Chapter 7: Diseases and Abiotic Damage Agents

Susan J. Frankel and I. Blakey Lockman[1]

Background

In what ways do plant diseases affect forest sustainability? How will disease disturbance regimes change given global warming and increasing population pressures? In this chapter, we review how plant diseases, caused by both biological pathogens and abiotic disturbance agents, influence forest sustainability—but note that our findings derive less from data and more from observations and professional judgment. Many forest pathogens (fungi, bacteria, viruses, nematodes) are microscopic, which predisposes them to nondetection because they cannot be seen with the naked eye and their symptoms are indistinctive. Further complicating our understanding of pathogen roles in disturbance are limitations in accurate attribution of the cause(s) of tree mortality. Typically, sampling and laboratory analysis are required to determine whether pathogens are contributing to mortality, even when tests are conducted, technological and financial constraints often result in an incomplete determination of the causal agent. Despite improvements in molecularly based (polymerase chain reaction, PCR) diagnostic methods, our knowledge as to pathogen distributions and ecological impacts remains limited (Das et al. 2016; Wingfield et al. 2015, 2017).

How Are Plant Pathogens, Including Abiotic Agents, Affecting Western Forests?

Western forests host a multitude of plant pathogens: microbes, parasitic plants, and other organisms that can cause disease in vegetation (tables 7.1 and 7.2) (Goheen and Willhite 2006, Hagle et al. 1987, Hepting 1971, Paine and Lieutier 2016). Tree or plant disease is defined as a malfunctioning of host tree or plant tissues by a pathogenic agent or environmental factor that leads to the development of symptoms (Agrios 2005). Forest diseases may be caused by biological organisms (e.g., mistletoes, fungi, Phytophthoras (oomycetes), and other organisms), as well as by direct damage to plants from nonliving, abiotic factors, primarily adverse environmental conditions such as drought, sunburn, or frost injury (Hansen and Lewis 1997, Manion and LaChance 1992, Sinclair et al. 1987). In this report, drought is treated in a separate chapter (see chapter 4). The effects and behavior of other biotic and abiotic diseases as they contribute to forest disturbance are briefly discussed below.

Forest diseases may be caused by both biological organisms and abiotic factors such as drought, sunburn, or frost injury.

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Table 7.1—List of common biotic diseases in Western U.S. forests

Scientific name—causal agent	Common name
Arceuthobium spp.	Dwarf mistletoe
Armillaria ostoyae	Armillaria root disease
Cronartium comandrae	Comandra blister rust
Cronartium ribicola	White pine blister rust
Cryphonectria parasitica	Chestnut blight
Dothistroma septosporum	Red band needle blight
Endocronartium harknessii	Western gall rust
Fusarium circinatum	Pitch canker
Geosmithia morbida	Thousand cankers
Heterobasidium irregulare, H. occidentale	Heterobasidion root disease (Syn. Annosum root disease)
Leptographium wageneri	Black stain root disease
Ophiostoma ulmi, O. novo-ulmi	Dutch elm disease
Phaeocryptopus gaumannii	Swiss needle cast
Phellinus sulphurascens, P. weirii	Laminated root rot
Phoradendron spp.	True mistletoe
Phytophthora cinnamomi	Phytophthora dieback
Phytophthora lateralis	Port-Orford-cedar root disease
Phytophthora ramorum	Sudden oak death, ramorum blight
Valsa sordida	Cytospora canker

Table 7.2—List of common abiotic diseases in the Western United States

Environmental factor	Disease or injury
Drought	Wilting, water stress, lack of transpiration, carbohydrate starvation
Ice accumulation	Freeze burn, branch breakage, and tree failure
Intense heat and drought	Sudden aspen decline, other declines, tree mortality
Flooding	Root suffocation, increased susceptibility to Phytophthoras, tree mortality
Lack of snow and early warming	Yellow-cedar decline, and other declines, freeze injury to new growth
Ozone and air pollution exposure	Leafspots, reduced growth
Snow accumulation	Uprooting from avalanche or crown damage
Storm damage	Flooding, branch breakage, tree failure
Unseasonal cold temperatures	Frost injury, bud damage, leaf burn, top die-back and tree mortality
Volcanism	Heat injury, smothering, or chemical toxicity
Wind damage	Windthrow or branch failure

Despite their cryptic nature, plant diseases (i.e., root diseases, wilts, cankers) profoundly influence forest composition, structure, and function (Boyce 1938, Ramsfield et al. 2016). Although fire and insect attack often appear dramatically across a landscape, damage from pathogens typically occurs more gradually. Nevertheless, plant diseases can be widespread and persistent; cumulatively, they can significantly shape forest openings by shortening tree lifespans and causing mortality. Impairment from plant diseases influences energy and water flux (Anderegg et al. 2013), carbon cycles (Cobb and Metz 2017, Hicke et al. 2012), and wildlife habitat quality (Boyd et al. 2013; Liebhold et al. 2017b, Loo 2009, Lovett et al. 2006). Both native and invasive pathogens can cause significant growth reduction, deformity, and mortality. Some of the more damaging native and nonnative pathogens are predicted to cause 15 percent or greater total basal area loss on more than 7.9 million ha across the West from 2012 to 2027 (fig. 7.1) (Krist et al. 2014). Pathogens interact synergistically with insects and fire to compound their effects on forests (Cobb and Metz 2017, Logan and Powell 2001, Metz et al. 2011, Parker et al. 2006). Disease development is very sensitive to environmental conditions, in particular temperature and moisture, so changes in climate patterns, including storm intensity and shifts in seasonality, will alter the behavior of biological pathogens and the nature of abiotic impacts on growth and mortality (Ayres and Lombardero 2000, Dale et al. 2001, Ramsfield et al. 2016, Sturrock et al. 2011).

Plant diseases profoundly influence forest composition, structure, and function.

In this review, we consider how pathogens influence disturbance and sustainability mainly in term of impacts to forest stocking, species composition, and related measures. Sustainability has many other important dimensions, i.e., provisioning of ecosystem services, which are considered in more detail in other chapters because pathogen impacts on most ecological processes are not well quantified.

Current Trends—Invasive Diseases (Pathogens) Are of Increasing Concern

Damage from invasive pathogens is on the rise as the number of pathogens detected continues to increase (Aukema et al. 2010, 2011; Ayres and Lombardero 2018; Liebhold et al. 2017; Santini et al. 2013; Wingfield et al. 2017). Exotic pathogen introductions are responsible for the most damaging forest pests ever witnessed in North American forests, including chestnut blight (*Cryphonectria parasitica*) (Anagnostakis 1987, Freinkel 2009); white pine blister rust (*Cronartium ribicola*) (Benedict 1981, Boyce 1938, Geils et al. 2010, Vitousek et al. 1996); and Dutch elm disease (*Ophiostoma ulmi* and *O. novo-ulmi*) (Brasier 1991, Strobel and Lanier 1981). Chestnut blight devastated Eastern U.S. forests, but introduced pathogens have killed and continue to destroy millions of trees and limit survival of their hosts in all parts of North America, including the Western United States (Liebhold et al. 1995, Mack et al. 2000).

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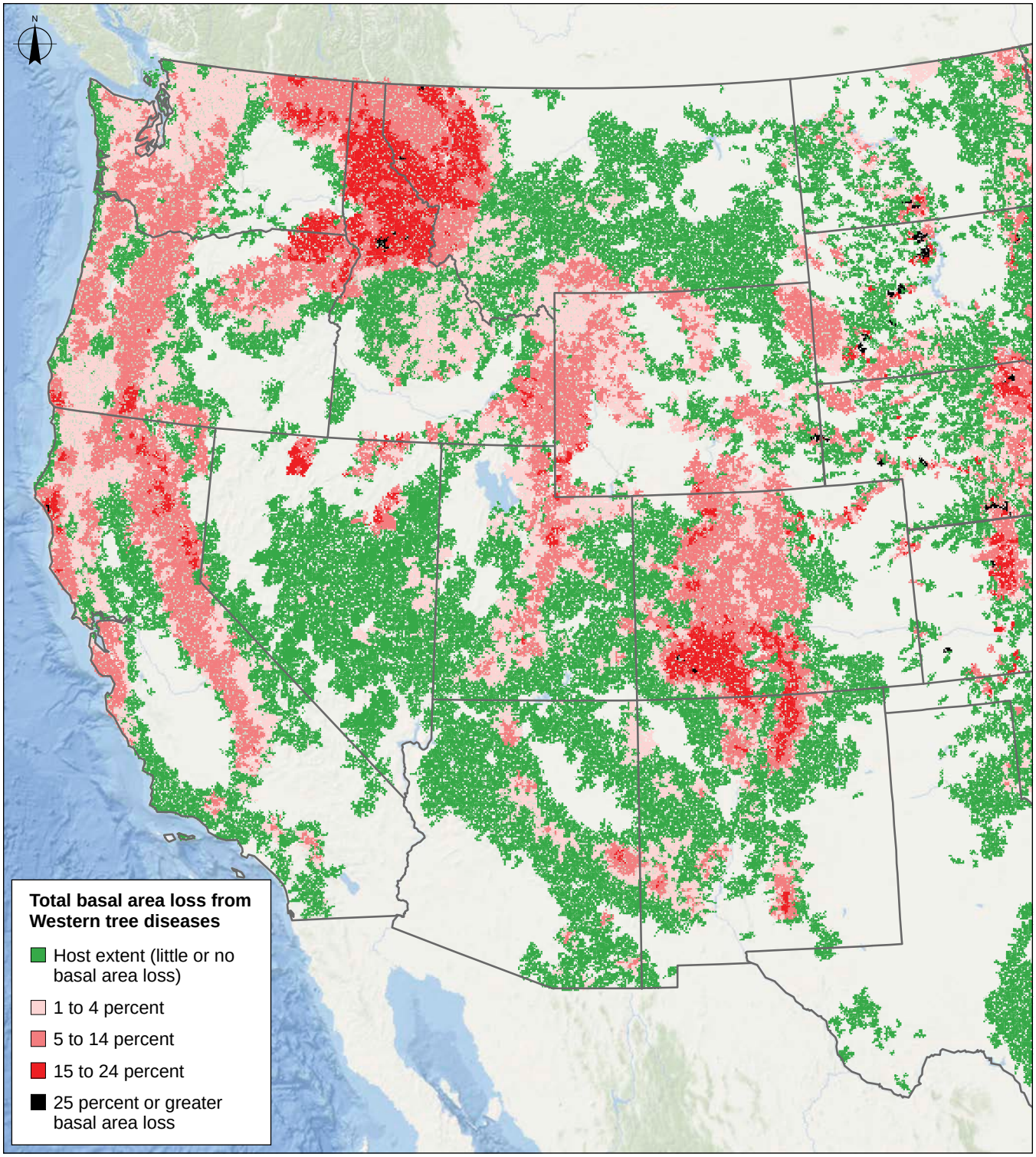

Figure 7.1—Predicted basal area loss from diseases in the Western United States. Diseases modeled are Armillaria root disease, aspen and cottonwood decline, dwarf mistletoes, Heterobasidion root disease, laminated root rot, Port-Orford-cedar root disease, sudden oak death, and white pine blister rust. (Data are from Krist et al. 2014).

Greater volumes of global trade and changes in import patterns that shift to new markets in portions of Europe, Asia, or South America will support continued establishment of new invasive species (Liebhold et al. 2017). Live plant imports are the most significant pathway for pathogen and insect transport into the United States; as nursery plants are increasingly grown overseas, the higher volume of imported plants will result in further pest introductions (Liebhold et al. 2012).

Capsule summaries for two highly damaging invasive pathogens in the West, sudden oak death (*Phytophthora ramorum*) and white pine blister rust (*Cronartium ribicola*), are provided below.

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Native Pathogens

Native pathogens are present throughout Western U.S. forest ecosystems, from coastal forests to high-alpine areas. The most widely dispersed native pathogens in the West are dwarf mistletoes (*Arceuthobium* spp.) (Hawksworth and Wiens 1996, Mathiasen et al. 2008). Obligately (only) parasitic, dwarf mistletoes can reduce growth, wood quality, seed production, and the lifespan of infected host trees. At times, however, they may be considered beneficial because their berries provide food for wildlife, and the witches' brooms they cause serve as favored nesting sites or habitat (Mathiasen et al. 2004).

Other significantly damaging native pathogens include root diseases: Armillaria root disease, Heterobasidion root disease, and laminated root rot (*Phellinus sulphurascens* and *P. weirii*). These root diseases have existed in parts of western forests for thousands of years, dating back to the most recent ice age, and all cause significant ecological impacts in many parts of the West (Shaw and Kile 1991, Washington State Academy of Sciences 2013). Overviews of these native diseases are provided below.

Both native and nonnative pathogens are present in western forests and their impacts depend on the stand management objectives and how they are implemented, or the land uses in place, such as whether the stands are plantations, managed stands, urban forests, or wilderness, in addition to other factors (Tubby and Webber 2010, Wingfield et al. 2015). Tree mortality in wildlands may contribute to biodiversity because reduced forest canopy creates openings that may provide habitat for shade-intolerant plants (Hansen and Goheen 2000). Conversely, plant death may reduce diversity; for example, in rare species habitat, the death of threatened or endangered plant species caused by the inadvertent introduction of pathogens during restoration plantings (e.g., *Phytophthora* spp.) may irreversibly degrade resource values (Rooney-Latham et al. 2015).

Abiotic Diseases

Depending on the environmental conditions, flooding, high winds, or intense heat may result in physical conditions that are beyond the capacity of trees or plants to endure. Abiotic injury is typically dependent upon the interaction of plants and climate, terrain, and geology. The most damaging abiotic injuries are caused by fire, drought, wind damage, snow (accumulation in crowns or as avalanches), ice accumulation in crowns, frost, flooding, ozone injury or air pollution damage, and landslides (Sinclair et al. 1987). Less frequent but significant damage occurs periodically from volcanic eruptions and glaciation (Gardiner and Quine 2000). Land development may also contribute to abiotic damage as a result of construction practices (Hauer et al. 1994), poor planting (Ware 1994), or fire injury from human ignitions (Stephens 2005, Syphard et al. 2007).

Biological pathogens contribute in many ways to abiotically driven die-offs; in particular, they increase stress by reducing physiological function, causing trees to die that could otherwise have recovered, thereby expanding and extending mortality events after the climatically induced stress is relieved (Worrall et al. 2010).

Megadisturbance

The abiotic diseases mentioned above are overshadowed by recent megadisturbances, in which interactions from increasing temperatures, drought, native insects, and pathogens have resulted in unprecedented levels of tree mortality in some forests (Allen et al. 2010, 2015; Millar and Stephenson 2015). It is difficult to predict responses of pathogens and other factors that interact in these extreme climate events (Allen et al. 2015), but widespread tree mortality in the Rocky Mountains (Berner et al. 2017, Wong and Daniels 2017) and California (Tree Mortality Working Group 2017) provides an indication of the severity and types of changes to expect in forest ecosystems.

Unprecedented Drought in the Sierra Nevada Mountains, 2010–2017

Tree mortality in the central Sierra Nevada Mountains in California has increased by an order of magnitude, from tens to hundreds of dead trees per square kilometer (Young et al. 2017); an estimated 129 million trees have died from 2010 to 2017, with more than 3.6 million ha of drought-stricken forests with approximately 62 million trees dying in 2016 alone (USDA FS 2017). Tree mortality—primarily of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and sugar pine (*P. lambertiana*)—is attributed to drought, native bark beetles, and other factors (Kolb et al. 2016), including pathogens that contributed an unquantified amount to total

mortality (California Tree Mortality Working Group 2017, USDA FS 2016). The tree mortality is extensive. For example, on the Sierra National Forest at elevations between about 1000 to 1500 m, 80 percent of the ponderosa and sugar pine trees more than 50.8 cm diameter at breast height (d.b.h.) have died, creating extensive landscapes with mostly dead trees (Ballard 2017). California's Tree Mortality Working Group reported the removal of 830,000 hazard trees to maintain safe conditions, with the Forest Service having removed almost 480,000 of these trees along 1355 km of roads, in 343 recreation sites, and around 135 communities, as well as having installed more than 556 ha of fuel breaks on six national forests in 10 counties (Gomes 2017).

This level of mortality is causing some forest type conversion to hardwoods or possibly other conifer species, but it will take decades for stands to reestablish and the impacts to be realized. Root disease fungi, dwarf mistletoes, and other native pathogens in these areas are expected to recolonize these stands, but the high level of uncertainty as to stand trajectory makes it difficult to predict the role that pathogens will play in influencing stand development or future disturbance.

Sudden Aspen Decline Illustrates the Role of Pathogens and Pests Following Drought Injury

In the early 2000s, a severe, hot, multiyear drought in the Southwestern United States incited sudden aspen decline of quaking aspen (*Populus tremuloides*) in Arizona, Colorado, Utah, and other states (Rehfeldt et al. 2009; Worrall et al. 2008, 2010). Sudden aspen decline, first observed in 2004, is characterized by rapid branch dieback and tree mortality on a landscape scale, without the involvement of a primary pest or pathogen. By 2008, it had been observed on more than 220 000 ha, or about 19 percent, of the quaking aspen type in the national forests of southwestern Colorado (Worrall et al. 2010). Marchetti et al. (2011) investigated the role of pathogens and insects in sudden aspen decline and found Cytospora canker (*Valsa sordida*), bronze poplar borer (*Agrilus liragus*), and aspen bark beetles (*Procryphalus mucronatus* and *Trypophloeus populi*) to be the most common pests in damaged areas, correlated with crown loss. They showed that sudden aspen decline fits the pattern of a true forest decline (Manion and LaChance 1992), with a predominance of secondary damage agents and no evidence that the mortality was caused by a primary pest; rather, the outbreak of secondary insects and pathogens increased the rate of mortality in aspen stands that were already affected by drought (the inciting factor). As is typical of responses to drought stress, populations of the pathogens and insects increased, allowing more vigorous trees to be attacked, thereby amplifying the impact of drought by killing trees that may have otherwise recovered.

Historical and Current Data: Management Approaches

To predict pathogens' contributions to forest disturbance, it is helpful to categorize the types of damage as root diseases, dwarf mistletoes, foliage diseases, rusts, Phytophthoras, or abiotic diseases, and consider them as disease groups with somewhat similar characteristics. Short descriptions of each are provided below.

Root Diseases

All forest types and tree species in western forests are affected by one or more root diseases.

Root diseases are the most damaging group of forest diseases in terms of tree volume loss in the United States (Krist et al. 2014). Root diseases are well distributed throughout the West (Lockman and Kearns 2016); all forest types and tree species are affected by one or more root diseases. Root disease pathogens kill trees, slow tree growth, decay wood, predispose trees to other biotic and abiotic agents, and cause trees to break off or uproot. All these impacts affect timber volume (Smith 1984), forest stand composition, and structure, ecosystem function (Hagle et al. 2000), personal safety (Filip and Goheen 1982), and carbon sequestration (Healey et al. 2016, Washington State Academy of Sciences 2013). Nearly all the root diseases affecting western ecosystems are caused by native pathogens, and as such, they have been long-term associates of the tree species they affect and are enduring components of the forest ecosystems they occupy. Climate change, management practices such as fire suppression and selective harvesting, and the introduction of exotic tree pathogens (e.g., white pine blister rust) have changed the historical roles of root diseases and, in many cases, have exacerbated their effects (Byler and Hagle 2000, Kliejunas 2011, Lockman and Kearns 2016).

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Root diseases, as a group, are one of the four top contributors to overall risk of tree mortality in the lower 48 states (along with oak decline/gypsy moth, mountain pine beetles, and southern pine beetles) (Lockman and Kearns 2016). Total basal area mortality rates of 25 percent or more are predicted to occur on nearly 930 777 ha in the Western States over a 15-year period (2012 to 2027) (fig. 7.2) (Krist et al. 2014).

In northern Idaho and western Montana, national forest land affected by root diseases has been measured at more than 2.3 million ha as determined by aboveground symptoms on U.S. Forest Service Forest and Inventory Analysis (FIA) plots (Lockman et al. 2015). This acreage equates to just under 40 percent of the land base on the seven national forests in northern Idaho and western Montana. Based on these area estimates, the volume lost from all root diseases in northern Idaho and western Montana is approximately 4.7 million m^3 per year. Volume growth impacts from root diseases often occur before a tree displays declining crown symptoms of infection aboveground (Cruickshank et al. 2011, Thies 1983), so actual volume lost is likely much more than estimated.

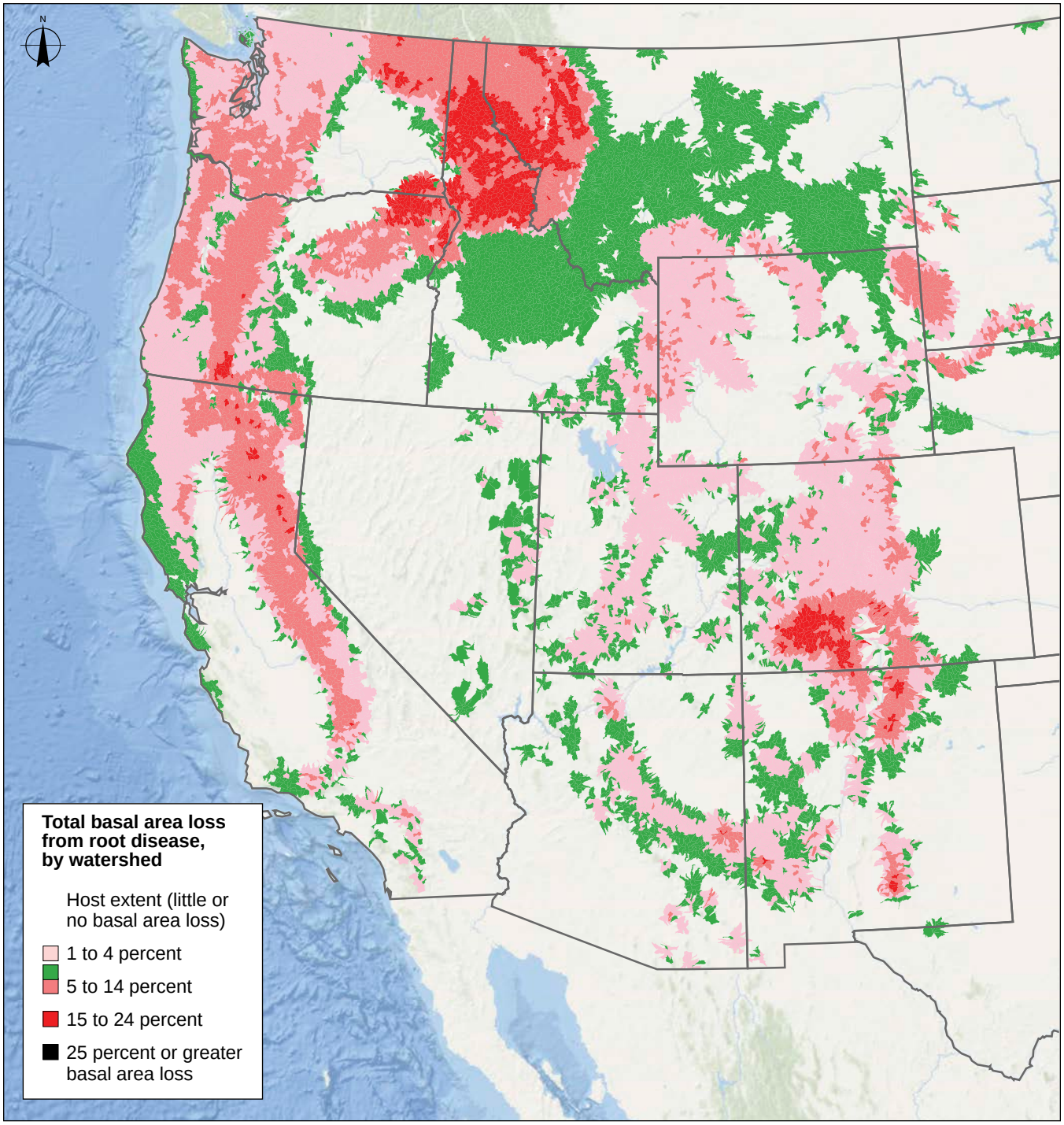

Figure 7.2—Predicted basal area loss from root diseases in the Western United States. Root diseases modeled are Armillaria root diseases, Heterobasidion root diseases, laminated root rot, and Port-Orford-cedar root disease (Data are from Krist et al. 2014).

Root disease pathogens have long-term and persistent impacts on the forest ecosystems they occupy because of their longevity on a site long after infected trees have died (Hagle et al. 2000). Root diseases kill millions of trees across the Western United States each year. This mortality occurs in large groups or as scattered small groups or individual trees, causing long-term openings in the forest canopy. Most of the fungi that cause root diseases survive saprophytically in root systems for years to decades, allowing them to become relatively permanent components on a site. This long-term presence can affect site productivity, along with the edaphic (related to soil) and physiographic features. Productivity is generally reduced by growth loss and mortality of host trees, which subsequently affects carbon sequestration. Root diseases can influence species composition by removing susceptible host trees and leaving tolerant species; and they can also modify successional pathways by changing forest structure and composition. Conversely, gaps and openings created by root diseases also allow for increased diversity in structure and species of plant life (Hansen and Goheen 2000, Kearns and Jacobi 2005). Additionally, root diseases create snags and down woody material, all of which affect wildlife habitat.

Management to minimize the impacts from many of the root diseases, such as Armillaria root disease and laminated root rot, involves converting or maintaining species that are tolerant to root diseases on the site. This can occur by regeneration harvest followed by planting tolerant species or using seed trees of a tolerant species to naturally regenerate a site, and precommercial and commercial thinning to favor root-disease-tolerant species. Other root diseases, such as black stain root disease in Douglas-fir (*Pseudotsuga menziesii*), can also be managed by minimizing damage to residual trees and harvesting during periods when the vectors of the causal fungus are at a minimum (Hansen et al. 1988, Rippy et al. 2005).

Dwarf Mistletoes

Dwarf mistletoes (*Arceuthobium* spp.) are parasitic plants that extract water and nutrients from living conifer trees (Shaw and Mathiasen 2013). Dwarf mistletoes are native components of western coniferous forests, having co-evolved with their hosts for millions of years. They cause reduced growth, decreased cone and seed production, tree mortality, and predisposition to other pathogens and insects (Hawksworth and Wiens 1996). The effects of dwarf mistletoes on individual trees are gradual, leading to measured impacts on ecosystem functions. These effects are generally scattered across a landscape, so significant impacts on ecosystem function may be detectable only across a long temporal scale and at a larger landscape level (Hawksworth and Wiens 1996). Fire suppression and silvicultural practices that favor dwarf mistletoes (e.g., regeneration harvest leaving dwarf mistletoe-infected

residuals over susceptible regeneration) have altered the historic levels of dwarf mistletoes and, in many cases, increased their severity and distribution across landscapes (Zimmerman and Laven 1984).

Dwarf mistletoes tend to be fairly host specific, and their distributions tend to loosely coincide with the distributions of their hosts (fig. 7.3). Mortality rates from dwarf mistletoes tend to be low. One to 15 percent of total basal area mortality resulting from dwarf mistletoes is predicted to occur on more than 1.2 million ha over a 15-year period (2012 to 2027) in the interior West, which includes Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming (fig. 7.3) (Krist et al. 2014). Although direct mortality rates are low, dwarf mistletoes play a significant role across the West as contributing agents to mortality in trees that are stressed by other factors, such as drought, insects, or root diseases (Byler 1978).

Direct mortality from dwarf mistletoes tends to be low, but dwarf mistletoes play a significant role as contributing agents to mortality in trees that are stressed by other factors.

Dwarf mistletoe management includes regeneration harvesting that allows for removal of infected overstory, planting of non-host species if maintaining an infected overstory, and removal of infected overstory to avoid infection of a susceptible understory (Hoffman 2010). Pruning to remove dwarf-mistletoe-infected branches in high-value trees can minimize hazards from brooms breaking out, reduce infection of understory trees, and increase the longevity of host trees (Maffei et al. 2016, Scharpf et al. 1988).

Foliage Diseases

Many foliage diseases are caused by numerous leaf- or needle-dwelling fungi, bacteria, and viruses (Sinclair et al. 1987). The symptoms, leafspots—discolored or necrotic areas—look similar, making it hard to identify a causal agent. In early disease stages, it may be difficult to distinguish between a benign spot and a serious pathogen that could lead to defoliation and growth loss. Foliar pathogens infect most all tree species and are particularly problematic in nurseries, plantations, or on ornamental plantings; however, significant damage in commercial forests occurs, as exemplified by Swiss needle cast and Dothistroma (red band) needle blight.

Swiss needle cast, *Phaeocryptopus gaeumannii*—
Swiss needle cast is a native foliar disease specific to Douglas-fir. The causal fungus, *Phaeocryptopus gaeumannii*, infects newly emerged needles in the spring and colonizes the intercellular spaces within needles (Hansen et al. 2000). Disease is caused by the pseudothecia (fungal fruiting body) physically blocking the stomata in the needles, which impedes uptake of carbon dioxide and water vapor needed for photosynthesis (Manter et al. 2005). Significant symptoms in native plantations were first noted in coastal Oregon in the late 1980s and early 1990s and have gradually increased in severity and spatial extent (Lee et al. 2017, Ritokova et al.

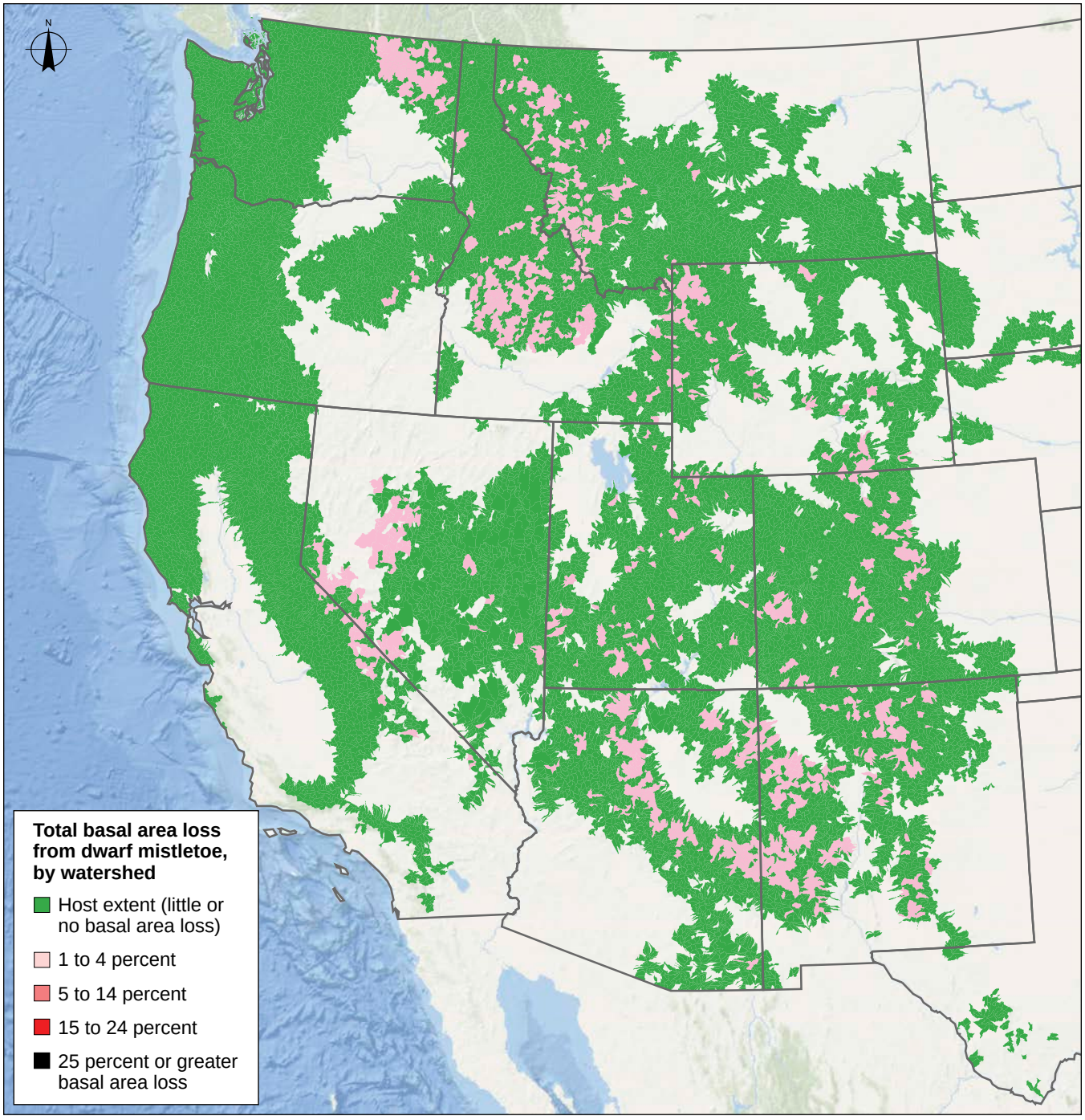

Figure 7.3—Predicted basal area loss from dwarf mistletoes in the Western United States. (Data are from Krist et al. 2014).

2016). Although much of the disease has been associated with young Douglas-fir plantations in the Sitka spruce(*Picea sitchensis*) zone, Swiss needle cast has been shown to affect older trees as well (Black et al. 2010). Aerial surveys have been used to map the extent of the disease, with the first flight occurring in 1996. In Oregon, the area affected has significantly increased in recent years from 53 050 ha in 1996 to 238 705 ha in 2015 (Ritokova et al. 2016). Although mortality is not attributed to this disease, significant growth losses have been documented. A 25-percent reduction in height growth and 35-percent reduction in basal area growth were measured in the more severely infected Douglas-fir plantations in the 1990s (Maguire et al. 2002). Radial growth in older trees can be decreased up to 85 percent in severely affected sites (Black et al. 2010).

A climate- and terrain-based model for Swiss needle cast severity in the western Oregon Coast Range has found strong correlations with mean daily temperature in late winter/early spring, with the best-fit model also including cumulative spring leaf wetness hours (Stone et al. 2008). As winter temperatures and spring/early summer precipitation continue to increase in current climate change scenarios, the area affected by severe Swiss needle cast will likely expand beyond the western Coast Range (Lee et al. 2017).

The increased development of Swiss needle cast along the Oregon Coast has been partially attributed to planting Douglas-fir into sites that typically have supported other species, such as western hemlock (*Tsuga heterophylla*), Sitka spruce, and red alder (*Alnus rubra*), with much less Douglas-fir than is currently present (Zhao et al. 2015). Impacts from Swiss needle cast can be minimized by planting mixed species to lessen potential disease losses, reducing the proportion of Douglas-fir on moderate- and high-severity sites, using seed adapted to the site, and avoiding planting offsite stock (Shaw et al. 2011).

Impacts from Swiss needle cast, a native foliar disease specific to Douglas-fir, can be reduced by planting mixed species and using seed and stock adapted to the site.

Dothistroma (red band) needle blight, *Dothistroma septosporum*— Dothistroma needle blight is one of the most damaging foliar diseases of pines in both the Northern and Southern Hemispheres (Drenkhan et al. 2016, Watt et al. 2009); the pathogen infects 82 pine species as well as other non-pine species, and can cause successive needle defoliation, reduced diameter and height growth, and tree mortality (Barnes et al. 2014). The global distribution of *D. septosporum* is considered an important example of the unintentional, human-assisted movement of a plant pathogen, facilitated by the establishment of *D. septosporum* in plantations planted outside their natural ranges, particularly on Monterey pine (*Pinus radiata* D. Don) (Barnes et al. 2014).

Recent outbreaks of Dothistroma needle blight have led to severe defoliation and subsequent mortality in localized areas of ponderosa pine in central Montana (James 2010); in limber pine, (*P. flexilis*) in eastern Montana, and in an extensive area of lodgepole pine (*P. contorta*) in British Columbia (Woods et al. 2005). Growth impacts are positively correlated to the amount of needles lost and are somewhat linear in younger trees, but a convex-curved relationship exists in older trees (Gibson 1972), in which older needles, which are infected first in disease progression, contribute less to growth than in younger trees. Mortality is a consequence of severe outbreaks and has occurred in limber pines in eastern Montana with greater than 90 percent of crowns affected by Dothistroma needle blight (Jackson and Lockman 2003). Similar infection levels leading to mortality were found in lodgepole pines in British Columbia (Woods 2003).

These outbreaks appear to be tightly tied to periods of warmer and wetter conditions in winter and spring (Jackson and Lockman 2003, Taylor and Schwandt 1998, Welsh et al. 2014, Woods et al. 2005), and if the current climate trend continues to favor warming with an increase in spring rains, there is a moderate likelihood of increased damage from this disease (Kliejunas 2011). Woods et al. (2016) found that, since the 1950s, four of the past five strong El Niño events coincided with reports of increased Dothistroma damage on several continents. The extent and severity of the current outbreak in British Columbia is also linked to an increase in prevalence of the host species there, where young lodgepole pine plantations have increased from 10 to 40 percent in managed stands (Woods et al. 2005).

Impacts from Dothistroma needle blight can be minimized by planting mixed species to lessen potential disease losses (Woods et al. 2005), reducing the proportion of susceptible pines on moderate- and high-severity sites, thinning to favor resistant trees or species, using seed adapted to the site, and avoiding planting offsite stock (James 2010).

Rusts—White Pine Blister Rust, *Cronartium ribicola*

Rusts are obligate parasites and may cause serious canker or foliar diseases. They often have complicated lifecycles that require more than one host plant species for disease to express, and may produce up to five types of spores. One of their spore types, uredial spores, are bright orange, hence during sporulation, the affected plant part appears “rusty” (Geils et al. 2010, Ziller 1974).

In the Western United States, the most damaging rust pathogen is *Cronartium ribicola*, a fungus native to Asia that is the cause of blister rust of white pines (*Pinus* spp.) and which was introduced to North America in the early 1900s (Maloy 1997). Infection by *C. ribicola* causes branch dieback, reproductive failure, and tree mortality. In the West, white pine blister rust is widely distributed (fig. 7.4); over

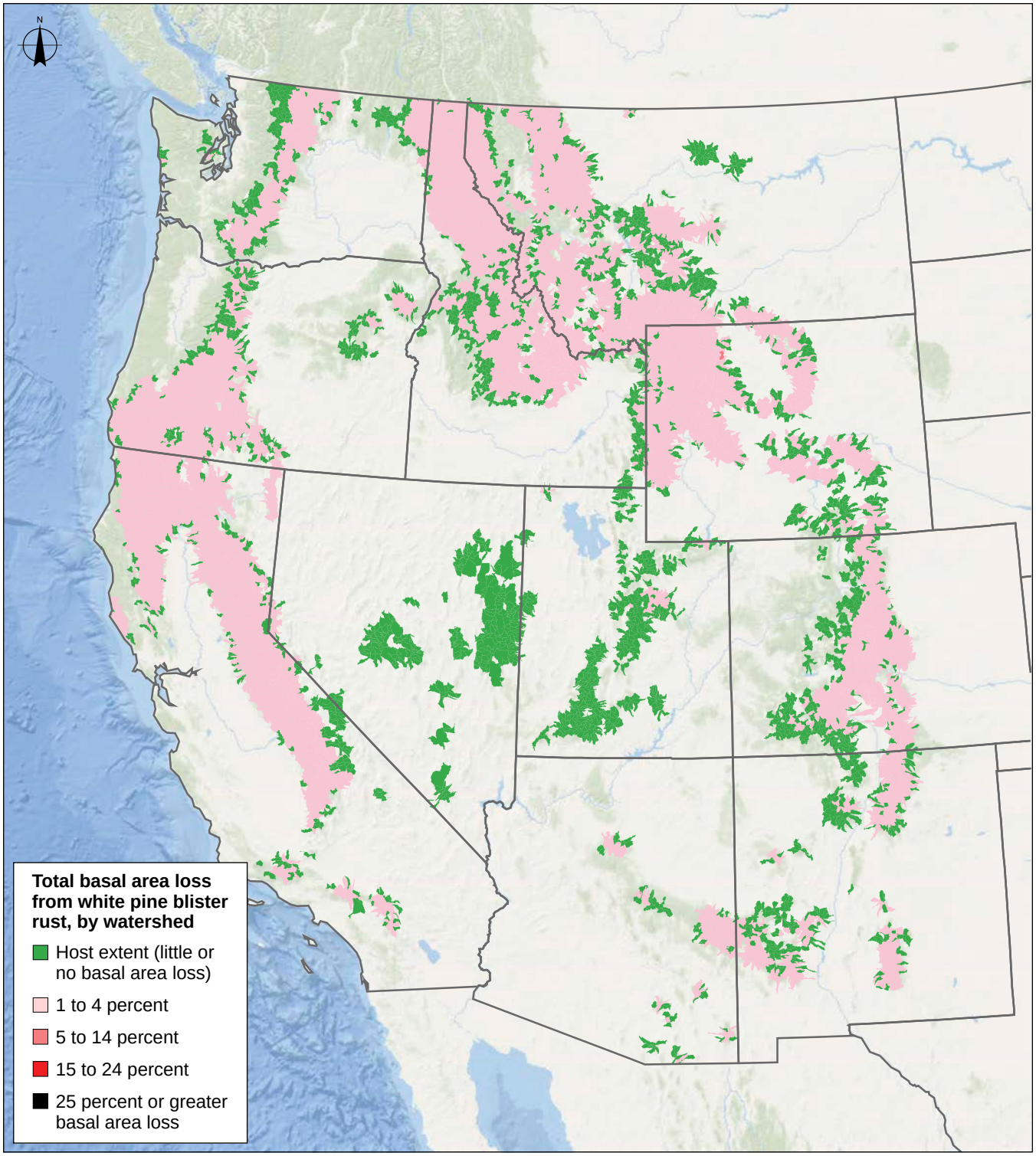

Figure 7.4—Predicted basal area loss from white pine blister rust in the Western United States. (Data are from Krist et al. 2014). Losses are based on current white pine cover type, which has been greatly diminished by past mortality from white pine blister rust, mountain pine beetle (*Dendroctonus ponderosae*), and harvesting (Neuenschwander et al. 1999).

White pine blister rust, caused by a nonnative fungus introduced in the early 1900s, over time has caused more damage than any other conifer disease in western forests.

time, the disease has caused more damage and more has been spent on control than any other conifer disease (Bega 1978). Control started in the 1930s with widespread removal of *Ribes* spp., the alternate host for white pine blister rust (Geils et al. 2010). Over time, individual trees were observed to be surviving white pine blister rust with little to no disease, so control efforts shifted into a program for breeding white pines resistant to white pine blister rust. Second- and third-generation trees bred for resistance are grown and outplanted. Genetically improved trees outperform wild trees when outplanted (Kearns et al. 2012), but they are not immune to the disease. Owing to the likelihood of blister rust damage, the number of western white pine (*P. monticola*) grown for reforestation has been reduced by 95 percent because forest managers consider it too risky to plant (Kinloch 2003), and there are few openings created to allow for outplanting stock. Of particular concern, synergistic effects of *C. ribicola*, drought, increasing temperatures, and outbreaks of mountain pine beetle (*Dendroctonus ponderosae)* are driving extensive mortality in high-elevation whitebark pine, (*P. albicaulis*) populations (Jules et al. 2016, Logan and Powell 2001).

Basal area mortality from white pine blister rust on all white pines is predicted to be low (Krist et al. 2014), but is based on current white pine cover type, which has been greatly diminished by past mortality from white pine blister rust, mountain pine beetle, and harvesting (Neuenschwander et al. 1999). One to 4 percent of total basal area mortality is predicted to occur on more than 4.7 million ha in the Western United States over a 15-year period, and 5 to 15 percent total basal area mortality is predicted to occur on nearly 0.8 million ha during the same period (2012 to 2027) (fig. 7.4) (Krist et al. 2014).

Management strategies to minimize impacts from white pine blister rust include planting of genetically improved stock resistant to white pine blister rust, thinning to improve growing conditions of host species, and pruning to remove the more susceptible lower branches and to remove nonlethal cankers before they are able to girdle the tree (Schwandt et al. 2013).

Phytophthoras, Sudden Oak Death, *Phytophthora ramorum*

Phytophthora is a fungus-like genus of microorganisms (Class Oomycetes) that includes water molds, diatoms, and brown algae. *Phytophthora* species thrive in water or moist conditions and produce swimming, flagellate spores, called zoospores. They are among the most damaging pathogens of forest, horticultural, or agricultural plants (Parke and Eberhart 2017).

A recent invader, *Phytophthora ramorum*, is now the leading biotic cause of tree mortality in California coastal forests and serves as an example of an aggressive

Sudden oak death, caused by a recent invasive pathogen, is now the leading biotic cause of tree mortality in California coastal forests.

pathogen causing disturbance along the Pacific Coast by preferentially attacking the largest, fastest growing host trees (Swiecki and Bernhardt 2006). This exotic, invasive, quarantine pathogen kills tanoak (*Notholithocarpus densiflorus*), coastal live oak, and other red oaks, but is known to infect more than 100 plant species including conifers, herbaceous plants, and ferns (Kliejunas 2010, Rizzo et al. 2005). Estimated to have been introduced sometime around 1980 to California on rhododendron, (*Rhododendron* sp.) nursery stock in landscape plantings (Mascheretti et al. 2008), *P. ramorum* escaped into the forest to kill millions of trees along the Pacific Coast, from the California central coast north to Curry County, Oregon (Grünwald et al. 2012). Tree mortality increased dramatically in the late 1990s in the San Francisco Bay Area, where more than 6 million people reside, so managing hazards (failing trees and falling branches) in residential areas, and along roadways and power lines, is a chronic concern (Frankel 2008). The pathogen is particularly disconcerting to some American Indian tribal members who rely on acorns for ceremonial use or food and may consider the primary host tree species, tanoak, to be sacred (Alexander and Lee 2010).

In heavily infested areas, such as on Mount Tamalpais (Marin County, California), the pathogen has caused type conversion of previously tanoak-dominated stands; tanoak is no longer a primary stand component (Klein et al. 2013). Tanoak stands managed by the Marin Municipal Water District are severely disease-transformed, which threatens the provisioning of drinking water and creates a high fire risk, so the district is conducting restoration trials in redwood-tanoak and Douglas-fir/tanoak forests to re-create an overstory component composed of less susceptible species, e.g., redwood (*Sequoia sempervirens*) and Douglas-fir (Cobb et al. 2017).

In Oregon from 2001 to 2012, an interagency team attempted to eradicate the pathogen, supported by the state's quarantine, which required destruction of infected and nearby host plants (Goheen et al. 2002). Eradication treatments eliminated disease from many infested sites, but the pathogen continued to slowly spread. Since 2001, the wildland quarantine area has expanded from 22 to 1333 km^2 in 2017, covering over 30 percent of Curry County, Oregon. Hundreds of thousands of tanoaks have died from *P. ramorum* in southwest Oregon (Goheen et al. 2017, Kanaskie et al. 2017). Environmental conditions along the Oregon Coast are highly conducive to disease development, and the pathogen, if untreated, is expected to expand north into Coos County and east into Josephine County (Association of Oregon Counties 2017).

In 2015, a second significant introduction of a new lineage of the pathogen was detected in Oregon, the first find of the *P. ramorum* EU1 lineage (European Union Lineage One) in a U.S. forest. This detection, on a tanoak tree about 1 mi (1.6 km)

north of a small private nursery (now closed) near the Pistol River (Curry County), underscores the importance of the nursery pathway for long-distance invasive pathogen movement (Grünwald et al. 2016).

Preventing the transport and outplanting of infested nursery stock is critical to avoid introducing pathogens to new areas.

Prevention of pathogen introduction via transport and outplanting of infested nursery stock is critical to avoid introductions to new areas (Grünwald et al. 2012). Quarantines are in effect in the United States and more than 67 other countries to prevent long-distance spread (Kliejunas 2010). Best management practices and strict sanitation may limit spread within nurseries (Parke and Grünwald 2012). Once the pathogen has been established in a forest, it is very difficult to control. Early detection, (conducted by aerial survey, waterway sampling, and ground surveillance) followed by hotspot eradication has slowed spread in Oregon (Kanaskie et al. 2017). To prevent infection, phosphonate may be injected or applied to the bark of high-risk trees, particularly on high-value coast live oak. High-value trees may also be protected by removing adjacent California bay laurels (*Umbellularia californica*), which serve as reservoirs for inoculum that can move via windblown rain to nearby oaks (Lee et al. 2011, Swiecki and Bernhardt 2013).

Abiotic Disease—Yellow-Cedar Decline

A good example of a species-specific abiotic disease is yellow-cedar decline, which has been observed across southeast Alaska for more than a century (Hennon and Shaw 1994, Sheldon 1912). Until recently, the cause of extensive mortality of Alaska cedar or yellow-cedar (*Callitropsis nootkatensis*), a culturally and economically important species, was unknown (Hennon et al. 2012). Over the past decade, Hennon and colleagues determined that, across more than 250 000 ha, Alaska cedar have died from climatic changes that cause a reduction in snow cover, promote early springtime thaws that trigger dehardening, and make the trees susceptible to root injury from freezing (D'Amore and Hennon 2006, Hennon et al. 2012, 2016).

Yellow-cedar decline is characterized by a slow decline in tree condition over several years. Affected forests are composed of standing, long-dead and recently dead and dying Alaska cedar and other tree species. Insects (*Phloeosinus* beetles) and pathogens (*Armillaria* spp. and other fungi) are contributing factors in yellow-cedar decline. Predisposing factors include landscape, site, and stand conditions (Hennon et al. 2008) that increase the probability that the fine roots of Alaska cedar will freeze during cold weather in late winter and early spring (Schaberg et al. 2008). Alaska cedar trees are healthy where snow persists past the last cold period in spring, or where they are deep-rooted on well-drained soils (Sturrock et al. 2011).

Conservation strategies that define suitable vs. unsuitable areas for Alaska cedar are recommended to determine areas where cedars are likely to survive and

thus are suitable for planting. Higher elevation sites with well-drained soils where snow or deeper rooting protect Alaska cedar roots from cold temperatures are most suitable, but may require thinning to ensure regeneration of Alaska cedar. In declining forests, salvaged wood from dead cedars may be economically valuable (Hennon et al. 2012).

Implications and Impacts of Pathogens on Sustainability

Interactions With Climate Change

The impacts of pathogens to forest sustainability are dependent upon (1) environmental conditions, (2) the distribution and density of host species, and (3) whether pathogens are present at the location. This simple model for disease expression, termed the "disease triangle," is one of the fundamental principles of plant pathology (Agrios 2005). If there are changes to any of these factors, disease patterns and pathogen impacts will change. Climate change and human population pressures alter the environmental influences (such as the amount of forest fragmentation) on plant pathogens and create new disease conditions. Changes in climate alter pathogens' ability to establish, infect, develop, and reproduce. The changes can be extreme, as in the drought that caused unprecedented levels of tree mortality in the Sierra Nevada Mountains from 2010–2017 (Tree Mortality Working Group 2017).

Changes in climate alter pathogens' ability to establish, infect, develop, and reproduce.

In the Western United States, examples of observed or predicted changes in pathogen behavior that are tied to climate change include increased damage from Swiss needle cast in the Pacific Northwest (Manter et al. 2005, Stone et al. 2008); Armillaria root disease on Douglas-fir (Klopfenstein et al. 2009); *Phytophthora cinnamomi* in Pacific Northwest forests (Burgess et al. 2017); and white pine blister rust on several species of white pines (Sturrock et al. 2011).

Similar to accelerated deterioration often observed in offsite plantings, as climate changes, plants growing in environments that are no longer suitable for them may be subject to increased damage from pathogens that attack stressed plants. As landscape-level stress intensifies, increased disturbance area, frequency, and intensity are likely, with pathogens playing a primary or secondary role (following, e.g., drought or heat stress).

Patterns of disturbance are expected to change as pathogens and their hosts adapt to new environmental conditions. The distribution of both hosts and diseases will change and a cascade of adaptations will ensue (Johnstone et al. 2016). The more rapid reproduction cycles of microbes relative to trees may give them an adaptive advantage over their hosts. Fungi and other types of pathogens may spread via wind or infested raindrops and settle in locations where the climate is newly

suitable for their survival and reproduction. Synchronicity between forest plants and pathogens will be disrupted by climate-driven changes in timing of budbreak in tree hosts, or temporal changes of pathogen spore release; these and other expected changes may alter disease incidence and severity given climate change (Sturrock et al. 2011). Drought increases stress, so trees severely infected by dwarf mistletoes may be more susceptible to insect attack, particularly bark beetles and wood borers (Kolb et al. 2016). Foliar fungal diseases and other diseases that require moisture for reproduction or spread are expected to decrease under extended drought periods (Kolb et al. 2016).

Impacts to Sustainability

Recent megadisturbances resulting from unprecedented drought, coupled with experimental findings on tree responses to warming (Adams et al. 2017a, 2017b), demonstrate that as areas warm, many forest disturbances will increase in size and frequency (Allen et al. 2015, Seidl et al. 2017). There remains much uncertainty as to how forest pathogen behavior and forest disease impacts will influence disturbance patterns given a warming and changing climate (Kolb et al. 2016). However, based on recent observations, unprecedented environmental conditions (i.e., extreme extended drought) will cause abiotic effects to increase, which may decrease the impact of biotic pathogens, because the hosts that the microbes attack will be killed by direct effects of heat, water stress, or other abiotic injury. This decrease in pathogen activity is predicted only under extreme situations (i.e., 80 percent tree mortality), such as occurred in parts of the central Sierra Nevada Mountains from 2015 to 2017 (Ballard 2017).

As areas transformed by megadisturbance are reforested, the increase in replanting may raise the potential for pathogen introductions or facilitate the spread of root diseases from living stumps to adjacent seedlings (Lockman and Kearns 2016). The risk of pathogen introduction may be elevated by planting of infested nursery stock, grading with contaminated equipment, or other human-mediated problems (Rooney-Latham et al. 2015).

Interactions Among Disturbance Agents

Under less extreme conditions, pathogens will continue to increase stress and damage trees directly or indirectly through interactions with insects, fire, and other disturbance agents (Sturrock et al. 2011). In areas that become overstocked, experience water-stress, or have been heavily affected by past land uses, trees may be prone to fire, beetle attack, or pathogen injury (Doblas-Miranda et al. 2017). If one of these mortality agents is favored, the mortality from the other agents may decrease because the number of suitable hosts has been reduced. Widespread fire

may reduce damage from pathogens as the heat produced can kill many microbes and dwarf mistletoes (Alexander and Hawksworth 1976, Shaw and Agne 2017) or eliminate the hosts they require for survival (Harrington and Hawksworth 1990). However, conversely, pathogens may influence fuels and stand structure to intensify fires (Metz et al. 2011, 2017).

Many management actions aimed at improving forest conditions may decrease detrimental impacts of forest pathogens, particularly thinning to reduce competition or brush control to enable seedling establishment (Jactel et al. 2009). However, precautions are needed during stand manipulations to avoid wounds that can serve as pathogen infection courts, or the creation of stand conditions that are favorable to mistletoes, root disease, or invasive pathogens (Muzika 2017). Additionally, although silvicultural treatments can reduce stress on residual trees in the short term, they also increase risk given the greater reliance placed on the remaining trees because the reduced density allows for larger trees, which can lead to hydraulic constraints (D'Amato et al. 2013). For each geographic area, prevention of known pathogen problems needs to be integrated into treatment strategies; e.g., in Oregon and Washington, species susceptible to laminated root rot (*Phellinus* spp.) should not be planted into areas with a history of root disease (Agne et al. 2018).

Management approaches to address climate change may inadvertently increase forest disease. In particular, assisted migration of tree species may allow pathogens to be introduced on nursery stock (Rooney-Latham et al. 2015). Introducing new plant species into new areas presents a risk that the environment will create conducive conditions for novel diseases.

Given the uncertainty of managing forests under a changing climate, increased monitoring of forest condition and pathogen distribution would enable wildland managers to respond to new invasive pathogens or newly aggressive native pathogens before they establish so widely that they become too expensive or logistically difficult to manage (Millar and Stephenson 2015). Species diversification and various planting configurations should be tried in new plantations (Thompson et al. 2009). Adaptive management approaches in which vegetation managers plan for the unexpected would increase resiliency against disturbance (Millar et al. 2007).

Increased monitoring of forest condition and pathogen distribution might enable managers to respond before new invasive pathogens become too expensive or difficult to manage.

Most forests will have to adapt to climate change without management intervention (Seidl et al. 2017, Spittlehouse and Stewart 2003), thus, in actively managed forest areas, decisions should be carefully designed to maximize the likelihood of tree survival and ecosystem benefits. Prescriptions for higher planting densities to account for anticipated losses to forest diseases should be avoided (Woods and Coates 2013).

Adapting to changing forest conditions resulting from climate change and other anthropogenic causes will require reconsideration of all aspects of forest management (i.e., yield tables, site quality indices) (D'Aprile et al. 2015), and expectations about the impacts of forest pathogens need to be reexamined as well. Unprecedented tree mortality is raising awareness of the vulnerabilities that forests face (Fettig et al. 2013); to sustain forests, we need a better understanding of the role of forest pathogens under current and anticipated future conditions and disturbance patterns. Needed actions include an increase in forest pathogen and climate change experimental data as well as detailed recording of observations of responses to warming, as well as inventory monitoring that more accurately attributes the cause of tree mortality so that ecological impacts of pathogens can be understood and addressed.

Conclusions

Changes in forest disturbance patterns, such as wildfires, will change the impacts of pathogens, creating novel forms of disruption to ecosystem services, as well as safety and management problems.

Changes in other forest disturbance patterns, such as wildfires, will change the impacts of pathogens, creating novel forms of disruption to ecosystem services, as well as safety and management problems. Tree mortality rates and growth responses will evolve over time, as pathogens and plant species adapt to one another (Zenni et al. 2017). Our ability to characterize pathogen issues under changing disturbance regimes is limited. If drought, fire, and other abiotic disturbances are extreme, the impact of pathogens may decrease because there will be fewer host plants for microbes to infect, and the weakest in the tree population will have been removed by other mortality agents.

Management approaches should consider the need to integrate historical, current, and predicted pathogen risks for their particular geographic area and to embed disease prevention into treatment strategies. Increased monitoring allows us to better understand the current impacts of pathogens on growth and tree mortality so that changes can be recognized and addressed. Prevention of pathogen invasions would lessen degradation of western forests.

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