greater than in the untied foliage units. Therefore, dwarf mistletoe-created brooms may increase spider abundance in this way.

Whole-tree water use

Whole-tree water use is a developing science, which has recently become more widely utilised in studies of individual tree ecophysiology, as well as whole-forest water regulation and use (Wullschlegel *et al.* 1998). Sala *et al.* (2001) used the 'sap flux' technique to quantify whole-tree water-use impacts of *A. douglasii* in Douglas-fir and *A. laricis* in western larch, whereas Meinzer *et al.* (2004) used the technique to study *A. tsugense* in western hemlock. These are the first such studies of dwarf mistletoe-infected trees. Sala *et al.* (2001) found that severely infected, large western larch had greater whole-tree water use than did large uninfected trees, whereas infected and uninfected Douglas-fir trees had no significant difference. Meinzer *et al.* (2004) found that large infected trees tend to use less water ($\sim 55 \text{ kg day}^{-1}$) than do large uninfected trees ($\sim 90 \text{ kg day}^{-1}$), an opposite effect from that described by Sala *et al.* (2001). Sala *et al.* (2001) found that the leaf area:sapwood area ratio increased in severely infected trees of both species, whereas Meinzer *et al.* (2004) determined that the leaf area:sapwood area ratio decreased in severely infected trees, probably owing to branch mortality (uninfected average 157 live and 34 dead branches *v.* infected trees average 100 live and 59 dead branches). The full implications of dwarf-mistletoe impacts on whole-tree water use await elucidation, and this area of investigation should be continued. Landscape-scale models that deal with productivity, forest hydrology and forest-atmosphere interactions may need to consider spatial extent of dwarf-mistletoe infection centres.

Carbon balance

The carbon balance of forests may be influenced by dwarf-mistletoe infestations also, but whole-stand studies using modern atmospheric techniques have not been completed. The basic paradigm is that severe dwarf-mistletoe infection reduces the diameter growth (wood production) of infected trees (Parmeter 1978; Hawksworth and Wiens 1996). Hawksworth and Wiens (1996) reported that reduced wood production (= reduced carbon sequestration?) because of dwarf mistletoes in western United States is ~ 11.3 million cubic metres per year,

whereas in western Canada it is ~ 3.8 million cubic metres per year. Whether this is due to decreases in foliage carbon acquisition, loss of assimilated carbon to dwarf mistletoe, or combinations with other factors is still unclear. Meinzer *et al.* (2004) found that leaf nitrogen content was 35% lower in infected western hemlock tree foliage, and foliar δ^{13} values were 2.8‰ more negative in infected than uninfected tree foliage, indicating that carbon accumulation and photosynthetic water use efficiency were sharply reduced at both the leaf and whole-tree scale. They estimated that owing to reduced photosynthesis and loss of leaf area from branch mortality, carbon accumulation was 60% lower in heavily infected trees than in uninfected trees. Alternatively, Logan *et al.* (2002) found no difference in nitrogen content or photosynthetic capacity in *Picea glauca* infected with *A. pusillum*. Research across several mistletoe-tree species systems that integrates leaf to whole-tree carbon-acquisition processes and is linked with eddy covariance techniques would greatly help understand how dwarf mistletoes influence carbon dynamics of whole trees and forests.

Mortality

Dwarf mistletoes influence mortality rates and processes of severely infected trees, compared with uninfected or lightly infected trees (Hawksworth and Johnson 1989; Filip *et al.* 1993; Roth 2001). In addition to the direct effect on hosts, dwarf mistletoes may also contribute to individual-tree susceptibility to fungal diseases (especially root diseases), insect agents of mortality (especially bark beetles; Coleoptera: Scolytidae) and environmental stress such as that caused by drought (Hawksworth and Wiens 1996). The increase in 10-year mortality rate (percentage of trees dying per decade) in severely infested stands over the mortality rate expected within uninfested stands was 21, 8, 23 and 34% for *A. abietinum* in *Abies concolor* (Gord. & Glend.) Lindl., *A. americanum* in *Pinus contorta*, *A. douglasii* in *Pseudotsuga menziesii* and *A. vaginatum* in *Pinus ponderosa*, respectively. The percentage increase in 10-year mortality rate for lightly infested stands compared with uninfested stands was 1, 2, 1 and 1%, respectively, in the same study. Roth (2001) studied mortality in dense 30–70-year-old *Pinus ponderosa* trees that grew up under an infested overstorey. The overstorey was removed and the mortality in a series of thinned and unthinned plots followed for a 22-year period. He found that 44% of the ponderosa pine trees died from *A. campylopodum*-associated mortality. From one perspective, this may be seen as a natural way over-crowded ponderosa pine stands are thinned (Roth 2001). Filip *et al.* (1993) investigated mortality of Douglas-fir associated with *A. douglasii*. The 10-year mortality rate was 5% in moderately infested stands and 4% in severely infested stands. Tree size was not related to mortality.

Community dynamics

The influence of *Arceuthobium* on community dynamics was first synthesised by Parmeter (1978), Tinnin *et al.* (1982) and Tinnin (1984). Parmeter (1978) integrated stand dynamics and knowledge concerning mistletoe damage on individual hosts (mortality, growth loss) to provide a perspective on spread, intensification and control of dwarf mistletoes. Tinnin *et al.* (1982) focused on witches' broom formation and its influence on ecosystem structure and function. They contended that brooms are of adaptive advantage to the parasite populations, in some cases to the host populations and in many cases affect biological diversity. For example, brooms in lodgepole pine, Douglas-fir and western larch may enhance susceptibility of the forest to fire. Since these three species are early successional species that require fire, fire may benefit these tree species because it prevents the late-successional tree species that replace them from becoming dominant. Tinnin (1984) contended that dwarf mistletoes do indeed have an impact on tree density, species composition and diversity within the community, physiognomy, and community spatial patterns, whereas Wanner and Tinnin (1989) subsequently demonstrated that *A. americanum* changes the population structure (increase in young trees relative to old) of lodgepole pine in Oregon.

Recently, Godfree *et al.* (2003a) reported that *A. americanum*, in *Pinus contorta*, reduced live basal area, increased bole-diameter variability, increased the density of saplings and seedlings, and decreased the density of tall-intermediate trees. By using the Hawksworth 6-class dwarf-mistletoe rating system (Hawksworth 1977) (DMR, 0 uninfected, 6 severely infected), they showed that a unit increase in stand-level DMR reduced live basal area by 1.32 m² ha⁻¹ and the density of dominant-sized trees by 45 trees ha⁻¹. They contended that the interaction of mistletoe and community dynamics is also greatly influenced by abiotic environmental factors, such as slope, aspect and frost behaviour (i.e. habitat type), which should not be ignored. In further studies of this system, Godfree *et al.* (2003b) found that severely infected lodgepole pine stands had more foliage in the lower canopy, and less foliage in the upper canopy, than did uninfested stands. This was partly caused by the shift to more small trees and fewer tall trees. The total canopy volume within these stands was similar, however.

Hawksworth *et al.* (1992) used plots in young (70-year-old) and old (>300-year-old) forests to compare spatial patterns of infection and growth impacts. Seventy-year-old forests had an average of 1.4 isolated infection centers per ha, whereas the old-growth forest had a majority of the plot infested, but lacked isolated infection centers. Presumably, forest succession leads to the coalescing of the isolated infection centers. Old surviving pines were more tolerant of mistletoe parasitism, having less impact on their growth rates, than did younger pole-sized

trees. Yet, over 29 years, the rate of mortality averaged 0.43% per year at old sites without dwarf mistletoe and 0.75% per year at old sites with dwarf mistletoe.

D. C. Shaw J. Chen, E. A. Freeman, D. M. Braun (unpubl. data) have investigated community influences of dwarf-mistletoe infestation in an old-growth Douglas-fir/western hemlock forest. Across a 12-ha plot, infected trees were isolated in groups which covered 33% of the plot. Infected trees were larger than uninfected trees, whereas within the infected trees, severely infected trees were larger than lightly infected trees. This distribution pattern is consistent with other dwarf mistletoes (Parmeter 1978) and positions the dwarf mistletoe for future spread. There was a negative association between infected and uninfected trees as a whole, whereas there was a positive association with lightly infected trees and uninfected trees, indicating that the infection centres were spreading. In this forest type, western hemlock does not become abundant for 200 years after major disturbance (fire), and hemlock dwarf mistletoe must survive in refugia during this time. Birds may be important in aiding distribution of dwarf mistletoe once western hemlock begins to become abundant again.

Conservation of dwarf mistletoes

Dwarf mistletoes are native plants that play an important role in the ecology of forest ecosystems. As previously stated, dwarf mistletoes are keystone species (Watson 2001) that have a disproportional influence on forest communities in relation to their small stature and biomass. Complete removal of dwarf mistletoes from forest ecosystems could therefore have a disproportional impact on forest ecology. Although dwarf mistletoes are considered pests in some forestry situations, they have a positive influence on many other species in forest ecosystems, having co-evolved with their hosts for millions of years. Therefore, in the emerging field of conservation biology, dwarf mistletoes should be considered along with other native plants as natural components of forest ecosystems that must be maintained on the landscape.

Are any dwarf mistletoes considered in danger of extinction because of management or habitat alteration? Only three taxa of *Arceuthobium* species are considered rare or endangered. *A. blumeri* was once listed as an endangered plant in the United States because it only occurs in one mountain range in southern Arizona. However, it is now known to be common in northern Mexico, so it was de-listed. Only *A. guatemalense* in Guatemala and southern Mexico might now be in some jeopardy of extinction—but this is difficult to assess accurately. *A. hondurensis* was thought to be a candidate for possible extinction in Hawksworth and Wiens (1972) because the known locations had been converted to agriculture or secondary forests; however, it has since been found in several locations in Mexico (Mathiasen *et al.* 2001, 2002).

Table 2. Comparison of *Arceuthobium* and *Amyema* characteristics

Feature	<i>Arceuthobium</i>	<i>Amyema</i>
Origin	Laurasian	Gondwanan
Species richness	42 worldwide, 34 New World	92 worldwide, 36 in Australia, 32 endemic
Growth form	Uniform, relatively small shrubs with reduced leaves; carbon, N and water parasites	Variable, medium–large, shrubby aerial hemiparasites, primarily water parasites
Age/longevity	May live as long as infected branch, aerial shoots not required	Unknown, but considerably less than host
Host range, specificity	Tends to be specific on one host, or group of related hosts, mostly Pinaceae	Highly variable; ranging from several congeneric host species, to over 100
Pollination	Wind and insect pollinated, generalists	Birds, primarily generalist nectarivores
Mode of dispersal	Hydrostatic expulsion and facultative epizoochory	Endozoochory
Dispersal agent	May use range of generalist birds and mammals	Birds, primarily three specialist frugivores
Effects on host	Major effects on growth, productivity, form and survival in heavily infected trees; little effect on lightly infected trees	Reduced growth rate, little effect on mortality
Effects on stand	Alteration of successional dynamics, sometimes mediated	Unknown through changed fire regime
Effects on diversity	Positive effect on vertebrate diversity, probably positive effect on invertebrates	Positive effect on vertebrate diversity

Comparison of *Arceuthobium* and *Amyema*

As summarised in Table 2, *Arceuthobium* and *Amyema* exhibit fundamental differences in their origin, life history and overall biology. *Arceuthobium* is restricted to coniferous forests of the Palearctic, where it parasitises a small number of hosts within two families. It is a small, long-lived plant with a well developed endophytic system, dependent on its host for both water and carbohydrates. *Amyema* is found in Australasia and adjoining regions where it parasitises a broad range of hosts in over 50 families. It is short-lived relative to its host, upon which it depends primarily for its water. Although neither group has specific pollinators—diffuse assemblage of insects and wind for *Arceuthobium*, and a broad range of birds and insects for *Amyema*—they differ greatly in their seed-dispersal strategy and subsequent establishment and growth. The effects of *Arceuthobium* on their hosts are dramatic and often deleterious, whereas *Amyema* rarely has any negative effects on host growth form or survival.

Despite these differences, it appears that *Amyema* may exhibit many similarities with *Arceuthobium* in terms of its interactions with animals and the influence it has on the distribution of other organisms. Although *Amyema* does not produce the characteristic witches' brooms associated with *Arceuthobium* infection, the shrubby clumps are a popular nest site for many Australian birds. Ongoing research has identified 238 species of birds recorded nesting within mistletoe clumps in Australia (Cooney *et al.*, unpubl. data), approximately three quarters of all terrestrial breeding species. Moreover, *Amyema* represents an important food source for many animals—both directly in terms of nectar, fruit and leaves, and also indirectly as a foraging substrate for

insectivorous birds. These interactions have been found to have an effect on the distribution patterns of particular species (Thompson and Owen 1964; Oliver *et al.* 2003) and diversity patterns of birds generally (Watson 2002). Although fragmentary, these findings are remarkably congruent with research on *Arceuthobium*–wildlife interactions, highlighting the analogous roles they play in their respective systems.

For both genera, the combined effect of these mechanisms is a strong influence of mistletoe occurrence on local diversity. Within a region, areas with more *Arceuthobium* and *Amyema* plants have been found to support greater species richness of birds, and also changes in the occurrence of mammals and arthropods. Using Watson's (2001) discussion, based on criterion of Power *et al.* (1996), both genera fit the definition of keystone resources because they are a minor vegetational component relative to total vegetation abundance, species richness and biomass, and they have a disproportional influence on forest biodiversity relative to their minor vegetational biomass. This is due to their influence on flower visitors, specialist herbivores, pathologic effects on hosts, forest structure and broom formation, and interaction with vertebrate ecology.

Gaps and future research priorities

Major gaps and research priorities for dwarf mistletoes include further research into whether animals that utilise dwarf mistletoes are really dependent on them, the role of mistletoes in the ecology of fires, especially outside the well studied ponderosa pine systems, and how has fire suppression in the western USA really affected dwarf-mistletoe populations. There is a pressing need to

understand the effect of dwarf mistletoes on community-level carbon, nutrient and water dynamics, as these factors are being modelled across the region, generally without regard to levels of dwarf-mistletoe infestations. The impacts of climate change on dwarf mistletoes is also an important question. The general question of the association of biodiversity, especially pollinator/flower visitor and specialist herbivores, needs more work. And finally, a synthetic approach to conservation biology and the role of dwarf mistletoes in ecosystem and landscape ecology across the western United States are needed.

Our understanding of *Amyema* ecology is at an earlier stage, with a series of fundamental questions requiring attention. Although there are isolated studies or anecdotal information about the effects of fire, interactions with pollinators, dispersers, herbivores and hosts, and effects of mistletoe on diversity, more studies are needed to establish the generality of existing findings. Several of these areas are the subject of ongoing research, but many questions related to *Amyema* ecology are yet to be explored, including their influence on hollow formation, the interactions between *Amyema*, fire and successional dynamics and the whole area of ecosystem ecology.

Do *Amyema* infections contribute to branch loss from the host and subsequent hollow formation, just as dwarf-mistletoe infection is considered one of the main mechanisms of top die-back, snag and hollow formation in host trees? Are areas with greater mistletoe density more prone to fire, and can mistletoe lead to changes in fire frequency and successional dynamics? These questions extend beyond the ecology of mistletoes and have an important bearing on our overall understanding of woodland and forest ecology.

Comparative studies of *Arceuthobium* and *Amyema* would be invaluable for evaluating similarities and differences between the two genera in terms of stand-level influences. Both groups appear to lack defences to fire, with occasional fires important in regulating local populations. Has fire suppression affected both species in a similar way? Have populations of *Arceuthobium* and *Amyema* increased because of fire suppression, or has the influence of fire suppression and resultant impacts on tree/host species succession changed the availability of hosts and lessened populations of mistletoes? Long-term mapped plots of both species would provide a comparison of a bird-dispersed hemiparasite *v.* a physically dispersed one. How do they differ in spatial patterns and what are the implications for population ecology? Is tree and branch mortality a factor in *Amyema* systems as it is in *Arceuthobium*, and what are the longer-term consequences of their differing dispersal syndromes?

Comparative studies are needed to determine whether *Arceuthobium* really is as different from all the other mistletoes as is suggested on the basis of the impact of the

plant on host water, carbon and nutrient dynamics. The general paradigm is that *Arceuthobium* has a much more negative impact on infested forests than other water-parasitic mistletoes in the Lorantheaceae. But this remains to be proven, given the lack of community-level studies on a range of factors in most mistletoe-dominated systems.

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