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# Management tactics to reduce bark beetle impacts in North America and Europe under altered forest and climatic conditions

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## 1 Introduction

Since the industrial revolution, atmospheric $CO_2$ has risen from ~270 to >400 ppm and methane emissions, which also play an important role in regulating climate, have nearly tripled (Turner, Frankenberg, & Kort, 2019). Although $CO_2$ enrichment has been shown to increase tree growth in some controlled studies and broad-scale analyses, the positive effects of $CO_2$ on tree growth is often negated by higher temperatures, droughts, low soil fertility, and air pollutants such as ground-level ozone. Warming amplifies precipitation deficits as higher temperatures result in higher levels of evapotranspiration and climatic water deficit. Wildfires, storms, insect and disease outbreaks, and other climatically enhanced events are becoming more frequent and severe in forests (Allen, Breshears, & McDowell, 2015; Seidl et al., 2017; Vose et al., 2018). Dyderski, Paź, Frelich, and Jagodziński (2018) projected changes in the distribution of 12 European tree species under three climate change scenarios (Representative Concentration Pathway (RCP) 2.6, RCP 4.5 and RCP 8.5) for 2061–80. Many pioneer species, such as Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.), were projected to lose suitable habitat. In North America, Prasad et al., (2020) projected changes in the distribution of 25 tree species under two climate change scenarios (RCP 4.5 and RCP 8.5) for 2071–2100 incorporating a migration model to assess colonization likelihoods. Many tree species in the

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conterminous USA were projected to lose suitable habitat (especially under RCP 8.5) while gains were projected in Alaska, USA and Canada.

Bark beetles (Coleoptera: Curculionidae, Scolytinae) are important disturbance agents in conifer-dominated forests in North America and Europe (Schafstall, Kuosmanen, Fettig, Knížek, & Clear, 2020; Table 1). Each bark beetle species exhibits unique host preferences, life history traits and impacts, but many exhibit a preference for colonizing larger-diameter trees growing in high-density stands with a high percent of host type (Fettig et al., 2007; Wermelinger, 2004). Many bark beetles use highly evolved chemical communications systems, involving pheromones, host volatiles and nonhost volatiles, during host finding, host selection, host colonization, and mating behaviors (Huber, Fettig, & Borden, 2021). Tree mortality attributed to bark beetles influence the function, structure, and composition of forests by regulating aspects of primary production, nutrient cycling, ecological succession, and the size, distribution, and abundance of trees. At endemic populations, bark beetles create small gaps in the forest canopy by killing individual trees or small groups of trees stressed by age, drought, defoliation, or other factors. In this context, few negative impacts are observed (Morris et al., 2017). This differs from the impacts associated with outbreaks, which may negatively affect many ecological goods and services including timber and fiber production, water quality, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among others (Fettig, 2019; Morris et al., 2018; Thom & Seidl, 2016).

Several recent bark beetle outbreaks have been incited by warming and drought (Bentz et al., 2010; Kolb et al., 2016; Jactel, Koricheva, & Castagneyrol, 2019; see Chapters 2–7). For example, in western North America, recent outbreaks of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have been severe, long lasting, and well documented, with >27 million ha impacted (Audley et al., 2020; Fettig, Progar, Paschke, & Sapio, 2021; Runyon et al., 2020). While mechanisms contributing to *D. ponderosae* outbreaks are complex and include density-dependent and density-independent factors (Bentz et al., 2010; Raffa et al., 2008; Sambaraju et al., 2012), an important inciting factor, particularly in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests, has been increases in minimum winter temperatures, which facilitate higher levels of brood survival during winter (see Section 10). Similarly, recent outbreaks of spruce beetle (*Dendroctonus rufipennis* (Kirby)) in western North America have increased in extent and severity. Again, increasing temperatures and, in some areas, prolonged periods of drought were important inciting factors (Sherriff, Berg, & Miller, 2011; see Section 11). In *D. rufipennis*, a facultative prepupal diapause may be avoided when late instar larvae are subjected to temperatures of <15°C for <20 d (Hansen, Bentz, Powell, Gray, & Vandygriff, 2011), allowing beetles to complete their lifecycle in one year compared to two years. This increases the possibility of exponential population growth (Hansen & Bentz, 2003) and the likelihood that *D. rufipennis* outbreaks will occur in an area.

**Table 1** Bark beetle species that cause substantial levels of tree mortality in conifer-dominated forests in North America and Europe.

| Common name | Scientific name | Common host(s) |
|---|---|---|
| Arizona fivespined ips | *Ips lecontei* | *Pinus ponderosa* |
| California fivespined ips | *Ips paraconfusus* | *P. contorta*, *P. lambertiana*, *P. ponderosa* |
| Douglas-fir beetle | *Dendroctonus pseudotsugae* | *Pseudotsuga menziesii* |
| Eastern fivespined ips | *Ips grandicollis* | *P. echinata, P. elliottii, P. taeda, P. virginiana* |
| Eastern larch beetle | *Dendroctonus simplex* | *Larix laricina* |
| Eastern six-spined engraver | *Ips calligraphus* | *P. echinata, P. elliotti, P. ponderosa, P. taeda, P. virginiana* |
| European spruce beetle | *Ips typographus* | *Picea abies*, *Pi. orientalis*, *Pi. yezoensis* |
| Fir engraver | *Scolytus ventralis* | *Abies concolor*, *A. grandis*, *A. magnifica* |
| Jeffrey pine beetle | *Dendroctonus jeffreyi* | *P. jeffreyi* |
| Larger Mexican pine beetle | *Dendroctonus approximatus* | *P. ponderosa* |
| Mountain pine beetle | *Dendroctonus ponderosae* | *P. albicaulis*, *P. contorta*, *P. flexilis*, *P. lambertiana*, *P. monticola*, *P. ponderosa* |
| Northern spruce engraver | *Ips perturbatus* | *Pi. glauca*, *Pi. x lutzii* |
| Pine engraver | *Ips pini* | *P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*, *P. resinosa* |
| Pinyon ips | *Ips confusus* | *P. edulis*, *P. monophylla* |
| Roundheaded pine beetle | *Dendroctonus adjunctus* | *P. arizonica*, *P. engelmannii*, *P. flexilis*, *P. leiophylla*, *P. ponderosa*, *P. strobiformis* |
| Sharp-dentated bark beetle | *Ips acuminatus* | *P. sylvestris* |
| Six-toothed bark beetle | *Ips sexdentatus* | *P. heldreichii, P. nigra, P. pinaster, P. sylvestris*, *Pi. orientalis* |
| Southern pine beetle | *Dendroctonus frontalis* | *P. echinata, P. engelmannii*, *P. leiophylla*, *P. ponderosa*, *P. rigida*, *P. taeda, P. virginiana* |
| Spruce beetle | *Dendroctonus micans* | *P. sylvestris*, *Pi. abies* |
| Spruce beetle | *Dendroctonus rufipennis* | *Pi. engelmannii*, *Pi. glauca*, *Pi. sitchensis, Pi. x lutzii* |
| Western balsam bark beetle | *Dryocoetes confusus* | *A. lasiocarpa* |
| Western pine beetle | *Dendroctonus brevicomis* | *P. coulteri*, *P. ponderosa* |

In California, USA, droughts are a regular occurrence, but the 2012–15 drought was characterized by large precipitation deficits and abnormally high temperatures and in some areas was the most severe in 1200 years (Griffin & Anchukaitis, 2014). This drought resulted in progressive canopy water stress of at least 888 million trees and severe canopy water stress of at least 58 million trees (Asner et al., 2016), and substantial mortality of dominant and co-dominant trees, much of which was attributed to western pine beetle (*Dendroctonus brevicomis* LeConte) (Fettig, Mortenson, Bulaon, & Foulk, 2019) (Fig. 1; see Section 9). Some consider the level of tree mortality recorded in California during this period to be unprecedented (Stephens et al., 2018). Similarly, following recent heat waves and droughts in Europe notable outbreaks occurred of the sharp-dentated bark beetle (*Ips acuminatus* (Gyllenhal)) (see Section 13) and European spruce beetle (*Ips typographus* (L.)) (Fig. 2; see Section 14). While climate change is intensifying bark beetle impacts in some regions, range expansions are occurring in other areas with species such as *D. ponderosae* in western North America (Cooke & Carroll, 2017; Cudmore, Bjőrklund, Carroll, & Lindgren, 2010) and southern pine beetle (*Dendroctonus frontalis* Zimmermann) in the eastern US (see Section 12) (Chapter 3).

Substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of tree mortality attributed to bark beetles (Fettig &

**FIG. 1** Much of California, United States, experienced a severe drought in 2012–15 inciting a large tree mortality event in the central and southern Sierra Nevada. In the most heavily impacted areas, 49% of trees died during 2014–17 (Fettig et al., 2019). *Pinus ponderosa* suffered the highest levels of tree mortality (90%). Mortality of *P. ponderosa* was highest at the lowest elevations, concentrated in larger-diameter trees and attributed primarily to colonization by *Dendroctonus brevicomis*, an important disturbance agent that readily colonizes drought-stressed *P. ponderosa* (Kolb et al., 2016). *Pinus lambertiana* exhibited the second highest levels of tree mortality (48%). Mortality of *P. lambertiana* was concentrated in the mid-diameter classes and attributed primarily to colonization by *Dendroctonus ponderosae* (Fettig et al., 2019). *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

**FIG. 2** During 2018–20, large outbreaks of *Ips typographus* occurred in central Europe incited by storm damage followed by extremely warm and dry weather. In Germany alone, ~178 million $m^3$ of sanitation and salvage were removed. *Photo credit: M. Kautz, Department of Forest Health Protection, Forest Research Institute Baden-Württemberg, Germany.*

Hilszczański, 2015). Suppression involves short-term tactics designed to address current infestations by manipulating beetle populations and often includes the use of sanitation harvests, insecticides, semiochemicals (i.e., chemicals released by one organism that elicit a response, usually behavioral, in another organism), or a combination of these and other treatments. Prevention is designed to reduce the probability and severity of future bark beetle infestations by manipulating stand, forest, and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and/or altering age classes and species compositions. Below, we provide an overview of the ecology and management of bark beetles in conifer-dominated forests followed by six case studies concerning the effects of altered forest and climatic conditions on bark beetle ecology and management. These case studies include (1) *Dendroctonus* spp. in yellow pine forests in the western USA, (2) *D. ponderosae* in pine forests in western North America, (3) *D. rufipennis* in spruce forests in western North America, (4) *D. frontalis* in pine forests in the eastern USA, (5) *I. acuminatus* in *P. sylvestris* forests in central Europe, and (6) *I. typographus* in *Pi. abies* forests in central Europe. We draw inference from the literature as well as from practical experience gained while working in forests in North America and Europe.

## 2 Development of outbreaks

Generally, two requirements must be met for a bark beetle outbreak to occur: (1) several years of favorable weather conducive to beetle survival and population growth and (2) an abundance of suitable and susceptible host trees. In short, bark beetle flight activity

depends on suitable weather during adult dispersal, and weather plays an important role in influencing beetle fecundity, fitness, phenology, and voltinism (Bentz et al., 2010). Increases in temperature may result in shortened life cycles, increased outbreak frequencies, and elevated impacts. Large-scale heat waves can synchronize outbreaks over large areas such as frequently observed with *I. typographus* in central Europe. From a forest management perspective, warming and drought often compromise our ability to mitigate the negative impacts exerted by bark beetles on forests (Bentz et al., 2020; Jönsson, Harding, Bärring, & Ravn, 2007; Netherer & Schopf, 2010).

During endemic populations, host trees weakened or damaged by other agents are often colonized and killed by bark beetles. For example, in Alaska, USA, endemic populations of northern spruce engraver (*Ips perturbatus* (Eichhoff )) infest forest debris, widely scattered individual trees, or small groups of trees. However, natural (e.g., flooding, wildfire, and windstorms) and anthropogenic-induced (e.g., road building, construction of utility rights-of-way and fire breaks, and logging activity) disturbances (Fig. 3) may produce large quantities of damaged, dead, or dying spruce, providing oviposition sites for *I. perturbatus* (Burnside et al., 2011). When favorable weather coincides with large amounts of host material, *I. perturbatus* populations may erupt resulting in mortality of apparently healthy trees over extensive areas (Holsten & Werner, 1987). Similarly, outbreaks of *I. typographus* in Europe (Komonen, Schroeder, & Weslien, 2011), pine engraver (*Ips pini* (Say)) in North America (Kegley, Livingston, & Gibson, 1997), and eastern

**FIG. 3** Bark beetle outbreaks occur when favorable weather and forest conditions coincide in time and space. In interior Alaska, United States, increased use of fuel reduction treatments and fire breaks to reduce the risk of wildfires to communities (above), increased interest in the use of wood-energy systems as alternatives to fossil fuels, and warming (Wolken et al., 2011) have heightened the need for development of effective tactics for management of *Ips perturbatus* (Fettig et al., 2013). *Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service.*

six-spined engraver (*Ips calligraphus* (Germar)), eastern five-spined engraver (*Ips grandicollis* (Eichhoff )), and small southern pine engraver (*Ips avulsus* (Eichhoff )) in the southern USA (Connor & Wilkinson, 1983; McNichol et al., 2019), among other species, are often precipitated by large-scale disturbances, such as severe storms or logging activity (Chapter 7). In the absence of such large-scale disturbances, damage to individual trees from subcortical insects (Boone, Aukema, Bohlmann, Carroll, & Raffa, 2011), defoliators (Wallin & Raffa, 2001), drought (Kolb et al., 2016, 2019), lightning strikes (Hodges & Pickard, 1971), and root pathogens (Klepzig, Raffa, & Smalley, 1991) may act as inciting factors and reduce host resistance which facilitates successful colonization by bark beetles.

## 3 Detection, survey, and risk and hazard rating models

In forested areas, management decisions are typically made at the stand level, whereas in urban areas, management decisions are made at the individual tree level. Information on the severity and extent of bark beetle infestations adequate to plan appropriate management tactics requires accurate detection and survey methods in both environments. These primarily range from trapping programs to monitor bark beetle populations to simple ground-based surveys to a broad array of aerial surveys using methods such as digital sketch mapping (Fettig & Hilszczański, 2015). Of note, the recent use of drones (Koontz, Latimer, Mortenson, Fettig, & North, 2021; Paczkowski et al., 2021; Schaeffer et al., 2021) and satellites (Abdullah, Skidmore, Darvishzadeh, & Heurich, 2019) to detect and map trees attacked by bark beetles (including newly infested trees) and of Lidar (light detection and ranging) to detect flying beetles (Li et al., 2020) hold promise for increasing efficiencies and reducing costs of bark beetle detection and survey. Biosurveillance with scent dogs or predatory wasps, electronic noses, acoustic detection, and laser vibrometry are important and promising technologies, especially when the focus is on discovery and eradication of invasive species (Poland & Rassati, 2019).

Risk and hazard rating models are also available to provide natural resource managers with means of identifying stand and forest conditions conductive to the initiation and spread of bark beetle infestations. In western North America, among the most notable risk and hazard rating model is that of Shore and Safranyik (1992) for *D. ponderosae* in *P. contorta*. Susceptibility is calculated based on four factors: (1) percentage of susceptible basal area (the cross-sectional area of a tree at 1.37 m in height) of trees $\geq$15 cm dbh (diameter at 1.37 m in height), (2) average stand age of dominant and co-dominant trees, (3) stand density of all trees $\geq$7.5 cm dbh, and (4) the geographic location of the stand in terms of latitude, longitude, and elevation. *Dendroctonus ponderosae* population data, referred to as a beetle pressure index, incorporates the proximity and size of *D. ponderosae* populations. The stand susceptibility index and beetle pressure index are then used to compute a stand risk index (Shore & Safranyik, 1992; Shore, Safranyik, & Lemieux, 2000). In Europe, phenological models such as PHENIPS and PHENIPS-TDEF are important hazard rating tools (Baier, Pennerstorfer, & Schopf, 2007; Matthews et al.,

2018). PHENIPS uses weather and topographical information to simulate when spring emergence of adult *I. typographus* occurs, as well as the potential development rates and emergence of subsequent generations. PHENIPS-TDEF includes a simple ecosystem water balance module (TDEF) which, based on prevailing weather conditions and a coarse description of forest stands, indicates when potential host trees become stressed by drought.

Several methods have been developed to predict tree losses attributed to Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) (e.g., Negrón, 1998; Shore, Safranyik, Riel, Ferguson, & Castonguay, 1999; Weatherby & Thier, 1993), roundheaded pine beetle (*Dendroctonus adjunctus* Blandford) (Negrón, 1997; Negrón, Wilson, & Anhold, 2000), *D. rufipennis* (e.g., Reynolds & Holsten, 1994, 1996; Schmid & Frye, 1976; Steele et al., 1996), *D. frontalis* (e.g., Billings & Hynum, 1980; Hedden, 1985; Reed, Burkhart, Leushner, & Hedden, 1981), and *D. brevicomis* (e.g., Hayes, Fettig, & Merrill, 2009; Liebhold, Berck, Williams, & Wood, 1986; Steele et al., 1996) in North America and to *I. typographus* in Europe (see Section 14). It is likely that the accuracy of some risk and hazard rating models are declining due to reductions in host tree vigor caused by climatic changes, forest densification, and other factors. As such, the threshold values identified in some models likely require revision (e.g., reductions in existing tree density thresholds associated with highly susceptible stands). For a related example, see Section 9.

## 4 Suppression

A successful suppression program requires prompt and thorough applications of the most appropriate tactics at a magnitude dictated by the bark beetle population and the spatial extent of the infested area. Of note, suppression is expensive, and therefore decisions regarding suppression are often made based on more practical concerns such as resource availability, market conditions, logistical constraints, and environmental concerns (Fettig & Hilszczański, 2015).

## 5 Sanitation

Sanitation involves the identification of trees infested by bark beetles, and subsequent felling and removal or treatment to destroy adults and/or brood beneath the bark. Where economically feasible, trees may be harvested and transported to mills where broods will be destroyed during processing. Otherwise, felled trees are burned, chipped, peeled, and debarked (Fig. 4) or treated with insecticides, fumigants, or by solarization (i.e., placement of infested material in the direct sun, which is often sufficient to kill brood beneath the bark in warmer climates) on site. In some cases, an emphasis is placed on sanitation of newly infested trees during the very early stages of colonization to reduce the quantity of aggregation pheromones released into the stand (Fettig, Gibson, Munson, & Negrón, 2014a). However, this is often difficult due to complications regarding the identification of newly infested trees, the level of responsiveness required in their prompt removal, and site accessibility limitations due to remoteness, steep terrain, and weather (e.g., heavy

**FIG. 4** Following sanitation, felled trees may be transported to mills where bark beetle broods will be killed during processing or treated in the field with tactics designed to kill the brood prior to emergence. Above, a log wizard is used to peel the bark of *Picea engelmannii* infested with *Dendroctonus rufipennis* in Utah, United States. *Photo credit: S. Munson, Forest Health Protection, USDA Forest Service.*

snow). Sanitation and salvage logging of windfelled spruce following windstorms is considered the most effective method of control for *I. typographus* and is widely implemented throughout Europe (see Section 14) (Chapter 7). In central Europe, Augustynczik, Dobor, and Hlásny (2021) simulated the removal of windfelled trees in stands randomly distributed on the landscape and in stands prioritized for salvage by an optimization algorithm using *i*Land, which simulates forest dynamics at the landscape scale (Seidl, Rammer, Scheller, & Spies, 2012). They reported spatially optimized salvage that removed 66% of windfelled trees reduced future tree losses to *I. typographus* by 55% and economic losses by ~69% compared to the reference condition (no salvage). Nonoptimized salvage, which removed the same volume of windfelled trees as optimized salvage, reduced damage by only 10%. In the southeastern USA, a unique variant of sanitation that includes removal of infested and some uninfested trees at small spatial scales (e.g., <0.4 hectare) is used for disrupting *D. frontalis* spot growth (see Section 12). Depending on the scale and extent of a bark beetle infestation, sanitation may have the added benefit of reducing stand susceptibility by influencing stand structure and composition.

## 6 Insecticides

Insecticides are regulated by federal, provincial, state, and local governments, and therefore their use for protecting trees from mortality attributed to bark beetles varies widely.

For example, hundreds of thousands of trees may be treated with insecticides to prevent colonization of these trees by *D. ponderosae* during outbreaks in the western USA, yet similar uses are banned for *I. typographus* in European countries (but insecticides may still be used to treat logs stored along forest roads in order to prevent colonization; see Section 14). In the USA, generally only high-value, individual trees growing in unique environments are treated. Most treatments for bark beetles involve bole sprays of contact insecticides applied from the root collar to the mid-crown until runoff. It is important that all parts of the tree that are likely to be colonized are adequately protected. For some *Ips* spp., this requires spraying most (≥7.6 cm diameter) branches (Fettig et al., 2006). Bole sprays are usually applied in late spring of the current year, or early fall of the prior year before flight activity occurs for the target bark beetle species. Length of residual activity varies by active ingredient, formulation, bark beetle species, tree species, and location. In most cases, at least one field season of protection can be expected with a single application (Fettig, Grosman, & Munson, 2013).

Researchers attempting to find safer, more portable, and long-lasting alternatives to bole sprays have evaluated the effectiveness of injecting small quantities of systemic insecticides directly into the tree bole (Grosman, Fettig, Jørgensen, & Munson, 2010; Grosman & Upton, 2006). Following injection, the product is translocated throughout the tree to the phloem where bark beetles feed. Injections can be applied at any time of year when the tree is actively translocating, but time (weeks to months) is needed to allow for distribution of the active ingredient within the tree prior to the tree being challenged by bark beetles (see Table 1 in Fettig, Munson, Grosman, and Blackford (2020) for appropriate timing in *P. contorta*, *P. ponderosa*, and *Pi. engelmannii*). Tree injections eliminate concerns regarding drift and reduce nontarget effects and applicator exposure compared to bole sprays (Fettig, Grosman, & Munson, 2013; Fettig, Munson, McKelvey, Bush, & Borys, 2008).

## 7 Semiochemicals

The primary semiochemicals associated with the most aggressive bark beetle species have been isolated and identified (Borden, 1997; Wood, 1982a; Zhang & Schlyter, 2004) and combined with an integrated understanding of their context in the chemical ecology of forests have led to the development of several management tactics (Seybold et al., 2018; Zhang & Schlyter, 2004). Aggregation pheromone components and other attractants, such as host volatiles, are commonly used in traps for survey and detection; population monitoring; predicting levels of tree mortality (e.g., Billings, 1988; Hansen, Bentz, Munson, Vandygriff, & Turner, 2006); timing of management tactics; and mass trapping (e.g., Bentz & Munson, 2000; Hübertz, Larsen, & Bejer, 1991). Attractants may also be used to induce infestation of individual or small groups of trees for a variety of research and management purposes.

Inhibitors, antiaggregation pheromones and nonhost volatiles, are used to protect individual trees and small-scale stands (Huber et al., 2021). Verbenone has received the most attention and is the primary antiaggregation pheromone of *D. ponderosae*, *D. frontalis*,

and *D. brevicomis*, but also causes inhibition in several other species, including *I. typographus* (Zhang & Schlyter, 2004). In North America, verbenone has been demonstrated effective for reducing tree mortality attributed to *D. ponderosae* and to some degree *D. frontalis*, but not *D. brevicomis* (Seybold et al., 2018). 3-Methylcyclohex-2-en-l-one (MCH), another antiaggregation pheromone, is highly effective for reducing colonization of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) by *D. pseudotsugae* (Ross, Gibson, & Daterman, 2015). Wallingford, Cha, Linn, Wolfin, and Loeb (2017) argued that one of the most successful applications of an inhibitor for plant protection is the use of verbenone for management of bark beetles.

The most common methods of applying inhibitors include nailing or stapling bubble capsule or pouch release devices at maximum reach to the bole of a host tree for individual tree protection, or nailing or stapling these release devices in a uniform grid (regardless of the vertical substrate used for attachment, but with application to host trees when possible) for stand protection (Fig. 5). Release devices should be applied prior to beetle flight for the current year. Bead, flake, and sprayable formulations have also been developed. Two notable recent advances include the development of SPLAT Verb for *D. ponderosae* (ISCA Technologies Inc., Riverside, California, USA; Fettig, Munson, Reinke, & Mafra-Neto, 2015) and SPLAT MCH for *D. pseudotsugae* (ISCA Technologies Inc.; Foote et al., 2020). Rather than a single release device, SPLAT is an amorphous, flowable controlled-release emulsion with chemical and physical properties that can be adjusted by small changes in composition and application (Fig. 5D). SPLAT formulations rapidly biodegrade compared to bubble capsules and pouches. This results in significant time and cost savings, as unlike bubble capsules and pouches SPLAT formulations do not need to be retrieved from the field. Gillette and Fettig (2021) suggest there exists an acute need for more intensive development of semiochemical-based tools and tactics given observed and projected increases in levels of tree mortality attributed to bark beetles.

## 8 Prevention

Thinning is widely accepted as an effective means of increasing the resistance and resilience of forests to bark beetles (Fettig & Hilszczański, 2015), a relationship that has been attributed primarily to changes in microclimate, tree spacing, tree competition, and tree vigor following thinning (Bartos & Amman, 1989; Knapp, Bernal, Kane, Fettig, & North, 2021; Thistle et al., 2004; Whitehead & Russo, 2005; Whitehead, Safranyik, Russo, Shore, & Carroll, 2004). For example, in western North America thinning from above or diameter-limit thinning and thinning from below (Cole & Cahill, 1976; McGregor, Amman, Schmitz, & Oakes, 1987) applied to increase residual tree spacing (Whitehead et al., 2004; Whitehead & Russo, 2005); to reduce basal area (Amman, McGregor, Cahill, & Klein, 1977; Bennett & McGregor, 1980; Cahill, 1978); and to remove trees with thick phloem (Hamel, 1978) reduce the susceptibility of *P. contorta* forests to *D. ponderosae* infestations. Thinning from below may optimize the effects of microclimate, inter-tree spacing, and tree vigor (Coops, Timko, Wulder, White, & Ortlepp, 2008; Whitehead & Russo, 2005), even


**FIG. 5** In many cases, the primary semiochemicals associated with the most aggressive bark beetle species in North America and Europe have been identified and synthesized. Common release devices include (A) bubble capsules, (B) pouches, (C) flakes, and (D) SPLAT (ISCA Technologies Inc.). New advances in the production of semiochemicals by microbes, regulatory streamlining, and the recent availablity of drone applications (Gillette & Fettig, 2021) will likely provide natural resource managers with cheaper and more effective means to mitigate tree mortality attributed to bark beetles in the future. *Photo credits: (A) R. Progar, Research and Development, USDA Forest Service, (B and D) C. Fettig, Pacific Southwest Research Station, USDA Forest Service, and (C) W. Murray, Department of Biological Sciences, San Jose State University.*

though residual trees are of diameter classes considered more susceptible to colonization by *D. ponderosae* (Mitchell, Waring, & Pitman, 1983; Waring & Pitman, 1980 but see Ager, McMahan, Hayes, & Smith, 2007). In Europe, *I. typographus* infestations are positively correlated with the proportion of spruce and/or age of spruce trees (Grodzki, 2010; Hilszczański, Janiszewski, Negrón, & Munson, 2006; Wermelinger, 2004; Zolubas, Negrón, & Munson, 2009) and the amount of forest edge (Kautz, Schopf, & Ohser, 2013; Schroeder & Lindelöw, 2002). As such, thinning and group selection must be carefully implemented to minimize the amount of forest edge.

Prevention should also account for the spatial distribution of forest cover types and host-tree species distributions. In many cases, treatments should be implemented to

increase forest heterogeneity (e.g., of tree ages, tree sizes, and tree species compositions) as homogeneous landscapes promote creation of large contiguous areas susceptible to similar disturbances. For example, several authors have suggested that shorter rotations and promotion of multiple, tree-age classes will minimize levels of tree mortality attributed to *D. ponderosae* (Safranyik, Shrimpton, & Whitney, 1974; Taylor & Carroll, 2004; Whitehead et al., 2004) and *I. typographus* (Hlásny et al., 2019). As such, at the landscape-level coordination of prevention activities across land ownerships is important.

## 9 Case study 1—*Dendroctonus* spp. in yellow pine forests in the western United States: Changes in forest structure and composition from fire suppression, livestock grazing, and climatic changes increase host-tree susceptibility

Outbreaks of *D. ponderosae*, *D. brevicomis,* and Jeffrey pine beetle (*Dendroctonus jeffreyi* Hopkins) in *P. ponderosa* and Jeffrey pine (*Pinus jeffreyi* Balf.) forests in the western USA (yellow pine forests, excluding those in New Mexico and Arizona, USA where *Ips* spp. cause most of the tree mortality attributed to bark beetles) have been well documented since the early 1900s (Eveden, 1945; Graham, Asherin, Battaglia, Jain, & Mata, 2016; Jenne & Egan, 2019; Miller & Keen, 1960). Each occurred within a window of time associated with a somewhat unique array of ambient conditions, including environmental factors such as duration, severity and spatiotemporal patterns of water availability, edaphic conditions, and resultant tree physiological stress (Guarín & Taylor, 2005; Hood, Baker, & Sala, 2016; Restaino et al., 2019). Additionally, forest characteristics, including the composition, structure, age, density, and landscape-scale abundance of yellow pines susceptible to bark beetles, fluctuate through time (Covington & Moore, 1994; Graham & Jain, 2005; Hagmann, Franklin, & Johnson, 2013; Taylor, 2010). The interactions of these characteristics have led to variability among the magnitude of bark beetle populations, exposure of stand conditions to divergent beetle population pressure, and resultant patterns of tree mortality.

The severity and spatial extent of modern bark beetle outbreaks in yellow pine forests have increased relative to the early 20th century. For example, as mentioned earlier, recent outbreaks of *D. brevicomis* in *P. ponderosa* forests in California may have been unprecedented compared to historic records, as pine mortality was widespread and commonly exceeded 80% in certain areas (Fig. 1). Outbreaks of *D. ponderosae* caused similar levels of *P. ponderosa* mortality across the Black Hills of South Dakota and Wyoming, USA during 2004–10 (Graham et al., 2016). Across Montana and northern Idaho, USA, *D. ponderosae* outbreaks have been spatially reconstructed with estimates of beetle-caused tree mortality within *P. ponderosa* spanning a 350,000-hectare extent during 1999–2015 (Lestina et al., 2019) and a 338,000-hectare extent during 1971–89 (Harley et al., 2019). This contrasts strikingly with the limited 12,000-hectare aggregate area of *P. ponderosa* impacted during

1909–45 ( Jenne & Egan, 2019). While the precision of area-impact estimates within early 20th century reports is not quantifiable, the magnitude of divergence relative to modern bark beetle outbreaks for northern Idaho and Montana suggest larger spatial areas were impacted during modern outbreaks. Wickman (2005) summarized work associated with outbreaks in the early 1900s and indicated "The drought-related stress to trees on millions of acres of ponderosa pine forests in the Inland West caused dramatic levels of tree mortality that could not be ignored by politicians."

Progressive changes in forest structure and composition have been well documented across yellow pine forests since the early 1900s. This includes a transition from low-density, open, and park-like forests comprised of large-diameter (>61 cm dbh) *P. ponderosa* and *P. jeffreyi* to dense, second-growth forests composed of smaller-diameter trees with increased densities of *Abies* spp. and *Ps. menziesii* in some locations (Covington & Moore, 1994; Graham & Jain, 2005; Hagmann et al., 2013; Smith & Arno, 1999; Taylor, 2010). These dense conditions resulted from extensive forest disturbance in the early 1900s, including timber harvesting that fueled local economies, wildfires, and bark beetle outbreaks, followed by periods of forest regrowth and densification that were promoted by fire exclusion and livestock grazing in the mid-20th century to today (Covington & Moore, 1994; Graham & Jain, 2005; Hagmann et al., 2013; Smith & Arno, 1999; Taylor, 2010) (Fig. 6). While few direct comparisons exist, an example of the magnitude of yellow pine forest densification is presented in Hagmann et al. (2013), which quantified a 300% increase in forest density (based on numbers of trees) by comparing modern and historic forest inventory data from sites in southern Oregon, USA.

Along with management influences, long-term climate dynamics, including the Pacific Decadal Oscillation and Atlantic Multi-Decadal Oscillation, have helped shape yellow pine forests (Jiang, Yu, & Acharya, 2019). Drier periods facilitate expansive wildfires and bark beetle outbreaks that are often temporally synchronized across large areas (Bollenbacher, Graham, & Reynolds, 2014; Morgan, Heyerdahl, & Gibson, 2008). Conversely, wetter periods are associated with substantial recruitment pulses and survivorship of *P. ponderosa* (Brown, 2006). For example, wetter conditions across Montana and northern Idaho from 1935 to 1974 were not conducive to widespread wildfires or bark beetle outbreaks while drier periods from 1919 to 1934 and from 2000 to present promoted regionally synchronized wildfires and bark beetle outbreaks (Bollenbacher et al., 2014; Hicke, Xu, Meddens, & Egan, 2020; Morgan et al., 2008). In effect, multidecadal wet periods since the early 1900s combined with fire exclusion promoted widespread forest densification. By 2012, these factors led to an estimated 14.4 million hectares of yellow pine forests being classified as moderately or highly susceptible to mortality from *Dendroctonus* spp. (Fig. 7; Krist et al., 2014).

## 9.1 Management

Historically, management tactics for *Dendroctonus* spp. in western yellow pine forests relied on sanitation of beetle-infested pines by felling and debarking (Fig. 8), decking

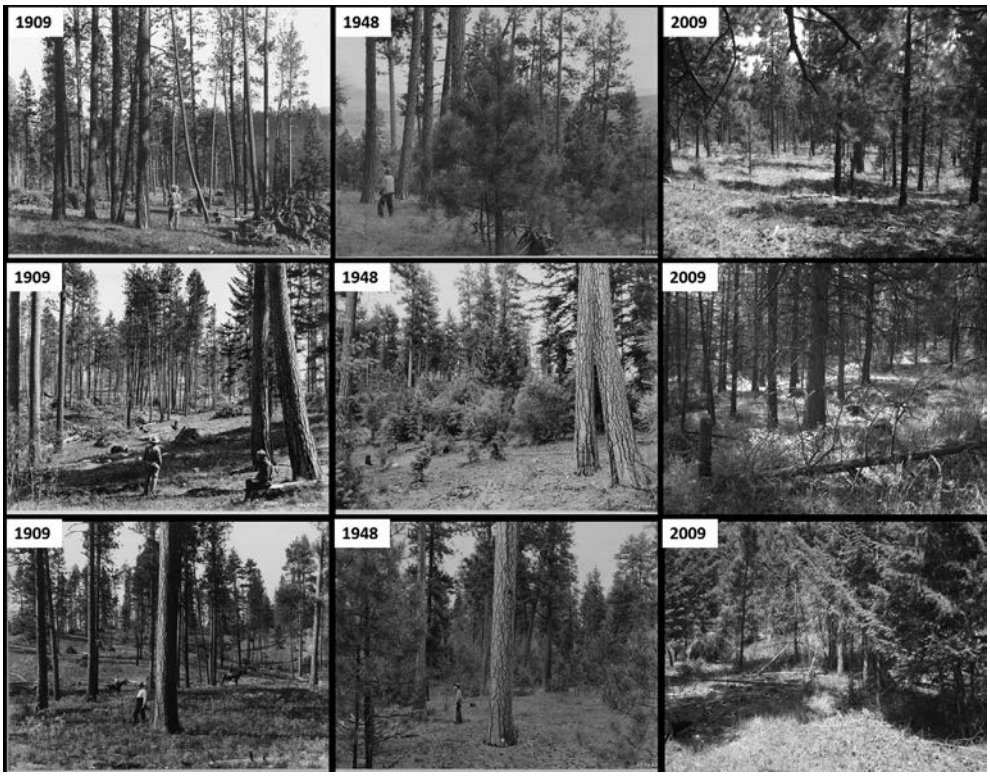


**FIG. 6** Time series photos depicting densification of *Pinus ponderosa* forests in the Lick Creek Drainage in western Montana, United States, 1909–2009. Today, similar conditions exist in many yellow pine forests in the western United States and resulted from extensive forest disturbance in the early 1900s followed by periods of forest regrowth promoted by fire exclusion and livestock grazing. *Photo credit: Hood, S. M., Lutes, D. C., Crotteau, J. S., Keyes, C. R., Sala, A., Harrington, M. G., et al. (2018). Lick Creek historic photographic series: A century of change in a ponderosa pine forest in Western Montana. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Research Data Archive.*

and burning, insecticides, or other techniques (Graham et al., 2016; Jenne & Egan, 2019; Miller & Keen, 1960; Wickman, 2005). These treatments were considered effective at causing brood mortality and, at times, halting the progression of small-scale, localized infestations. However, they were largely ineffective at preventing infestations across landscapes comprised of susceptible host trees (Eveden, 1945; Jenne & Egan, 2019; Miller & Keen, 1960; Wickman, 2005). After summarizing 40 years of control efforts in northern Idaho and Montana, Eveden (1945) called for "Additional research…[to] provide a foundation upon which both artificial control and the preventative efforts of silvicultural management must stand."

From 1960–90s, long-term studies were established by the USDA Forest Service and university colleagues to identify conditions in yellow pine forests resistant to *Dendroctonus* spp.-caused tree mortality. Findings across studies indicated thinning to

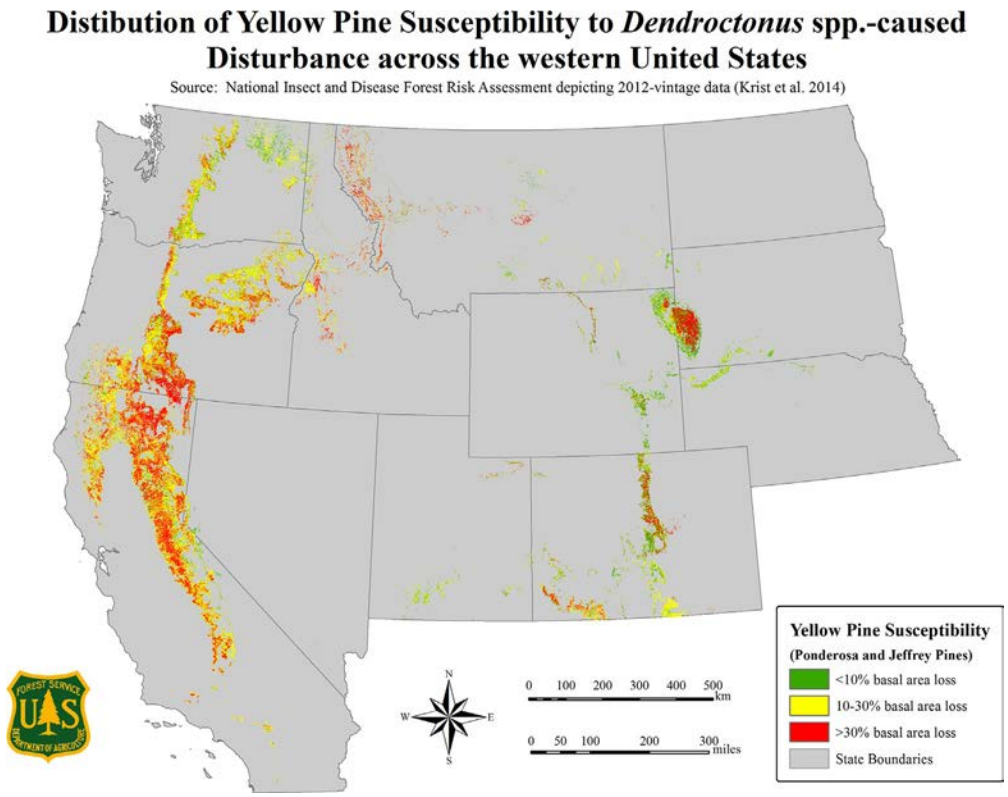


**FIG. 7** Yellow pine susceptibility to *Dendroctonus* spp. across the western United States. About 82% of western yellow pine forests are moderately or highly susceptible to tree mortality (Krist et al., 2014).

residual stand densities of 200–240 stand density index (SDI) (a measure of stocking based on the number of trees per unit area and dbh of the tree of average basal area; Reineke, 1933; Stage, 1968) provided adequate resistance under most circumstances (e.g., Cochran & Barrett, 1993, 1995, 1998; Oliver, 1995). However, Kolb et al. (2007) cautioned against extrapolation of results from time periods during which "large numbers of lethal bark beetle attacks…rarely occur." To that end, Egan et al., (unpublished data) analyzed data from 662 plots (0.041 to 0.8-hectare plots, including >62,000 trees) surveyed 1959–2016 across yellow pine forests in the western USA (Table 2). All plots were dominated by *P. ponderosa* or *P. jeffreyi* and were stratified by exposure to (1) low to moderate bark beetle pressure (infestation severity ≤30% of susceptible pines in or adjacent to the survey plot) or (2) severe bark beetle pressure (infestation severity >30%) during the study period. Resistance was defined by survivorship of susceptible-sized (>10.2 cm dbh) pines as "high-level resistance" where ≥90% pine survivorship occurred; "moderate-level resistance" where ≥70% survivorship occurred; and "low resistance" where <70% survivorship occurred. The objectives were (1) to identify variations in annual and summer precipitation across study locations from 1948 to 2018 and (2) to determine whether the

**FIG. 8** In North America, historical management practices relied upon the detection and sanitation of beetle-infested trees, including *Pinus ponderosa* colonized by *Dendroctonus brevicomis*, California, United States, 1930. These treatments were considered effective at causing brood mortality and, at times, halting the progression of localized infestations. Today, other tactics are favored over sanitation for management of bark beetles in North America, but sanitation remains the primary means of control for *Ips typographus* and other bark beetles in Europe. *Photo credit: J. Patterson, USDA Forest Service.*

200–240 SDI thresholds identified in earlier studies promoted adequate resistance to modern (2000–18) *Dendroctonus* spp. infestations.

Precipitation conditions over multidecade time segments were evaluated with standard precipitation index (SPI), a metric to facilitate temporal comparisons of wet, dry, and neutral conditions across spatio-temporal sites after standardization to site-specific reference conditions (Guttman, 1999). Findings indicate annual and summer dry conditions occurred more frequently during 2000–18 than during earlier time segments (Fig. 9). Conversely, 1980–99 had frequent wet conditions and very limited frequency of dry annual and summer conditions. The period 1980–99 is when numerous studies were executed to derive the current stand density thresholds (200–240 SDI) used by natural resource managers today to promote stand resistance to bark beetles in yellow pine forests.

Of the 662 plots, most plots (88%) from the period 1980 to 1999 were exposed to low-moderate beetle pressure, while most plots (74%) from 2000 to 2018 were exposed to severe bark beetle pressure (Table 2). In general, failures in bark beetle resistance increased with increasing stand density. High-level resistance within plots exposed to low-moderate *Dendroctonus* spp. pressure failed (defined by % of plots failing to have resistance at $\geq$10%) when stand density was 200–249 SDI and above (Fig. 10, top, blue line), validating thresholds identified in earlier studies when plots were exposed to low-moderate beetle pressure. Moderate-level resistance within plots exposed to low-moderate *Dendroctonus* spp. pressure failed only rarely (Fig. 10, top, red line). However,

**Table 2** Attributes of studies compiled for assessment of bark beetle resistance from research plots located in yellow pine forests in the western United States, 1956–2016.

| Study | Location | Period | Bark beetle pressure[a] | No. plots | *Dendroctonus* spp. | Stand density index |
|---|---|---|---|---|---|---|
| Cochran and Barrett (1993) | Oregon | 1959–1989 | Low-moderate | 20 | *D. ponderosae* | 74–300 |
| Hall and Davies (1968) | California | 1961–1965 | Severe | 4 | *D. ponderosae* | 193–550[b] |
| Cochran and Barrett (1998) | Washington | 1964–1993 | Low-moderate | 88 | *D. ponderosae* | 21–437 |
| Cochran and Barrett (1995) | Oregon | 1967–1991 | Low-moderate | 68 | *D. ponderosae* | 48–257 |
| McCambridge and Stevens (1982) | South Dakota Wyoming | 1979–1980 | Low-moderate | 6 | *D. ponderosae* | 74–383 |
| Oliver (1995) | California | 1979–1994 | Low-moderate | 59 | *D. ponderosae* *D. brevicomis* | 25–350 |
| Graham et al. (2016) | South Dakota Wyoming | 1985–2006 | Low-moderate | 40 | *D. ponderosae* | 78–375 |
| Egan et al. (2011) | California | 1991–1996 | Severe | 72 | *D. jeffreyi* | 66–539 |
| Graham et al. (2016) | South Dakota | 1994–2010 | Severe | 84 | *D. ponderosae* | 61–391 |
| Jørgensen et al., unpublished data | Idaho | 1999–2016 | Low-moderate | 14 | *D. brevicomis* | 15–229 |
| Egan et al. (2010) | California | 2001–2007 | Severe | 36 | *D. ponderosae* *D. brevicomis* | 68–368 |
| Egan et al. (2010) | California | 2001–2007 | Low-moderate | 22 | *D. ponderosae* *D. brevicomis* | 161–550[b] |
| Hood et al. (2016) | Montana | 2005–2012 | Severe | 42 | *D. ponderosae* | 45–328 |
| Briggs et al., unpublished data | Colorado | 2008–2011 | Severe | 17 | *D. ponderosae* | 52–229 |
| Egan et al. (2020) | Montana | 2010–2014 | Severe | 24 | *D. ponderosae* | 49–256 |
| Fettig et al. (2019) | California | 2013–2016 | Severe | 66 | *D. brevicomis* | 93–550[b] |

[a] Low to moderate bark beetle pressure, infestation severity ≤30% of susceptible pines in or adjacent to survey plots during the study period; severe bark beetle pressure, infestation severity >30%.

[b] Maximum stand density index (SDI) is indicated for 2x plots on productive sites in California in which SDI computations exceeded 550 SDI.

for plots challenged by severe *Dendroctonus* spp. pressure, high-level resistance failures occurred at 100–149 SDI (Fig. 10, bottom, blue line) and moderate-level resistance failures occurred at 150–199 SDI (Fig. 10, bottom, red line). Overall, these results suggest that substantially lower stand densities are required to maintain adequate levels of resistance in contemporary yellow pine forests than previously considered by most natural resource managers. Of note, it appears stand density levels <100 SDI are required to promote high levels of resistance, and those <150 SDI are required to promote moderate levels of

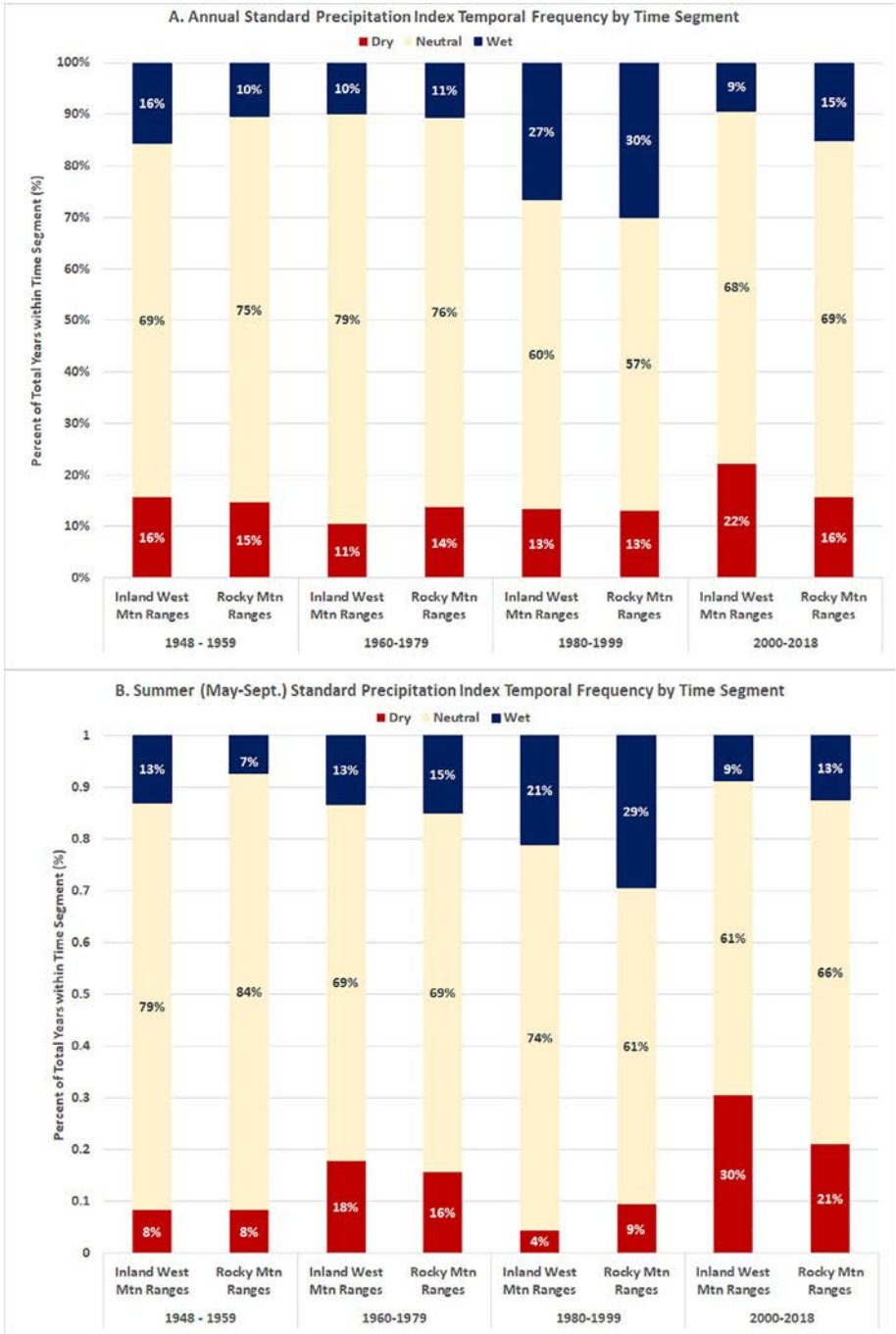


**FIG. 9** Temporal frequency of standard precipitation index-designated condition classes by time segment averaged across yellow pine research plots in the western United States compiled for Rocky Mountain and Western Mountain Ranges.

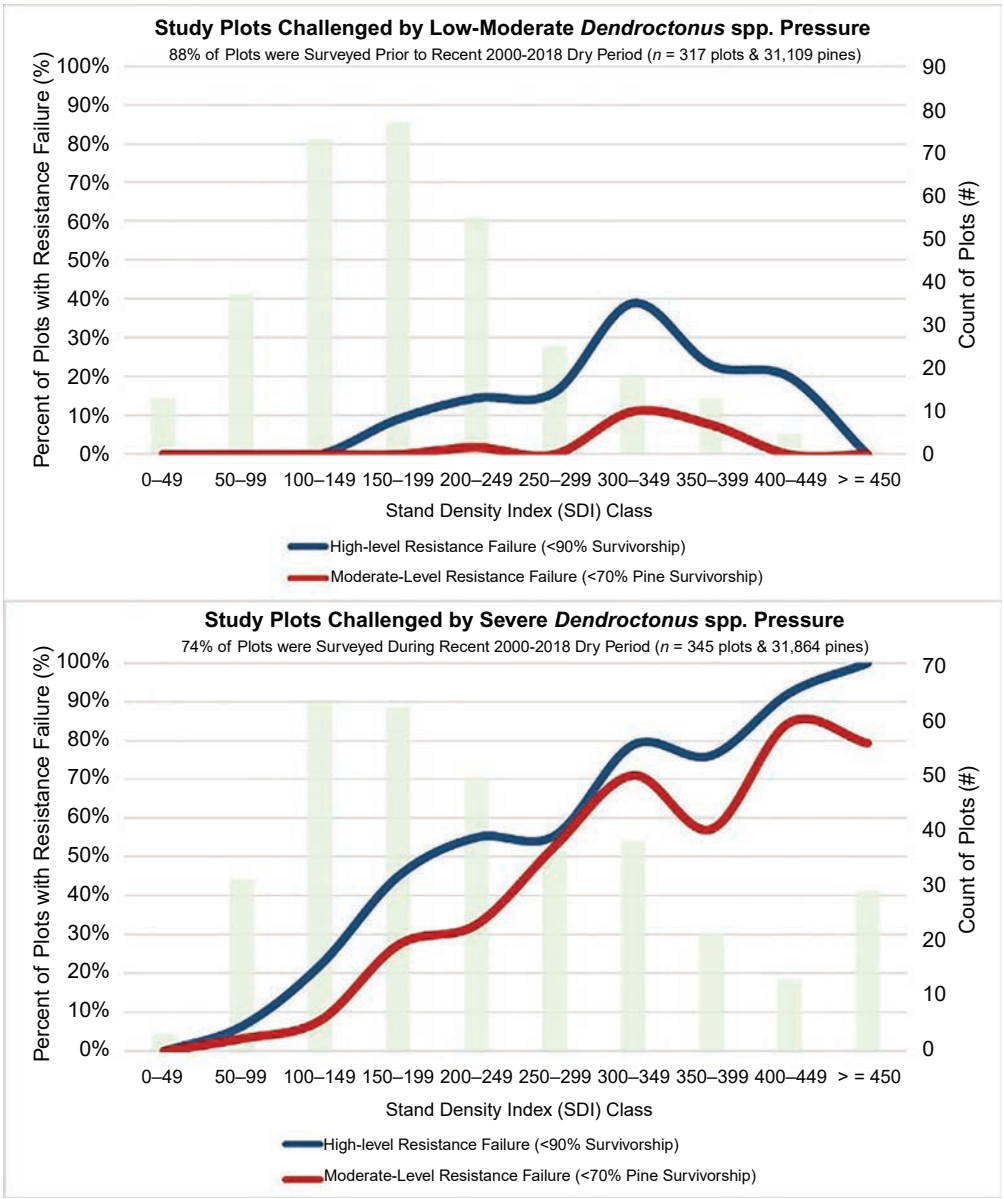


**FIG. 10** Distribution of resistance failures by stand density index class for yellow pine research plots in the western United States exposed to low-moderate and severe *Dendroctonus* spp. pressure (based on infestation severity in or adjacent to the research plots).

resistance to severe *Dendroctonus* spp. population pressures (Egan et al., unpublished data). Maintaining western yellow pine stands at these densities would represent a substantial change from current management prescriptions (e.g., maintenance of 200–240 SDI).

## 10 Case study 2—*Dendroctonus ponderosae* in pine forests in western North America: Climatic changes increase beetle overwintering survival and host susceptibility

*Dendroctonus ponderosae* is a major disturbance agent in conifer-dominated forests of western North America where it colonizes about 15 tree species, most notably, *P. contorta*, *P. ponderosa*, sugar pine (*Pinus lambertiana* Dougl.), limber pine (*Pinus flexilis* E. James), western white pine (*Pinus monticola* Dougl. ex D. Don), and whitebark pine (*Pinus albicaulis* Engelm.) (Negrón & Fettig, 2014). *Dendroctonus ponderosae* has a wide geographic distribution extending from northern Mexico north to central British Columbia and from the Pacific Coast east to South Dakota, Wyoming, and Nebraska, USA (Costello & Schaupp, 2011; Safranyik et al., 2010; Wood, 1982b). Host trees occur further north of this distribution; however, the latitudinal and elevational limits are determined by climatic conditions unsuitable to beetle development (Mock et al., 2007; Safranyik, Shrimpton, & Whitney, 1975). The severity of recent *D. ponderosae* outbreaks may have exceeded the range of historic variability in some areas, and recent outbreaks have occurred in areas where they were rare or previously unrecorded.

*Dendroctonus ponderosae* exhibits a preference for large-diameter (>41 cm dbh) *P. contorta* growing in densely stocked stands (Amman et al., 1977). Larger-diameter trees offer thicker phloem suitable for larval development and population increases (Amman, 1972). Trees growing in dense stands exhibit increased host tree stress because of increased competition for resources such as nutrients, water, and sun light. This compromises the defensive mechanisms of trees, particularly resin production which is the most important defensive mechanism (Waring & Pitman, 1985). Dense stands may also offer more suitable habitat for *D. ponderosae* by moderating temperatures thereby reducing mortality of *D. ponderosae* due to high subcortical temperatures during summer; by reducing the dispersion and dilution of aggregation pheromones within stands used to facilitate mass attacks; and by providing inter-tree distances that better facilitate infestation development and spread (Amman & Logan, 1998; Bartos, 1988; Bartos & Amman, 1989; Geiszler & Gara, 1978; Thistle et al., 2004; Whitehead & Russo, 2005). As a native insect and natural disturbance agent, *D. ponderosae* contributes to shaping forest structure and composition through tree mortality at multiple spatial and temporal scales (Axelson, Alfaro, & Hawkes, 2009; Dordel, Feller, & Simard, 2008; Klutsch et al., 2009). However, *D. ponderosae* outbreaks often cause substantial challenges for natural resource managers and landowners as dead trees pose safety hazards for lengthy periods (Audley et al., 2021); negate silvicultural investments; and influence recreation, wildlife

habitat, wildfires and hydrologic processes, among other factors, in a variety of ways (Negrón & Cain, 2018).

## 10.1 Management

Management of *D. ponderosae* generally has two primary objectives (1) suppression of localized populations sufficient to reduce numbers of trees killed at small-spatial (e.g., <1 ha) scales and (2) prevention to reduce the probability and severity of future infestations (Fettig et al., 2014a; Fettig, Gibson, Munson, & Negrón, 2014b). Of note, the efficacy of semiochemical-based techniques, including the use of verbenone, varies depending on *D. ponderosae* population levels and environmental conditions, among other factors (Progar, Gillette, Fettig, & Hrinkevich, 2014). Undoubtedly, the most effective suppression technique is the use of insecticides sprayed on the bole of host trees prior to beetle flight. When beetles land on these trees while seeking hosts, they are killed following contact with the insecticide (Fettig et al., 2006, 2008). The efficacy of thinning has been well documented for prevention, particularly in *P. contorta* and *P. ponderosa* forests (Fettig et al., 2014a; Whitehead & Russo, 2005). Most thinning data, however, come from small experimental plots (<2 ha), and there is still a need to evaluate the effectiveness of thinning for the prevention of *D. ponderosae* infestations at larger spatial scales. Thinning is likely most effective when implemented at least a few years before an infestation or outbreak occurs (Fettig et al., 2007); however, recent work confirms the value of thinning during *D. ponderosae* outbreaks (Negrón, Allen, Ambourn, Cook, & Marchand, 2017).

Management tactics to mitigate levels of tree mortality attributed to *D. ponderosae* will need to evolve as climate change influences the geographic distribution of *D. ponderosae* and its host trees. An important factor to consider is how stand susceptibility may change over time. Currently, a variety of simple models are available to assess the probability of *D. ponderosae* infestations and the extent of tree mortality that can result. These models vary in accuracy and reliability (Bentz, Amman, & Logan, 1993), but the purpose is to offer general guidelines to natural resource managers to identify areas of higher susceptibility when *D. ponderosae* populations increase and to prioritize these areas for management. There is a need to revisit these models (see related example in Section 9 for yellow pine forests). Some stands are thinned specifically for *D. ponderosae* prevention. More often, however, contemporary forest management, particularly at lower elevations (<1981 m), focuses on returning forests to more historical conditions using thinning and prescribed burning to reduce the severity of wildfires (Stephens et al., 2012). While the associated suite of management prescriptions used will reduce overall stand density, prescriptions also often call for leaving clumps of trees (Tinkham et al., 2017). These clumps, characterized by a complex matrix of tree groups of varying numbers of trees interspersed with gaps of no or few trees, emulate historical conditions and are thought to promote resilience. However, clumps may increase the overall risk of infestation by *D. ponderosae* as host trees within clumps experience higher levels of competition (Negrón, 2020). Despite recent evidence to the contrary from mixed-conifer forests in California (Knapp et al.,

2021), this concern warrants further investigation in other forests where *D. ponderosae* is an important disturbance agent.

One of the most significant changes in bark beetle management will be prioritization of where to focus tools and tactics. For example, tree populations at the margins of elevational and latitudinal constraints are likely to experience increased stress making host trees more susceptible to *D. ponderosae*. The use of semiochemicals may prove to be particularly useful in these locations. However, the use of verbenone for tree protection could be affected by climate change as the release of verbenone from commercial devices is temperature driven (Progar et al., 2014). Today, one application of verbenone per year is sufficient to protect *P. contorta* from colonization by *D. ponderosae* each year, but this may not be the case with continued warming. Additionally, with warming *D. ponderosae* may increase the length of its flight activity period. The combination of these events could result in having to reapply verbenone a second time each year. Further, a key factor in effective sanitation is the prompt identification and removal of recently infested trees, and a longer flight period would increase surveillance needs. Relatedly, warming and increases in solar radiation may reduce the duration that insecticides remain effective on tree boles (Zhong, Hastings, Hain, & Monahan, 1995) increasing application frequencies.

Climate change is likely to increase host tree stress and to compromise host tree defensive systems. Overall, this may lead to forest conditions that are more suitable for *D. ponderosae*. However, in some areas (e.g., higher elevations) tree growth may be enhanced because of climate change resulting in higher tree vigor (i.e., assuming stand density is appropriately managed over time). Research on how management tactics may need modification, in conjunction with improving our knowledge of the effects of climate change on *D. ponderosae* and its host trees, is required to improve the efficacy of current and evolving management tactics for *D. ponderosae*.

## 11 Case study 3—*Dendroctonus rufipennis* in spruce forests in western North America: Climatic changes increase beetle voltinism and host susceptibility

*Dendroctonus rufipennis* is the most important forest insect causing mortality of mature spruce in western North America. Outbreaks have occurred from Alaska to Arizona, USA, however the beetle's range extends east through all Canadian Provinces into the northeastern USA. Although *D. rufipennis* will colonize all species of spruce (Holsten, Thier, Munson, & Gibson, 1999), preferred hosts include white spruce (*Picea glauca* [Moench] Voss), Lutz spruce (*Picea X lutzii* Little), Sitka spruce (*Picea sitchensis* [Bong.] Carr.), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). Blue spruce (*Picea pungens* Engelm.) is occasionally colonized, but usually only during infestations precipitated in *Pi. engelmannii* where most *Pi. pungens* survive. Recently, Ott, Fettig, Munson, Runyon, and Ross (2021) identified physical and chemical characteristics that render *Pi. pungens* less

susceptible to colonization than *Pi. engelmannii* in stands where the two species are sympatric.

Maroja, Bogdanowicz, Wallin, Raffa, and Harrison (2007) utilized mtDNA and microsatellite data to examine the genetic structure of *D. rufipennis* populations throughout their range to reconstruct *D. rufipennis* phylogenies. The beetle is differentiated into three genetically distinct groups that have likely been isolated since the early-to-mid Pleistocene. The two northern groups colonize *Pi. glauca, Pi. lutzii,* and *Pi. sitchensis* from Alaska to Newfoundland, Canada. A second group infests *Pi. engelmannii* in the Rocky Mountains, whereas the third group is further subdivided into two groups with populations in Utah and Arizona, USA, being distinct from populations in British Columbia, Canada, and Colorado, Montana, and Washington, USA.

Outbreaks of *D. rufipennis* have occurred sporadically throughout time, but recent outbreaks have increased in extent and severity (Berg, Henry, Fastie, DeVolder, & Matsuoka, 2006; DeRose & Long, 2012; DeRose, Long, & Ramsey, 2011; Dymerski, Anhold, & Munson, 2001; O'Connor, Lynch, Falk, & Swetnam, 2015; U.S. Department of Agriculture, Forest Service, 2016a) (Fig. 11). Hebertson and Jenkins (2008) found that outbreak initiations in a given area occurred once every 19 years in Utah and Wyoming. However, they also noted *D. rufipennis* outbreaks in Utah experienced a return interval of ~73 years in some locations. Outbreaks in British Columbia and northwest Colorado occur about every 100 years (Veblen et al., 1994; Zhang, Alfaro, & Hebda, 1999), and about every 40–60 years in the Colorado Front Range (Hart, Veblen, Eisenhart, Jarvis, & Kulakowski, 2014). Data obtained from USDA Forest Service aerial detection surveys (U.S. Department of Agriculture, Forest Service, 2019) indicate the most severe and extensive outbreaks occurred in Alaska, Colorado, and Utah during 1997–2019. Recent outbreaks in Utah resulted in loss of >90% of large (>41 cm dbh) spruce in some stands (DeRose & Long, 2007; Dymerski et al., 2001).

Like other bark beetles, populations of *D. rufipennis* are influenced by interactions of endogenous and exogenous factors (Raffa et al., 2008). Exogenous factors include random

**FIG. 11** A *Dendroctonus rufipennis* outbreak in *Picea engelmannii* forests in Utah, United States. Warming and droughts have been implicated as important inciting factors. *Photo credit: S. Munson, Forest Health Protection, USDA Forest Service.*

and nonrandom events such as windthrow, wildfire, and seasonal weather patterns (Kärvemo, 2010). Endogenous factors include the availability of susceptible hosts, habitat suitability, inter- and intraspecific competition, beneficial and antagonistic associates, and natural enemies. Historically, *D. rufipennis* completed its life cycle in two years throughout most of its range. On warmer sites at lower elevations, the life cycle could take one year and up to three years on colder sites at higher elevations (Schmid & Frye, 1977). In a 2-year life cycle, adult emergence generally occurs in early summer soon after temperatures become suitable for flight (Dyer, 1973; Holsten & Hard, 2001; Safranyik & Linton, 1987).

In more recent years, warming and prolonged periods of drought have been implicated in the extent and severity of *D. rufipennis* outbreaks (Sherriff et al., 2011). In the subalpine zone of the Rocky Mountains, climate change is predicted to result in an increase in the frequency and severity of *D. rufipennis* outbreaks (Bentz et al., 2010; Foster, Shuman, Shugart, & Negrón, 2018). Modeling results show that *D. rufipennis* infestations acted to facilitate competition with invading lower-elevation tree species (Foster et al., 2018), resulting in an increase in the biomass of other tree species at the expense of *Pi. engelmannii*, likely influencing the distribution of future outbreaks. Temperature directly affects many *D. rufipennis* life-history traits that influence population success including diapause, cold hardening, and development time (Bentz & Jönsson, 2015). Under warm conditions, life cycles are enhanced, and beetles may develop to pupal and adult stages by fall of the year that egg laying occurs (Dyer, 1970; Dyer & Hall, 1977). Overwintering survival is also enhanced by warming (Miller & Werner, 1987). However, contrary to the positive direct effects of warming on *D. rufipennis* populations, Hart, Veblen, Schneider, and Molotch (2017) showed that recent outbreaks in Colorado were incited by drought.

## 11.1 Management

Several suppression techniques are available to limit the negative impacts of *D. rufipennis* on forests (Bentz & Munson, 2000), but efficacy is generally limited to small spatial scales. Sanitation has been employed at multiple scales with varying successes ( Jenkins, Hebertson, & Munson, 2014), and insecticides are commonly used to protect individual spruce in recreation sites, administrative sites or near homes and cabins (Fettig, Grosman, & Munson, 2013). MCH and other inhibitors have been evaluated for tree protection with mixed results (Seybold et al., 2018). In response to recent outbreaks, Hansen et al. (2017) examined a combination MCH and AKB (linalool, β-caryophyllene and leaf alcohols) as a repellent for *D. rufipennis*. MCH and AKB were quite effective for protecting individual trees in all studies except in Alaska and warrants further examination.

Prevention offers the best alternative for reducing the long-term susceptibility of forests to *D. rufipennis* by creating mosaics of stand structures, tree ages, and tree species compositions (DeRose & Long, 2010). In Alaska, Holsten et al. (1999) indicated thinned stands maintained higher tree vigor reducing susceptibility to *D. rufipennis*. Based on studies compiled by Schmid and Frye (1977), Alexander (1987) recommended thinning to reduce spruce composition to <65%, to remove larger diameter spruce resulting in

residual spruce averaging ~30 cm dbh, and to maintain basal area to ~18 $m^2$/hectare in the central and southern Rocky Mountains. Thinning also promotes tree regeneration creating the structural and tree age class diversity necessary to perpetuate spruce. A retrospective assessment of thinning by Hansen, Negrón, Munson, and Anhold (2010) found that treated stands had fewer infested trees and less infested basal area than untreated stands, and lower proportions of infested trees and infested basal area. Most of this difference, however, occurred in smaller-diameter trees (8–28 cm dbh) with little difference in larger-diameter trees. Table 3 provides an example of a postharvest diameter class distribution in *Pi. engelmannii* where a full range of diameter classes is the objective for an uneven-aged prescription.

## 12 Case study 4—*Dendroctonus frontalis* in pine forests in the eastern United States: A native bark beetle goes invasive

*D. frontalis* has an extensive range but exerts its most notable impacts in the southern USA where enormous economic and ecological losses can occur (Clarke & Nowak, 2010). Economic impacts have reached hundreds of millions of dollars a year and have averaged ~$43 million (USD) per year since 1960 (Pye, Holmes, Prestemon, & Wear, 2011). The last major *D. frontalis* outbreak caused ~$1 billion (USD) in damage over a four-year period (Nowak, Klepzig, Coyle, Carothers, & Gandhi, 2015). *D. frontalis* has a wide host range inclusive of all southern yellow pines, and pitch pine (*Pinus rigida* Mill.) and eastern white pine (*Pinus strobus* L.). In the southern USA, loblolly pine (*Pinus taeda* L.) and shortleaf pine (*Pinus echinata* Mill.) are preferred hosts (Clarke & Nowak, 2010). Unlike bark beetle species in western North America and Europe, *D. frontalis* outbreaks have been less frequent and severe in recent decades in the southern USA (Asaro, Nowak, & Elledge, 2017). However, there have been notable outbreaks in Central America (Gomez, Sathyapala, & Hulcr, 2020) and in the northeastern USA (Dodds et al., 2018; Lombardo, Weed, Aoki, Sullivan, & Ayres, 2018), the latter which led to the hypothesis that *D. frontalis* is expanding its range northward due to climate change (Dodds et al., 2018; Lombardo et al., 2018). In the past decade, extensive mortality of *P. rigida* occurred on Long Island, New York, USA, an

**Table 3** An example of an uneven-aged stand structure resistant to mortality from *Dendroctonus rufipennis* in *Picea engelmannii* forests in the western United States.

| Dbh class (cm)[a] | Trees/ha | Basal area ($m^2$/ha) | Stand density index |
|---|---|---|---|
| 5 | 473 | 0.9 | 15 |
| 15.2 | 127 | 5.6 | 50 |
| 25.4 | 144 | 7.4 | 60 |
| 35.5 | 84 | 8.3 | 60 |
| 47.7 | 48 | 3.3 | 50 |
| Total | 876 | 25.5 | 235 |

[a] Mid-point of 10-cm dbh (diameter at 1.37 m in height) class.

area considered to be beyond the native range of *D. frontalis* (Clarke & Nowak, 2010). Tree mortality has also been recorded in several small areas in Connecticut, USA, and trapping surveys have detected *D. frontalis* farther north than the species had been documented (Connecticut, Massachusetts and Rhode Island, USA) (Dodds et al., 2018).

## 12.1 Management

In the southern USA, where *D. frontalis* has long been recognized as an important forest insect pest, there is a well-coordinated state and federal integrated pest management (IPM) program in place (Clarke, 2001; Nowak, Asaro, Klepzig, & Billings, 2008). This includes a pheromone-based trapping program implemented in spring to identify areas with rising *D. frontalis* populations, aerial surveys to detect spots, suppression measures to limit levels of tree mortality attributed to *D. frontalis*, and prevention efforts to mitigate future impacts (Clarke, 2001; Nowak et al., 2008). *D. frontalis* relies on an intricate and well-developed pheromone communication system to initiate and grow infestations known as spots. Suppression of spots is based on disrupting pheromone communication (Clarke, 2001; Nowak, Meeker, Coyle, Steiner, & Brownie, 2015), and common tactics include cut-and-leave (Fig. 12) and cut-and-remove.

Prevention tactics consist mainly of planting the appropriate pine species to the site based on climatic and edaphic factors (especially longleaf pine (*Pinus palustris* Mill.) where appropriate, which is less susceptible to colonization by *D. frontalis* than other southern yellow pines), thinning at the appropriate time and prescription (~18.4 $m^2$/hectare of basal

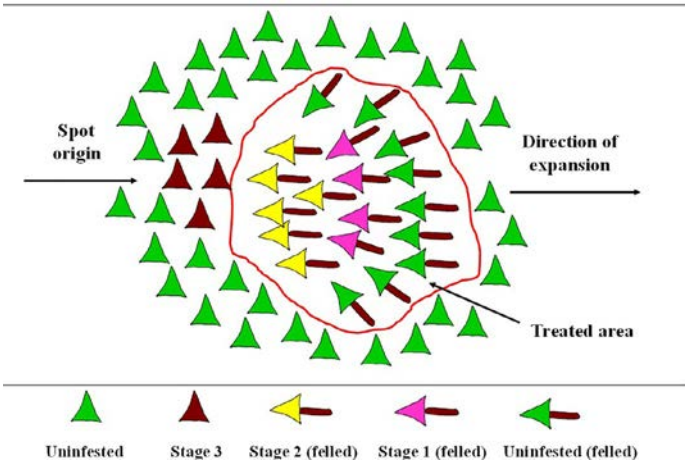


**FIG. 12** Cut-and-leave is a sanitation method used for suppression of *Dendroctonus frontalis* spots in the southern United States. Felling currently infested trees (stages 1 and 2) and a buffer strip of uninfested trees at the head of the spot will halt spot growth under most circumstances. Stage 3 trees were killed by earlier generations of *D. frontalis*. Unlike many bark beetle species in western North America and Europe, *D. frontalis* outbreaks have been less severe in recent years in the southern United States (Asaro et al., 2017); however, the beetle has expanded its range in the northeastern United States.

area) and maintaining an open stand structure in the understory and midstory. These techniques have multiple benefits including increased stand value, improved wildlife and pollinator habitat, and increased stand resilience, including to variations in climatic conditions. The Southern Pine Beetle Prevention Program (U.S. Department of Agriculture, Forest Service, 2016b) provides a comprehensive and integrated approach for preventing and reducing the impacts of *D. frontalis* on federal, state, and private forests. This strategy was developed at the request of the USA Congress, and to date nearly 607,000 hectares have been treated and >15,000 landowners have participated in state run cost-share programs (Fig. 13). A logger incentive program was developed to help facilitate treatment of small tracts of land and to help maintain the rural-based logging industry. Since the Southern Pine Beetle Prevention Program started in 2003, there has not been a multi-year, multi-state *D. frontalis* outbreak, which has allowed this program to focus on prevention instead of suppression. The Southern Pine Beetle Prevention Program serves as a model of success for managing bark beetle impacts under altered forest and climatic conditions. Elements of its structure could easily be adapted for management of other bark beetles in North America and Europe.

Thinning pine stands has been shown to prevent *D. frontalis* spot initiation and growth (Nebeker & Hodges, 1983; Nowak, Meeker, et al., 2015). It has long been understood that pines in forests with low basal area produce more resin, a tree defensive mechanism that


**FIG. 13** The Southern Pine Beetle Prevention Program, managed by the USDA Forest Service, represents a comprehensive and integrated approach for managing *Dendroctonus frontalis* on federal, state, and private forests in the southern United States. To date, nearly 607,000 hectares have been treated under this program, and >15,000 landowners have participated in state run cost-share programs. The Southern Pine Beetle Prevention Program serves as a model of success for managing bark beetle impacts in North America. *Photo credit: J. Nowak, Forest Health Protection, USDA Forest Service.*

thwarts attacking *D. frontalis*. Several studies have demonstrated a relationship between increased oleoresin production and reduced tree susceptibility to *D. frontalis* (Hodges, Elam, Watson, & Nebeker, 1979; Hodges & Lorio, 1975; Lorio, 1986; Nebeker & Hodges, 1983). Increases in tree spacing due to thinning have also been shown to reduce stand susceptibility. Gara and Coster (1968) demonstrated that the likelihood of an adjacent tree being colonized by emerging *D. frontalis* significantly decreased as inter-tree spacing exceeded ~6 m.

There is concern that due to climate change *D. frontalis* populations will extend further into the northern USA than recently observed. In anticipation of this range expansion, relevant state forestry agencies should consider developing IPM programs now for future use. In the northeastern USA, an IPM system is being developed (Dodds et al., 2018), but there are hurdles to successful implementation. For example, effective suppression and prevention depends on suitable markets for sale of harvested trees to be financially practical. In the northeastern USA, few markets exist for this material. Furthermore, there is a lack of institutional knowledge among natural resource managers in the northeastern USA concerning the survey, detection, prevention, and suppression of *D. frontalis*; a condition likely to become more common in other regions as other bark beetle species expand their ranges. Two positives do exist, however. First, the Southern Pine Beetle Prevention Program represents a well-developed and successful model for addressing *D. frontalis*. Second, standard prescriptions for managing *P. rigida* ecosystems in the northeastern USA overlap with prescriptions for prevention of *D. frontalis* infestations (Nowak, Meeker, et al., 2015). In the end, developing markets for pine timber and biomass and persuading the public about the benefits of effective IPM for *D. frontalis* will help address the unique challenges of managing this notable forest insect pest in its expanded range.

## 13 Case study 5—*Ips acuminatus* in *Pinus sylvestris* forests in central Europe: Climatic changes increase host susceptibility and create a "new" forest insect pest

*Pinus sylvestris* is one of the most widespread tree species in the world (Nikolov & Helmisaari, 1992) and ranges from Spain and Turkey north to Norway and east to Siberia, Russia. The species has also been introduced to North America and New Zealand (Meason & Mason, 2014). In central Europe, *P. sylvestris* covers almost 60% of the total forest area and hosts large numbers of organisms. Among them, bark beetles and other cambiophagous species play important ecological roles.

One of the primary bark beetle species that colonizes *P. sylvestris* is *I. acuminatus*, which is widespread throughout almost all of Europe except in Portugal. On the Scandinavian Peninsula, *I. acuminatus* crosses the Arctic Circle. In Asia, it occurs in Siberia, Kazakhstan, Mongolia, Japan, Korea, and the northern part of China and has also been recorded in Asia Minor and Syria (Löbl & Smetana, 2011). Colombari, Battisti, Schroeder, and Faccoli (2012) reported that *I. acuminatus* withstands temperatures down to –34°C

in winter by lowering the molecular weight of fluids in their bodies. Such adaptations mean that this thermophilic species copes well in colder climates and short-term temperature drops in winter do not pose a major threat to its survival in most locations. In central Europe, *I. acuminatus* occurs in *P. sylvestris* forests in lowland and mountainous areas, but until recently infestations were rare. As such, *I. acuminatus* was generally not considered an important forest insect pest (Bakke, 1968) until the early 21st century when outbreaks occurred in several southern and central European countries (Plewa & Mokrzycki, 2017; Siitonen, 2014) (Fig. 14). Due to drought and other factors, *I. acuminatus* is now regarded as an important forest insect pest throughout much of its range. During 2015–19, a notable increase in the economic importance of *I. acuminatus* occurred in Poland where drought was identified as the most important inciting factor. In 2015, activity was generally limited to southeastern Poland where sanitation was employed on ~230 hectares of pine forest. By 2019, tree mortality and branch dieback were observed throughout Poland. As a result, suppression was conducted on ~26,000 hectares in 2019.

The minimum air temperature at which *I. acuminatus* initiates flight ranges from ~14°C in the southeastern Alps (Colombari et al., 2012) to 18°C in France (Jamin, 1977), while relative humidity must be <50% (Vallet, 1981). Such conditions allow full development of a second generation each year, even if only a part of the population can produce a second generation. As a result, there are two main periods of tree colonization. In Poland, the first begins the first half of May and lasts until mid-June. Under favorable conditions with appropriate temperatures and little or no rainfall, the second begins the second half of July and lasts until mid-August (Plewa & Mokrzycki, 2017).

**FIG. 14** A *Pinus sylvestris* stand heavily impacted by *Ips acuminatus* in Poland. *I. acuminatus* is now regarded as an important forest insect pest throughout much of its range. *Photo credit: J. Hilszczański, Department of Forest Protection, Forest Research Institute, Poland.*

Additionally, it is likely that part of the population produces a sister generation (i.e., females complete oviposition, re-emerge, and replenish their energy reserves) (Plewa & Mokrzycki, 2017). Research conducted in the Italian Alps shows that *I. acuminatus* from sister generations in summer most often inhabit trees in the immediate vicinity of the infestation (Colombari, Schroeder, Battisti, & Faccoli, 2013).

### 13.1 Management

As with other species of bark beetles in central Europe, sanitation is the most feasible tactic for reducing localized populations of *I. acuminatus* but is expensive to implement. In addition, the overlap between *I. acuminatus* generations causes difficulties in precisely timing sanitation (Colombari et al., 2013), which should be concentrated near infestations from the previous year. Large spots account for most of the observed tree mortality, so sanitation should be focused on these areas as soon as crown discoloration appears, which can be rapid during periods of drought. This strategy will remove beetles from the spring generation prior to emergence and before they infest new host trees (Colombari et al., 2013). Faccoli, Finozzi, and Colombari (2012) found a significant correlation between the number of *I. acuminatus* caught in pheromone-baited traps and the number of damaged trees. However, recent studies on attractants for *I. acuminatus* indicate they are likely not attractive enough to ensure catches sufficient for effective population suppression by mass trapping (Sukovata, Jaworski, & Plewa, 2021).

*I. acuminatus* feed in the upper parts of trees. As such, new infestations are often difficult to detect initially. Infested trees usually show few or no symptoms in the early stages of an infestation and are hard to distinguish from healthy trees. The first signs of *I. acuminatus* infestation are often not visible until the end of June or early July when needles turn red and the bark at the infested site begins to crack or bear traces of woodpecker activity. To address some of these issues, aerial detection surveys are being deployed over Polish State Forests for initial detection of infested stands followed by the use of drones equipped with optical and multispectral cameras. Photos collected from drones allow for identification of dead and weakened trees, which are manually or automatically digitized into classes (Fig. 15) and used to locate trees for sanitation.

## 14 Case study 6—*Ips typographus* in *Picea abies* forests in central Europe: Climatic changes and the legacy of off-site plantings increase forest susceptibility

*Ips typographus* is the most important forest insect pest in Europe, and the most significant disturbance agent in *Pi. abies* forests (Grégoire, Raffa, & Lindgren, 2015) (Chapter 4). Outbreaks are usually driven by other disturbances, such as windstorms, which provide an abundance of host material that fosters rapid increases in population densities (Komonen et al., 2011), and the landscape-scale connectedness of host and beetle populations (Seidl et al.,

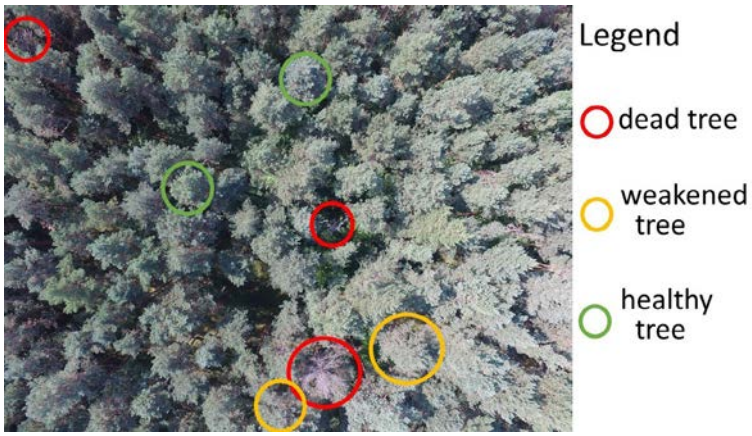


**FIG. 15** In Europe, detection of beetle-infested trees for sanitation is usually accomplished with ground-based surveys. However, in recent years, aerial detection surveys are being deployed over Polish State Forests for initial detection of stands infested by *Ips acuminatus* followed by drone surveys. *Photo credit: J. Hilszczański, Department of Forest Protection, Forest Research Institute, Poland.*

2016) (Chapters 4, and 7). Due to vast forest exploitations in the past and current wood demands, *Pi. abies* is now widely distributed outside its native range and is frequently found on unsuitable sites in central Europe where it is highly susceptible to *I. typographus*. In recent years, a notable outbreak of *I. typographus* occurred in central Europe incited by storm damage and extremely warm and dry weather (Fig. 16). In Germany alone, during 2018–20, tree losses occurred on >285,000 hectares and were estimated at 178 million $m^3$ (Bundesministerium für Ernährung und Landwirtschaft (BMEL), 2020), approximately half of which was attributable to *I. typographus* outbreaks.

Studies suggest that current and future outbreaks of *I. typographus* are exacerbated by climate change (Hari, Rakovec, Markonis, Hanel, & Kumar, 2020; Seidl et al., 2017). Increasing temperatures lead to a prolonged flight period and faster development, and eventually to an increased number of *I. typographus* generations within a year (Jacoby, Lischke, & Wermelinger, 2019). Population size grows exponentially with every additional generation (i.e., assuming similar reproductive capacities among generations). Warming and drying cause temporal drought stress to spruce trees, rendering them more susceptible to colonization by *I. typographus*. Further, under severe water stress resin production is reduced compromising host-tree defenses (Netherer et al., 2015). More frequent heat waves and droughts in Europe (Hari et al., 2020) will not only foster direct tree mortality but will also lead to an increase in large-scale *I. typographus* outbreaks. Even though most forestry agencies in central Europe now focus on converting *Pi. abies* forests to more climate-adapted tree species, such as European beech (*Fagus sylvatica* L.) (Thom, Rammer, & Seidl, 2017), *I. typographus* outbreaks are likely to impede overall progress as patches of spruce are still required for management of light conditions and establishment of other shade-tolerant tree species.

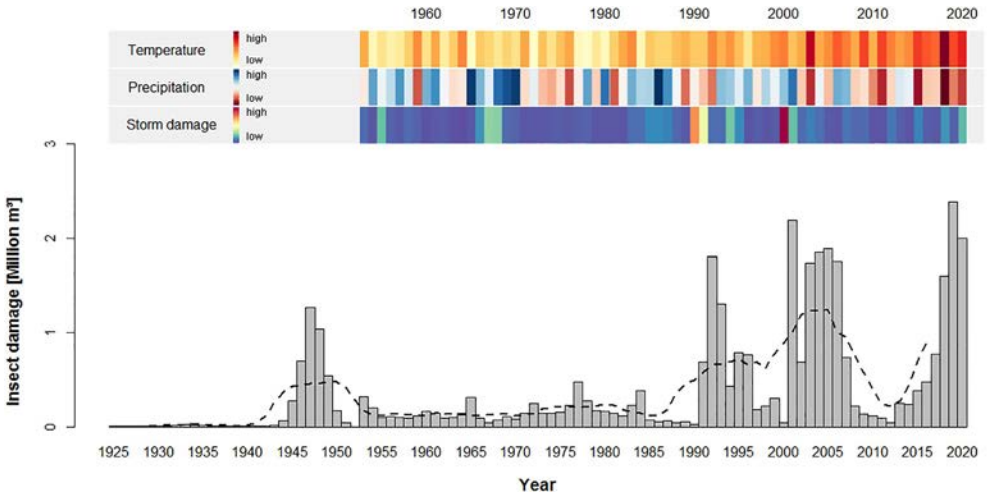


**FIG. 16** Sanitation felling across all tree species, but mostly attributed to *Ips typographus* in *Picea abies*, in Baden-Württemberg, Germany, from 1925 to 2020 (no data for 1952; *dashed line*: centered 9-year rolling average) and related climate and storm damage from 1953 to 2000. Temperature and precipitation data refer to months April–September at a reference station at 800 m elevation (data for years <1953 were not consistently available).

## 14.1 Management

In accordance with directives from the European Union, bark beetle management is based on the principles of IPM, with its main components of prevention, monitoring, and sanitation (Bentz et al., 2020). While prevention and monitoring are employed continuously, sanitation is dependent on current levels of infestation. Prevention primarily includes thinning, diversifying tree ages and tree species compositions, and limiting reforestation of spruce to suitable sites only (Dobor, Hlásny, & Zimová, 2020; Neuner et al., 2015). Ground-based surveys of susceptible stands occur on a regular basis and are conducted as frequently as every week or two in April–September depending on the level of activity. Monitoring of *I. typographus* flight and stages of development are provided by a network of pheromone-baited traps and observations on trees in the field (LWF, 2016). Phenological models based on weather data (Baier et al., 2007; Jacoby et al., 2019) support monitoring on a regional scale. The search for infested trees in fall and winter is also critical to reduce population densities through sanitation prior to the spring flight period. Furthermore, salvage logging is employed to reduce host breeding materials resulting from storm or snow breakage damage. In both cases, the material is removed and transported to sawmills and/or wet and dry storages, or is debarked, chipped, milled or burned on site as soon as possible (Fig. 17). If necessary, insecticides or fumigants may be used to treat logs stored along forest roads (FVA, 2020; Wermelinger, 2004). While the use of verbenone has been successful for bark beetle management in North America, its use for suppression of *I. typographus* in Europe is currently under investigation. Like the use of nonhost volatiles (Unelius, Schiebe, Bohman, Andersson, &

**FIG. 17** Examples of measures used to destroy brood following sanitation harvesting for *Ips typographus*, including wet storage to minimize beetle development (or to prevent colonization of uninfested logs following salvage logging (top left), chipping (top right), insecticide sprays (bottom left), and debarking (bottom right). *Photo credits: Department of Forest Health Protection, Forest Research Institute Baden-Württemberg, Germany.*

Schlyter, 2014), verbenone may prove helpful for reducing colonization of logs at storages or of windthrown trees in forests.

Once a large-scale *I. typographus* outbreak develops, such as observed in 2018–20, suppression becomes more difficult as the availability of foresters, other natural resource managers, forest labor, equipment, and other resources is limited. Further, the long-term availability of insecticides for treatment of logs is in jeopardy given regulatory and ecological concerns. As such, prevention is becoming more important, with the goal of keeping levels of tree mortality attributed to *I. typographus* as low as possible for as long as possible. Some argue this just delays the amount of tree mortality that will occur once outbreaks develop, and that many forests dominated by *Pi. abies* in central Europe are not likely to be sustained under climate change (Dobor, Hlásny, & Zimová, 2020).

Further optimization of *I. typographus* management will be crucial under climate change. Recent advances in computer and smart phone App-based recording and documentation of infested trees detected through ground-based surveys are promising. Such spatially and temporally explicit information can be sent immediately to field crews that implement sanitation. Dynamic early-warning systems are another promising field of research. For instance, automatized comparison of time-series satellite imagery (e.g., in

combination with machine-learning algorithms) can provide *I. typographus* infestation data with high spatial and temporal resolution at large spatial scales (Zhan et al., 2020). Infestation risk maps help support decisions as to when and where to focus monitoring and management (Mezei et al., 2014). Dynamic risk maps are under development (Puhlmann & Hallas, 2020), which based on daily and forecasted weather data assess infestation risk more accurately.

Climate change calls for intensified research focused on improving *I. typographus* monitoring and management. In parallel, multinational strategies are required for dealing with the consequences of recurrent, large-scale outbreaks of *I. typographus* in central Europe. This means the necessary organizational and structural components must be available to adequately address the issue, including, but not limited to, funding instruments to support private landowners, well-trained personnel, viable markets for sale of timber and other biomass produced during sanitation and salvage, and suitable forest road networks (Dobor et al., 2020). With such measures, spruce forests may persist in central Europe but will differ in structure and composition from contemporary spruce forests.

## 15 Conclusions

The world's forests are increasingly vulnerable to tree mortality because of the direct and indirect effects of climate change (Allen et al., 2015) with notable consequences not only to forest health, but to human health. There are also important feedbacks that further influence climate and land use at a global scale. In conifer-dominated forests of North America and Europe, bark beetle outbreaks will be responsible for much of the projected tree mortality. As a result, natural resource managers will be increasingly challenged to manage bark beetle populations; to maintain resilient and productive forests; and to facilitate recovery of landscapes impacted by bark beetles, other disturbances, and their interactions (Leverkus et al., 2021). As discussed, there is a wide array of tools and tactics available to reduce the severity and extent of bark beetle infestations when properly applied at appropriate spatial and temporal scales. However, under altered forest and climatic conditions the use of these tools and tactics must evolve and adapt, while applications must intensify to account for the overall increase in susceptibility of conifer-dominated forests to bark beetles. As such, prioritization of the use of tools and tactics will become increasingly important due to constraints imposed by limitations in resources, infrastructure and markets, among other factors. For example, tree populations at the lower margins of elevational and latitudinal constraints are likely to experience higher levels of mortality, and thus these areas likely justify increased surveillance and management.

The use of some tools and tactics will continue with only slight modifications to account for changing conditions. Perhaps the best example of this is the need to thin to lower stand densities in some contemporary forests than previously considered to maintain adequate levels of resistance to bark beetles (e.g., as demonstrated in

Section 9 for yellow pine forests in the western USA). In other cases, efforts will be required to convert highly susceptible forests to less-susceptible forests of more climate-adapted tree species, while still providing the goods and services that society expects from these forests (e.g., as mentioned in Section 14 for *Pi. abies* forests in central Europe). The impacts of many bark beetle species are expected to increase due to altered forest and climatic conditions, but some may decrease while others (e.g., as demonstrated for *D. frontalis* in Section 12) may decrease in some areas yet become invasive in other areas. Relatedly, numerous efforts are underway in North America and Europe to refine and develop tools and tactics for notable bark beetles, and for species that are increasing in pest status due to altered forest and climatic conditions (e.g., as demonstrated for *I. acuminatus* in Section 13). In all cases, proper implementation demands knowledge of the effects of climatic and other changes on forests, and of the institutional, social, and environmental factors that influence adaptive capacity (Cottrell et al., 2020). Furthermore, we must build stronger relationships among stakeholders, communities, and agencies; train and retain sufficient numbers of professionals to execute the necessary work; and develop communication platforms that increase awareness of the issue and support for related management efforts.

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