



The influence of variation in host tree monoterpene composition on secondary attraction by an invasive bark beetle: Implications for range expansion and potential host shift by the mountain pine beetle



Jordan L. Burke*, Allan L. Carroll

Department of Forest and Conservation Sciences, Faculty of Forestry, The University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada

ARTICLE INFO

Article history:

Received 17 July 2015

Received in revised form 18 September 2015

Accepted 27 September 2015

Keywords:

Dendroctonus

Climate change

Range expansion

α -Pinene

Pheromone production

ABSTRACT

The range of mountain pine beetle (*Dendroctonus ponderosae*) has expanded in recent years to include many evolutionarily naïve forests in western Canada. These forests include novel populations of the principal host species, lodgepole pine (*Pinus contorta*), the novel species jack pine (*Pinus banksiana*), and their hybrids (*P. contorta* × *P. banksiana*). These novel forests are chemically and physically different than native forests, and recent studies have shown beetle reproductive performance is enhanced in these novel habitats. We conducted a field experiment to determine the effect of differing host chemistry, specifically α -pinene content, on secondary attraction by foraging mountain pine beetles. Alpha-pinene is the precursor molecule for the production of *trans*-verbenol, the main aggregation pheromone for this beetle species. We found that elevated relative concentrations of α -pinene in bolts significantly increased their attractiveness to *in situ* mountain pine beetles. Seventy-five percent of attacks were found on infested bolts with the most α -pinene relative to other monoterpenes. Other measures of terpene chemistry between bolt types could not explain the pattern of attacks. This result suggests that elevated concentrations of α -pinene could increase the rate of aggregation and attack success by the mountain pine beetle in novel pine forests. Newly invaded hybrid and jack pine in the western boreal forest are reported to contain 3–4 times the relative concentration of α -pinene than lodgepole pines in forests in which the beetle has coevolved. These elevated concentrations may help the mountain pine beetle overcome some of the potential restraints for establishment and spread in the boreal forest, such as low pine volume and connectivity, and continue expanding its range.

Crown Copyright © 2015 Published by Elsevier B.V. All rights reserved.

1. Introduction

Due to their short life cycles, high reproductive potential and mobility, and physiological sensitivity to temperature changes, herbivorous insects are highly susceptible to variations in weather and climate (Deutsch et al., 2008; Logan et al., 2003; Musolin, 2007; Parmesan, 2006). To date, the most common response by insect species to a warming environment involves distributional changes, including both range expansions (Hickling et al., 2006, 2005; Parmesan et al., 1999), and range contractions (Visser and Holleman, 2001; Wilson et al., 2005). Range shifts have often resulted in novel herbivore–host plant associations (Braschler and Hill, 2007; Cullingham et al., 2011), and where these have occurred, evidence suggests herbivore impacts may be greater than

expected due to insufficiently co-evolved plant defenses (Cudmore et al., 2010; Raffa et al., 2013).

The recent, unprecedented outbreak by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in western North America has seen the species expand its range north in latitude and up in elevation into novel habitats (Aukema et al., 2008; Carroll et al., 2004). Historically, the mountain pine beetle was restricted to areas west of the Rocky Mountains and at latitudes <56°N (Safranyik and Carroll, 2006). Its distribution was not limited by host availability, but by the adverse effects of climate (Carroll et al., 2004; Safranyik, 1978; Sambaraju et al., 2012; Bentz et al., 2010). The beetle has expanded its range due in part to increases in temperature resulting from climate change (Carroll et al., 2004), and to forest management practices that have favored highly susceptible forests conditions (Taylor and Carroll, 2004). In 2002, dispersing mountain pine beetles breached the Rocky Mountain geoclimatic barrier and spread into north-central Alberta (Giroday et al., 2011; Safranyik and Carroll, 2006;

* Corresponding author.

E-mail address: jordan.lewis.burke@gmail.com (J.L. Burke).

Safranyik et al., 2010). Since then, infestations have been detected in the Northwest Territory (north of 60° latitude), and within 50 km of the Alberta/Saskatchewan border (110°W longitude) (A L Carroll, pers. obs.). In the historic range in western Canada, the principal host of the mountain pine beetle is lodgepole pine (*Pinus contorta* Douglas var. *latifolia*), but it can successfully reproduce in most native and introduced *Pinus* species in North America (Furniss and Schenk, 1969). As a consequence of its abrupt range expansion, the beetle has established within habitats comprising novel (i.e. putatively evolutionarily naïve (Cudmore et al., 2010)) populations of lodgepole pine, a novel host species in jack pine (*Pinus banksiana* Lamb.), and the intermediate hybrid (*P. contorta* × *P. banksiana*) zone (Cullingham et al., 2011).

Jack pine is a principal species of the transcontinental boreal forest, and the rapid expansion by mountain pine beetle into this novel host type has raised concern that the beetle could spread across North America (Logan and Powell, 2001; Nealis and Peter, 2009; Safranyik et al., 2010). It has been observed that mountain pine beetle reproductive performance is enhanced in evolutionarily naïve lodgepole pine forests as compared to evolutionarily experienced forests, in the form of increased attack densities (Clark et al., 2010) and the number of surviving offspring produced per female (Cudmore et al., 2010). Population genetic studies have revealed that the beetle has been undergoing a post-Pleistocene demographic expansion northward (Bentz et al., 2010; Mock et al., 2007), following behind an earlier expansion by lodgepole pine (Cwynar and MacDonald, 1987; MacDonald and Cwynar, 1985). Thus, the beetle has likely been absent from the boreal region since at least the last glaciation period.

Mountain pine beetles feed in the phloem tissue of their host trees, and therefore must overcome the complex physical and chemical defenses produced by the trees. Sub-outbreak (i.e. endemic) populations characteristically comprise very low densities that are restricted to colonizing trees with impaired defenses (Safranyik and Carroll, 2006). These trees are usually weakened by biotic or abiotic agents, and are normally occupied by other species of bark beetles that are specialists on defensively impaired trees (Safranyik and Carroll, 2006; Smith et al. 2011). If conditions (e.g., mild winters that increase over-winter survival; hot/dry summers that increase colonization success) facilitate reduced generation mortality, populations may increase through an incipient-epidemic phase to the outbreak, or epidemic phase, in which they can colonize and kill many hectares of large-diameter, thick-phloem trees by way of pheromone-mediated aggregation and mass attack (Berryman, 1982). Attraction to infested hosts is termed “secondary attraction”, as opposed to “primary attraction” by foraging pioneer beetles in response to host characteristics (Pureswaran and Borden, 2003). Boone et al. (2011) demonstrated that host selection behavior and preference changes with population density, where endemic mountain pine beetles prefer trees with weak defenses, and epidemic beetles prefer trees with strong defenses (measured by the content of defensive chemicals in the resin). Trees with strong defenses are generally healthier, have thicker phloem, and therefore provide greater quantity and quality of resources for offspring development. These trees also tend to be very abundant in mature pine-dominated landscapes, and so this behavior is an adaptation that provides access to plentiful, high-quality resources in the absence of interspecific competition (Raffa et al., 2008).

Pinus spp., such as lodgepole pine, have evolved highly effective defenses against attack by bark beetles (Franceschi et al., 2005). When severed, constitutive resin ducts in the bark exude resin that physically and chemically repels attacking beetles (Berryman, 1972; Shrimpton and Whitney, 1968). If beetles overwhelm the constitutive defenses, penetrate the bark and encounter the live tissues beneath, an induced response is initiated that involves

the breakdown of parenchyma cells, formation of traumatic resin ducts, and the production of secondary resin containing higher concentrations of toxic terpenes and phenolic chemicals (Franceschi et al., 2005; Safranyik and Carroll, 2006). Mountain pine beetles have evolved to take advantage of host defensive chemicals, particularly in the use of the monoterpene resin constituent α -pinene as a pheromone precursor. Alpha-pinene is converted to *trans*-verbenol via cytochrome p-450 mediated hydroxylation by females upon initiation of attack (Blomquist et al., 2010; Gries et al., 1990; Keeling and Bohlmann, 2006; Pierce et al., 1987). There are other aggregation pheromones utilized by mountain pine beetles, such as *exo*-brevicomin, but *trans*-verbenol is the primary semiochemical for initiation of mass attack (Borden et al., 1987; Progar et al., 2014). Epidemic mountain pine beetles respond in a dose-dependent fashion to *trans*-verbenol, but not to *exo*-brevicomin, which is synthesized *de novo* by males and is therefore mostly independent of host tree chemistry (Blomquist et al., 2010; Miller et al., 2005). Mountain pine beetle's dependence on *trans*-verbenol for secondary attraction suggests that variations in host tree α -pinene content across populations and species may affect the beetle's aggregation rates and attack success, as α -pinene is the direct precursor of *trans*-verbenol. Evidence indicates that mountain pine beetles in newly invaded pine forests have begun to encounter elevated concentrations of α -pinene. Comparison of lodgepole pine phloem chemistry reveals more α -pinene in naïve populations (Clark et al., 2010), and jack pine monoterpene profiles are predominantly comprised of α -pinene (Clark et al., 2014; Taft et al., 2015b). Recent studies have also shown α -pinene content of the phloem is directly related to the production of *trans*-verbenol by feeding female mountain pine beetles (Erbilgin et al., 2014; Taft et al., 2015a). In this study, we evaluated the hypothesis that α -pinene content will influence the secondary attraction of mountain pine beetles in an active infestation. Our prediction was that higher α -pinene concentrations in infested bolts will be more attractive to foraging beetles.

2. Methods and materials

2.1. Experimental site selection

To assess aggregation by mountain pine beetles in response to differing levels of α -pinene within their hosts, we conducted a field study within the historic range of the beetle (Safranyik and Carroll, 2006) near Oliver, British Columbia, Canada (N49.110°, W119.177°; elevation ~1300 m) in July of 2012. Sites were established in mature lodgepole pine stands, with a few interspersed aspen (*Populus tremuloides* Michx.) and western larch (*Larix occidentalis* Nutt.). Stands were 80–100 years-old and averaged ~20 m²/ha basal area with ~600 stems per hectare, which are conditions considered highly suitable for mountain pine beetle outbreak (Shore and Safranyik, 1992). Stands were located in the transition between the Interior Douglas-fir and Montane Spruce biogeoclimatic zones (<https://www.for.gov.bc.ca/hre/becweb/>). Epidemic mountain pine beetle infestations were observed (i.e. clusters of large-diameter trees with foliage “fading” from yellow to red) sporadically throughout the area.

2.2. Trap bolt selection and preparation

Naïve lodgepole (LPN), jack pine (JP), and lodgepole × jack pine hybrid (HYB) bolts were harvested near Slave Lake, Alberta, Canada [LPN: N54°51' W115°18', elev. 900 m; JP: N55°04' W114°06', elev. 577 m; HYB: N55°33' W114°53', elev. 652 m], from sites that had been thoroughly genotyped by Cullingham et al. (2011), and immediately transported to the experimental site. Experienced

Download English Version:

<https://daneshyari.com/en/article/6542623>

Download Persian Version:

<https://daneshyari.com/article/6542623>

[Daneshyari.com](https://daneshyari.com)