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Are novel plant chemicals friends or foes of native invasive insect herbivores?

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Summary – Mountain pine beetle (MPB, *Dendroctonus ponderosae*) has recently breached the geo-climatic barrier of the northern Rocky Mountains and invaded novel jack pine (*Pinus banksiana*) forests in western Canada. This breach signifies an unprecedented climate change-induced invasion of a new plant biome by a native insect. The mechanism underlying this host range expansion is unknown, but likely involves phytochemicals that play critical roles in the MPB biology. Thus far, studies have investigated jack pine suitability to MPB as a host and examined compatibility of its chemicals with beetles and their microbial symbionts. Based on these studies, I have identified five phytochemical mechanisms that have likely facilitated the host expansion of MPB. First, relative to the historical host of MPB (lodgepole pine, *P. contorta*), jack pine not only quantitatively lacks toxic defense chemicals, but also contains large amounts of chemicals that promote MPB host colonization. Second, prior to the arrival to naïve jack pine forests, invasion of a zone of hybrids of jack and lodgepole pines by beetles likely improved their success in the jack pine as hybrids show chemical characteristics of both novel and historical hosts. Third, jack pine chemistry is compatible for beetle pheromone production, aggregation on the host trees, and larval development. Fourth, compatibility of jack pine chemistry with the microbial symbionts of MPB maintains beneficial interactions with their host. Finally, jack pine contains low amounts of defense and attraction inhibitory compounds, and high amounts of pheromone precursor and synergistic compounds that make historical hosts susceptible to MPB. I conclude that compatibility of chemicals of jack pine to MPB and its symbionts has likely facilitated the biological invasion.

Introduction

Climate change has facilitated the invasion of novel habitats by both exotic and native herbivorous insects across globe (Walther *et al.,* 2009). Exotic insects become invasive when they cause significant economic and/or ecological impacts in the plant biome of their introduced range. Similarly, native insects that had historically been limited in their distribution by climatic barriers have overcome these barriers and become invasive by expanding their range into novel habitats (Battisti *et al.,* 2006; Walther *et al.,* 2009). In North America, mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae) has expanded its host range from lodgepole pine (*Pinus contorta*) to the novel jack pine (*P. banksiana*) in western Canada (Erbilgin *et al.,* 2014). Yet, the mechanisms underlying this unprecedented host expansion have not been clearly defined. In particular, whether phytochemicals have contributed to the host expansion of MPB has not been fully described even though they mediate beetle's interaction with host trees (Raffa *et al.,* 2008). Such understanding can have important implications for the climate change-driven host expansion of native invasive insects and also contributes to the functions of novel plant chemicals in the future plant-insect interactions.

Periodic MPB outbreaks have caused widespread mortality of pine trees in western North America (Raffa *et al.,* 2008). The historical range of MPB covers a large portion of western conifer forests, extending from Mexico to western Canada. Within this range, MPB colonizes numerous pine species including lodgepole pine. Frequent epidemics of MPB have occurred in the past but these eruptions were historically limited by cold temperatures (Barber *et al.,* 2000). However, recent climatic changes have led the current MPB eruption to expand from beyond its historical range to areas where they usually do not outbreak (Cudmore *et al.,* 2010). As MPB expands easterly in Alberta, Canada it has spread across the lodgepole × jack pine hybrid zone, and more recently invaded jack pine forests in north-eastern Alberta (Erbilgin *et al.,* 2014).

Jack pine is a foundation species throughout Canadian boreal forests which extend into the US upper Midwest and New England. The range of jack pine reaches into those of several important eastern pine species and thus, MPB expansion into jack pine forests can also provide a potential conduit for MPB to spread to eastern North America (Ayres & Lombardero, 2000). Although jack pine populations in Alberta seem to be suitable for MPB, our understanding of host expansion is hampered by the fact that its mechanistic basis is still poorly understood.

Plants have developed broad primary and secondary metabolites to cope with herbivorous insects (Howe & Jander, 2008). These metabolites affect insect biology from oviposition selection to offspring fitness. Primary (availability of nitrogen and carbon-based compounds, such as carbohydrates and lipids) and secondary (defensive) metabolites affect host plant suitability (Berenbaum, 1995; Awmack & Leather 2002; Hansen & Moran, 2014). Incompatibility (unsuitable for the biology of the organism) of these metabolites with the invasive insects can influence their establishment success, population dynamics, and potential for invasiveness (Becerra, 1997; Awmack & Leather, 2002; Hansen & Moran, 2014).

Three features of MPB's interaction with host tree chemicals are particularly relevant to its relationship with hosts (Raffa *et al.,* 2005; Safranyik *et al.*, 2010). First, beetles must overcome host defenses to reproduce. They employ two main strategies to overcome host defenses. Pheromone-mediated mass aggregation depletes the first tier of defenses (constitutive) and the introduction of phytopathogenic fungi vectored by the colonizing beetles into the host rapidly destroy the phloem and vascular tissues, further compromising the defenses. When host defenses are overwhelmed, beetles mate, construct oviposition galleries, and lay eggs. Emerging larvae complete development under the tree bark and emerge as adults. Failure to kill the host usually results in failed reproduction due to toxic secondary compounds such as resin. Monoterpenes are a major constituent of resin along with diterpene resin acids (Keeling & Bohlmann, 2006). These chemicals act as both physical and chemical barriers against beetles and their microbial associates. Second, pheromone production in MPB is closely linked to host chemicals (Blomquist et al., 2010). For example, host monoterpene α-pinene precursor female MPB aggregation pheromone, *trans*-verbenol. Pheromones function in mate finding, locating hosts, overwhelming host defenses, and resource partitioning. Finally, MPB mass aggregation involves co-evolved interactions between volatile host chemicals and pheromones as some host chemicals either synergize or inhibit beetle attraction to its aggregation pheromones (Borden *et al.,* 2008).

In this review, I compare and contrast the chemical profiles of historical (lodgepole pine) and novel (jack pine) hosts, integrate host chemistry with the MPB host colonization behavior, and provide mechanistic explanations for how differences between host species can potentially affect the beetle behaviors that govern host acceptance for mating and oviposition. I primarily focus on biologically relevant chemicals, mainly monoterpenes, and explain how each individual compound has played a potential role in the MPB host expansion (Table 1). This is the first comprehensive review on the phytochemical mechanisms underlying invasion of a new plant biome by a native-invasive forest insect species, particularly in bark beetles which contain several outbreak species throughout the world. I identify five phytochemical mechanisms that have likely facilitated the host expansion of MPB into the jack pine forests (Fig. 1).

Approach

I searched the Web of Science and Scopus using terms like "jack pine or lodgepole pine chemistry (monoterpenes, phenolics, terpenes, fatty acids) and mountain pine beetle" and identified 59 papers published 2006 to 2018. Off these, I selected those solely on the chemistry of mature trees as ontogeny can influence tree chemistry (Erbilgin & Colgan, 2012). Among the remaining papers, I only included those reported units as dry weight of phloem tissue, because amounts reported vary substantially between "dry" and "fresh" tissues as well as between foliage and phloem (n=12). In cases where units of compounds reported in some studies were not clear, I personally contacted the authors of such papers and obtained the units. There were fewer studies reporting the enantiomeric ratios of monoterpenes and these were also included in my synthesis (n=4). For induced defenses, I only included those papers incorporated real or simulated (via inoculation with fungi symbiotic to MPB such as *Grosmannia clavigera*) beetle attacks (n=6). If studies were conducted in my lab, I revisited the full data (not all data were reported in published papers) and obtained the necessary information to be included in the tables. Depending on the mechanism listed below, the number of papers included varied from one (Table 3) to six (Tables 2, 4). Due to a small number of papers available, I did not conduct metaanalysis which may indicate bias in my conclusion (Pigott, 2012). Thus, I reported the lowest and highest means (and SE) for each compound from each study. The sample size of trees in these papers ranged from 5 to 10 trees per study.

1. Jack pine appears to have less pronounced constitutive and induced chemical defenses than a historical host of MPB

Conifer chemical defenses contain different classes of compounds such as terpenes and phenolics (Keeling & Bohlmann, 2006). These chemicals are constitutively present in trees, providing immediate resistance to attacks. If the attack persists and the insect is not deterred, a "second tier of defense" in the form of an induced response is triggered to protect the tree. Induced defenses rise rapidly following beetle attacks and within a few days, can occur at concentrations that can inhibit or repel later-arriving beetles and alter the growth of their microbial fungi (Raffa *et al.,* 2005). Among terpenes, monoterpenes are the most studied due to their importance to MPB behavior (Chiu *et al.,* 2017; Erbilgin *et al.,* 2017a; Reid *et al.,* 2017) and to tree resistance (Boone *et al.,* 2011; Erbilgin *et al.,* 2017b). Conifers also contain other classes of compounds such as fatty acids that can be toxic to MPB (Ishangulyyeva *et al.,* 2016). Fatty acids are major components of plant lipids and can be synthesized into derivatives such as jasmonic acid used in plant defenses against insect herbivory.

Even though jack and lodgepole pines appear to be genetically similar (Cullingham *et al.,* 2013), there are some differences in the amounts of chemicals that affect MPB behaviour. For example, the main monoterpenes of jack and lodgepole pines are α-pinene and β-phellandrene, respectively (Table 2). The amounts of many other chemicals differ greatly between the two species. Jack pine has more (–)-α-pinene, which is a precursors to the female MPB aggregation pheromone, *trans*-verbenol. In contrast, lodgepole pine has more (+)- and (–)-limonene, 3-carene, 4-allylanisole, linoleic acid, and α-linolenic acid that either act as anti-feedants or aggregation inhibitors. Lower abundance of these toxic and inhibitory compounds in jack pine may likely improve host entry by MPB (Ishangulyyeva *et al.,* 2016; Chiu *et al.,* 2017; Erbilgin *et al.,* 2017b; Reid *et al.,* 2017). Although some compounds like α-pinene can be anti-feedants on beetles at high concentrations (Chiu *et al.,* 2017), higher abundance of such compounds also leads to greater production of *trans*-verbenol (Taft *et al.,* 2015a). Constitutive phenolics are not known to contribute to defense against MPB nor other bark beetles, but this may due largely to a lack of investigation (Erbilgin *et al.,* 2017a).

Studies have also investigated the induced defenses of pines. Defense responses are commonly induced by inoculating trees with a MPB-associated fungus and measured by estimating concentration of monoterpenes in the phloem and necrotic tissues (i.e., lesions) (Arango-Velez *et al.,* 2016; Cale *et al.,* 2017; Erbilgin *et al.,* 2017a). Concentrations of biologically relevant chemicals showed differences between pine species (Tables 3, 4). Shortly after induction (within 7 days) toxic compounds like limonene, 3-carene, and 4-allylanisole were rapidly induced in much greater amounts in lodgepole than in jack pines. For example, amounts of (–)-limonene and 3-carene were four and two times higher in lodgepole pine, respectively. Likewise, 4-allylanisole, which inhibits beetle attraction to its aggregation pheromone, was about two times higher in the historical host. All these compounds were also associated with resistant lodgepole pines in Alberta (Erbilgin *et al.,* 2017b). In contrast, less toxic, beetle-beneficial compounds were present in higher quantities in jack pine including (–)-α-pinene, which was 21 times higher. The toxicity of α-pinene, β-phellandrene and terpinolene is comparably much less than limonene or 3-carene (Chiu *et al.,* 2017; Reid *et al.,* 2017).

Delayed induced defenses (usually 6-8 weeks after inoculations) showed similar patterns as the rapid induced defenses in the phloem or lesion between species (Table 4). For example, (–)-limonene and 3-carene concentrations were 58 and nine times higher in lodgepole than in jack pines, respectively. In contrast, (–)-α-pinene was two times higher in jack than in lodgepole pines. 4-Allylanisole was about five times higher in the lodgepole pine. Furthermore, quantification of defense chemicals in the lesion between species indicated a much stronger but similar pattern (Table 4). In almost all cases, jack pine lesion contained higher amounts of less toxic, beneficial compounds and lower amounts of more toxic and harmful compounds.

Based on these differences in defenses between species, I conclude that jack pine failed to provide an immediate resistance to MPB attacks due to high concentrations of pheromone precursor (α-pinene) and pheromone synergist (terpinolene and myrcene) compounds as well as due to low concentrations of toxic (limonene, 3-carene) and attraction-inhibitive (4-allylanisole) compounds in its phloem (Fig. 1, Mechanisms #1-3). Furthermore, jack pine induced responses did not inhibit or repel later-arriving beetles because, in part, it had lower concentrations of defense compounds like (–)-limonene or 3-carene with which to kill attacking beetles, or attraction inhibitive compounds like 4-allylanisole to stop arriving beetles, while concentrations of both pheromone precursor and pheromone synergists increased several fold. Likewise, concentrations of highly toxic fatty acids were considerably lower in jack pine. All these differences between the novel and historical hosts have led to successful colonization of jack pine by MPB.

(2) Invasion of hybrid zone of jack and lodgepole pine trees likely improved MPB success in jack pine

Hybridization of closely related trees is a common phenomenon in natural forests and happens when two fertile species cross and produce progeny. In north-central Alberta, lodgepole and jack pines naturally hybridize and create a hybrid zone where both pure species and their hybrids co-exist together. Genetic analysis of both species in this zone indicated that the hybrid ancestry was biased toward lodgepole pine but gene flow between species was equal (Cullingham *et al.,* 2012).

Shortly after the invasion of lodgepole pine forests in Alberta in 2006-2007, beetles arrived to the hybrid zone and spent several generations here before flying into the more jack pine dominated forests in north-eastern Alberta in 2011 (Cullingham *et al.,* 2013, Lusebrink *et al.,* 2013). Chemical profile of hybrids is intermediate between both pine species (Table 2). For example, hybrids have proportionally less β-phellandrene than lodgepole pine, but more than jack pine. Likewise, concentrations of 3-carene, α-pinene and myrcene in the hybrid were intermediate between the two species. Basically, hybrid trees provide a mixture of monoterpenes of both species, although they appear to closely resemble lodgepole rather than jack pines, supporting genetic data (Cullingham *et al.,* 2012, 2013). Lusebrink *et al.* (2013) further investigated the effects of induced defenses of hybrids on MPB reproduction and reported that fitness of beetles emerged from hybrid trees was similar to those emerged from lodgepole pine (Erbilgin *et al.,* 2014). Furthermore, concentrations of induced chemicals of hybrids again intermediate between the two pine species (data now shown). Likewise, fungal inoculations of mature hybrid trees with *G. clavigera* indicated successful infection (Lusebrink *et al.,* 2013).

Invasion of the hybrid forests has three important consequences for the MPB host expansion (Fig. 1, Mechanism #4). First, hybrid trees provided MPB and its microbial symbionts behavioral and physiological flexibility for accepting trees with chemically different profiles prior to moving to jack pine forests. Second, since hybrid trees contain similar biologically relevant compounds as lodgepole pine, these chemicals certainly helped beetles to accelerate their acceptance of jack pine. Third, emergence of brood from hybrids signifies that MPB can successfully complete its development on a chemically different host species. In short, MPB and its symbionts likely used the hybrid forests as “stepping stone” prior to invasion of jack pine forests.

(3) Chemical similarity between novel and historical hosts likely facilitated the host expansion of MPB

Host specificity is directly related to the herbivore’s invasion potential as it determines the herbivore’s ability to reproduce and invade (Becerra, 1997). Although not all insect invasions are successful (Bertheau *et al.,* 2010), they may capitalize on the “evolutionary naivety” of novel host plants and exploit them as effectively as their historical hosts (Walther *et al.,* 2009). Several hypotheses were proposed to explain the role of host plant suitability during an insect host expansion (Feeny 1991). They all emphasize that novel plants are suitable for colonization by insects if their secondary compounds are related to those of the insect’s ancestral hosts (Berenbaum, 1995; Becerra, 1997; Murphy & Feeny, 2006; Erbilgin *et al.,* 2014).

Although jack and lodgepole pine have different chemical profiles, both contain the same compounds that are biologically relevant to MPB (Table 2). For at least three reasons, chemical similarity of jack and lodgepole pines has promoted the MPB host expansion through exploitation of common host compounds for its aggregation, colonization, and establishment on jack pine (Fig. 1, Mechanism #5). First, jack pine phloem contains an essential monoterpene precursor (α-pinene) for the production of MPB pheromones (Blomquist *et al.,* 2010). In fact, the emission of *trans*-verbenol was about three times higher on jack pine than on the lodgepole pine (Erbilgin *et al*., 2014), likely due to higher α-pinene content in the jack pine phloem (Table 2). Emission of male aggregation pheromone, *exo*-brevicomin was similar between species (Erbilgin *et al.,* 2014). Second, the fitness of beetles emerged from jack pine was superior in terms of body size relative to those emerged from lodgepole pine (Lusebrink *et al.,* 2016). Body size can influence beetle ecology as larger female beetles can disperse farther, have better survival ability, and lay more eggs than smaller females (Graf *et al.,* 2012). Third, female beetles emerged from jack pine consumed proportionally less mass during flight than those emerged from lodgepole pine, indicating that they could arrive at the host with greater body mass that is convertible to eggs (Erbilgin *et al.,* 2014).

In addition to secondary compounds, Ishangullyeva *et al.* (2016) also evaluated whether fatty acid profile of jack pine impede host colonization by MPB and *G. clavigera* (Tables 1, 2). The study has found that tissues of jack or lodgepole pine amended with synthetic fatty acids at concentrations representative of either host species were compatible with developing MPB larvae. Likewise, *G. clavigera* grew similarly in media amended with fatty acids at concentrations present in jack or lodgepole pine phloem. Furthermore, sampling of different jack pine populations across Canada indicated that the composition of fatty acids was similar to the different populations of lodgepole pine sampled. These results demonstrate that the composition of fatty acids of jack pine can be compatible with MPB and its fungal symbionts.

In short, these results demonstrate that differences between historical and novel hosts do not constrain their use by MPB. This conclusion is supported by the results of earlier studies by Ehrlich & Raven (1964) and others, who proposed that chemical similarity between host plants provides strong basis for the overall pattern of host shifts by herbivorous insects.

(4) Co-evolutionary interactions between microbial symbionts and MPB are maintained on jack pine

Microbial symbionts can benefit their insect hosts in a variety of ways (Adams *et al.,* 2009, 2013; Chung *et al.,* 2013; Thompson *et al.,* 2013) and are critical for the host's development and survival (Lukasik *et al.,* 2013), and thus can influence the range expansion of their insect hosts (Adams *et al.,* 2013). MPB is associated with symbiotic fungi and bacteria (Therrien *et al.,* 2015). Symbiotic fungi facilitate beetle nutrition, either directly by serving as a substrate, or indirectly by digesting and concentrating tree nutrients (Goodsman *et al.,* 2012). *Grosmannia clavigera* was also shown to detoxify toxic terpenes (DiGuistini *et al.,* 2007). Successful host colonization by beetles usually makes trees available to other types of fungi, mainly saprophytic, such as *Aspergillus* and *Trichoderma*. These fungi directly compete with the symbiotic fungi for unused phloem and thus can substantially influence the survival of immature stages of MPB (Therrien *et al.,* 2015).

Bacteria are also frequent associates of bark beetles, but how they influence beetle development and survival are not clear (Adams *et al.,* 2013; Therrien *et al.,* 2015). Some bacteria have been shown to accelerate nitrogen accumulation in beetle galleries (Morales-Jiménez *et al.,* 2013). In addition, bacteria may also simulate growth or germination of MPB symbiotic fungi (Adams *et al.,* 2009), inhibiting fungal antagonists (Scott *et al.,* 2008) or degrading tree defense chemicals in vitro (Boone *et al.,* 2013). *Pseudomonas* and *Stenotrophomonas* species are the two of most common associates of MPB and carry genes that encode for terpene metabolism (Adams *et al.,* 2013).

Therrien *et al.* (2015) investigated how interactions between four bacterial associates, and two symbiotic and two opportunistic fungi affect performance of MPB in phloem of lodgepole and jack pines (Table 5). Overall, MPB produced more larvae and established longer ovipositional and larval galleries in phloem predominantly colonized by either of two symbiotic fungi *G. clavigera* or *Ophiostoma montium* than by opportunistic fungi, *Aspergillus* and to a lesser extent, *Trichoderma*. The same pattern occurred in both tree species. In addition, bacterial impact on beetle performance varied depending on particular fungus-bacterium combinations and tree species. *Pseudomonas* sp. D4-22 and Hy4T4 in lodgepole pine and *Pseudomonas* sp. Hy4T4 and *Stenotrophomonas* in jack pine reduced antagonistic effects by the two opportunistic fungi, resulting in a larger offspring.

I purpose three processes by which MPB may have benefited from microbial symbionts during host expansion (Fig. 1, Mechanism #6). First, symbionts can detoxify jack pine secondary compounds. Microbial associates on MPB oviposition galleries are found to have genes involved in terpene degradation (DiGuistini *et al.,* 2007; Adams *et al.,* 2013) and that these associates reduced concentrations of host terpenes in vitro (Boone *et al.,* 2013), resulting in improved beetle development (Therrien *et al.,* 2015). Second, microbial symbionts can lower deleterious effects of competitive fungi (*Aspergillus* and *Trichoderma*) on beetle performance on jack pine (Therrien *et al.,* 2015). In particular, beetles in jack pine had longer oviposition galleries and more offspring per female when *Aspergillus* and *Pseudomonas* sp. were together, compared to *Aspergillus* alone. This is likely a result of competitive exclusion of antagonistic fungi by the symbiotic fungi and/or inhibition of antagonistic fungi by bacterial-derived toxins (Scott *et al.,* 2008). Finally, co-evolutionary interactions between MPB and microbial symbionts maintained on the jack pine, suggests that interactions between MPB and microbial associates do not constraint MPB's reproduction in jack pine, and may potentially help MPB to establish in the novel host by creating favorable subcortical environments for brood similar to the beetle's historical host (Adams *et al.,* 2013; Boone *et al.,* 2013 Cale *et al*., 2017).

(5) Comparison to MPB-resistant lodgepole pine trees further reveals jack pine trees susceptibility to MPB

During periodic MPB outbreaks, some individual trees showed resistance to MPB colonization and survived at high beetle densities. Erbilgin *et al.* (2017b) analyzed the host chemistry of surviving lodgepole pine trees and compared them with those that were not attacked by MPB. Surviving resistant trees were characterized by higher concentrations of defense (limonene, 3-carene) and inhibitory (4-allylanisole) compounds, and lower concentrations of precursor (α-pinene) and synergistic (myrcene and terpinolene) compounds (Table 2). Overall, the study showed that several key host tree compounds (individually or collectively) may have interfered with the emission of bark beetle pheromones, inhibited beetle attraction to aggregation pheromones, and restricted the ability of beetles to excavate oviposition galleries and oviposit.

Further comparison of secondary compounds and fatty acids between resistant lodgepole pine and jack pine revealed that the latter species has low concentrations of defense and inhibitory compounds and high concentrations of precursor and synergistic compounds (Fig. 1, Mechanism

#7; Table 2). In particular, jack pine had lower limonene (5.9-15.6 times) and 4-allyanisole (2.3-2.9 times), but higher α-pinene (1.3-10.4 times) concentrations. Likewise, all fatty acids that are toxic to MPB were lower in jack pine than in resistant lodgepole pines. In particular, linoleic acid was at least four times higher in the resistant lodgepole pine. Together, all these results demonstrate that when jack pine trees are attacked by MPB, they are likely to promote MPB aggregation due to high levels of pheromone precursor or synergists and low levels of toxic chemicals.

Conclusions and future directions

From an evolutionary perspective, plants develop optimal strategies for balancing various functional traits such as growth, defense, and reproduction based on their life history strategy, source-sink relationships, and biotic pressures (Herms & Mattson, 1992; Raffa *et al.,* 2017). However, climate change has not only altered these species-specific evolutionary processes, but also accelerated the invasion of novel habitats by insects. As a result, the outcome of plant-insect interactions has become less predictive in both co-evolved and novel plant-insect systems (Jamieson *et al.,* 2017). In particular, we have a limited understanding of how variation of defense compounds within a species that has evolved under historical conditions (Moreira *et al.,* 2014) is sensitive to the changing climate and will affect the invasive insects. Thus, we need a new predictive framework for addressing these challenges in forestry, in part because studies commonly focus on the post-invasion processes and pre-invasion processes including accessing suitability of novel host plants are usually ignored. The present review should contribute towards the development of a more inclusive and mechanistic conceptual framework for host range expanding insects. However, for example, we do not know how the chemotypic variation across different jack pine populations (Taft *et al.,* 2015a,b) will affect MPB invasion. Likewise, it is unknown how specific defense strategies that have evolved with native herbivorous insects will influence biological invasions. For example, lodgepole pine phloem contained qualitatively and quantitatively more monoterpenes than foliage, and jack pine foliage had more monoterpenes than phloem, suggesting interspecific variation in the allocation of defenses between plant organs (Erbilgin & Colgan, 2012; Erbilgin *et al.,* 2017a). Such differences make sense evolutionarily because the primary herbivore of jack pine is a defoliator, while MPB is the most pronounced insectivorous threat for lodgepole pine. Thus, forecasting plant responses that account for co-evolved interactions will provide more realistic predictions of tree responses to invasive insects.

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Table 1. The roles pine (*Pinus* spp.) chemicals play in *Dendroctonus ponderosa* activity.

Host compounds	Known activity in *D. ponderosa*	References[4]
Monoterpenes		
(–)-α-Pinene	Pheromone precursor; aggregation inhibitor[1], anti-feedant[2]	Erbilgin et al. 2017a; Chiu et al. 2017
(+)-α-Pinene	Pheromone precursor; pheromone synergist; anti-feedant[2]	Chiu et al. 2017
Terpinolene	Pheromone synergist	Klutsch et al. 2017
Myrcene	Pheromone synergist; anti-feedant[2]	Chiu et al. 2017; Klutsch et al. 2017
(–)-Limonene[3]	Anti-feedant	Chiu et al. 2017; Erbilgin et al. 2017 a,b
(+)-Limonene	Anti-feedant	Chiu et al. 2017; Reid et al. 2017
3-carene	Anti-feedant; aggregation inhibitor[1]	Erbilgin et al. 2017a,b; Chiu et al. 2017; Reid et al. 2017
(–)-β-Phellandrene	Attractant[1]; anti-feedant[2]	Chiu et al. 2017
Phenylpropene		
4-Allylanisole	Aggregation inhibitor; anti-feedant	Erbilgin et al. 2017a, b
Fatty Acids		
Linoleic Acid	Anti-feedant	Erbilgin et al. 2017b
Palmitic Acid	Anti-feedant	
Behenic Acid	Anti-feedant	
α-Linolenic Acid	Anti-feedant	

[1] (–)-α-Pinene and 3-carene may function as an absolute or dose-dependent aggregation pheromone inhibitor.

[2] At very high doses, (+)-α-pinene and myrcene can be toxic, but its toxicity is much less than limonene or 3-carene.

[3] With the exception of α-pinene, it is unknown how the enantiomeric ratios of other monoterpenes affect *Dendroctonus ponderosa* biology.

[4] Only references after 2017 were added. References prior to 2017 were shown at Erbilgin *et al*. (2017b).

Table 2. Mean (± SE) constitutive concentrations (ng/mg dry weight of phloem tissue) of known biologically relevant chemicals quantified from phloem of *Pinus contorta*, *P. banksiana,* and their hybrids in *Dendroctonus ponderosa*.

Host compounds	*P. contorta* (min-max range) [1]	*P. contorta* [2]	*P. banksiana* (min-max range) [3]	Hybrid of *P. contorta*-*P. banksiana* [4]
(–)-α-Pinene	152 ± 11 – 227 ± 33	152.4 ± 11.2	55 ± 9 – 735 ± 216	110 ± 31
(+)-α-Pinene	41 ± 5 – 100 ± 17	40.9 ± 5.1	196 ± 27 – 1466 ± 212	281 ± 61
Total α-Pinene	193 ± 13 – 326 ± 44	193.4 ± 12.6	250 ± 19 – 2001 ± 489	392 ±92
Terpinolene	30 ± 3 – 48 ± 6	29.6 ± 2.7	4 ± 1 – 19 ± 11	18 ± 3
Myrcene	46 ± 4 – 72 ± 9	46.1 ± 4.3	5 ± 1 – 22 ± 5	63 ±5
(–)-Limonene	49 ± 15– 154 ± 45	154.1 ± 45.3	23 ± 3 – 59 ± 9	185 ± 52
(+)-Limonene	11 ± 2 – 65 ± 20	65.1 ± 19.7	6 ± 1 – 13 ± 3	23 ± 5
Total Limonene	60 ± 16 – 219 ± 64	219.2 ± 636.4	14 ± 4 – 37 ± 3	208 ± 57
3-carene	89 ± 19 – 275 ± 65	242.6 ± 31.4	45 ± 12 – 155 ± 102	180 ± 15
β-Phellandrene	875 ± 138 – 2700 ± 495	899.7 ± 45.7	4 ± 1 – 13 ± 3	906 ± 130
4-Allylanisole	19 ± 4 – 35 ± 5	35.4 ± 4.8	12 ± 3 – 15 ± 3	15 ± 3
Linoleic acid	31 ± 5 – 318 ± 8	318 ± 8	30 ± 5 – 75 ± 8	N/A
Palmitic Acid	8 ± 2 – 74 ± 2	62 ± 2	7 ± 2 – 14 ± 3	N/A
Behenic Acid	7 ± 1 – 12 ± 1	9 ± 0.4	5 ± 1 – 13 ± 2	N/A
α-Linolenic acid	3 ± 0.4 – 39 ± 1.5	39 ± 1.5	4 ± 1 – 42 ± 4	N/A

[1] Goodsman et al. 2013; Erbilgin et al. 2014, 2017a, b; Ishangulyyeva et al. 2016 (data only from Alberta); Roth et al. 2018

[2] Only lodgepole pine trees that survived at high beetle densities during *D. ponderosa* outbreak in Alberta reported at Erbilgin et al. 2017b

[3] Erbilgin & Colgan (2012); Taft et al (2015a, data only from Alberta); Erbilgin et al. 2014, 2017a,b; Ishangulyyeva et al. 2016 (data only from Alberta); Lusebrink et al. 2016.

[4] Lusebrink et al. 2013.

Table 3. Rapid induced mean (± SE) concentrations (ng/mg dry weight of phloem tissue) of known biologically relevant chemicals quantified from *Pinus contorta* and *P. banksiana* lesions in *Dendroctonus ponderosa*.

Host compounds	*P. contorta*[1]	*P. banksiana*[2]
(–)-α-Pinene	230 ± 40 – 530 ± 110	7630 ± 1960 – 11160 ± 2480
(+)-α-Pinene	90 ± 16 – 310 ± 65	14510 ± 4970 – 17220 ± 4260
Total α-Pinene	320 ± 57 – 2440 ± 420	22140 ± 6931 – 28380 ± 6740
Terpinolene	160 ± 20 –1000 ± 120	190 ± 54 – 340 ± 75
Myrcene	260 ± 30 – 920 ± 80	40 ± 10 – 270 ± 10
(–)-Limonene	710 ± 140 – 1140 ± 160	280 ± 48 – 320 ± 75
(+)-Limonene	390 ± 75 – 450 ± 89	190 ± 40 – 195 ± 46
Total Limonene	1100 ± 216 – 1800 ± 400	470 ± 88 –515 ± 121
3-carene	1400 ± 160 – 7220 ± 1300	1550 ± 450 – 3310 ± 540
β-Phellandrene	8470 ± 825 – 31800 ± 3590	80 ± 10 – 240 ± 40
4-Allylanisole	57 ± 8 – 110 ± 11	29 ± 5 – 50 ± 9

[1,2] Cale et al. (2017)

Table 4. Mean (± SE) induced concentrations (ng/mg dry weight of phloem tissue) of biologically relevant chemicals quantified from *Pinus contorta* and *P. banksiana* phloem and lesions in *Dendroctonus ponderosa*.

Host compounds	*P. contorta*		*P. banksiana*	
	Phloem[1]	Lesion[2]	Phloem[3]	Lesion[4]
(–)-α-Pinene	292 ± 38	6235 ± 892	510 ± 90	15329 ± 2807
(+)-α-Pinene	122 ± 9	3972 ± 424	196 ± 15	68092 ± 7734
Total α-Pinene	414 ± 47 – 497 ± 54	10207 ± 1316	646 ± 84 – 1106 ±147	83421 ± 10541
Terpinolene	121 ± 16 – 599 ± 92	2206 ± 413	9 ± 1 – 48 ± 7	2457 ± 512
Myrcene	352 ± 84 – 415 ± 67	4622 ± 752	13 ± 2 – 45 ± 7	3219 ± 467
(–)-Limonene	6269 ± 896	5235 ± 542	108 ± 10	350 ± 47
(+)-Limonene	126 ± 13	446 ± 57	15 ± 4	338 ± 54
Total Limonene	510 ± 35 – 6395 ± 910	5681 ± 599	123 ± 6 – 313 ± 52	688 ± 102
3-carene	193 ± 23 – 962 ± 74	8030 ± 1012	48 ± 3 – 112 ± 13	11358 ± 2162
β-Phellandrene	2700 ± 450 – 5492 ± 850	134879 ± 15770	1 ± 0.2 – 26 ± 3	1099 ± 233
4-Allylanisole	108 ± 16	Not Available	22 ± 4	Not Available

[1] Goodsman et al. 2013; Erbilgin et al. 2014, 2017a; Lusebrink et al. 2016; Roth et al. 2018.

[2] Erbilgin & Colgan (2012); Taft et al (2015, data only from Alberta); Erbilgin et al. 2014, 2017a; Lusebrink et al. 2016.

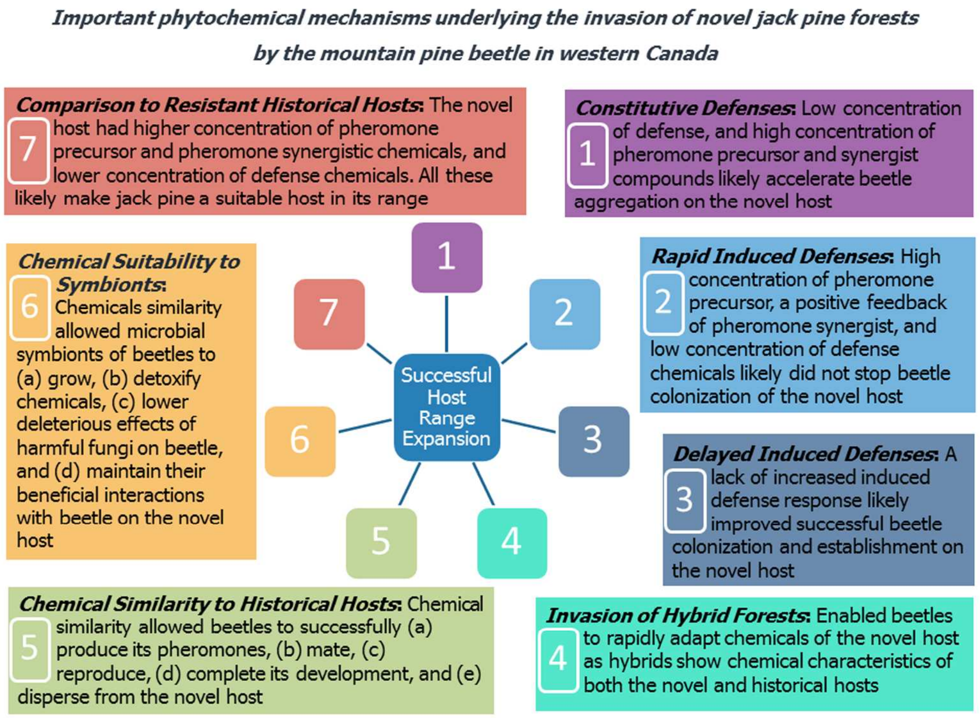
[3] Erbilgin et al. 2017a; Lusebrink et al. 2016.

[4] Erbilgin et al. 2017a; Lusebrink et al. 2016.

Table 5. Differences in *Dendroctonus ponderosae* female gallery lengths, number of larvae per treatment, and length of larval galleries per treatment between different bacterium–fungus combinations in *Pinus contorta* and *P. banksiana*.

Treatments	Female Gallery Length	Number of Larvae	Larval Gallery Length
Grosmannia clavigera (Gc) alone	⬛	⬛	⬛
Ophiostoma montium (Om) alone	⬛	🟫	⬛
Trichoderma (Tr) alone	⬛	⬛	⬛
Aspergillus (Ag) alone	⬛	▨	▨
Gc + Bacillus	▨	▨	▨
Om + Bacillus	▨	▨	▨
Tr + Bacillus	🟧	🟫	🟦
Ag + Bacillus	▨	▨	▨
Gc + Pseudomonas sp. D4-22	🟫	⬛	🟫
Om + Pseudomonas sp. D4-22	▨	▨	▨
Tr + Pseudomonas sp. D4-22	🟫	🟫	🟫
Ag + Pseudomonas sp. D4-22	🟫	🟧	🟫
Gc + Stenotrophomonas	▨	▨	▨
Om + Stenotrophomonas	🟫	🟫	🟫
Tr + Stenotrophomonas	▨	▨	▨
Ag + Stenotrophomonas	🟦	⬛	🟦
Gc + Pseudomonas sp. Hy4T4	▨	▨	▨
Om + Pseudomonas sp. Hy4T4	🟫	⬛	🟧
Tr + Pseudomonas sp. Hy4T4	🟧	⬛	▨
Ag + Pseudomonas sp. Hy4T4	🟦	⬛	🟧

Black boxes indicate no difference between tree species. Dark brown ($P < 0.01$) and light brown ($P < 0.05$) boxes indicate *P. contorta* was superior over *P. banksiana* while blue box indicates that *P. banksiana* was superior to *P. contorta*. Gray boxes indicate that there was not sufficient data for one *Pinus* species or the other. Data were shown in Therrien et al. (2015).



Important phytochemical mechanisms underlying the invasion of novel jack pine forests by the mountain pine beetle in western Canada

7 ***Comparison to Resistant Historical Hosts*:** The novel host had higher concentration of pheromone precursor and pheromone synergistic chemicals, and lower concentration of defense chemicals. All these likely make jack pine a suitable host in its range

1 ***Constitutive Defenses*:** Low concentration of defense, and high concentration of pheromone precursor and synergist compounds likely accelerate beetle aggregation on the novel host

6 ***Chemical Suitability to Symbionts*:** Chemicals similarity allowed microbial symbionts of beetles to (a) grow, (b) detoxify chemicals, (c) lower deleterious effects of harmful fungi on beetle, and (d) maintain their beneficial interactions with beetle on the novel host

2 ***Rapid Induced Defenses*:** High concentration of pheromone precursor, a positive feedback of pheromone synergist, and low concentration of defense chemicals likely did not stop beetle colonization of the novel host

3 ***Delayed Induced Defenses*:** A lack of increased induced defense response likely improved successful beetle colonization and establishment on the novel host

5 ***Chemical Similarity to Historical Hosts*:** Chemical similarity allowed beetles to successfully (a) produce its pheromones, (b) mate, (c) reproduce, (d) complete its development, and (e) disperse from the novel host

4 ***Invasion of Hybrid Forests*:** Enabled beetles to rapidly adapt chemicals of the novel host as hybrids show chemical characteristics of both the novel and historical hosts

Important phytochemical mechanisms underlying the invasion of novel jack pine forests by the mountain pine beetle in western Canada

254x190mm (300 x 300 DPI)