An Analysis of the Effect of Mountain Pine Beetles on North American Pine Forests Due to Climate Change

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Abstract

The mountain pine beetle, *Dendroctonus ponderosae*, are an ecologically significant organism because of the services they provide and the damage they inflict to large areas of pine forests. Before the recent change in climate, they were an essential food source for many other organisms and were essential for the health of the forest and habitat creation. Recent trends in global temperature have allowed mountain pine beetle populations to expand beyond their native range, creating many ecological disruptions like disease, changes in hydrology and water quality, impacts on wildlife, and reducing vital carbon sinks. Mitigation efforts like control burning and pesticide use can help minimize impacts of large scale outbreaks, but may not be enough to keep up with the shifting climate.
Introduction

Montane ecosystems make up a large portion of North America. These montane ecosystems play an intricate role in water ecology, biodiversity, and even the economies of areas surrounding them. As the climate begins to warm because of human activity, these ecosystems are experiencing a great deal of stress due to the invasion of pine beetle populations (*Dendroctonus ponderosae*). The tree species found in the forests of North America are equipped to combat shifting climatic conditions, but not large scale infestations of pine beetles. As the climate begins to warm, higher winter temperatures allow larger numbers of pine beetles to survive in areas where they would normally freeze.

The goal of this project is to analyze the effects of pine beetle populations on the forests of North America. This will include various forest systems in North America, including the Boreal Forest, Rocky Mountains, and others. These areas contain high densities of tree species such as ponderosa and lodgepole pine, the preferred food source for pine beetles. The pine beetles burrow through the bark of the trees to the trunk, where they feed and produce larvae. Their infestation is also associated with fungal infections within the tree that inhibit growth of the tree and the transport of nutrients, leading to rapid tree mortality. They also indirectly affect wildfires, wildlife, and hydrology.

Climate change is allowing the pine beetle to survive winter conditions that would otherwise limit their population. The main concern is the adverse environmental effects associated with the deaths of large quantities of trees due to the pine beetle’s expansion. Areas that receive snow pack in winter will begin to have earlier occurrences of snow melt due to the lack of canopy to block solar radiation. This effect can also disrupt the seasonal flow of
downstream rivers, creating greater flood risks during winter storms. It is also believed that the increase in deadfall provides additional fuel for forest fire events.

*Mountain Pine Beetle Ecology*

The mountain pine beetle (*Dendroctonus ponderosae*) is a species of bark beetle native to the forests of North America. It prefers pine-dominated forests, as their primary food source consists of species such as lodgepole, ponderosa, and white bark pine. Under normal climatic conditions, mountain pine beetles play an important role in pine forest ecosystems. By attacking old and weakened trees, young trees are able to develop and keep the forest healthy (Ministry of Forests 1995). They also provide an essential food source for many insectivore species like woodpeckers (Morrissey et al. 2008). Although mountain pine beetles are ecologically beneficial, their geographic expansion due to climate change causes many ecological problems because of their burrowing habits and rapid reproduction rates.

The life cycle of a mountain pine beetle is relatively simple, despite their large ecological impact. When mountain pine beetles reach maturity, they land on ideal trees, that are either too weak to defend themselves or have been overwhelmed by other beetles, and burrow through the bark into the phloem (Raffa et al. 2008). The phloem is the tissue that transports nutrients and organic materials created during photosynthesis and nutrient uptake from the root system on which the mountain pine beetles feed (Turgeon and Wolf 2008). Once successfully burrowed in a host tree, the beetles cut into the wood and create corridors in which they can lay their eggs. The newly hatched larvae feed on the phloem and vascular tissue, creating additional corridors that end in chambers where larvae transition to the pupal stage and then emerge as adults (Turgeon and Wolf 2008).
When pine beetles successfully burrow into a healthy host tree, the tree activates defenses to kill the pests. Resin containing toxins and acids are secreted at the burrowing site in an attempt to suffocate and/or poison intruding pine beetles (figure 1) (Bohlmann et al. 2000). The concentration of toxins in the resin rises as pine beetle attacks continue, up until a point where the beetles can no longer physically defend against the toxins (Raffa and Smalley 1995). Pine beetles have their own defense against the host trees by avoiding particularly healthy and resistant trees (Wallin 2004), and also using pheromones to attract additional pine beetles to the host tree for a large-scale invasion. To avoid particularly resistant hosts, adult pine beetles have sophisticated chemoreceptors that allow them to identify specific species of trees and their defense capabilities (Huber et. al 2004). The large-scale invasion of a host tree is followed by the release of pheromones by successfully burrowed pine beetles, which can attract thousands of beetles within a few days (Raffa and Berryman 1983). The rapid increase in pine beetles exhausts the defenses of the host tree and allows more beetles to survive and reproduce within the host. However, the large-scale invasion creates overcrowding and competition. To reduce this problem, successfully burrowed pine beetles excrete repellant pheromones that drive nearby pine beetles away and keep new ones from targeting the host tree (Ginzel et al. 2007).

The success of the mountain pine beetle is completely reliant on the resistance of the host trees. When stands of pine trees (or other species) become stressed due to drought or changing climate they become susceptible to invasion. Most of their resources are allocated to mediating external stressors, which leaves little energy to be spent on immune system defenses against pine beetle invasions or fungal infections. Climate change is the main force allowing pine beetles to expand further from their normal climatic range and to take advantage of an increasing number of environmentally stressed host trees.
Human-induced climate change is at the basis for the geoclimatic expansion of the mountain pine beetle and other pine forest pest species. Global human population is projected to rise toward 8.5 billion by 2100 (Bradshaw and Brooke 2014) and as countries become more developed over the next century, energy needs, and land requirements will cause an increase in the amount of greenhouse gases in the atmosphere, assuming drastic restructuring of energy infrastructures does not occur. Fossil fuels are the primary energy source for most countries, with fossil fuel energy consumption accounting for 86.4% of the world’s total energy consumption (U.S. EIA 2017). During the last few decades, global atmospheric temperature have increased due to an increase in global greenhouse gas emissions. The global average temperature has risen 0.85 degrees Celsius and is projected to rise another 1 to 2 degrees Celsius by 2100 (IPCC 2013).

If current trends continue and the human population continues to emit greenhouse gases at unsustainable rates, we will see a vast increase in the areas of pine forests affected by mountain pine beetles. As we know based on their ecology, pine beetle populations are limited by freezing temperatures in the winter, primarily during their pupal development stage, and prefer lower elevation pine forests (Raffa et al. 2008). Under normal winter conditions, severe cold weather events reduce the odds of finding trees that have been killed by mountain pine beetle outbreaks by approximately 80%, showing the importance regular cold snaps have on limiting outbreaks (Sambaraju 2011).

However, as global temperatures increase 1-2 degrees Celsius in areas like the Boreal forest in Canada, and the Sierra Nevada in California, mountain pine beetle populations will begin to expand. Studies conducted by Sambaraju et al. 2011, showed that small increases in temperatures result in new outbreaks at higher elevations, then at latitudes further north into
regions that were previously uninhabitable. Some research also shows that climate change also affects the ability of trees to defend themselves against mountain pine beetle attack. High elevation pine species like whitebark pine aren't adapted as well to defend against mountain pine beetles because they have very little ecological interaction with them (Raffa et al. 2012). As temperatures begin to allow mountain pine beetles to survive at higher elevations, the weak defenses of high elevation tree species will allow the pine beetles to expand their population with little resistance (figure 2).

**The Ecological Effects of Mountain Pine Beetle Invasions**

*Wildfire Ecology*

Over the last three decade mountain pine beetles and forest fires have increased in severity and frequency in North American forests due to climate change. Following outbreaks of mountain pine beetles the fuel load on the forest floor, combined with the increase in number of snags (Raffa et al. 2008) seems to have a potential to effect the behavior and severity of wildfires. However, North American forests actually show that mountain pine beetle outbreaks have little influence on wildfires. The most notable determinant of the severity of wildfires is climate. While pine beetle outbreaks may add additional variables that could affect fuel load, prolonged drought and increased temperatures show more of a relationship to more frequent and severe wildfires (Kulakowski and Jarvis 2011).

Although most studies have found that mountain pine beetle outbreaks do not affect the severity or frequency of wildfires, the fuel load added to the forest floor could affect the behavior of wildfires by adding more downed woody debris that results in longer burn times, as well as other factors (Lutes et al. 2009). Post outbreak forests have much higher levels of course woody
debris (Raffa et al. 2008), which can contribute to classifications of burning ranging from 100 hour to 1000 hour. These classifications determine behavioral aspects of wildfires, such as smoke production, burn time, and soil heating (Keane et al. 2009). Therefore, the increase in course woody debris following a mountain pine beetle outbreak may have an influence on wildfire behavior, contrary to the majority of research done on the subject. Due to current climate variability and the increase in abundance of mountain pine beetles, more research will need to be conducted to accurately determine the relationship between mountain pine beetle outbreaks and wildfire ecology.

*MPBs As Disease Vectors*

Mountain pine beetles not only damage and kill host pine trees by burrowing and consuming the phloem, they also act as vectors for symbiotic, disease fungal species to become established in host trees. The most common of the symbiotic fungal species is *Grosmannia clavigera*, or commonly known as blue stain fungus (Mercado et al. 2014). Pine beetles have special structures on their bodies called mycangia that help transport the spores of blue stain fungi and allow for both species to benefit from one another (Lieutier et al. 2009). When a pine beetle becomes established, the fungi provide a barrier from the trees defenses by detoxifying the resin secreted by the host tree (DiGuistini et al. 2011), allowing for a safer environment for the beetles to further their establishment and reproduce. In addition, when the fungi become established within a pine beetle gallery they are able to redirect essential nutrients to the areas of phloem that are lacking in these nutrients (Bleiker and Six 2007). According to Bentz and Six (2006), there is some evidence that suggests that the symbiosis between the fungi provide chemicals that are essential for the production of pheromones in adult beetles needed for reproduction and maturation.
The transportation ability of the pine beetles and their ability to rapidly infect host trees greatly benefits the symbiotic blue stain fungi. Without the help of the pine beetles, the fungi would not be able to survive the external defenses of the host and the competition from other fungal species (Mercado et al. 2014). The external defenses are bypassed during establishment and when the pine beetles excavate within the host tree, they create openings that allow the fungi to establish throughout the tree without excess interspecies competition. Adams et al. (2008), also showed that certain bacterial communities being carried internally by pine beetles assisted in the growth of the blue stain fungi after establishment in a host.

The highly beneficial symbiotic relationship between blue stain fungi and mountain pine beetles is problematic for affected pine forests. When blue stain fungus becomes successfully established in a pine host, it starts to infect the xylem and phloem (Ballard et al. 1982), which are essential nutrient transport systems for the host tree. The fungi intercept the flow of nutrients, which it then uses for growth. Once it has expanded to the heartwood, the host tree can no longer grow radially (Mercado et al. 2014). This process takes approximately five weeks (Solheim 1995), and when combined with the invasion of pine beetles, results in rapid death (less than one year) for host trees (Craighead 1928). When host trees are infected separately with blue stain fungus and pine beetles, their death rates are highly variable and are rarely rapid (Wilson and Gartner 2012). The rapid death in host trees becomes a positive feedback. As pine beetles expand due to climatic shifts, more trees will be affected, increasing the probability of infected hosts that have both pine beetles and blue stain fungus (Raffa et al. 2008). With more hosts containing both pathogens, rapid death rates will increase, thus increasing the migration of beetles from one host to the next due to their need for healthy hosts. The possible resulting effect is an uncontrollable outbreak of pine beetles happening at rates that are too rapid to apply mitigation efforts. Without
the limiting effects of extreme winter conditions, mountain pine beetles and blue stain final spores will be able to survive in large numbers and infect broader ranges of pine forests.

There are also economic implications for the introduction of fungi in stands of trees by mountain pine beetles. When host trees are affected by fungi alone, the wood remains relatively strong and salvageable for timber companies or other entities (Diguistini et al. 2007). However, the destruction caused by fungi combined with pine beetles reduces the value of the timber and in some cases, makes the timber unsalvageable. This removes one of the only benefits from massive outbreaks of pine beetles, economic gains from timber harvesting. In British Columbia alone unsalvageable damage from pine beetles and fungus cost the government billions of dollars a year with little return from timber harvests (B.C. Forestry Service 2016).

**Hydrological Effects**

The rapid mortality of tree species in mountain pine beetle affected areas also has negative implications for the hydrology of these regions by affecting snowmelt and nearby stream ecology. When forests that have been subject to an outbreak of mountain pine beetles reach the “Red” phase (phase at which the needles turn red and fall off), the canopy cover begins to thin out (Carroll et al. 2004). When afflicted trees cover a large area, the movement into the red phase causes an increase in snowpack due to the loss of canopy that would normally block it (Penn et al. 2016). The loss of canopy cover has also been attributed to increased surface temperatures and an increase in wind speed. With the increase in wind speeds and temperatures, the surface snowpack melts faster, at a rate of about one week quicker than normal conditions (B.C. Ministry of Environment 2008).
The increase in snowmelt following a mountain pine beetle outbreak effects nearby streams by increasing stream flows and causing more erosion. The peak flows of streams contribute to the habitat of fish and other species within the stream. When peak flows are abnormally high due to earlier peak flows, it could alter the habitat and livelihood of organisms by displacing prey species and degrading spawning grounds (Wong 2008). Increased water temperatures occur because of the loss of canopy cover because of the decrease in amount of shade. Fish adapted to cold water with high dissolved oxygen will suffer from the imbalance and their eggs will become less likely to spawn, resulting in a decrease in their populations following an MPB outbreak (Wong 2008).

Wildlife Impact

In contrast to the negative effects of large-scale (thousands of hectares) pine beetle outbreaks, many species of birds and mammals show a positive relationship to small scale tree mortality cause by pine beetles (Drever and Martin 2007). Most species of woodpeckers, with the exception of ground nesting species, benefit from increases in pine beetles because of the availability of food, and the increased potential for nesting habitats (Saab et al. 2007). Saab et al. (2014), found that the survival rates of avian insectivores, after a large-scale pine beetle infestation, showed a rapid increase as opposed to the pre-infestation period. Positive relationships are also present for mammalian species that rely on pine beetles as a food source and for the habitat created by downed woody debris.

Mountain pine beetle outbreaks may be beneficial to some wildlife species in the small-scale, however, the large-scale effects could prove to be unfavorable. Most nesting species in pine forests rely on fresh pine needles as a source for nest construction and cover from predators (Bull et al. 2007). However, after large scale outbreaks these resources become limited due to the...
quick death of the host trees. The nesting birds then have to forage for other materials in which they are not accustomed to building nests with and deal with less canopy protection, which can have an effect on their offspring’s survivability (Steventon and Daust 2009).

Mountain pine beetles also have the potential to disrupt whitebark pine ecosystems. There is a mutualistic relationship between the Clark’s nutcracker and whitebark pine, in that the nutcracker is the primary source for seed dispersal for the whitebark pine species. When large infestations of mountain pine beetles effect whitebark pine stands, they produce less seeds, therefore limiting the amount of resources for the Clark’s nutcracker. Under normal conditions the nutcracker would only consume a portion of the seeds and disperse the rest, because of the abundance of seeds. When the seed production is limited, the Clark’s nutcracker will consume a greater percentage of seeds while dispersing fewer seeds. This reduces the reproductive success of whitebark pine trees, which diminishes its population over time (Khrone 2016).

The decrease in healthy tree stands and increase in downed woody debris also presents a problem for large herbivores like deer and elk. These types of animals rely on relatively open forests in order to migrate and evade predators (Mosher 2011). The increase in downed woody debris after a pine beetle outbreak makes it easier for predators to trap and kill the large herbivores. It also means small mammals, which are a secondary food source for predators, have an increased amount of favorable habitat to evade predators. Unable to catch smaller prey, wolves and mountain lions would then turn to hunting large herbivores than can be easily trapped in the cluttered understory, instead of wasting time and energy sifting through debris to find the smaller, less filling prey (Mosher 2011).

Although not very well studied, fish can also be affected indirectly by the ecological damage of expanding mountain pine beetle populations. With an increase of snow reaching the
forest floor, it is expected that streams in affected areas will have higher peak flows during melting seasons, which can be exacerbated by climate change. The high peak flows can also cause an increase in sediment in the water, which has the potential to disrupt water quality and macroinvertebrate communities within the stream. Fish species in areas where pine beetles are endemic prefer high water quality and will most likely be affected by ecological disturbances due to increased outbreaks (Redding et al 2008).

**Carbon Feedback**

Large scale outbreaks of mountain pine beetles in North America and Canada have caused the loss of upwards of 90 million acres of pine forest (Ministry of Forests 2014). The extensive pine forests of western North America act as carbon sinks, meaning they sequester carbon dioxide from atmosphere, and if they are lost, that stored carbon will be released back into the atmosphere (Kurz et al. 2008). The carbon dioxide increase will be a result from an increase in forest fires, and the release of carbon due to decomposition (Parkins and McKendrick 2007). This massive loss of timber has negative implications on the atmosphere itself and can even act as a positive feedback for further expansion of pine beetles and their disease counterparts.

Kurz et al. (2008), explored the consequences of the pine forests shifting from being carbon sinks to carbon sources. Their study, conducted in 2008, used models to predict the net biomass production (amount of carbon either sequestered or released to/from the atmosphere) of select sections of forests. The study area included a 375,000 km² section of pine forest in British Columbia unaffected by pine beetle outbreaks in the region. That area of forest was estimated to be removing 0.59 megatons of Carbon per year under regular ecological conditions. However, introducing a large scale pine beetle outbreak using the ecological prediction models, showed
that the same section would shift to a carbon source that would release 18 megatons of carbon into the atmosphere over a 17 year period. The models also took into account effects due to pine beetle outbreaks other than tree mortality, such as increased forest fire severity and carbon outputs due to timber harvesting. This study shows that increases in mountain pine beetle outbreaks due to climate change will cause increases in carbon dioxide emissions, further exacerbating the results of climate change and expanding the range of the pine beetles.

**Mitigation**

*Controlled burning*

Controlling insect populations, especially the mountain pine beetle, is particularly difficult because of their reproduction rates and geographical range. Mitigating their effects on pine forests is a problem with only a few solutions, one being controlled burning of afflicted areas. Controlled burning is common among forest management practices, but mainly to reduce fuel loads on the forest floor to prevent crown fires and to add nutrients to soils that have been starved due to decades of fire suppression. However, controlled burns have recently been considered as a possible mitigation tool to limit the damage created by large scale outbreaks of pine beetles (Tabacaru and Erbilgin 2014).

Crown fires, and sometimes mid-canopy fires, can benefit mountain pine beetles by providing weakened hosts for colonization. However, low-level prescribed burns may limit the ability of mountain pine beetles to reach epidemic levels, and even decrease their population over a relatively short period of time (~ two years) (Safranyik and Carroll 2006). Studies have shown that predator species of mountain pine beetles increase in abundance in fire injured host trees due to the increase abundance of prey in the area (Tabacaru and Erbilgin 2014). The release
of pheromones aided by symbionts of mountain pine beetles has also been shown to attract parasites (Boone et al. 2008) that also take advantage of the increase in pine beetle populations following a prescribed burn. The rapid increase in predators and parasites parallels the increase in pine beetles until eventually their numbers are reduced. Tabacaru et al. observed that following a prescribed burn, populations of mountain pine beetles declined rapidly over a period of three years, mostly due to high mortality rates caused by predation.

Other opportunistic insects, like other species of pine beetle species also take advantage of weakened host trees following a prescribed burn (Tebacaru et al. 2014). When other insects are nearby, especially in similar or larger numbers, the pheromones secreted by the mountain pine beetle become less effective and they are less likely to reproduce (Safranyik and Carroll 2006). They also have difficulty competing for food and brood space within host trees. Since mountain pine beetles are outcompeted easily, this becomes another approach to the effectiveness to prescribed burns as a mitigation technique. However, following a controlled burn some studies show that these results can be highly variable (Tebacaru et al. 2014).

Use of Pesticides

The use of pesticides on forest stands recently affected by mountain pine beetle outbreaks is also a solution to try and minimize ecological damage. In an attempt to contain mountain pine beetle populations, many forest services and industries use the organic pesticide monosodium methanearsenate (MSMA), due to its easy application and low cost (Morrissey et al. 2008). The MSMA pesticide is used most effectively when the pine beetles have already established a brood and have moved to the larval stage of their development. When MSMA is injected into a tree, it travels through the nutrient pathways of the tree, where it is consumed either directly or indirectly, thus resulting in the mortality of the tree and the pine beetles (Manville et al. 1988).
Since MSMA is also fatal to the host tree, only a few trees within the affected area are injected, which can possibly lessen the mortality of mountain pine beetles. Morrissey et al. (2008) and the British Columbia Ministry of Forests and Range (2004) found that the effectiveness of the MSMA pesticide ranged from 55% to 88% (figure 3). The low efficiency estimate from the British Columbia Ministry of Forests and Range was attributed to dry climatic conditions and incorrect treatment time (Morrissey et al. 2008). If application of MSMA is done during the correct development stage of the beetles and under preferable climatic conditions, the effectiveness of the pesticide will be closer to 88%. Although these results can be highly variable depending on location and climate, when combined with other mitigation efforts, the use of MSMA provides additional support for limiting mountain pine beetle populations.

The main issue behind the use of the MSMA pesticide is the possibility of bioaccumulation of arsenic in insectivore species, primarily woodpeckers. The effect on woodpecker species is actually limited due to emergence of other pine beetle species and wood boring insects (Morrissey et al. 2008). Many insectivore bird species have been shown to consume a variety of insects, which means less MSMA is accumulated from mountain pine beetles. Some species of woodpecker also prefer to consume other species of insects that attack the tops of trees that are weakened from MPB attacks. MSMA accumulation in the tree is primarily located toward the middle and lower half, therefore insects at the top of the tree are either not affected, or affected at lower concentrations (Maclauchlan 1988). This means woodpeckers feeding on insects at the tops of the trees are exposed to MSMA at much lower concentrations, thus decreasing the likelihood of toxicity (Morrissey et al. 2008).
Conclusion

Mountain pine beetles are an essential organism in pine forest ecosystems. They provide an extensive food source for insectivore species as well as create habitat opportunities for mammals and other small organisms that live on the forest floor (Morrissey et al. 2008). Mountain pine beetles also help thin out the forests by reducing the amount of old, weak trees. This allows for saplings to grow and become established, thus enhancing the overall health of the forest.

However, the geographical expansion of mountain pine beetles due to climate change creates a lot of ecological problems. Higher elevation tree stands cannot defend against outbreaks and the resulting tree mortality will have a negative effect on the wildlife that rely on these habitats for shelter and food. Grizzly bears rely on whitebark pine stands at high elevation as an important food source for hibernation (Raffa et al. 2012). These tree stands also provide even distribution of snow melt that aids in the overall health of stream systems and nourishes ground level plant species. With the introduction of large scale outbreaks of mountain pine beetles, these ecological systems become threatened. The occurrence and severity of wildfires in afflicted areas also increases, which can have damaging effects on local economies and national parks.

Very few mitigation techniques are available to minimize mountain pine beetle outbreaks, but when implemented, can reduce outbreak level populations. Controlled burning is the most common solution but some studies show that mountain pine beetles benefit from burned areas. Pesticides are also used to decrease populations, but their toxicity has yet to be thoroughly studied enough for large scale use. The best course of action is to minimize human induced climate change by any means, because if temperatures allow mountain pine beetles to expand, it will be extremely difficult and costly to minimize their damage.
Figure 1; Raffa et al 2008. Image of a host tree defending against invasion by secreting toxic resin.
Figure 2 Raffa et al. 2008. Arial view of a large-scale outbreak in British Columbia.

Figure 3 Morrissey et al. 2008. Graph of the effectiveness of MSMA against pine beetle species. The reference is as untreated host tree.
References Cited


interactions between yeasts and bacteria and the fungal symbionts of the


56(3):460–466.


–2341.

Bentz, B.J., And D.L. Six. 2006. Ergosterol content of fungi associated with *Dendroctonus

ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *Ann.


Bleiker, K.P., and D.L. Six. 2007. Dietary benefits of fungal associates to an eruptive

herbivore: Potential implications of multiple associates on host population dynamics.


and evolutionary aspects of defense-related terpenoids in conifers.

*Recent Advances in Phytochemistry* 34: 109–149.

Boone, C.K., Six, D.L., Raffa, K.F., 2008. The enemy of my enemy is still my enemy:

competitors add to predator load of a tree-killing bark beetle. *Agric. Forest

Entomol.* 10, 411–421.

Bradshaw, C. J., & Brook, B. W. (2014). Human population reduction is not a quick fix for

environmental problems. *Proceedings of the National Academy of Sciences*, 111(46),

16610-16615.


Ginzel MD Bearfield JC Keeling CI McCormack CC Blomquist GJ Tittiger C. 2007.. Antennally mediated negative feedback regulation of pheromone production in the pine engraver beetle, Ips pini.. Naturwissenschaften . 94: 61-64.

Huber DPW Ralph S Bohlmann J. 2004.. Genomic hardwiring and phenotypic plasticity of terpenoid-based defenses in conifers.. Journal of Chemical Ecology . 30: 2399-2418.


Lieutier, F., A. Yart, And A. Salle. 2009. Stimulation of tree defenses by ophiostomatoid fungi can explain attack success of bark beetles on conifers.


