

REVIEW ARTICLE

Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada

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- Abstract**
- 1 Natural and recurring disturbances caused by fire, native forest insects and pathogens have interacted for millennia to create and maintain forests dominated by seral or pioneering species of conifers in the interior regions of the western United States and Canada.
 - 2 Changes in fire suppression and other factors in the last century have altered the species composition and increased the density of trees in many western forests, leading to concomitant changes in how these three disturbance agents interact.
 - 3 Two- and three-way interactions are reviewed that involve fire, insects and pathogens in these forests, including fire-induced pathogen infection and insect attack, the effects of tree mortality from insects and diseases on fuel accumulation, and efforts to model these interactions.
 - 4 The emerging concern is highlighted regarding how the amount and distribution of bark beetle-caused tree mortality will be affected by large-scale restoration of these fire-adapted forest ecosystems via prescribed fire.
 - 5 The effects of fire on soil insects and pathogens, and on biodiversity of ground-dwelling arthropods, are examined.
 - 6 The effects of fire suppression on forest susceptibility to insects and pathogens, are discussed, as is the use of prescribed fire to control forest pests.

Keywords Bark beetles, conifers, dwarf mistletoes, fire suppression, fuel accumulation, fungal pathogens, insect biodiversity, prescribed fire, soil organisms, wood borers.

Introduction

Fire, insects, and diseases are natural, integrated components of western forests in North America (Martin, 1989; Harvey, 1994). The recurring disturbances they cause are essential to creating and maintaining these forests (Hessburg *et al.*, 2000). The combined effects of fire, competition for light and water, and native forest insects and pathogens have in-

teracted for millennia to produce a forested landscape dominated by seral or pioneering species of conifers (McDonald *et al.*, 2000). However, changes in fire suppression, anthropogenic factors (e.g. livestock grazing; forest management practices such as high grade timber harvesting or failure to thin stands enough to maintain healthy densities of trees; more people living in forested areas at the urban–wildland interface) and climate in the last century have altered these interactions (Baker & Veblen, 1990; Hadley & Veblen, 1993; Hagle *et al.*, 2000b; Hessburg *et al.*, 2000; Dale *et al.*, 2001). McDonald *et al.* (2000; p. 195) emphasized that ‘Since fire has been the dominant recurring historic disturbance in western forests, the key to maintenance of ecosystem function is a full understanding of time–space interactions among fire, management activities, insects, and disease’.

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Here, we review relationships among fire, insects and diseases for coniferous forests of the Interior West that have frequent fire return intervals (≤ 200 years). Similar reviews have been published for other geographical areas and fire regimes. For example, McCullough *et al.* (1998) emphasized the boreal forests of North America, although they included information about coniferous forests in the Interior West and northern Rocky Mountains. Here, the focus is on drier systems where fire is observed more often and has historically been responsible for most nutrient cycling (Harvey, 1994). Interactions among fire, insects and pathogens differ between forests that have evolved with low-intensity, frequent fires and those with high-intensity fire regimes (Martin, 1989). Although, discussion is limited to coniferous tree species of the western United States and Canada, analogous relationships are observed in arid forest systems around the world.

Literature was examined pertaining to forests in interior western North America: northern Rocky Mountains (Alberta, British Columbia, Idaho, Montana, Wyoming), central Rocky Mountains (Colorado, Utah), southern Rocky Mountains (Arizona, New Mexico), Cascade Range (east-slope Washington, Oregon, and California), eastern Washington, eastern Oregon, north-eastern California, and the Sierra Nevada Mountains (California, Nevada) (Fig. 1). The dominant trees in these coniferous forests include true firs (*Abies* spp.), western larch (*Larix occidentalis* Nuttall), spruces (*Picea* spp.), pines (*Pinus* spp.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), giant sequoia (*Sequoia gigantea* (Lindl.) Decne.), western red cedar (*Thuja plicata* Donn ex D. Don) and hemlocks (*Tsuga* spp.). The major forest pathogens that interact with fire are dwarf mistletoes (*Arceuthobium* spp.) and fungi that cause root diseases (e.g. genera *Armillaria*, *Heterobasidion*, *Leptographium*, *Phellinus*, *Rhizina*), various types of decays (e.g. *Cryptosporus*,

Echinodontium, *Fomitopsis*, *Gleophyllum*, *Letinus*, *Oligoporus*, *Phaeolus*, *Phellinus*, *Perenniporia*, *Tyromyces*), rust diseases (e.g. *Cronartium*, *Endocronartium*) and stains (e.g. *Ambrosiella*, *Ophiostoma*, *Raffaella*) (Table 1). The most prevalent insects associated with fire are bark beetles/engravers (e.g. *Dendroctonus*, *Hylastes*, *Hylurgops*, *Ips*, *Pityogenes*, *Pityophthorus*, *Pseudohylesinus*, *Scolytus*) and ambrosia beetles (e.g. *Gnathotrichus*, *Monarthrum*, *Trypodendron*, *Xyleborus*) in the subfamily Scolytinae (Coleoptera: Curculionidae) (Table 1). Unless noted otherwise, the insects referred to in this review are members of the Scolytinae. Two insect defoliators (the western spruce budworm [*Choristoneura occidentalis* Freeman] (Lepidoptera: Tortricidae)] and the Douglas fir tussock moth [*Orygia pseudotsuga* [McDunnough]] (Lepidoptera: Lymantriidae)] also interact with fire in these forests (Table 1).

Insects, fire or pathogens acting alone or in concert can stress conifer trees and weaken their defenses, thus making them more susceptible to other pests (Miller & Keen, 1960; Fischer, 1980; Gara *et al.*, 1985; Littke & Gara, 1986; Piirto *et al.*, 1998). Trees weakened by pathogens and/or insects may also suffer greater mortality during fire than healthy trees (Harrington & Hawksworth, 1990; Conklin & Armstrong, 2001). Two-way interactions between fire and pathogens, or fire and insects, are commonly documented in the literature, but explicit mention of three-way relationships are rare. The review begins with two examples of interactions among insects, pathogens and fire found in the literature, followed by a review of pathogens that are likely to be vectored by insects after fire, and then two-factor interactions are covered, plus the effects of fire suppression on forest susceptibility to insects and pathogens. The review ends with information on the use of prescribed fire to control insects or pathogens.

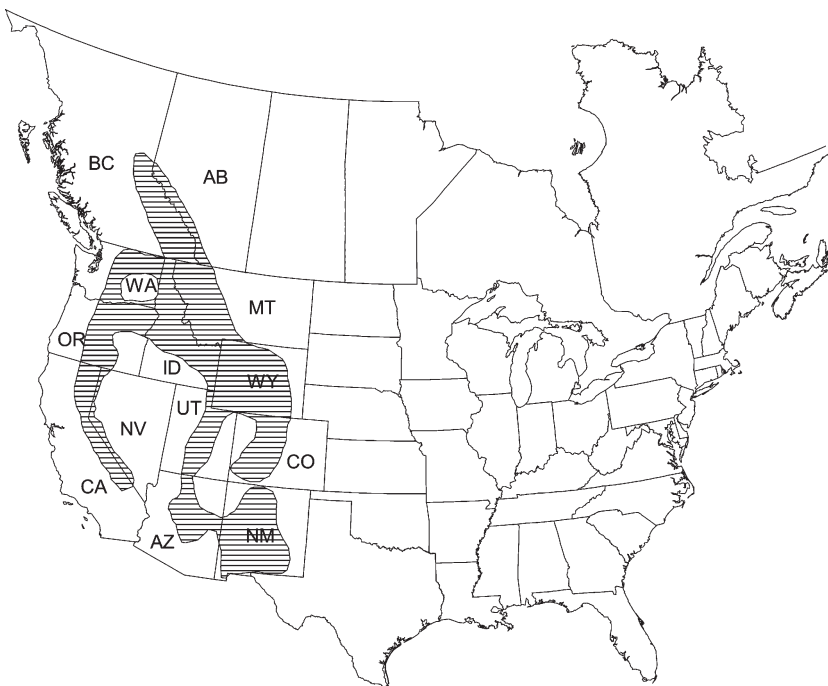


Figure 1 Map of the continental United States and the southern Canadian provinces, with the approximate geographical areas of the coniferous forests covered in this review indicated with shading. AB, Alberta; AZ, Arizona; BC, British Columbia; CA, California; CO, Colorado; ID, Idaho; MT, Montana; NM, New Mexico; NV, Nevada; OR, Oregon; UT, Utah; WA, Washington; WY, Wyoming.

Table 1 Scientific and common names of the main genera and species of insect and pathogen pests included in this paper; for species, the major forest types they occur in are also shown

Genus/species	Common name	Major forest type/ Ponderosa/Jeffrey pine	Lodgepole pine	Mixed conifer	Spruce-fir/ mountain hemlock
Insects					
<i>Arhopalus</i>	Roundheaded borers	–	–	–	–
<i>Arhopalus productus</i>	None	X	X	X	X
<i>Asemum</i>	Roundheaded borers	–	–	–	–
<i>Asemum striatum</i>	None	X	X	X	X
<i>Choristoneura</i>	Budworm, leafroller, and tortrix defoliators	–	–	–	–
<i>Choristoneura occidentalis</i>	Western spruce budworm	–	–	X	X
<i>Dendroctonus</i>	Bark beetles	–	–	–	–
<i>Dendroctonus adjunctus</i>	Roundheaded pine beetle	X	–	–	–
<i>Dendroctonus brevicomis</i>	Western pine beetle	X	–	–	–
<i>Dendroctonus frontalis</i>	Southern pine beetle	X	–	–	–
<i>Dendroctonus jeffreyi</i>	Jeffrey pine beetle	X	–	–	–
<i>Dendroctonus ponderosae</i>	Mountain pine beetle	X	X	–	–
<i>Dendroctonus pseudotsugae</i>	Douglas-fir beetle	–	–	X	–
<i>Dendroctonus rufipennis</i>	Spruce beetle	–	–	–	X
<i>Dendroctonus valens</i>	Red turpentine beetle	X	X	–	X
<i>Ergates</i>	Roundheaded borers	–	–	–	–
<i>Ergates spiculatus</i>	None	X	X	X	X
<i>Gnathotrichus</i>	Ambrosia beetles	–	–	–	–
<i>Hylastes</i>	Bark beetles	–	–	–	–
<i>Hylastes macer</i>	None	X	–	–	–
<i>Hylastes nigrinus</i>	None	–	–	X	–
<i>Hylurgops</i>	Bark beetles	–	–	–	–
<i>Ips</i>	Engraver beetles	–	–	–	–
<i>Ips pilifrons</i>	None	–	–	–	X
<i>Ips pini</i>	Pine engraver	X	X	–	X
<i>Leptura</i>	Roundheaded borers	–	–	–	–
<i>Leptura oblitterata</i>	None	X	X	X	X
<i>Monarthrum</i>	Ambrosia beetles	–	–	–	–
<i>Orygia</i>	Tussock moths	–	–	–	–
<i>Orygia pseudotsuga</i>	Douglas-fir tussock moth	–	–	X	X
<i>Pissodes</i>	Weevils	–	–	–	–
<i>Pissodes fasciatus</i>	None	–	–	X	–
<i>Pityogenes</i>	Twig beetles	–	–	–	–
<i>Pityogenes knechteli</i>	None	X	X	–	–
<i>Pityophthorus</i>	Twig beetles	–	–	–	–
<i>Pityophthorus confertus</i>	None	X	X	–	–
<i>Pseudohylesinus</i>	Bark beetles	–	–	–	–
<i>Pseudohylesinus nebulosus</i>	Douglas-fir pole beetle	–	–	X	–
<i>Scolytus</i>	Bark beetles	–	–	–	–
<i>Scolytus ventralis</i>	Fir engraver	–	–	X	X
<i>Steremnius</i>	Weevils	–	–	–	–
<i>Steremnius carinatus</i>	None	–	–	X	–
<i>Trypodendron</i>	Ambrosia beetles	–	–	–	–
<i>Trypodendron lineatum</i>	Striped ambrosia beetle	X	X	X	X
<i>Xyleborus</i>	Ambrosia beetles	–	–	–	–
Pathogens					
<i>Ambrosiella</i>	Stain fungi	–	–	–	–
<i>Arceuthobium</i>	Dwarf mistletoes	–	–	–	–
<i>Arceuthobium americanum</i>	Lodgepole pine dwarf mistletoe	–	X	–	–
<i>Arceuthobium vaginatum cryptopodum</i>	Southwestern dwarf mistletoe	X	–	–	–
<i>Armillaria</i>	Root disease fungi	–	–	–	–
<i>Armillaria ostoyae</i>	Armillaria root disease	X	X	X	X
<i>Cronartium</i>	Rust fungi	–	–	–	–
<i>Cronartium comandrae</i>	Comandra blister rust	–	X	–	–
<i>Cronartium ribicola</i>	White pine blister rust	–	–	X	–
<i>Cryptoporus</i>	Decay fungi	–	–	–	–
<i>Cryptoporus volvatus</i>	Gray-brown saprot	X	X	X	X

Continued

Table 1 Continued

Genus/species	Common name	Major forest type/ Ponderosa/Jeffrey pine	Lodgepole pine	Mixed conifer	Spruce-fir/ mountain hemlock
<i>Echinodontium</i>	Decay fungi	–	–	–	–
<i>Echinodontium tinctorium</i>	Rust-red stringy rot	–	–	X	X
<i>Endocronartium</i>	Rust fungi	–	–	–	–
<i>Endocronartium harknessii</i>	Western gall rust	X	X	–	–
<i>Fomitopsis</i>	Decay fungi	–	–	–	–
<i>Fomitopsis pinicola</i>	Brown crumbly rot	X	X	X	X
<i>Gloeophyllum</i>	Decay fungi	–	–	–	–
<i>Gloeophyllum odouratum</i>	None	–	X	–	–
<i>Heterobasidion</i>	Root disease fungi	–	–	–	–
<i>Heterobasidion annosum</i>	Annosus root disease	X	X	X	X
<i>Lentinus</i>	Decay fungi	–	–	–	–
<i>Lentinus lepideus</i>	Lentinus butt rot	–	X	–	–
<i>Leptographium</i>	Root disease fungi	–	–	–	–
<i>Leptographium wageneri</i>	Black stain root disease	X	–	X	–
<i>Oligoporus</i>	Decay fungi	–	–	–	–
<i>Oligoporus sericeomollis</i>	Brown cubical butt and pocket rot	–	–	–	–
<i>Ophiostoma</i>	Stain fungi	–	–	–	–
<i>Ophiostoma clavigerum</i>	Blue stain	X	X	–	–
<i>Ophiostoma montium</i>	Blue stain	X	X	–	–
<i>Phaeolus</i>	Decay fungi	–	–	–	–
<i>Phaeolus schweinitzii</i>	Schweinitzii butt rot	X	X	X	–
<i>Perenniporia</i>	Decay fungi	–	–	–	–
<i>Perenniporia subacida</i>	Yellow root rot	–	X	–	–
<i>Phellinus</i>	Decay and root disease fungi	–	–	–	–
<i>Phellinus weirii</i>	Laminated root disease	–	X	–	X
<i>Pholiota</i>	Decay fungi	–	–	–	–
<i>Pholiota carbonicola</i>	Charcoal pholiota	–	X	–	–
<i>Raffaella</i>	Stain fungi	–	–	–	–
<i>Rhizina</i>	Root disease fungi	–	–	–	–
<i>Rhizina undulata</i>	Rhizina root disease	–	–	X	–
<i>Sistotrema</i>	Decay fungi	–	–	–	–
<i>Sistotrema brinkmannii</i>	None	–	X	–	–
<i>Tyromyces</i>	Decay fungi	–	–	–	–

Interactions among fire, insects and pathogens

Fire, root decay and bark beetles

Lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) forests are susceptible to cycles of damage to trees from fire, followed by pathogen-induced decay that predisposes trees to mortality from bark beetle attack; in turn, this causes increased fuel build-up, and continuation of the decay/insect/fuel accumulation cycle (Geizler *et al.*, 1980; Geizler, 1981; Gara *et al.*, 1985; Littke & Gara, 1986; Gara, 1988). These forests have mean fire-return intervals of approximately 25–90 years (Wright & Bailey, 1982).

Such cycles start with low–severe intensity fires, which can scar tree boles and damage root systems of lodgepole pine (Littke & Gara, 1986). Fire-damaged roots in eastern Oregon were frequently infected by fungi associated white rots such as *Leptographium* spp. and *Paceliomyces* spp. and years later by brown rots in the Basidiomycetes, such as *Oligoporus sericeomollis* (Rom.) Pouz. (Gara *et al.*, 1985; Littke & Gara, 1986; Gara, 1988). This fungus causes a

brown cubical heart rot of living and dead conifers throughout western and eastern North America, Europe and Asia (Gilbertson & Ryvardeen, 1987). Geizler *et al.* (1980) and Geizler (1981) reported that fire-scarred boles may be infected by decay fungi such as Schweinitzii butt rot (*Phaeolus schweinitzii* (Fr.) Pat.). However, it is more likely that the white and brown rots reported in later investigations were the principal decay agents and that they attacked fire-damaged roots rather than the fire-scarred boles (Littke & Gara, 1986).

Mountain pine beetles (*Dendroctonus ponderosae* Hopkins) attack trees infected with decay more often than trees without decay; beetles can subsequently spread to neighbouring healthy trees (Geizler *et al.*, 1980; Geizler, 1981; Gara *et al.*, 1985; Littke & Gara, 1986; Gara, 1988). Given the right conditions, mountain pine beetle populations can reach epidemic levels that cause widespread mortality of lodgepole pine, leading to fuel accumulations that later support intense fires. Lodgepole pines are thin-barked, shallow-rooted conifers, and the majority of trees die in severe fires. However, residual trees infected with decay fungi may survive fires and provide a source of inoculum for continuation of the decay cycle (Boyce, 1961).

Dwarf mistletoe, bark beetles and fire

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forests can be vulnerable to cycles of weakening of tree defenses from dwarf mistletoe infection, predisposing trees to mortality from mountain pine beetle attack, leading to accumulated fuels that support severe fires. This ultimately results in maintenance of the fire-adapted early seral host species that are the primary host of the mistletoe. In this case, the cycle starts with south-western dwarf mistletoe [*Arceuthobium vaginatum* (Willd.) Presl ssp. *cryptopodum* (Engelm.) Hawksw. and Wiens] that infects Rocky Mountain ponderosa pine (*P. ponderosa* var. *scopulorum* Engelm.) in Arizona, New Mexico, Colorado, Utah, western Texas and Mexico (Hawksworth & Wiens, 1996). Dwarf mistletoe infection predisposes ponderosa pines in Colorado to mountain pine beetle attack, which may result in extensive tree mortality (Johnson *et al.*, 1976; McCambridge *et al.*, 1982). For example, in the study by McCambridge *et al.* (1982) of north-central Colorado, 25% of the original live pines and 49% of the pine stems per acre were killed in a mountain pine beetle outbreak. Plots with dwarf mistletoe infection had approximately two-fold greater beetle mortality compared with plots without infection (McCambridge *et al.*, 1982). Widespread beetle-induced mortality in mistletoe-infected stands may result in fuel build-ups that cause eventual fires to burn intensely (Lotan *et al.*, 1985). High mortality on a scale more than 40 ha could result in large fire-induced forest openings surrounded by areas thinned by fire. In the short term, fire-weakened trees would be susceptible to bark beetles but, subsequently, areas cleared and thinned by fire would be more resistant to beetle attack and would have decreased dwarf mistletoe abundance. However, in the long term, retention of fire as a disturbance factor would encourage the continued prevalence of fire-adapted early seral host species such as ponderosa pine, the primary host of south-western dwarf mistletoe (Wicker & Leaphart, 1976). Bark beetles may also interact with pathogens other than dwarf mistletoes (e.g. annosus root disease [*Heterobasidion annosum* (Fr.) Bref.]) to cause significant mortality and fuel accumulation (Sherman & Warren, 1988).

Kenaley (2004) recently established that a similar relationship exists between south-western dwarf mistletoe infested ponderosa pines in northern Arizona and increased susceptibility to attack by *Ips* bark beetles. He concluded that when *Ips* outbreaks occur in dwarf-mistletoe infested ponderosa pine stands, the beetles preferentially attack and kill severely infected, intermediate size pines. Kenaley (2004) suggested that, although elimination of these stressed, intermediate size trees by *Ips* beetles may improve the long-term vigour and health of these forests, the bark beetle-killed trees with dwarf mistletoe also contribute to a large build-up of standing and downed fuel, thus exacerbating the fire hazard.

Insects as vectors of pathogens after fire

Insects spread fungi to fire-stressed trees in many western forest ecosystems. For example, Piirto *et al.* (1998) reported that the entomogenous fungus *Tritrachium* sp. was more

common in fire-scarred giant sequoia than in unburned trees. A large percentage of some bark beetle species carry decay fungi. Harrington *et al.* (1981) reported that 80% of Douglas-fir beetles (*Dendroctonus pseudotsugae* Hopkins) carried several types of fungi. Examples include *Fomitopsis pinicola* (Schwartz: Fr.) Karst, which causes brown crumbly rot; *Cryptoporus volvatus* (Pk.) Shear., which causes grey-brown saprot; and other decay fungi. Although the implication is that the beetles could convey decay fungi to uninfected trees because they carry spores of these fungi, transmission has not actually been demonstrated.

Insects can disseminate spores of the fungus that causes black stain root disease to the fire-weakened trees they attack (Safranyik *et al.*, 1975); the disease is a potentially lethal disorder caused by *Leptographium wageneri* (Kendrick) Wingfield. There are three strains of the fungus: one strain kills Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), lodgepole pine and ponderosa pine; another kills pinyon (*Pinus edulis* Engelm.); and the third kills Douglas-fir (Sinclair *et al.*, 1987). Black stain root disease can spread from infection centres at up to 7 m/year and is considered a major threat to Douglas-fir and ponderosa pine under management in western forests. Thies *et al.* (2001) found that ponderosa pine sites in the Blue Mountains of Oregon burned by prescribed fire had greater abundances of beetles infesting roots and lower boles; the beetles were possible vectors of black stain root disease. Sinclair *et al.* (1987) reported that *Hylastes macer* (LeConte) bark beetles are a likely vector of this disease in ponderosa pine. Insects that may act as vectors in Douglas-fir forests include the weevils (Coleoptera: Curculionidae) *Steremnius carinatus* (Mannerheim) and *Pissodes fasciatus* LeConte, and the bark beetles *Hylastes nigrinus* (Mannerheim) and *Hylurgops* spp. (Thies *et al.*, 2000).

Dendroctonus bark beetles have evolved a complex relationship of symbiosis, competition and antagonism with blue stain fungi and parasitic mites (Klepzig *et al.*, 2001). *Dendroctonus* beetles native to North America may have co-evolved with their most common fungal associates because most species introduce their own unique species of mycangial fungi to their hosts (Owen *et al.*, 1987; Six & Paine, 1999). Mountain pine beetles attack fire-weakened trees (Fischer, 1980; Geizler *et al.*, 1984; McHugh, 2001) and carry at least two species of blue stain decay fungi in their mycangia that may contribute to host tree mortality (Krebill, 1975; Safranyik *et al.*, 1975; Solheim, 1995; Solheim & Krokene, 1998). The two fungi are *Ophiostoma montium* (Rumb.) von Arx and *Ophiostoma clavigerum* (Robins.-Jeff. and Davids.) Harrington; the latter fungus is the primary invader of sapwood and is probably the more virulent of the two (Solheim & Krokene, 1998).

Trees killed by fire attract sapwood-feeding insects and heartwood-borers (e.g. several genera of ambrosia beetles and roundheaded borers [Coleoptera: Cerambycidae]; Lowell *et al.*, 1992), but they do not generally attract *Dendroctonus* bark beetles (DeNitto *et al.*, 2000). Sapwood feeders like ambrosia beetles contribute to deterioration of fire-killed timber by introducing stain fungi such as *Ambrosiella* spp. and *Raffaella* spp.; the combination of boring and fungal action has its greatest effect in wetter coastal forests

(Furniss & Carolin, 1977). It is unclear as to what extent introductions of stain fungi by insects in inland forests hasten the rate of tree-fall because insect activity also loosens bark. Bark loss increases the rate of drying and retards decay (Lowell *et al.*, 1992). When insects do induce rapid deterioration of fire-killed trees, they may also accelerate wind-throw of the dead trees. Wind-thrown trees are frequently deteriorated by stem decays (Lowell *et al.*, 1992). Decay organisms may thereby reduce the number of years required for ground fuels to accumulate in areas burned by crown fire. Ground fires that occur with abundant coarse fuels may carry farther and burn hotter than in areas without abundant downed trees (Rothermel, 1983).

Trees in the genera *Pinus*, *Abies* and *Pseudotsuga* that were recently killed by fire are often substrates for *Cryptoporus volvatus*, a fungus that causes a white sapwood rot (Gilbertson & Ryvarden, 1986) commonly known as grey-brown saprot (Hawksworth *et al.*, 1985). Globular sporophores of the fungus, frequently referred to as 'popcorn conks', are formed annually and grow from insect holes in the bark (Hayashi *et al.*, 1996). The fungus may also grow on live trees weakened by fire or insects (Hayashi *et al.*, 1996) and it can enhance sapwood decay of trees attacked by subcortical insects (Harrington & Shaw, 1981). Although *C. volvatus* is generally thought to be insect disseminated (Castello *et al.*, 1976; Harrington *et al.*, 1981; Hayashi *et al.*, 1996), Harrington & Shaw (1981) reported that wind-disseminated spores were released through perforations in the volva.

Interactions between fire and pathogens

Fire-induced pathogen infection

There is evidence for a few western tree species, in particular lodgepole pine, that fire produces entrance courts and/or weakens trees so that pathogens may become established. The evidence for root decays invading fire-damaged roots in lodgepole pine has already been discussed. Littke & Gara (1986) reported that fire-damaged roots, not fire scars, were the most common entrance points for decay fungi in lodgepole pine. Approximately 70% of fire-scarred trees in their study also had fire-damaged roots; *Pholiota carbonicola* A.H. Sm. & Hesler was the primary invader of freshly scorched roots. Six years after fire, common decay fungi included *Perenniporia subacida* (Pk.) Donk (the fungus that causes yellow root rot), *Heterobasidion annosum* (annosus root disease), *Lentinus lepideus* (Fr.) (*Lentinus* butt rot), and *Sistotrema brinkmannii* (Bres.) J. Eriksson. Fungi isolated from heart-rot columns of trees damaged by fire 84 years earlier included *Oligoporus sericeomollis* (a brown cubical rot; reported as *Poria asiatica*) and *Gloeophyllum odouratum* (Fr.) Imaz. (also a brown cubical rot) (Littke & Gara, 1986).

Piirto *et al.* (1998) observed that fire in giant sequoia ecosystems resulted in more abundant decay fungi in fire-scarred trees and a higher incidence of above-ground decay than in unburned areas. Closer investigation may reveal that decays in above-ground fire scars are not contiguous with heartwood decays (Littke & Gara, 1986).

Laminated root disease and fire

A negative feedback loop appears to drive the system composed of the laminated root disease fungus *Phellinus weirii* (Murr.) Gilb., the host trees mountain hemlock *Tsuga mertensiana* (Bong.) Carr. and lodgepole pine, and fire (Dickman & Cook, 1989). Laminated root disease infestations are typically characterized by dead and dying trees that provide a substantial fuel supply and a means for surface fire to climb into the crown layer (Dickman & Cook, 1989; Dickman, 1992). Laminated root disease increases the probability of fire via fuel accumulation, but then fire reduces the fuels that harbour the fungus. Fire also favours lodgepole pine rather than mountain hemlock because it is more resistant to the fungus, although the early seral lodgepole pines can still harbour the fungus. A shift in species composition to lodgepole pine after fire decreases the availability of the primary host of laminated root disease (mountain hemlock). Greater proportions of lodgepole pine in the stand decrease the probability of crown fire until the pines become mature and suffer mortality due to bark beetles, stem gall and lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.). If no fire occurs, the site becomes increasingly dominated by mountain hemlock again and *P. weirii* populations increase thereby reinitiating the cycle.

Dwarf mistletoes and fire

Fire history has been an important factor in determining the distribution and abundance of dwarf mistletoes in western North America (Heinselman, 1970; Alexander & Hawksworth, 1975; Wicker & Leaphart, 1976; Koonce & Roth, 1980, 1985; Hawksworth & Johnson, 1989; Hawksworth & Wiens, 1996; Kipfmüller & Baker, 1998; Conklin, 2000). These studies on wildfire and dwarf mistletoe interactions have all concluded that the natural fire-dwarf mistletoe ecological relationship has largely been disrupted by fire suppression in western North America. This disruption has led to an increase in the severity and distribution of dwarf mistletoes in most cases (Hawksworth, 1975; Zimmerman & Laven, 1984; Hessburg & Beatty, 1985; Maffei & Beatty, 1988; Hawksworth & Wiens, 1996; Conklin, 2000; Shaw *et al.*, 2004).

Natural fires in dwarf mistletoe-infested western forests usually served to limit the distribution of these parasites but, in some cases, may have favoured their spread and intensification. Stand replacing fires can completely eradicate an area of dwarf mistletoes when all their hosts are destroyed because dwarf mistletoes will spread into the newly regenerated forest at much slower rates than their hosts. By contrast, fires that burn in a mosaic pattern can leave behind dwarf mistletoe-infected trees that will infect susceptible regeneration after the fire (Jones, 1974; Baranyay, 1975; Hawksworth, 1975; Hreha & Weber, 1979; Hawksworth & Johnson, 1989).

Fire suppression may have decreased dwarf mistletoe abundance in some situations. In stands where frequent fires maintained early seral trees 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 species are not very susceptible

to lodgepole pine dwarf mistletoe, the abundance of this dwarf mistletoe may be reduced where fire suppression has been effective in lodgepole pine forests of the Rocky Mountains (Hawksworth, 1975; Lotan *et al.*, 1981).

Dwarf mistletoe infection often increases live tree consumption during fires because infected trees may have a greater abundance of highly flammable fuels such as resin-soaked branches, dead witches' brooms and dead needles (Koonce & Roth, 1980, 1985; Harrington & Hawksworth, 1990; Zimmerman *et al.*, 1990). In addition, dwarf mistletoe-infected trees do not self-prune lower branches as frequently as uninfected trees and so the live crowns of infected trees often extend closer to the ground. This creates a vertical fire ladder for ground fires, increasing the potential for fires to consume whole trees and spread into the crowns of nearby trees, and then possibly to the crowns of entire stands or forests.

Dwarf mistletoes also cause increased fuel accumulations in severely infested stands (Brown, 1975; Koonce & Roth, 1985; Conklin & Armstrong, 2001; Hoffman, 2005). In ponderosa pine forests, Koonce & Roth (1985) reported 73% greater aerial fuels (live and dead witches' brooms) in dwarf mistletoe-infested stands than in un-infested stands. Conklin & Armstrong (2001) reported that much of the higher mortality in dwarf mistletoe-infested plots they prescribed burned in New Mexico might have been due to increased ground fuels such as down logs and dead witches' brooms that burn intensely and for a long duration. Koonce & Roth (1985) speculated that dwarf mistletoe-infected branches persisted in surface fuels because of their increased average diameter and tendency to be resinous. Hoffman (2005) found that moderately and severely dwarf mistletoe-infested ponderosa pine stands in northern Arizona had significantly higher total fuel loads than similar un-infested stands. These studies have clearly demonstrated that fuel loads in dwarf mistletoe-infested forests are greater than in un-infested forests, and therefore dwarf mistletoe-infested stands are at greater risk to have high-intensity fires in the future.

Prescribed fire has been proposed as a means of directly decreasing dwarf mistletoe populations and for reducing the potential for spread of dwarf mistletoes (Alexander & Hawksworth, 1975). The direct effects of fire on dwarf 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 (Koonce & Roth, 1980; Conklin & Armstrong, 2001). Prescribed fires can reduce the potential for spread of dwarf mistletoes, particularly after thinning treatments, because periodic low-intensity ground fires can be used to deter regeneration and eliminate infected advanced regeneration, at the same time as maintaining a reduced tree spacing, which reduces dwarf mistletoe spread (Alexander & Hawksworth, 1975; van der Kamp & Hawksworth, 1985).

Interest in the interactions between dwarf mistletoes, wildfires and prescribed fires in western coniferous forests has increased dramatically during the last 10 years. This is because more forest managers have been recommending the re-introduction of natural fire cycles into fire-dependent forest

ecosystems as part of programmes to improve forest health and reduce the possibilities of catastrophic wildfires in dense, unhealthy western forests. The Healthy Forests Initiative introduced in 2002 and the Healthy Forests Restoration Act of 2003 (HFRA, 2003) are both aimed at reducing fire hazard in fire-prone western forests using both thinning and prescribed fire. Consequently, further research is clearly warranted on how dwarf mistletoes affect fire behaviour, and on how prescribed fires affect the survival, reproduction and spread of dwarf mistletoes.

Interactions between fire and insects

Fuel accumulation

Lodgepole pine forest dynamics are intimately related to fire and insects (Lotan *et al.*, 1985; McCullough *et al.*, 1998). Large lodgepole pines are more susceptible to mountain pine beetle attack than small trees because phloem must be ≥ 2.5 mm thick to support good beetle reproduction (Amman & Safranyik, 1985). As a result, mature stands with high percentages of basal area in trees with phloem thickness > 6 mm are especially susceptible to mountain pine beetle outbreaks (Berryman & Stark, 1985). Alfaro *et al.* (2004) hypothesized that lodgepole pine stands in the south central area of British Columbia alternate between states where they are susceptible or resistant to mountain pine beetle outbreaks on average every 42 years; stands are susceptible when they are overstocked, mature (usually ≥ 80 years old) and have many large diameter trees. Trees killed by mountain pine beetles create abundant ground fuels; beetle outbreaks in mature stands cause extensive mortality that may become a large contiguous fuel base (Brown, 1975; Stuart *et al.*, 1989; Parker & Stipe, 1993). When fires are ignited, the resulting burns are often intense, killing the majority of mature trees, and clearing soil for regeneration from seeds released by the serotinous cones (Lotan *et al.*, 1985). Young trees in postfire stands will not support a bark beetle outbreak until they age significantly. This familiar cycle has been observed in every western state and province where lodgepole pine occurs (Koch, 1996).

There is also a long-standing notion (Hopkins, 1909) that Engelmann spruce (*Picea engelmannii* Parry ex. Engelm.) mortality induced by outbreaks of the spruce beetle (*Dendroctonus rufipennis* Kirby) increases fuel loads and the probability of stand-replacement fires in subalpine spruce-fir forests (Schmid & Frye, 1977). Any disturbance that produces downed host material can potentially contribute to the rapid increase of spruce beetle populations (e.g. windthrow, logging slash, snow avalanche) (Jenkins *et al.*, 1998). The literature has frequently suggested that fire occurrence increases after spruce beetle outbreaks (Hopkins, 1909; McCullough *et al.*, 1998).

However, Baker & Veblen (1990) proposed that spruce beetle outbreaks in subalpine forests are not as closely associated with fire as previously thought. Spruce beetle outbreaks that do not result in fire may perform a similar function in subalpine ecosystems that produce the same

vegetation patterns; in fact, beetle outbreaks may be a more common disturbance agent than fire (Baker & Veblen, 1990; Veblen *et al.*, 1994). The primary fire/insect interaction in spruce-fir forests may simply be that insect outbreaks do not occur in young postfire stands (Veblen *et al.*, 1994). For example, postfire spruce stands are not subject to *D. rufipennis* outbreaks until they reach at least 70 years of age (Veblen *et al.*, 1994).

Recent work by Bebi *et al.* (2003) and Kulakowski *et al.* (2003) also failed to support the often-suggested increase in fire occurrence expected to follow spruce beetle outbreaks, based on quantifying the spatial associations of fire and spruce beetle outbreaks over more than a century in a sub-alpine forest landscape in north-western Colorado. Bebi *et al.* (2003; p. 369) concluded that 'Following the widespread 1940s spruce beetle outbreak, there was no increase in fire density in affected stands compared with unaffected stands'. Their results, based on analyses at a broad landscape scale, were consistent with former watershed scale findings (Veblen *et al.*, 1994); crown fires reduced the subsequent occurrence of spruce beetle outbreaks in young postfire stands because beetles primarily attack mature trees. Bebi *et al.* (2003) also noted that the interactions they studied between fire and spruce beetle outbreaks were spatially highly variable in relation to topographic variables.

Fire-induced insect attack

Large wildfires in the West have caused widespread tree mortality in the recent past (Mutch *et al.*, 1993). For example, Swetnam (1990) and Swetnam & Betancourt (1998) concluded that the potential for regionally synchronized wildfires has increased in the south-western United States because a wet period in the decades after the 1970s led to fuel accumulation, which has been followed by an apparent drought after the late 1990s. Also, an ever-increasing acreages area is treated with prescribed fire every year (Fettig, 2004). As a result, insect attack of burned trees may become a more important issue.

Trees that are killed by fire are generally infested only by woodwasps (horntails; Hymenoptera: Siricidae) or wood borers in the beetle families Cerambycidae (longhorned beetles or roundheaded wood borers) and Buprestidae (flatheaded or metallic wood borers) (McCullough *et al.*, 1998; DeNitto *et al.*, 2000). These insects generally do not build up and attack neighbouring green trees (DeNitto *et al.*, 2000). Wood borers occasionally attack dead parts of live ponderosa pines (e.g. dead portions of the cambium or areas previously attacked by *Dendroctonus* or *Ips* bark beetles; McHugh, 2001). Buprestids and cerambycids are sometimes classified as either sapwood or heartwood feeders (Lowell *et al.*, 1992). Some of the most common heartwood borers are cerambycid roundheaded borers such as *Ergates spiculatus* (LeConte), *Arhopalus productus* (Lec.), *Asemum striatum* (L.) and *Leptura oblitterata* Haldeman (Lowell *et al.*, 1992). Ambrosia beetles are one of the most common sapwood feeders that attack fire-killed Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), spruce and true firs (Lowell *et al.*, 1992); western species are typically in the genera *Trypodendron*, *Gnathotricus*, *Monarthrum* and *Xyleborus* (Furniss & Carolin,

1977). Ambrosia beetles enhance deterioration of fire-killed timber by introducing stain fungi (Lowell *et al.*, 1992).

Natural disturbance regimes from fire plus native pathogens and insects such as bark beetles appear to have functioned in a balanced manner across the landscape in many forests of Interior Western North America to create ecosystems that were resilient to perturbation (Hessburg *et al.*, 2000). Similarly, Schowalter *et al.* (1981) concluded that, historically, low-intensity surface fires combined with non-epidemic populations of the southern pine beetle (*Dendroctonus frontalis* Zimmermann) probably provided many beneficial ecosystem functions in south-eastern coniferous forests. For example, both fire and bark beetles reduce competition among trees, but the competitive release caused by bark beetle outbreaks has much longer lasting effects on tree growth rates compared with fire (Veblen *et al.*, 1994). Surface fires help recycle nutrients sequestered in the litter and understory, whereas bark beetles release nutrients by killing large senescent trees and thinning stands (Schowalter *et al.*, 1981). Together, fire and tree mortality from bark beetles creates a positive feedback loop that encourages nutrient system stability (Everett *et al.*, 2000).

Nonetheless, bark beetles are typically considered as the most important damaging insects after fires because they commonly attack trees that were weakened but not killed by fire (Miller & Patterson, 1927; Fischer, 1980; Ryan & Reinhardt, 1988; Amman & Ryan, 1991; McCullough *et al.*, 1998; Bradley & Tueller, 2001; Conklin & Armstrong, 2001; Thies *et al.*, 2001; Fowler & Sieg, 2004). However, successful attack of burned trees by bark beetles is by no means certain and depends on several factors (DeNitto *et al.*, 2000). Trees must be scorched sufficiently so that their defenses are weakened. Tree species with thicker bark (e.g. ponderosa pine and western larch) are less likely to suffer fire-induced damage (Ryan & Reinhardt, 1988; Reinhardt & Ryan, 1989; Ryan & Frandsen, 1991) and may be more able to defend themselves against insect attack than thinner-barked trees. There must also be a sufficient supply of undamaged inner bark in fire-affected trees to provide food for the beetle's offspring. Fires must occur close to a time when the adult beetles are flying and searching for new host trees to colonize. If trees are not attacked soon after a fire, the phloem may become too dry before the next beetle flight season. Finally, a population of beetles must be within flight distance of fire-weakened trees (DeNitto *et al.*, 2000).

The propensity for bark beetles to attack fire-damaged trees has led to an emerging concern about how the amount and distribution of bark beetle-caused tree mortality will be affected by large-scale restoration of fire-adapted forest ecosystems in the Interior West via prescribed fire (Ganz *et al.*, 2003; Wallin *et al.*, 2003; Fettig, 2004). There has been a dramatic increase in the use of prescribed fire and/or mechanical fuel treatments to reduce hazardous fuels throughout much of the western United States after the implementation of the National Fire Plan in 2001, and the passage of the Healthy Forests Restoration Act of 2003 (P.L. 108-148) (Fettig, 2004). Prescribed fire is a necessary tool that has great promise for restoration of these forests, but it is also crucial to understand the effects it has on secondary

mortality agents such as bark beetles. This concern extends to the use of prescribed burns to manage pine forests in other regions of North America (McCullough *et al.*, 1998; Santoro *et al.*, 2001; Sullivan *et al.*, 2003).

The next sections discuss susceptibility of fire-weakened trees of six common species of western conifers to insects, primarily bark beetles. Tree species are listed in order of greatest resistance of mature trees to fire (Agee, 1993).

Douglas-fir. Fire weakening of Douglas-fir typically increases the probability of attack by Douglas-fir beetles (Furniss, 1965; Pasek, 1991; Flanagan, 1996; Rasmussen *et al.*, 1996; Hagle *et al.*, 2000a; Fowler & Sieg, 2004). Despite their thick bark, mature Douglas-firs often suffer severe mortality after fire because Douglas-fir beetles are attracted to trees with only moderate amounts of crown scorch (Furniss, 1965; Pasek, 1991; Flanagan, 1996). A high percentage of large diameter Douglas-fir that are initially classified as surviving a fire may ultimately die due to beetle attack (Weatherby *et al.*, 1994). Populations of Douglas-fir beetles may build up in burned areas and attack neighbouring unscorched trees (Pasek, 1991). Additional tree mortality, especially of small diameter Douglas-fir, can be caused by Douglas-fir pole beetles [*Pseudohylesinus nebulosus* (LeConte)] and wood borers (Rasmussen *et al.*, 1996).

Ponderosa pine. Crown scorch, cambial injury, and root injury are, in order of decreasing importance, sources of ponderosa pine mortality from prolonged exposure to moderate fire intensities (Flanagan, 1996). Fire-damaged ponderosa pines are susceptible to several species of bark beetles including western pine beetle (*Dendroctonus brevicomis* LeConte), mountain pine beetle, red turpentine beetle (*Dendroctonus valens* LeConte), roundheaded pine beetle (*Dendroctonus adjunctus* Blandford), pine engraver [*Ips pini* (Say)] and other *Ips* species, plus buprestid and cerambycid wood borers (Furniss & Carolin, 1977; Fischer, 1980; Flanagan, 1996; Conklin & Armstrong, 2001; Thies *et al.*, 2001; McHugh *et al.*, 2003; Fowler & Sieg, 2004). Red turpentine beetles rarely causes mortality by themselves (Fischer, 1980), rather they weaken trees that may then be overcome by other bark beetles (Furniss & Carolin, 1977). Pine engravers may build up in slash before attacking live trees or an *Ips* attack may precede or succeed an attack by western pine beetle (Fischer, 1980).

Bark beetles typically attack higher proportions of ponderosa pines with greater crown damage from fire compared with trees that have less crown damage (McHugh *et al.*, 2003; Wallin *et al.*, 2003). However, trees must have enough green phloem and live buds to permit new needle growth for western pine beetle attack to occur (Fischer, 1980). Trees with more than 50% crown scorch have much higher rates of mortality from western pine beetle than trees with less than 50% crown scorch (Miller & Keen, 1960; Conklin & Armstrong, 2001). Crown scorch during ponderosa pine's growing season may have more severe effects on trees and consequently results in greater risk of insect attack than dormant season scorch (Fischer, 1980). One of the mechanisms driving increased beetle susceptibility of severely scorched trees may be decreased resin flow (constitutive and induced resin volume) (Wallin *et al.*, 2003).

Large-scale field experiments are underway in the interior ponderosa pine forests of California to determine how prescribed fire and other silvicultural techniques affect bark beetle-caused mortality (Fettig, 2004). Early results from high-diversity burned plots in the Blacks Mountain Experimental Forest indicate that many of the large diameter ponderosa pines are succumbing to western pine beetle infestations, with similar rates of mortality continuing for 5 years post-treatment. Alternatively, in the low-diversity burned plots, the largest levels of tree mortality have been caused by borer species rather than by primary scolytids or the direct effects of fire.

Zausen *et al.* (2005) used large treatment stands replicated across a ponderosa pine landscape in northern Arizona to examine the longer-term impacts of operational silvicultural treatments on tree physiological characteristics, growth and bark beetle occurrence among three different forest conditions (unmanaged stands, stands thinned 8–16 years ago, and similarly thinned stands that were broadcast burned). Tree mortality due to bark beetles in 2003–04 was very low (< 0.1%) in all stands and did not differ among the treatments, suggesting remarkable resistance of these ponderosa pines to bark beetles, even at high tree densities. Furthermore, the effects of prescribed fire on the response variables they measured were negligible or indistinguishable from the effects of thinning, suggesting that prescribed fire had no longer-term effects on tree physiology or susceptibility to bark beetle attack.

Jeffrey pine. In California, bark beetles attacked Jeffrey pines more often in plots burned by autumn prescribed fire than trees in unburned areas (Bradley & Tueller, 2001). Red turpentine beetles (*D. valens*) attacked 22.9% of burned trees but attacked no trees in unburned areas. Fresh Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins) attacks were also only observed in burned trees; furthermore, they only attacked trees that were previously attacked by *D. valens*, suggesting that *D. valens* predisposes fire-injured trees to *D. jeffreyi* attack (Bradley & Tueller, 2001).

Bradley & Tueller (2001) conducted one of the few fire/insect relationship studies that included random selection of study plots with replication of treatments; this allowed development of logistic regression models to determine the factors associated with bark beetle attack of Jeffrey pines. Red turpentine beetles were more likely to attack trees with smaller diameter at breast height (d.b.h.), more crown scorch, more bole char, and trees with a soil burn rating of 'extreme'. Jeffrey pine beetles also attacked trees with more crown scorch, more bole char, and a higher soil burn rating. Similarly, attacks by *Ips* beetles occurred more often on trees with more crown scorch, more bole char and a smaller d.b.h. Because larger diameter trees have better thermal resistance to fire, they are injured and stressed less by fire and thus may be less susceptible to bark beetle attack after fire (Ryan & Reinhardt, 1988; Regelbrugge & Conard, 1993; Bradley & Tueller, 2001).

Ganz *et al.* (2003) studied the effects of prescribed fire in California forest ecosystems on susceptibility of forest stands of Jeffrey and ponderosa pine to bark beetle attack. An unexpected and surprising result from these two case studies is that red turpentine beetles and pine engravers are causing

significant postburning beetle-induced mortality with both autumn and spring prescribed burns. The high levels of pine mortality caused by red turpentine beetles and pine engravers led Ganz *et al.* (2003) to call for a re-evaluation of the traditional perceptions that these species are not primary mortality agents in Jeffrey and ponderosa pines. They also cautioned that tree mortality from bark beetles can reduce stocking levels of pine trees, which may not be the result managers want if prescribed burning is being used to restore the competitive advantage to pine species by thinning out shade-tolerant, understory fir trees.

Lodgepole pine. These pines may be most sensitive to fire-induced girdling at or near the ground (Rasmussen *et al.*, 1996). Geizler *et al.* (1984) found that percent root-kill was the most important fire-related variable in predicting mountain pine beetle (*D. ponderosae*) attack of lodgepole pine. However, Rasmussen *et al.* (1996), observed that attack of fire-damaged trees by mountain pine beetles was negligible (0.8%) compared with attack by *I. pini* (44%) or twig beetles (*Pityophthorous confertus* Swaine and *Pityogenes knechtli* Swaine) (no percentage given). Gara *et al.* (1985) reported that *D. ponderosae* attacked undamaged and lightly damaged lodgepole pine, and *I. pini* attacked moderately to severely fire-damaged trees. According to Stock & Gorley (1989), fire-stressed lodgepole pines were severely attacked by *D. ponderosae* and were also attacked by *Ips* spp. and striped ambrosia beetles [*Trypodendron lineatum* (Olivier)].

Alternatively, Elkin & Reid (2004) found that mountain pine beetles did not preferentially attack lodgepole pines that were artificially burned to simulate different intensities of spring ground fires. Reproductive success of the beetles was also unaffected by the fire damage treatments. The only response observed by Elkin & Reid (2004) was increased beetle attack success on fully burnt trees that had low beetle attack densities. The authors concluded that fire damage to lodgepole pines only affects mountain pine beetle population growth in areas where attack densities are low.

Engelmann spruce. This spruce is a relatively thin-barked fire-sensitive species (Agee, 1993; Rasmussen *et al.*, 1996). Engelmann spruce trees with intermediate amounts of basal-circumference-killed by fire (e.g. 40–80%) may be more susceptible to infestation by insects than trees with more or less scorch (Rasmussen *et al.*, 1996; Ryan & Amman, 1996). Spruce beetles attack fire-injured Engelmann spruce most frequently, although *Ips pilifrons* Swaine and buprestid and cerambycid wood-borers also attack this species (Rasmussen *et al.*, 1996). Fire-weakened Engelmann spruce often fall in windstorms after wildfire. This may result in epidemic populations of spruce beetles in large burned areas (Gibson *et al.*, 1999).

Subalpine fir. *Abies lasiocarpa* [Hook.] Nutt. is a thin-barked tree species and does not generally survive fire vigorous enough to burn all sides of the bark (Amman & Ryan, 1991). Thinner barked trees in the Interior West also generally tend to have shallower roots, which are susceptible to fire induced mortality (Ryan, 1990). Most of the subalpine fir investigated after the 1988 Yellowstone fires in Wyoming were severely girdled and infested by wood borers (Buprestidae and Cerambycidae) (Amman & Ryan, 1991;

Rasmussen *et al.*, 1996). Amman & Ryan (1991) concluded the subalpine fir remaining after the Yellowstone fires were too severely burned (minimum basal injury by fire = 81%) to be susceptible to bark beetle infestation.

Insect biodiversity

Fire can alter populations of ground-dwelling arthropods through changes in the postfire vegetation communities (Lightfoot, 1996) and by creating a mosaic of habitats due to diverse fire intensities (McCullough *et al.*, 1998). As a result, these arthropod communities may have different compositions within a single fire (Lightfoot, 1996). As vegetation communities change in the years after fire, insect communities may change as well (Fellin, 1980b, 1980c; Lightfoot, 1996; Villa-Castillo & Wagner, 2002). For example, in the first few weeks after fire, fewer species and individuals of ground-dwelling arthropods may occur in burned areas than in unburned areas (Pippin & Nichols, 1996), possibly because the cover substrates some species require were destroyed (Christiansen & Lavigne, 1996). However, more species may be observed in burned than in unburned areas as the vegetation responds a decade after fire (Villa-Castillo & Wagner, 2002). Studies by Gandhi *et al.* (2001) in western Alberta emphasized the importance of residual patches of unburned high-elevation coniferous forests left naturally by wildfires in providing important habitat patches for a number of surface-dwelling carabid and staphylinid beetle species (Coleoptera: Carabidae and Staphylinidae); this included populations of glacial relict beetles that were restricted to these locally stable and moist forests.

Dajoz (1998) reported a greater abundance of pyrophilous insect species in burned trees, low insect diversity in burned areas, and a smaller mean size of species in burned areas. According to Dajoz (1998), the following families and genera in the order Coleoptera include pyrophilous species in California and Arizona: Carabidae (*Sericoda* and *Nomius*), Buprestidae (*Melanophila*), Cerambycidae (*Monochamus*), Cucujidae (some species of *Laemophloeinae*) and Latridiidae (*Corticaria*). Dajoz (1998) also concluded that fire suppression after the early 1900s had modified forest structure and that many pyrophilous insect species were becoming rare or extinct.

The majority of literature on fire effects on ground-dwelling arthropods describes effects on ground beetle populations (Coleoptera: Carabidae) (Fellin, 1980a; Dajoz, 1998; Thies *et al.*, 2001; Villa-Castillo & Wagner, 2002). Villa-Castillo & Wagner (2002) reported that ponderosa pine stands that had been thinned and burned with prescribed fire 7 years before had higher ground beetle diversity than unmanaged and thinned-only stands. The carabid *Cyclotrachelus constricta* (Say) was most characteristic of the thinned and burned treatment and was associated with native forbs and large woody debris.

Northern Arizona ponderosa pine stands that had experienced catastrophic wildfire 2 years before had very different ground beetle assemblages than unmanaged or thinned and burned stands, and they had the highest ground beetle

diversity (Villa-Castillo & Wagner, 2002). However, the species of ground beetles in these stands were characteristic of dry and open areas rather than forests (*Amara farcta* LeConte, *Amara quenseli* Schönherr, and members of the genus *Harpalus*). The carabids *Agonum placidum* Say and *Harpalus* spp. were positively correlated with the presence of exotic graminoids that were common in stands after wildfire. Ground beetles native to forests were most common in thinned and burned stands.

Season of burn may affect ground beetle communities. Thies *et al.* (2001) reported that the Simpson diversity index for carabids in the southern Blue Mountains of Oregon was greater for fall compared with spring prescribed burns or unburned units. This may be from carabids being less affected in the fall because they are quiescent and underground, or it may be related to the low-intensity and heterogeneous nature of spring burns.

Niwa & Peck (2002) determined the short- and longer-term (ranging from < 1–15 years old) effects of prescribed understory fuel reduction burning on communities of both carabid beetles and spiders (Araneae) in the litter of a managed forest ecosystem in south-western Oregon. Four of the five carabid beetle species they analysed were more abundant in the unburned sites. Four of the seven spider families analysed were also more abundant in unburned sites, whereas the other three spider families were more numerous in burned sites. No differences in species richness or diversity were detected for either spiders or carabid beetles, and the relationship between abundance and time after burning was weak. Although this study was not designed to directly measure prey availability, the data associated with the pitfall trap catches indicated ants (Hymenoptera: Formicidae) were significantly more abundant in burned than in unburned sites, but *Collembola* (springtails) within litter and *Diplopoda* (millipedes) were found in significantly greater abundance in unburned sites.

Aside from the Carabidae, Sánchez-Martínez & Wagner (2002) reported that ambrosia beetles (*Gnathotrichus* spp.) and the predator *Enoclerus* sp. (Coleoptera: Cleridae) only occurred in stands burned by wildfire. These species could be considered indicator species for areas that have experienced crown fires in northern Arizona ponderosa pine forests. Sánchez-Martínez & Wagner (2002) also observed that southern pine beetle and western pine beetle were more abundant in thinned stands and thinned plus burned stands than in unmanaged stands and stands affected by wildfire. However, the relatively higher abundance was not sufficient to allow them to be classified as indicator species.

Modelling the interactions

Methods need to be developed to quantify the frequency with which insects, disease and fire interact and the strength of these relationships. McDonald *et al.* (2003) proposed that accurate mapping of vegetation subseries will facilitate analysis of landscape interactions among fire and forest pests.

Two recent studies addressed interactions among fire, diseases and insects in western forests to examine how

pathogens and insects influence landscape scale patterns of fire behaviour. Reich *et al.* (2004) present practical and efficient models that estimate the spatial distributions of different types of fuel created by forest diseases at landscape scales. Lundquist (2006) quantified the relative importance of co-occurring fuel-generating disturbances and other factors using structural equation modelling. Lundquist (2000) previously adapted this method of path analysis models to describe *Armillaria* root disease complexes; he concluded that root disease, insects and fire do interact to create forest openings. However, the models needed further development because they accounted for little of the variation within the systems investigated (Lundquist, 2000).

Atkins & Lundberg (2002) demonstrated the utility of using USDA Forest Service Forest Inventory Analysis (FIA) data in combination with the Forest Vegetation Simulator (FVS) model, and its Fuels and Fire Effects and Insect and Pathogen Extensions, to characterize current and future hazards related to fire, insect and disease for large geographical areas. They concluded that the FVS model and FIA data provide a powerful tool to help land managers and policy-makers assess conditions and provide a basis for making decisions about how to allocate resources to reduce hazards from fire, insects and pathogens. However, they cautioned that limitations in using this tool must be recognized due to several weaknesses they discovered in the base model and extensions.

Hawkes *et al.* (2004) summarized the results from a three-year Canadian research project to examine the impact of mountain pine beetle on lodgepole pine stand dynamics in British Columbia (BC) and southern Alberta. The three components of the project were to assess the effects of mountain pine beetle on stand dynamics, to project beetle impacts on stand and fuel dynamics with Prognosis^{BC} (the BC variant of the FVS) and the Northern Idaho variant of the Fire and Fuels Extension (FFE), and to estimate mountain pine beetle outbreak and fire return intervals. Hawkes *et al.* (2005) subsequently determined how well-suited the Prognosis^{BC}-FFE model is for projecting postoutbreak mountain pine beetle stand and fuel dynamics and potential fire behaviour in lodgepole pine-dominated stands in central interior British Columbia. The authors found that the model is sensitive to differences in stand structure and composition over time, although it has limitations because of several factors, including additional sources of un-modelled mortality from mountain pine and *Ips* species beetles. The British Columbia Ministry of Forests Prognosis^{BC} development team is currently developing a growth and yield model linked to a fuel and snag dynamics modelling system that will be able to help resource and fire managers determine impacts of mountain pine beetle outbreaks, particularly on timber supply and making salvage decisions (Hawkes *et al.*, 2005).

Li & Barclay (2004) and Li *et al.* (2005) used a theoretical modelling approach to study the interaction of fire and mountain pine beetle via forest age structure. The results of their simulation suggest that the temporal dynamics of lodgepole pine forests susceptible to mountain pine beetle attack are complex and depend on the fire history of the stand for areas that are experiencing large and irregular stand-replacement fires (Li *et al.*, 2005). A stable lodgepole pine forest

age-distribution might never be achieved if the landscape is subjected to large and irregular fire disturbances (Li & Barclay, 2004).

Effects of fire on soil insects and pathogens

The effects of fire on soil organisms depend largely on fire intensity and duration. Fast moving fires in fine fuels such as grass likely have little effect on soils and their microbial communities, whereas slow moving fires in moderate to heavy fuels probably have the greatest effects because they transfer large amounts of heat to the forest floor (Neary *et al.*, 2000). Soil mesofauna may be drastically reduced after hot wildfires but prescribed burns that remove only the litter layer may have only small effects (Mitchell & Martin, 1980). Prescribed fires are mostly of low to moderate severity, and have little effect on the porosity, structure, bulk density and moisture of forest soils except under slash piles (Neary *et al.*, 2000).

Niwa *et al.* (2001) emphasized that the direct effect of fire on arthropods inhabiting soil, litter and coarse woody debris depends on fire intensity, seasonal timing, and the amount of litter and other fuels consumed. They also noted that the literature concerning disturbance effects on these arthropods in forested ecosystems is sparse, and that results vary with stratum and taxonomic group. In general, burning appears to have greater effects on arthropods inhabiting the forest floor compared with those that reside in the soil (Niwa *et al.*, 2001).

Low-intensity fires may increase soil nutrient availability, tree health and resistance to pathogens and insects. Prescribed burning in south-western ponderosa pine forests can increase soil nutrient availability (Covington & Sackett, 1992; Kaye & Hart, 1998). Heterotrophic microbes can be negatively affected by removal of organic material but autotrophic microbes may be positively affected (Neary *et al.*, 2000). Improved seedling survival on burned seedbeds may be partially due to removal of fungi that cause seed decay, damping-off, and seedling root-decay (Parmeter, 1977). Prescribed fire may improve tree health due to mineralization of nutrients sequestered in organic material (Neary *et al.*, 2000). Healthy, vigorous trees may be less susceptible to insects such as bark beetles (Waring & Pitman, 1985) or pathogens such as *Armillaria* (Shaw & Kile, 1991). Alternatively, fire damage during high-intensity fires may predispose trees to decays (Littke & Gara, 1986) and insect attack (Furniss & Carolin, 1977; Fischer, 1980; Flanagan, 1996; McHugh *et al.*, 2003).

Fall prescribed burns may decrease populations of *Armillaria ostoyae* (Romagn.) Herink, a saprophytic and weak parasitic fungus that can become an aggressive tree-killing pathogen when it causes *Armillaria* root disease (Shaw & Kile, 1991). The fungus can survive in dead roots for at least 50 years. Filip & Yang-Erve (1997) reported that, in Oregon, the amount of *Armillaria* recovered from infected wood segments buried at 8 cm below ground was significantly less in stands burned in fall prescribed fires than in unburned stands or in stands burned during the spring season. Wood segments

buried with an antagonistic fungus (*Trichoderma harzianum* Rifai) showed a decrease in *Armillaria* beginning 8–10 months after prescribed burning. Previous research in laboratory settings indicated that *Trichoderma* isolates from burned soils were more antagonistic to *Armillaria* than isolates from unburned soils (Reaves & Shaw, 1990). However, prescribed fire had no effect on *Armillaria* populations at depths of 30 cm, and roots that harbour *Armillaria* are normally present at depths much greater than 30 cm. Filip & Yang-Erve (1997) concluded that the direct effects of prescribed fire on *Armillaria* populations in infected wood segments are negligible. The effects of prescribed burning on naturally occurring infected roots have not been examined.

Effects of fire suppression on forest susceptibility to insects and pathogens

Constraint of biological decomposition processes is common in dry forests of the inland western United States (Harvey, 1994). Historically, fire, insects and pathogens did much of the work in cycling nutrients in western forests (Haack & Byler, 1993). Fire return intervals have, however, lengthened by as much as two orders of magnitude from approximately 1910 onwards (McCune, 1983; McCullough *et al.*, 1988). Fire sensitive tree species that are susceptible to insects and pathogens have invaded sites where they were previously excluded by frequent fire (Hagle *et al.*, 2000b). Tree species that were formerly distributed in a mosaic pattern now form continuous-canopy forests in many areas of the Intermountain West (Agee, 1994). Forests may now be more susceptible to both insects (Savage, 1994) and pathogens (Hagle *et al.*, 2000b), suggesting that these two disturbances are filling the void of fire where conditions have changed as a result of fire suppression (Harvey, 1994). The next sections summarize how fire suppression has changed susceptibility of three major forest types in the Interior West to various insects and pathogens.

Ponderosa pine forests

Historically, frequent fire exerted a controlling influence on seedling survival in ponderosa pine forests of the West. Fire suppression in these forests has lengthened fire return intervals (Brown & Sieg, 1996) and allowed the disjunct groups of even-aged trees that were typical of presettlement forests to become spatially connected by thickets of stagnated trees (Agee, 1994). When older trees are removed, the younger residual stands are susceptible to attack by western and mountain pine beetles. If older trees remain they often eventually succumb to beetle attack because of competition for resources with younger trees (Lehmkuhl *et al.*, 1994). In stands regenerated from stand-replacement fires, tree densities have remained high due to subsequent fire suppression, leading to high hazard ratings for bark beetles (Lehmkuhl *et al.*, 1994). Density of ponderosa pine trees is often positively correlated with mortality from mountain pine beetles (Sartwell & Stevens, 1975; Stevens *et al.*, 1980;

McCambridge *et al.*, 1982; Mitchell *et al.*, 1983; Sherman & Warren, 1988).

The diameter distributions of these forests have been skewed toward smaller trees from decades of timber harvesting and survival of in-growth during fire suppression; this has also changed susceptibility to insects. The western pine beetle prefers mature ponderosa pine (150–300 years old) with a d.b.h. of 60–81 cm (Miller & Keen, 1960). On the other hand, forests with smaller trees and a small range of diameters may be more vulnerable to mountain pine beetles, which commonly attack a large proportion of trees with a d.b.h. of 23–33 cm (Olsen *et al.*, 1996). However, forests that currently have a low abundance of large diameter trees because of fire suppression may become more susceptible to western pine beetle over time as the stands reach larger diameter classes (Sánchez-Martínez & Wagner, 2002).

Prior to 2001, 'unhealthy' stand conditions in south-western ponderosa pine forests, caused in part by fire suppression, did not always result in bark beetle outbreaks. Despite dense stands of mid-sized diameter trees in northern Arizona, large beetle outbreaks did not occur in the 20th century (Sánchez-Martínez & Wagner, 2002). The only records of mountain pine beetle outbreaks in northern Arizona are from the Kaibab Plateau prior to the 1930s, and a moderate infestation on the Kaibab in the mid 1970s (Parker & Stevens, 1979; Parker, 1980). Sánchez-Martínez & Wagner (2002) reported only small infestations of bark beetles in their study sites; populations of *Ips* spp. were increasing, but western pine beetles were decreasing, resulting in a zero net change of mortality rates.

The situation has changed dramatically over time; the South-western Region (Arizona and New Mexico) experienced unprecedented increases in bark beetle activity from 2001 to 2003 (USDA, 2005; Zausen *et al.*, 2005). The recent bark beetle outbreak was probably drought induced, given that the entire Region has been in the grip of an extreme drought for approximately the past 10 years (Adams & Kolb, 2004; McPhee *et al.*, 2004). This prolonged drought, in combination with overstocked forest conditions, is almost certainly the major factor that precipitated the outbreak. For example, ponderosa pine mortality caused by *Ips* beetles in Arizona increased from endemic levels of approximately 1684 ha in 2000, to approximately 26 676 ha in 2001, and peaked at approximately 193 977 ha in 2002 (USDA, 2005). *Ips*-caused mortality subsequently declined to approximately 159 048 ha in 2003 and to approximately 34 223 ha in 2004 (USDA, 2005); it continued to decrease in 2005 due to a wet winter and spring in 2004–05 (Crimmins *et al.*, 2005). However, climatologists caution that an occasional wet year is not uncommon during an extended period of drought (McPhee *et al.*, 2004). It appears the Region may be at the beginning of a major bark beetle outbreak cycle, especially if the drought persists (as it did in the winter of 2005/6, which was one of the driest winters on record for Arizona), although the impacts on tree mortality will probably vary among different geographical areas. For example, Zausen *et al.* (2005) found minimal bark beetle impacts on tree mortality from 2003 to 2004 at their mid-elevation (2160–2440 m)

ponderosa pine study sites in northern Arizona, in spite of the widespread mortality from bark beetles that occurred in ponderosa pine forests near the lower extent of their elevational range in Arizona (approximately 2000 m) from 2001 to 2003.

Dense stands of ponderosa pine have proven more susceptible to bark beetles than open grown stands. Tree mortality from mountain pine beetles was significantly higher in stands with basal areas of 27–35 m²/ha compared with stands with area ≤ 20 m²/ha (Sartwell & Stevens, 1975; Mitchell *et al.*, 1983). Resin flow, an important tree resistance mechanism to bark beetles, was lower in high-density compared with lower-density stands (Feeney *et al.*, 1998; Kolb *et al.*, 1998). Pheromone-baited trap captures of western and southern pine beetles were greater in unmanaged, higher density ponderosa pine stands in northern Arizona than in managed, lower density stands, although catches of pine engraver beetles did not differ among treatments (Zausen *et al.*, 2005).

However, Mitchell *et al.* (1983) reported that the mountain pine beetle avoids highly dense stands composed of small diameter trees that are unsuitable for insect reproduction. Kolb *et al.* (1998) also suggested that trees growing in very dense stands (with basal areas ≥ 78 m²/ha) may also be at low risk of attack by bark beetles because small diameter trees with thin phloem are unsuitable for insect reproduction. Stands with moderate basal areas (18.4–27.6 m²/ha) may be more at risk to bark beetle attack (Kolb *et al.*, 1998).

Where wildfires occur despite continued attempts at fire suppression, fire-induced root and cambium injury may lead to pathogen establishment and insect outbreaks. In forests with a history of frequent fire, years of fire suppression have led to significant accumulations of duff (Ryan, 1990). When these ground fuels burn, the hot fires can injure fine and coarse roots (Ryan, 1990), which can then predispose trees to attack by pathogens and insects (Gara *et al.*, 1985; Littke & Gara, 1986). Bole injury can also lead to establishment of decay organisms in limited cases (Piiro *et al.*, 1998). As a result, even fires that never reach tree crowns can cause increased pathogen and insect activity.

Prior to fire suppression, ponderosa pine stands may have been too sparse to allow spread of dwarf mistletoe seed (Conklin, 2000). Control of understory fire in south-western ponderosa pine ecosystems has allowed the establishment of stands much more dense than the open park-like forests of presettlement times (Covington & Moore, 1994; Chang, 1996; Dahms & Geils, 1997). Koonce & Roth (1980) observed that stands with low tree densities generally have lower levels of dwarf mistletoe infestation than stands with higher tree densities. Today, many stands may be at densities optimal for spread of the parasite. However, if stands become too dense, rate of spread is reduced (Hawksworth, 1961). Broom development is also reduced in stands with high tree density (Koonce & Roth, 1985), potentially mitigating dwarf-mistletoe-related flammability in dense stands. If dense stands are thinned and fire is reintroduced, lack of broom development will alter fire behaviour. Because brooms require long periods of time to develop, fire suppression will have long-term effects on fire behaviour, even where forest restoration is attempted.

Mixed conifer forests

In mixed conifer forests of the south-western United States, fire suppression has led to a shift in species composition that has altered susceptibility to defoliating insects. Forest stands most at risk to the western spruce budworm are multistoried with true firs (e.g. white fir, *Abies concolor* [Gord. and Glend.] Lindl. ex Hildebr.) and Douglas-fir in the understory. Fire suppression has increased the fire return interval, permitting historically less susceptible stands to accumulate fire-sensitive tree species vulnerable to budworm defoliation (Linnane, 1986; McCullough *et al.*, 1998). Hadley & Veblen (1993) reported that a combination of fire suppression and extensive burning during 19th century European settlement in ponderosa pine/Douglas-fir stands of the Colorado Front Range had increased landscape homogeneity and the area of forests reaching a stage of development susceptible to western spruce budworm outbreaks. These forests were relatively 'middle aged' and more homogenous than young postfire stands or old-growth stands (> 250 years old) (Hadley & Veblen, 1993). Similar changes have occurred in the mid-elevation forests on the eastern slope of the Cascade Mountains, resulting in forests that are more susceptible to western spruce budworm outbreaks because they have higher numbers of trees like grand fir that are fire-intolerant and shade-tolerant, late successional species (Hummel & Agee, 2003).

In many forests of the northern Rocky Mountains, fire suppression has resulted in a proliferation of shade tolerant species such as true firs and a decline in fire-adapted species such as ponderosa pine and western larch (Habeck & Mutch, 1973; Byler *et al.*, 1994; Gibson *et al.*, 1999). True firs have thinner bark and generally suffer greater mortality in fires than thicker barked trees (Minore, 1979; Ryan & Reinhardt, 1988). The shift in relative abundance of tree species has resulted in a concomitant shift in pathogen and insect species in the northern Rocky Mountains (Byler *et al.*, 1994). Timber harvesting and the effects of white pine blister rust (*Cronartium ribicola* Fisch.), a non-native fungus, have coincided with fire suppression to exacerbate declines in pine abundance in this region (Hagle *et al.*, 2000b; McDonald *et al.*, 2000).

Fire suppression and white pine blister rust also appear to have played significant roles in determining trajectories for sugar pine (*Pinus lambertiana* Dougl.) populations in the central and southern Sierra Nevada Mountains of California (van Mantgem *et al.*, 2004). However, there was no clear suggestion that high stand densities resulting from fire exclusion were correlated with increased severity of blister rust attack. In other words, van Mantgem *et al.* (2004) did not find any evidence of a possible relationship between disease and fire history (e.g. that dense stands result in poor growing conditions that increase susceptibility of sugar pines to blister rust attacks).

In pre-European settlement forests of the northern Rocky Mountains, both stand replacing and mixed severity fires maintained dominance by western larch and western white pine (*Pinus monticola* Dougl. ex D. Don) (Byler *et al.*, 1997). Root diseases killed Douglas-fir and true firs and favoured disease-tolerant western white pine and western larch. As

western white pine forests aged, they became increasingly susceptible to mountain pine beetle outbreaks. Such outbreaks caused mortality that increased the probability of stand-replacement fire. Western white pine and western larch were the dominant early seral species to initially colonize burned sites (Byler *et al.*, 1997).

The combined effects of approximately 80 years of fire suppression, the introduction of white pine blister rust, and timber harvesting of the comparably higher value pines, resulted in forests with a greater component of Douglas-fir and true fir (Byler *et al.*, 1997). These shade tolerant, climax species are highly susceptible to root diseases (Byler *et al.*, 1997; Gibson *et al.*, 1999). In forests of northern Idaho, the current prevalence of root diseases may result in a major transition to western red cedar and western hemlock (Byler *et al.*, 1997). The shift from pine to fir may also result in declines in mountain pine beetle activity and stem decays and increases in the activity of bark beetles that attack Douglas-fir and grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) (Byler *et al.*, 1994).

One example of how the decline of pines and proliferation of true firs affects forest pathogens is the incidence of the Indian paint fungus (*Echinodontium tinctorium* (Ell. & Ev.) that causes rust-red stringy rot in true firs and hemlocks. Hagle *et al.* (2000b) reported that the Indian paint fungus became more common in western Montana and Idaho forests from 1935 to 1975. The increased abundance was probably due to fire suppression and forest management practices that contributed to increases of the three species of trees that are the primary hosts for Indian paint fungus: grand fir, sub-alpine fir and western hemlock (Hagle *et al.*, 2000b). The percent of the study area covered by these tree species rose from 16.4% in 1935 to 41.1% in 1975 in one of two study landscapes, and from 11.4% to 48.8% in the other (Hagle *et al.*, 2000b). Observations by Hagle *et al.* (2000b) also showed that multistoried stands, which allow the fungus to spread more rapidly, became more common due to fire suppression. In the same time period, the relatively small area covered by ponderosa pine declined by approximately 50%.

Fire suppression has also affected the incidence of needle diseases occurring in the northern Rocky Mountains by changing the abundance and species composition of understory plants (Hardison, 1976). Hardison (1976) reported that fire suppression had allowed the persistence of understory plants and trees that were readily infected by needle diseases such as comandra blister rust (*Cronartium comandrae* Pk.). However, fire suppression may have also reduced the abundance of *Ribes* spp. (currants and gooseberries), the alternate host of white pine blister rust thereby to some extent mitigating the effects of this exotic disease (Hardison, 1976).

During the fire suppression era, a similar decrease in pine and increase in fir abundance has been observed in eastern Oregon and Washington, albeit with different species. Ponderosa pines dominated much of the forested area east of the Cascade Crest before widespread fire suppression was implemented in the 1930s (Hall, 1977; Filip & Goheen, 1984; Mutch *et al.*, 1993; Huff *et al.*, 1995; McCullough *et al.*, 1998). However, the abundances of grand fir, white fir, and Douglas-fir in these forests increased to unprecedented levels

after effective fire suppression (Hall, 1977; Filip & Goheen, 1984; Mutch *et al.*, 1993; Filip, 1994; Huff *et al.*, 1995). Concomitant with the change in species diversity, Filip & Goheen (1984) observed significant mortality induced by *Armillaria*, laminated and annosus root diseases. In north-eastern and central Oregon, Filip (1994) reported grand fir mortality from fir engraver (*Scolytus ventralis* LeConte), western spruce budworm, and *Armillaria* root disease. Epidemic insect populations have caused widespread mortality in much of north-eastern Oregon (Mutch *et al.*, 1993). Forest diseases and insects could now be considered the dominant force for nutrient cycling in these forests and they may become even more so in the absence of catastrophic wildfires (Filip, 1994).

Forest susceptibility to the Douglas-fir tussock moth has increased as firs have replaced pines in northern California, eastern Oregon, and eastern Washington (Wickman, 1978; Williams *et al.*, 1980; McCullough *et al.*, 1998). Douglas-fir and true firs became more abundant and encroached on ponderosa pine sites in north-eastern Washington and east-central Oregon, probably because fire suppression allowed the more fire-sensitive, shade-tolerant fir species to survive (Williams *et al.*, 1980). At the same time, Douglas-fir tussock moth outbreaks became more common in sites that were previously dominated by ponderosa pine, leading to the recommendation to reintroduce fire to limit the area occupied by hosts of the tussock moth (Williams *et al.*, 1980). In north-eastern California, fire suppression and harvesting of overstory pines allowed development of large acreages with increased amounts of white fir, which is highly susceptible to Douglas-fir tussock moth (Wickman, 1978). Ferrell (1996) reported that, like forests throughout most of the West, fire exclusion practices in Sierra Nevada forests had contributed to the development of overly dense stands and have promoted tree species that are susceptible to insects and pathogens.

Lodgepole pine forests

Lodgepole pine forests historically experienced periodic stand-replacement fires; fire suppression has resulted in large areas occupied by mature forests in the Rocky Mountains (Holland, 1986) and in British Columbia (Taylor & Carroll, 2004). These mature forests are often characterized by large amounts of mortality caused by mountain pine beetle and other agents (Brown, 1975). Fires will eventually burn hot and over large areas because suppression of high-intensity fire is not possible with current technology (Skinner & Chang, 1996). Because fires may be burning on larger scales than in the past, insects and diseases such as the mountain pine beetle and root decays also seem to be operating at larger scales (Hessburg *et al.*, 1994, 2000).

In forests where high-intensity fire regimes historically prevailed, tree population dynamics in the post-fire-suppression era may result in increased insect infestation in forests that were initiated some time ago by stand-replacement fires. Roe & Amman (1970) concluded that in the absence of fire, consecutive mountain pine beetle attacks in lodgepole stands promoted conversion from even-aged to uneven-aged stands.

They also found that the mountain pine beetle promoted succession to spruce and fir by removing the largest lodgepole pines in the stand. If fire is suppressed in lodgepole pine forests longer than the usual return interval of 80–90 years, a large amount of pine seed builds up, and regeneration in burned stands is so abundant that average seedling fitness is reduced (Raffa & Berryman, 1987). Dense stands of lodgepole pine may become stagnated and susceptible to insect attack (Waring & Pitman, 1985). If stands are protected from fire past approximately 150 years of age, succession usually proceeds to *Larix–Pseudotsuga* or *Picea–Tsuga* complexes. These tree species are subject to a different suite of pathogens and insects than lodgepole pine. Shade tolerant tree species that invade sites formerly dominated by pines may also suffer severe insect mortality because they may be poorly adapted to these sites (Wickman, 1978).

In limited cases, fire suppression may have decreased the abundance of lodgepole pine dwarf mistletoe. Fire suppression has allowed the establishment of fire sensitive climax species such as *Picea* and *Abies* in lodgepole pine stands where frequent fires of the presettlement era formerly maintained this early seral dwarf-mistletoe-susceptible tree species. With an increase of tree species that are not principal hosts of lodgepole pine dwarf mistletoe, the abundance of this mistletoe may be reduced (Hawksworth, 1975; Lotan *et al.*, 1981).

Prescribed fire for control of pathogens and insects

Control of insects and pathogens in forests of inland western North America has been one of the goals of prescribed fire from at least the 1980s, although it has not been widely used for this purpose (Simmerman & Fischer, 1990; Weber & Taylor, 1992). Controlled fire can be used to directly destroy insects or fungi, or to alter forest characteristics to make forests less susceptible to insects or pathogens. By reintroducing fire into ecosystems where burns have become rare, it may be possible to reduce fuel levels in western forests to bring the size and intensity of fires within the range of historical variability and reduce the prevalence of tree species that allow the build up of insects and diseases. If practiced on a large enough scale, this approach should begin to reverse some of the changes brought about by fire suppression.

When considering the use of prescribed fire for control of forest insects and pathogens, the merits of thinning and burning must be compared with burning alone. Burn only treatments can be less expensive because sawyers do not need to be contracted, roads do not need to be built and forest inventories are often not performed (Price, 1991). However, because of fuel build-ups during the last century of fire suppression, preliminary cutting, piling, and burning may need to precede prescribed fire (Simmerman & Fischer, 1990; Thies *et al.*, 2001). In areas of extreme fuel build-up, appropriate conditions for prescribed fire may occur so rarely that burn only treatments may not be practical. Thinning prior to burning has the added advantage of keeping fire close to the ground

and thereby reducing crown damage in retained trees (Graham *et al.*, 1999). Thinning and other partial harvesting treatments are also easier to use than prescribed fire to achieve targeted post-treatment tree densities and species compositions.

Fungal pathogens

Many fungal plant pathogens are known as 'diseases of the site' because they persist in dead plant materials under the soil surface (e.g. root decays). Burning roots and debris has long been used to destroy sources of inoculum (Hardison, 1976). Because fire often burns intensely in stumps and root systems (Thies, 1990), fire may have historically been a mechanism for reducing inoculum; however, there is little data testing this hypothesis for the interior western United States and Canada. Fire does destroy inoculum of most pathogens that sporulate on dead materials on the ground (Parmeter, 1977). Exposure to grass and pine needle smoke reduced spore germination of the fungi associated with western gall rust [*Endocronartium harknessii* (J. P. Moore) Y. Hirat.] and annosus root disease, and it decreased mycelial growth of the fungi associated with annosus and black stain root diseases in a laboratory experiment (Parmeter & Uhrenholdt, 1975). In Douglas-fir forests, fire did not reduce spored production of the fungus associated with laminated root disease (Wallis, 1976). Fire may inhibit *Armillaria* root disease on or near the ground surface but has little effect deep in the soil (Filip & Yang-Erve, 1997).

An important caveat to consider is that fungal pathogens can enter trees damaged or stressed by fire (Littke & Gara, 1986; Piirto *et al.*, 1998). There is also evidence that spores of the fungus associated with *Rhizina* root decay [*Rhizina undulata* (Fr.)] germinate when exposed to high temperatures, such as those produced by fire (Thies, 1990). This root disease primarily causes mortality in Douglas-fir seedlings in clearcuts; however, its relatively low incidence makes it a minor consideration when planning most prescribed fires (Thies, 1990).

Dwarf mistletoes

Prescribed fire can be used both for direct reduction of dwarf mistletoe inoculum and to make forests less susceptible to the parasite (Conklin & Armstrong, 2001; Shaw *et al.*, 2004). Direct effects of fire on dwarf mistletoes include scorch pruning of infected branches and witches' brooms, mortality of severely infected trees, and reductions in mistletoe seed crops from dehiscence of mistletoe plants exposed to smoke and heat. Prescribed fire can also be used to alter susceptibility of forests to dwarf mistletoe spread, particularly after thinning treatments have been applied. Buffers without host trees prevent the spread of this parasite if they are wider than mistletoe seed can disperse. Because most tree species are more sensitive to fire when they are small, periodic understory fires can deter regeneration in buffers and eliminate potentially infected advanced regeneration (Alexander & Hawksworth, 1975; van der Kamp & Hawksworth, 1985). Forest stands thinned to basal areas low

enough to reduce dwarf mistletoe spread can also be maintained by understory fire.

Insects

Prescribed fire has been used to directly destroy ground dwelling arthropods and bole-infesting insects like bark beetles (McCullough *et al.*, 1998), but it has rarely been used to control defoliating insects. Prescribed burning of the forest floor can directly kill many forest floor arthropods and remove forest litter required by these insects for food and shelter (Fellin, 1980b, 1980c); this topic was addressed in the previous section on 'Insect biodiversity'.

Perhaps the simplest use of prescribed fire to reduce forest susceptibility to insects is disposal of thinning slash by burning to prevent build-ups of *Ips* spp. bark beetles (Amman, 1975; Mitchell & Martin, 1980; Smith *et al.*, 1983; Alexander, 1986; Parker, 1991). Prescribed fire can also be used to directly destroy *Ips* brood in infested slash (Smith *et al.*, 1983; Parker, 1991). However, care must be taken to avoid scorching residual trees that can make them susceptible to *Ips* attack (Mitchell & Martin, 1980).

Bark beetles over-wintering in trees can also be destroyed by fire; infested trees are burned standing or after they are felled (Amman & Safranyik, 1985). Winter felling and burning of individual infested trees is a common direct control technique used in British Columbia (Stock & Gorley, 1989). Synthetic pheromones may be used to ensure beetle attraction to existing infestations before burning (Safranyik *et al.*, 2001). Production of mountain pine beetles in lodgepole pines attacked prior to prescribed fire may be reduced by approximately 50% (Safranyik *et al.*, 2001). Vigorous burns may be necessary to cause appreciable brood mortality (Stock & Gorley, 1989; Safranyik *et al.*, 2001). However, the costs of direct control may exceed the value of the trees to be saved in large outbreaks (Amman & Safranyik, 1985). Furthermore, direct control is only a temporary measure; forest susceptibility to bark beetles must ultimately be reduced for long-term pest management (Amman & Safranyik, 1985).

Conclusions

After more than a century of fire suppression, the present-day coniferous forests of interior western North America are largely different in structure and composition compared with pre-European settlement times (Veblen *et al.*, 1994; Gibson *et al.*, 1999). The higher densities of old trees, heavy fuel loads and nonfire adapted species that characterize the current forests have led to concomitant changes in the insects and diseases that are the most important agents of disturbance in these forests (Byler *et al.*, 1994; Hummel & Agee, 2003). In recent years, large wildfires have accompanied the alterations in disease and insect activity in the western United States (Swetnam, 1990; Swetnam & Betancourt, 1998). Hessburg *et al.* (1994, 2000) predicted that populations of forest insects and diseases are likely to be greater than historical levels if large wildfires persist in the West, and if we continue large-scale reintroduction of fire into forests where it has long been suppressed.

A clear understanding of the relationships among fire, insects, and pathogens can help frame the costs and benefits of management practices designed to restore more natural fire cycles to these fire-adapted ecosystems. Increased insect and pathogen activity often occurs in forests where fire has been suppressed. However, restoration of natural fire regimes via prescribed burning in forests where fire has long been controlled can also result in increased populations of insects and pathogens (Thies *et al.*, 2001; Fettig, 2004). Consequently, decisions about how, when, and where to restore fire will need to consider the effects of fire on the susceptibility of trees to insects and diseases, and weigh this against the ecological and economic costs of wildfires that will inevitably occur in many forests if nothing is done. A detailed knowledge of the potential effects of prescribed fire on insect and pathogen communities should be used to make proposed fire treatments as effective as possible. Land management agencies are often under pressure to achieve quick results. As a note of caution, rapid and wide-scale implementation of intense prescribed fires to restore these ecosystems may lead to unintended and undesirable large increases in tree mortality from insects and diseases. This is particularly true in forests in the Intermountain West with historically low-intensity, frequent fire regimes. Because fire, insect and pathogen interactions are different in these low-intensity, frequent-fire regime forests (Martin, 1989), gradual introduction of smaller and cooler fires may be necessary to reduce potential unwanted responses from insects and diseases. As efforts are increased to reintroduce fire to western forests, the effects of prescribed burns on insect and pathogen communities must also be monitored to ensure that land management objectives are met.

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