Commentary

Pine terpenoid defences in the mountain pine beetle epidemic and in other conifer pest interactions: specialized enemies are eating holes into a diverse, dynamic and durable defence system

Joerg Bohlmann

Michael Smith Laboratories, University of British Columbia, Vancouver, BC, Canada V6S 1Z4; Corresponding author (bohlmann@msl.ubc.ca)

Received May 23, 2012; accepted June 5, 2012; handling Editor Danielle Way

During the last 15 years, an epidemic of mountain pine beetle (MPB; Dendroctonus ponderosae Hopkins) and its associated fungal pathogens (e.g., Grosmannia clavigera Robinson-Jeffrey & R.W. Davidson) has swept through ~15 million hectares of lodgepole pine (Pinus contorta Douglas) forests in western Canada and has also infested large areas of pine forests in the northwestern USA. The pine-killing symbiosis of MPB and blue-staining fungi has left behind landscapes of dead trees, an economic scramble and the potential for massively increased carbon emissions from decaying trees (Kurz et al. 2008).

Fuelled by an overabundance of suitable host trees and following the trail blazed by warming climates, rapidly growing populations of the MPB/fungus complex have continued to defy some traditional predictions as to when and where this epidemic would reach its limits: we now know that the MPB epidemic has spread further north and climbed into higher elevations than predicted (Samarasekera, 2012); it has crossed the Rocky Mountain ‘barrier’ from west to east; and—as recently documented with molecular markers (Cullingham et al. 2011)—the MPB has successfully expanded its eastern host range from lodgepole pine into Jack pine (Pinus banksiana Lamb.). Jack pine has become a frontline host species through which the MPB and its vectored fungal pathogens have gained entrance into a wide landscape of boreal forest east of the Rocky Mountains (Safranyik et al. 2010, Cullingham et al. 2011). Unlike its sibling species, lodgepole pine, whose range is historically overlapping with that of MPB and its fungi, Jack pine may not have co-evolved its defences with the MPB/fungus disease system, which offers new uncertainties as to how the epidemic will play out. The major defences of pines against insect pests and fungi include specialized chemicals such as terpenoids of oleoresin and phenolics, as well as anatomical structures such as thick bark, constitutive and traumatic resin ducts and specialized phloem parenchyma cells (Franceschi et al. 2005). Oleoresin presents both a physical and chemical defence system against stem-boring insects and is composed mostly of monoterpenes and diterpene resin acids (Trapp and Croteau 2001, Keeling and Bohlmann 2006a, 2006b). As a physical barrier of complex chemical composition, resin flow at wound sites upon beetle attack, mobilization of resin flow and additional formation of resin directed towards the sites of bark beetle and fungal activity after entering the tree, as well as variation of resin volume and composition, present a complex set of parameters that have to be considered in the assessment of host tree defence capacity and how this capacity may be affected by tree health, environment and pests (Raffa et al. 2005, Boone et al. 2011, Ott et al. 2011, Clark et al. 2012, Novick et al. 2012).

Terpenoid defences, including accumulation of oleoresin and volatil emissions, and their underlying biochemical pathways are well characterized in several conifer species (Keeling and Bohlmann 2006a, 2006b). Species of spruce such as Norway spruce (Picea abies Karst.), white spruce (Picea glauca (Moench) Voss) and Sitka spruce (Picea sitchensis (Bong.) Carr.) have been established as a reference system for information on anatomical, chemical, biochemical, molecular and genomic aspects of conifer terpenoid defences (Zulak and Bohlmann 2010, Hall et al., 2011, Hamberger et al., 2011, Keeling et al. 2011). Species of spruce have also been characterized for the roles of terpenoids in tree–insect or tree–fungal interactions (e.g., Byun-McKay et al. 2006, Zeneli et al. 2006,
These and other studies have shown that terpenoid defences of conifers are diverse and variable: monoterpenes, sesquiterpenes and diterpenes, including the diterpene resin acids, accumulate with dozens of chemically different compounds in any given conifer tree and the profiles of these chemicals show considerable inter- and intra-specific variations, even between closely related genotypes of the same species (e.g., Robert et al., 2010, Hall et al., 2011). Terpenoid defences of conifers are also dynamic: aside from changes during the growing season and over the many years of tree growth and development, terpenoid quantities and their qualitative composition in the oleoresin and volatile emissions can change dramatically in response to real and simulated insect or fungal attack (e.g., Martin et al. 2002, 2003, Byun-McKay et al. 2003, Miller et al. 2005, Zulak et al., 2009).

In this issue, Erbilgin and Colgan (2012) report on some of the dynamics of induced Jack pine terpene chemicals in response to a suite of real and simulated fungal treatments, including inoculation with the MPB-associate *G. clavigera*, and they identified differences in the response to individual treatments and between mature and juvenile trees. This work provides a basis for comparison with the previously established knowledge of constitutive and induced lodgepole pine terpenoid defence systems in the MPB/*G. clavigera* epidemic (Boone et al. 2011, Ott et al. 2011). Recent work in the lodgepole pine system has made major strides in untangling information about the variation of terpenoid chemical defences affected by tree genetics and environment (Ott et al. 2011), and their variable effectiveness in the different real-world scenarios of endemic, incipient and epidemic MPB pressure (Boone et al. 2011). In ongoing genomic research (J. Bohlmann and D.E. Hall, unpublished results), the genes and enzymes for the biosynthesis of terpenes are now being investigated in both Jack and lodgepole pines to identify genomic and mechanistic underpinnings of the observed variations reported by Boone et al. (2011), Ott et al. (2011) and Erbilgin and Colgan (2012).

One of the overriding questions in the characterization of terpenoids in pine hosts of the MPB/fungal epidemic is how beetles and fungi cope with these tree defences. While conifer terpenoid defences provide a strong and durable shield of protection against most generalist herbivores and non-pathogenic fungi, they are not a perfect barrier against a relatively small number of species of specialized insect pests and fungi. These specialists, which under suitable environmental or forest management conditions cause massive damage to conifer forests, have evolved some unique biochemical, physiological, ecological or behavioural adaptations to cope with the host tree defences. While the resin load of a 100-year-old pine tree may appear like a monstrous tsunami against an individual beetle, mass attack by large numbers of con-specific insects in concert with dense fungal inoculation can overwhelm and exhaust the defence capacity of the tree. Much shorter generation times of beetles, compared with the trees, may have provided an additional edge in the evolution of molecular mechanisms by which beetles cut through the pine’s defensive pitch.

Mechanisms of beetles to cope with, undermine or even take advantage of pine terpenoid defences are numerous. Volatile terpenoid emissions play important roles as semiochemicals in host recognition and can serve as precursors for bark beetle pheromones (Seybold et al. 2000). The molecular mechanisms of olfaction and pheromone formation in the MPB are now being elucidated using genomic approaches (Aw et al. 2010, Keeling et al. 2012). Likewise, comprehensive genome and transcriptome analyses of the MPB-associated *G. clavigera* revealed mechanisms of coping with monoterpenoid defences (Diguistini et al., 2011). This fungus has a unique molecular system to actively transport and tolerate monoterpenoid compounds of the host pine defence, and also uses select monoterpenes as a carbon source to support fungal growth (Diguistini et al., 2011).

In summary, while a tree-centric perspective may have been prevailing for some time in the literature on conifer defence systems, bark beetles and fungi can eat some painful holes into simplified concepts of terpenoid defences of pines. While terpenoid defences are diverse, dynamic and often durable, through the evolution of specialist beetles and fungi, they also present a source of attractive information, signals and food for the tree’s most ferocious natural enemies.

In addition, terpenes are also an ideal biofuel of hydrocarbons which, in nature, let pine forests easily go up in flames (Bohlmann et al., 2011). A high content of flammable terpene hydrocarbons may also increase fire hazards in saw mills now processing massive amounts of MPB-killed pines.

**Acknowledgments**

I thank Ms Karen Reid and Dr Carol Ritland for outstanding project management support. I thank Ms Kate Wilczak for reading of the manuscript.

**Funding**

Work by the author and much of the recent work by others on the MPB system has been supported with funds for the Tria Project (www.thetriaproject.ca) provided by Genome Canada, Genome British Columbia and Genome Alberta. Support for research on conifer defence in the author’s laboratory was also supported by Genome Canada and Genome British Columbia through the Treenomix Project (www.treenomix.ca) and the SMarTForests Project (www.smartforests.ca), and by the Natural Science and Engineering Research Council of Canada (NSERC).
References


