



RESEARCH ARTICLE

Bark Beetle Outbreaks: Economic, Ecological Impacts, and Allelochemicals in ManagementMuhammad Zubair Ashraf¹, Kanakachari Mogilicherla^{2*}¹Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Czech Republic²ICAR-Indian Institute of Rice Research (IIRR), Rajendra Nagar, Hyderabad, Telangana, India**ARTICLE INFO****ABSTRACT**

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Tree-killing bark beetles (Coleoptera: Curculionidae: Scolytinae) are highly devastating insect pests of coniferous trees worldwide. Global warming, drought stress, and poor management of forests favor beetle infestation. Climate change has enhanced the magnitude of bark beetle attacks, causing tree mortality and economic loss. Phloem-feeding beetle genera i.e. *Dendroctonus*, and *Ips* have an overwhelming impact on coniferous forests and recently beetle infestation and outbreak escalated. Synthetic pesticides play an important role in protection but cause environmental effects. Thus, there is a dire need for alternative integrated insect pest management methods. Plant secondary metabolites referred to as allelochemicals are biological compounds naturally produced in conifers resin ducts. Coniferous Allelochemicals are the first line of chemical defense against tree-killing bark beetles. Alkaloids, terpenoids, and phenols are the most compelling compounds of secondary metabolites of conifers. In this review, we described the plant-based allelochemicals and their role in pest management of tree-killing beetles. Conifer allelochemicals protect trees by deterring infestation, inhibiting feeding, and poisoning, and by alluring beetles through traps and influencing beetle behavior and physiology. Allelochemicals offer environmentally friendly, sustainable control of insect pests. In this study, we conclude that allelochemicals provide various promising opportunities for novel and ecologically friendly solutions for the control of tree-killing bark beetles.

INTRODUCTION

The bark beetle is an important biotic factor that significantly alters forest dynamics. Beetles inhabit forests globally (Hulcr et al., 2015), outbreaks of beetles cause tree mortality and due to global climate change bark beetles are expanding their range, elevational distribution, and changing host preferences (Raffa et al., 2015). The structure of the forest ecosystem and its functioning has been disturbed by bark beetle strongly, also affecting species composition, disturbance regimes like wildlife, carbon sink, nutrient cycle, and ecosystem hydrology (Morris et al., 2017). Bark beetle disturbance can have, hence, significant consequences for the preservation of ecosystem services in the future (Hlásny et al., 2019). Scientists have acclaimed the bark beetle outbreak as a significant factor for forest ecosystems worldwide considering the influence of global climate change. These beetles play a crucial part in forest ecosystem processes like surface albedo, carbon water fluxes, and global climate change.

In this review, we focused on the bark beetle species that damaged the coniferous forests and their economic and ecological effects. We explained bark beetle biology, the life cycle, and the effect of climate change on beetles. Then we present the mechanism of host allelochemicals and their role in deterrence and toxicity to beetle.

Bark beetle biology

The bark Beetles are smaller cylindrical insects, taxonomically classified in the Scolytinae (Latreille,1804) subfamily, Curculionidae family, and Coleoptera (Linnaeus,1758) order. 6000 beetle species are identified in the Scolytinae subfamily and less than 1 % can colonize and cause healthy tree mortality (Hulcr et al., 2015). Coniferous tree-killing bark beetles can cause important economic and environmental impacts (Morris et al., 2017). In this review, we mainly focused on North American and European coniferous forest species of *Dendroctonus*, *Tomicus*, and *Ips* genera.

Bark beetles all their life besides the dispersal phase during the adult stage, spend their lives breeding, and feeding gallery chambers inside plant bark tissues (Raffa et al., 2015) also few species overwinter in forest tree debris (Schebeck et al., 2017). The bark beetle life cycle consists of host tree selection for colonization and reproduction, development through all the larval instars, pupate, and dispersal after maturation (Sauvard, 2004). Still, there are variations among species of tree-killing bark beetles such as reproductive strategies, for example, monogamous or polygamous, number of generations each year, and host selection. It affects the host tree colonization, dispersal, and potential population outbreak.

After the selection of a susceptible host beetle attacks and colonizes the tree for production, the beetle bores through phloem and excavates galleries to select the mating partners. In *Dendroctonus* genera and *Tomicus* which is a monogamous species, females are the pioneers while in the genus *Ips* polygamous males are the ones who initiate galleries (Lieutier et al., 2015; Six and Bracewell 2015 (Cognato, 2015). Pioneer beetles produce aggregation pheromones to attract the mating partner on a new host (Blomquist et al., 2010). Female beetles oviposit eggs in galleries to produce brood. Through mass attack species such as *Dendroctonus rufipennis*, *D. ponderosae*, and *I. typographus* overwhelm the defense of the host tree (Blomquist et al., 2010). The mass attack counts on factors like the density of the beetle, host tree defensive metabolites, and the health of individual host trees (Boone et al., 2011).

Bark beetles along with associated symbiotic microorganisms (fungi) is capable of causing tree mortality, which also helps in the detoxification of tree secondary metabolites (Chiu et al., 2019). Antiaggression pheromones are released to deter further infestation after successful colonization of the host tree to decrease conspecific competition (Wood, 1982). Depending on tree size, the nutritional quality of the host, and bark beetle species infestation, the host tree is typically available for up to two generations of beetle per year (Raffa et al., 2016). Larvae excavate perpendicular galleries to maternal chambers and start eating phloem along with blue fungi. After pupation, individuals bore in phloem i.e. in *Ips sexdentatus* or in *Tomicus piniperda* which bore in outer bark (Lieutier et al., 2015). The maturation period required in beetles before they start reproduction and dispersal in *Ips* and *Dendroctonus* takes place in the natal host (Six and Bracewell, 2015), after maturation beetles disperse to select a new susceptible host tree. However, the *Tomicus* species starts feeding on the same host twigs and shoots. Dispersal of bark trees and selection of hosts are influenced by biotic and abiotic factors like beetle fitness, temperature, tree density, and wind (Kautz et al., 2016; Jones et al., 2019). Usually, dispersal happens from a few hundred meters to a few kilometers (Doležal et al., 2016). However, beetles do cover long-distance distances when flight is assisted by wind currents. *D. ponderosae* has been documented more than 24 km from the natal host tree (Evenden et al., 2014) furthermore *I. edentates* and *I. typographus* can fly above 40 km distance (Nilssen, 1984, Jactel and Gaillard, 1991).

Host selection

The Bark beetles widespread infestations and colonization are complex and supported by climate change, and extreme draughts which lead to devastating effects on coniferous forests (Seidl and Rammer, 2017). Host tree response under stress and drought is varied across species. Fallen, stress trees provide breeding material for tree-killing bark beetles to transition from endemic to pandemic situation (Hroššo et al., 2020). Fully grown adult beetles locate a suitable host, bore, mate, and lay eggs in galleries under the bark. Larvae and adult beetles feed to maturity on tree phloem. Brood adults emerge and migrate to find new hosts (Raffa et al., 2015). Successful beetle infestation results in tree mortality. Hundreds of beetles attack

simultaneously to colonize trees and block nutrient transport. Single species of tree-killing beetle can breed on one tree and can breed up to 3 generations before tree bark gets exhausted (Krokene, 2015). Bark beetles attack hosts in intermittent events followed by a non-outbreak phase where they reproduce. In the endemic phase, the beetle population is controlled by host tree defensive chemicals and weather and natural enemies. Due to favorable conditions beetles surpass threshold level and overwhelm the stressed tree defense through an aggression mechanism (willian et al., 2004).

Bark beetle and climate change

Bark beetle outbreaks are facilitated by droughts and wind to some extent (Negrón and Huckaby, 2020). Contemporary, bark beetle outbreaks in North America and Europe are changed than previously observed, suggesting the role of climate change and its role in new infestation patterns (Fettig et al., 2022). Beetle outbreaks are more grave and frequent, and the length of beetle attacks is longer than past (Hlásny et al., 2021). Warmer temperature enhances beetles' generations per year, expanding their dispersal beyond the historical typical range with the risk of becoming an invasive species i.e. *D. ponderosae* (Cudmore et al., 2010). Phloem eating beetle species are colonizing formerly noninfested coniferous species, indicating their expansions in host preferences (Raffa et al., 2013).

Economic impact

Over the past two decades, a huge number of conifer species spanning millions of hectares (ha) in Canada and Mexico have been infested, colonized, and killed by bark beetles (Fettig et al., 2022). 36 million hectares of coniferous forest land have been affected by tree-killing bark beetle in the western USA, belonging to *Ips* and *Dendroctonus* genera (USDA, 2020). US\$2 billion annually loss is experienced by the USA due to timber loss due to tree-killing bark beetle infestation. An outbreak of *D. ponderosae* caused the mortality of 14 million ha *Pinus contorta* in British Columbia and converted it to a carbon source from a carbon sink (Woods et al., 2010). Bark Beetles from *Ips* and *Tomicus* genera are the main drivers of tree infestation and outbreaks of beetle which caused recent tree mortality across Europe. *Ips typographus* is the most aggressive species among all tree-killing beetles which affected the spruce forest in Europe in the last decade (Patacca et al., 2023). Between 2017-2019 in the Czech Republic *I. typographus* beetles killed greater than 23 million m³ of spruce forest (Hlásny et al., 2021). 260 million USD worth of economic loss was experienced in the Czech Republic during the year 2018-2019 due to the *Ips typographus* outbreak (Gandhi et al., 2022).

Allelochemicals and Their Role in Insect-Plant Interaction

Insect pests interact and damage plants around the globe which leads to the development of complex defensive systems including chemical mechanisms. This evolution of plants determines insect population diversity. Secondary metabolites play a crucial role in defense mechanisms and Insect-plant interactions are called allelochemicals (Ibanez et al., 2012). Plants counter herbivore attacks through induced defense response. Plants produce defensive metabolites that protect against insect attacks (Yan et al., 2014). Phytoanticipins (stored) and phytoalexins (active) are two metabolites that form in plants. They protect the tree by inhibiting or intoxicating the insects and cause negative effects on the digestion of herbivores. Insects and plants are in continuous interaction. Plants provide food and shelter to insects and in return, they lay eggs and help with pollination (Newman, 2014). Plants evolved multiple resistances to overcome insect pest damage (Schoonhoven et al., 1998). Constitutive and induced defense mechanisms consist of morphological attributes and secondary plant metabolites to protect plants against insects. Anti-feeding compounds are plant secondary metabolites that inhibit insect feeding (Block et al., 2019). Metabolites are divided into subgroups like alkaloids, glucosinolates, cyanogenic glycosides, terpenoids, and phenolics (Polumackanycz et al., 2020). The main groups of allelochemicals are Allomones, Repellents, Suppressants, Deterrents and Toxins. Their main role is to suppress inhibiting, prevent feeding and ovipositing, and produce chronic or acute toxic effects to insect pests. The production of secondary phenolic metabolites varies significantly among tree species, tree parts, ages, and regions (Mbata and Payton, 2013).

Conifers produce a wide range of allelochemicals that can inhibit the growth or development of other plants and organisms, playing a key role in plant interactions by affecting competition, herbivory, and mutual relationships, with their method of allelochemical production being particularly intricate (Despland et al., 2016).

In coniferous species, tree defense against beetles depends on terpenoids with polyphenols which are produced in resin ducts of the plant xylem (Copolovici et al., 2012). These secondary metabolites are evenly distributed in the roots, shoots, and needles of conifers. Terpenoids comprise different groups e.g., monoterpenoids, sesquiterpenoids, diterpenoids, and triterpenoids. Terpenes protect plants against insect pests indirectly by increasing and luring natural enemies of beetles. They released a blend of volatiles that attract beneficial insects including predators and parasitoids of beetles (Bond et al., 2004). A few Monoterpenoids e.g. D-limonene, pulegone, and myrcene used as the primary ingredients of essential oils which are used against many insects. The toxicity of 10 predominant monoterpenes of *P. contorta* against the bark beetle mountain pine beetle suggested that carene, myrcene, terpinolene, enantiomers of α -pinene, β -pinene, and limonene triggered beetle mortality (Tao et al., 2003). Some plant oils are neurotoxic when beetles feed on them. The most noticeable symptoms include hyperactivity, and hyper-excitation, followed by brisk knockdown and paralysis (Singh et al., 1988).

Due to the attractant behavior of few monoterpenes, I can potent synergist along with pheromones of *Dendroctonus* species which is not influenced by host orders solely. Turpentine can be used in baited traps for *D. frontalis* to increase the catch along with its attractive pheromone (Billings, 1985, Sullivan, 2016). Combinations of monoterpenes result in up to 30 times increase in catches of *D. ponderosae* contrasted to pheromone alone (Borden et al., 2008).

Scots pine shows different concentrations of phenolic compounds in its dried bark, needles, and heartwood are 76.0, 17.5, and 1.1 mg/g, respectively, while wood samples have tannic acid equivalent concentrations ranging from 6.7 to 13.6 mg/g (Kahkonen et al., 1999, Venalainen et al., 2004). Norway spruce's knot wood can have phenolic concentrations ranging from 10-15% to 30% by dry weight (Willfor et al., 2003). Terpenes, which impart the distinctive scent of conifers and can adversely affect plants and insects due to their volatility, and non-volatile phenolics, which inhibit the growth of neighboring plants by disrupting their metabolic processes, are both crucial in plant interactions. Conifer resins, containing toxic substances that deter pests like bark beetles and affect their feeding, development, and reproduction, serve as a defense mechanism that helps minimize damage to conifer foliage and bark (De Silva et al., 2015). The current review is investigating the potential use of conifer allelochemicals for natural pest control in forest management.

Verbenone, is a monoterpene ketone with two enantiomeric forms: (-)-*S*- and (+)-*R*-verbenone. It was initially discovered as an oxidation product in coniferous turpentine oil (Blumann and Zeitschel, 1913). It can be present in various coniferous bark beetle host species (Szmigielski et al., 2012).

Verbenone is produced under aerobic conditions when α -pinene (conifer resin) or verbenol are present (Ramakrishnan et al., 2022). Through autoxidation, the spontaneous conversion of verbenol happens and results in verbenone (Dvořakova et al., 2007) and its irreversible process.

Verbenone is a widely recognized bark beetle repellent which is a well-studied and established phenomenon, and stands as a prominent bark beetle aggregation inhibitor (Mafrá-Neto et al., 2022). Verbenone seems to be ubiquitous only among the Scolytinae family. Verbenone inhibitory effect against bark beetle through the baited traps in the field is positively associated with verbenone dosage (Lopez et al., 2013; Byers et al., 2018, 2020).

Table 1: Allelochemical conifer source, Application methods, and their efficacy.

Allelochemical Source	Application Mode	Localization of Compound	Insect Suppression	Reference
Monoterpenes				

α -Pinene	Natural resin, essential oils, spray fumigant, tropical application, pheromone trap	Resin ducts of bark, needles	Deterrence of bark beetle bark beetles. Inhibits feeding and development. In a pheromone trap a lure agent.	(Faccoli et al., 2005 Fang et al., 2021 Chiu et al., 2017 Moliterno et al., 2023 Mamoci et al., 2022)
β -Pinene	Natural resin, essential oils, spray fumigant, tropical application	Resin ducts of bark, needles	Deterrence of bark beetles. Inhibits feeding and development. In the pheromone trap a lure agent.	(Faccoli et al., 2005 Fang et al., 2021 Chiu et al., 2017 Moliterno et al., 2023 Mamoci et al., 2022)
Limonene	Foliar application, essential oils	Resin ducts of bark, needles	Repels beetles and inhibits feeding	(Faccoli et al., 2005 Fang et al., 2021 Chiu et al., 2017 Moliterno et al., 2023 Mamoci et al., 2022)
Myrcene	Natural resin, essential oils, spray fumigant, tropical application	Resin ducts of bark, needles	Repels bark beetles. Inhibits feeding and development. In the pheromone trap a lure agent.	(Faccoli et al., 2005 Fang et al., 2021 Chiu et al., 2017 (Moliterno et al., 2023 Mamoci et al., 2022)
Diterpenes				
Abietic Acid	Resin extraction, topical application	Resin ducts of bark, needles	inhibits feeding and development; effective against bark beetles.	(Kopper et al., 2005 Schiebe et al., 2012 Lopez et al., 2020)
Pimaric Acid	Resin extraction, topical application	Resin ducts of bark, needles	Toxic and deterrent effects on insects; reduces beetle infestations.	(Kopper et al., 2005 Schiebe et al., 2012 Lopez et al., 2020)
Sesquiterpenes				
Farnesene	Foliar application, essential oils	Resin ducts	Repellent to beetles and insects; effective in preventing beetle infestation.	(Gonzalez et al., 1995 Kendra et al., 2014 Gonzalez et al., 2014 Cheney et al., 2019)
Germacrene D	Foliar application, essential oils	Resin ducts	Inhibits feeding and development of various beetles and caterpillars.	(Gonzalez et al., 1995 Kendra et al., 2014 Gonzalez et al., 2014 Cheney et al., 2019)
Tannins				
Catechins	bait trap to lure.	Needles	Repels insects; deters feeding and reduces larval development.	(Solar et al., 2006 Keefover et al., 2016)
Resin Acids				
Resin Acid Esters	Natural resin, topical treatment	Resin ducts, spruce wood	Toxic to bark beetles; reduces infestation rates.	(Chiu et al., 2019)
Phenolic Compounds				

Flavonoids	Fumigant, spray	Tropical	Tree needles	Repels insects; inhibits feeding and larval growth.	(Pereira et al., 2024; Hammerbacher et al., 2019; Schnarr et al., 2022)
Phenolic Acids	Fumigant, spray	Tropical	Bark, wood	Acts as a repellent; reduces feeding and survival rates of insects.	(Pereira et al., 2024; Hammerbacher et al., 2019; Schnarr et al., 2022)
Cinnamic Acid	Fumigant, spray	Tropical	Bark, wood	Deterrent to various insects; reduces feeding and development. Inhibits detoxification,	(Pereira et al., 2024; Hammerbacher et al., 2019; Schnarr et al., 2022)

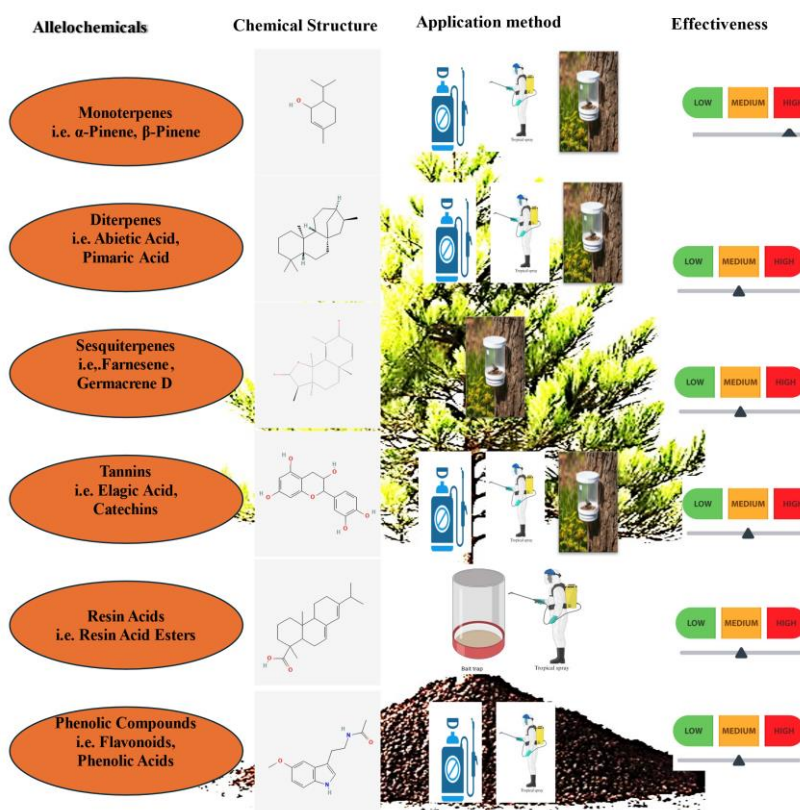


Figure 1: Allelochemicals in conifers

CONCLUSION

Current beetle infestation demands novel, effective, sustainable, and eco-friendly beetle management methodologies. The use of coniferous allelochemicals (secondary metabolites) with toxic and deterrent effects is an environmentally acceptable beetle management strategy. Devastating bark beetle attacks occurred due to stress and rise in temperature. These naturally occurring metabolites play an important role in constituting tree defense. The role and potential of many secondary metabolites of conference have not been investigated yet. Therefore, it is necessary to conduct new experiments concerning beetle inhibiting and deterring the properties of conifer allelochemicals. Additionally, adding these allelochemicals

with other Ipm strategies like biological control, using allelochemicals as synergists or habitat modification can enhance overall effectiveness in bark beetle control methodologies. Furthermore, by understanding how climate change and increase in temperature will affect the production and effectiveness of these secondary metabolites bark beetle adaptive control strategies can be developed.

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AMZ conceptualization. AMZ prepared the first draft wiring. AMZ and KM finalized the table and figure and prepared the final draft. All authors read and approved the final version of the draft.

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Data Availability Statement

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Conflicts of Interest

The authors disclose no conflicts of interest.

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