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Attraction of red turpentine beetle and other Scolytinae to ethanol, 3-carene or ethanol + 3-carene in an Oregon pine forest

Rick G. Kelsey* **and Douglas J. Westlind***

USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331, U.S.A

Abstract

1 Red turpentine beetle *Dendroctonus valens* LeConte is a non-aggressive bark beetle in North America that attacks weakened or recently dead pines, as well as their fresh logs or stumps. Fire-injured ponderosa pines releasing stress-induced ethanol are often attacked. The oleoresin from these trees frequently contains 3-carene as a major component mixed with α- or β-pinene. 3-Carene lures usually attract more *D. valens* than α- or β-pinene lures or 1 : 1 : 1 mixtures, whereas the attraction of ethanol + 3-carene lures has never been tested.

2 Funnel traps with ethanol, 3-carene or ethanol + 3-carene lures, and a no lure blank, were set-up as a randomized complete block design in a pine forest near La Pine, Oregon, U.S.A., from 23 April until 11 June 2015.

3 *Dendroctonus valens*, *Hylastes nigrinus*, *Hylurgops reticulatus*, *Hylurgops porosus* and *Hylastes gracilis* exhibited similar responses, with highest numbers captured in traps with ethanol + 3-carene. The response by the first three species was confirmed as synergistic.

4 *Ips* spp., *Pityogenes* spp., *Gnathotrichus* spp., *Pachysquamus subcostulatus* and *Hylastes macer* composed a second group whose numbers captured with ethanol lures were similar or greater than the 3-carene or ethanol + 3-carene lures. A reduced *H. macer* response to ethanol + 3-carene was confirmed as an interruption.

Keywords 3-Carene, *Dendroctonus valens*, ethanol, host selection, kairomones, synergism.

Introduction

Red turpentine beetle *Dendroctonus valens* LeConte (Coleoptera: Curculionide: Scolytinae) is a native North American bark beetle found in pine forests on both sides of the Great Plains but not in the south-eastern states (Owen *et al*., 2010; Taerum *et al*., 2013). Its behaviour is typically nonaggressive, colonizing weakened, dying or recently dead pines, plus their fresh logs and stumps. Fire-stressed trees are particularly vulnerable to attacks by *D. valens* (Bradley & Tueller, 2001; McHugh *et al*., 2003; Perrakis & Agee, 2006; Schwilk *et al*., 2006; Hood *et al*., 2007; Fettig *et al*., 2008, 2010; Six & Skov, 2009; Youngblood *et al*., 2009), although they do not contribute substantially to post-fire tree mortality (Fettig *et al*., 2008; Owen *et al*., 2010; Fettig & McKelvey, 2014; Negrón *et al*., 2016).

Correspondence: Rick G. Kelsey. Tel.: +1 541 750 7368; fax: +1 541 758 7760; e-mail: rkelsey@fs.fed.us

*Present address: USDA Forest Service, Pacific Northwest Research Station, 3200 Jefferson Way, Corvallis, OR 97331, U.S.A.

In the U.S. Intermountain region, the probability of post-burn attacks by *D. valens* may be predicted by bole or crown scorch heights (Negrón *et al*., 2016). These injuries are related to the internal heat stress that the tree tissues experience and their associated physiological responses, including ethanol synthesis and accumulation, which contributes to the primary attraction of *D. valens* (Kelsey & Westlind, 2017a, b). For example, ethanol concentrations in phloem and sapwood 2 cm above the gallery entrance holes of pioneering *D. valens* on fire damaged ponderosa pine *Pinus ponderosa* Douglas ex P. Lawson & C. Lawson were greater than those in tissues from opposite sides of the same tree without a nearby gallery, as well as tissues from unattacked neighbours with similar visual fire damage (Kelsey & Westlind, 2017b). In addition, almost all other preferred host materials for *D. valens* are under some form of physiological stress known to induce ethanol synthesis (Sjödin *et al*., 1989; Kelsey, 1994a, b; von Sydow & Birgersson, 1997; Kelsey & Joseph, 1999; Kelsey *et al*., 2013, 2014). In conifer tissues, ethanol is always associated with some quantity of monoterpenes that are continuously released into the atmosphere from

healthy and stressed stem tissues (Rhoades, 1990; Gara *et al*., 1993). This may explain why *D. valens* exhibits a stronger primary attraction to traps baited with ethanol + host oleoresin or + individual monoterpenes than to traps with only ethanol lures (Vité & Gara, 1962; Gandhi *et al*., 2010).

Combining ethanol with host monoterpenes lures usually attracts more *D. valens* than the monoterpene lures alone. Traps with 1 : 1 ethanol : turpentine lures in declining red pine *Pinus resinosa* Aiton plantations in Wisconsin caught 60-fold more *D. valens* than traps baited with only turpentine in a preceding year (Klepzig *et al*., 1991). In California, traps releasing ethanol + [1 : 1 : 1; (+)-α-pinene : (−)-β-pinene : (+)-3-carene] captured 1.2-fold more *D. valens* than traps with just the monoterpene mixture, although the difference was not statistically greater (Fettig *et al*., 2004). The influence of ethanol on primary attraction has also been demonstrated by increasing its release rate at the same time as holding the associated monoterpene lure release rate constant, resulting in high release ethanol lures that attract 3.3-fold more beetles than those with a low ethanol release rates when combined with 1 : 1 α-pinene : β-pinene (Joseph *et al*., 2001). The response to increased ethanol release rates when α-pinene was the monoterpene lure depended on the chiral form, with an increased beetle response to ethanol : (−)-α-pinene of 5 : 1 over the 1 : 1 baited traps; the opposite response was observed with ethanol : (+)-α-pinene 5 : 1 versus 1 : 1 lures (Erbilgin *et al*., 2001). Finally, there are examples where ethanol + α-pinene baited traps capture substantial numbers of *D. valens* over a field season without comparisons with other lure types (Dodds, 2014).

Host oleoresin or individual host monoterpenes without ethanol also function as primary attractants for *D. valens* (Vité & Gara, 1962; Klepzig *et al*., 1991; Sun *et al*., 2004; Erbilgin *et al*., 2007). The three-component lure with 1 : 1 : 1 (+)-α-pinene : (−)-β-pinene : (+)-3-carene is used as a standard bait to monitor and study red turpentine beetle (Fettig *et al*., 2004, 2006, 2007; Gaylord *et al*., 2006). Tests comparing those three components individually have shown (+)-3-carene to be the most preferred compound in North America, as well as in China (Sun *et al*., 2004; Erbilgin *et al*., 2007) where *D. valens* is an invasive species that has been associated with millions of dead and dying *Pinus tabuliformis* Carr. from 1999 onwards (Sun *et al*., 2013). A preference for (+)-3-carene aligns with various North American pine species that produce it as one of their major xylem resin components (Smith, 2000). However, there are examples where *D. valens* responds in greater numbers to other compounds. In California, traps baited with (−)-β-pinene caught more beetles than those with (+)-3-carene or a mixture of α-pinene enantiomers, and trap catches increased with each increase in (−)-β-pinene release rate (Hobson *et al*., 1993). Oleoresins from *P. tabuliformis* hosts in China contain α-pinene as the major component, plus substantial β-pinene, limonene and myrcene, whereas they only have minimal amounts of (+)-3-carene (Liu *et al*., 2011; Xu *et al*., 2014). *Pinus tabuliformis* with a larger diameter (30 cm), and with α-pinene as the major resin component, is preferred over smaller trees (10 cm) with an almost equal mix of α- and β-pinene (Liu *et al*., 2011). Oleoresin from large trees or a mimic blend was more attractive to *D. valens* in laboratory choice tests than the oleoresin or mimic blend of small trees (Liu *et al*., 2011). Although (+)-3-carene is often the preferred host kairomone, these beetles maintain a broad attraction plasticity to other host monoterpenes.

With ethanol present in many of the stressed pine hosts colonized by *D. valens*, and their preference for 3-carene, which is often the dominant monoterpene in ponderosa pine, we were interested in how these beetles would respond to ethanol + 3-carene lures relative to each lure separately. The present study aimed to compare the attraction of *D. valens* with traps baited with ethanol, 3-carene, ethanol + 3-carene, as well as a no lure blank.

Materials and methods

Study site

The study site is located approximately 6 km, aerial distance East of La Pine, Oregon, U.S.A. (43° 39.465′N; 121° 24.360′W) at an elevation of 1384 m. Prior to thinning in April 2014, the overstory in this area was dominated by uneven aged ponderosa pine and a minor component of lodgepole pine *Pinus contorta* Douglas ex Loudon, with diameters ranging from 18–76 cm, and a basal area from 9–23 m^2/ha. The understory was composed of lodgepole pine (60%) and ponderosa pine (40%) with 494–4942 trees/ha. Thinning treatment objectives were to maintain large ponderosa dominance interspersed with some lodgepole, at a target basal area of 11–13 m^2/ha, and no more than 334 trees/ha. Noncommercial stems and slash were piled for later burning and remained through the 2015 trap period.

Trap set-up

The experiment was set-up as a randomized complete block design with 15 blocks each containing four, Lindgren style, 16-unit multiple-funnel traps. Blocks were set up as parallel lines positioned at least 50 m apart, whereas traps within blocks were set at least 30 m apart. Each trap was secured to a metal rod with a 90° bend at the top for attachment, with catch cup bottoms 10–20 cm above the forest floor. Traps were at least 3 m from any potential host trees. The four test lures, ethanol, 3-carene, ethanol + 3-carene and a blank (no lure), were randomly assigned to traps within each block and attached on 23 April, 2015. Lures were not re-randomized within blocks between trap periods. Ethylene glycol antifreeze was added to the catch cups to kill and preserve beetles (Miller & Duerr, 2008), which were collected on 1, 16, 29 May and 11 June 2015.

Ethanol and 3-carene lures were obtained from Synergy Semiochemicals Corp. (Canada). (+)-3-Carene was released from low density polyethylene bottles inside a thin, white plastic bag, and ethanol UHR (ultrahigh release) from membrane pouches (approximately 31 by 10 cm when folded midway lengthwise). The release rates provided by the supplier were approximately 100–200 mg/day for 3-carene and 300 mg/day for ethanol, depending on temperature. The top ends of the ethanol lures were attached outside the sixth funnel above the catch cup, with ethanol at the bottom of the pouch near the third funnel. Single 3-carene lures were also attached at the third funnel but, when combined with ethanol lures, they were secured to the lower end

of the pouches so that both vapours would mix thoroughly as released.

Statistical analysis

Beetle responses to lure main effects and their interaction was evaluated with a randomized complete block 2^2 factorial analysis of variance (ANOVA) design with two lure types (ethanol and 3-carene), each at two levels (absent, present). The total number of beetles caught in each trap was summed over the entire period for each species and then analyzed separately by the generalized linear mixed models procedure (PROC GLIMMIX) in SAS, version 9.4 (SAS Institute, 2012) using a Poisson distribution for count data with a log link function. Block was modelled as a random effect and lure combination as a fixed effect. Assumptions of normality and equal variance of the residuals were checked during analysis through the use of quantile–quantile and residual versus predicted plots, respectively. $P < 0.05$ was considered statistically significant for the ANOVA model results. The least squares means and 95% confidence intervals were back-transformed for presentation.

A synergistic beetle response was defined as a combined ethanol + 3-carene lure trap catch greater than the sum of the trap catches by the two individual lures in conjunction with a significant interaction term in the analysis. An interruption was defined as combined ethanol + 3-carene lure trap catch lower than the sum of the trap catches by the two individual lures in conjunction with a significant interaction term in the analysis.

Results

Almost 14 000 Scolytinae beetles, representing 14 species or genera groups, were captured over the entire trap period. The cumulative catch for five species was over 500 beetles each, and the other nine were all less than in 200 total, with the 10 most abundant being analyzed statistically (Table 1). Based on similarities in beetle response patterns to ethanol + 3-carene lures, relative to the individual lures, species were further divided into two groups of five (Figs 1 and 2). The first group (Fig. 1) had mean ethanol + 3-carene catches that were equal or greater than the sum of means for traps with individual ethanol and 3-carene lures. Additionally, the catch by 3-carene lures was higher than or similar to traps with ethanol lures. All these species were attracted to lures with 3-carene or lures with ethanol, except *H. gracilis* LeConte, which did not respond to lures with just ethanol. *Dendroctonus valens*, *Hylastes nigrinus* (Mannerheim 1852) and *Hylurgops reticulatus* Wood responded synergistically to the ethanol + 3-carene lures (Ex3C *P* values) (Fig. 1), which also attracted the greatest number of *Hylurgops porosus* (LeConte 1868) but not sufficiently higher than the sum of both individual lures to be a statistical synergism. The response of *Hylastes gracilis* to ethanol + 3-carene lures was comparable to adding the catches from individual ethanol and 3-carene lures (Ex3C *P* values) (Fig. 1).

The second group of five species (Fig. 2) was characterized by mean ethanol + 3-carene catches being lower than the sum of means for traps with individual ethanol and 3-carene lures. In addition, the numbers caught by 3-carene lures were lower

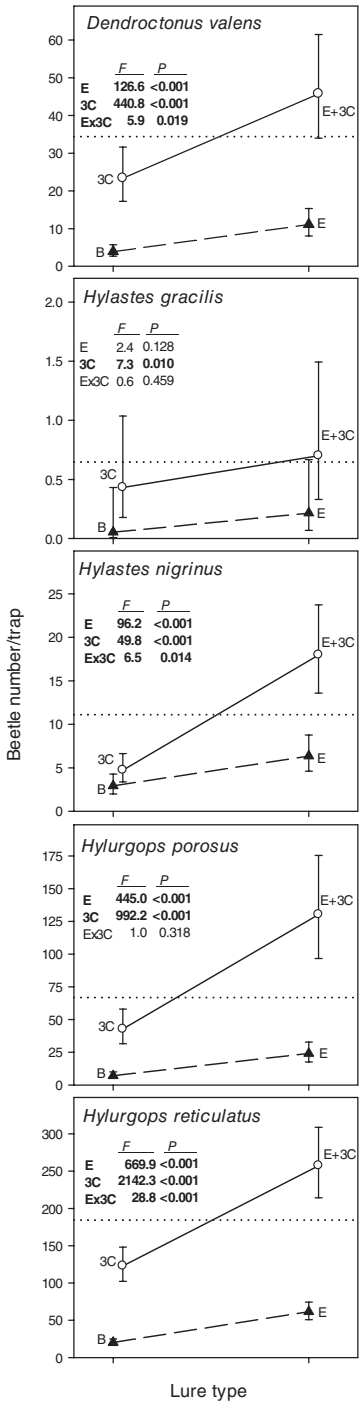

Figure 1 Mean number of beetles trapped by lure type ($n = 15$) for the five species with a trap catch by ethanol + 3-carene lures matching or exceeding the summed catch by traps with separate ethanol and 3-carene lures (horizontal dotted line), in a ponderosa pine forest near La Pine, Oregon from 23 April until 11 June, 2015. Symbols are back-transformed geometric means and the 95% confidence interval (CI), offset horizontally to eliminate CI overlap. The results of the analysis of variance shown in bold indicate statistical significance (d.f. = 1,42 for all species). The solid line connects traps with 3-carene lures present, and the dashed line connects traps without 3-carene. Lure type: B, blank; 3C, 3-carene; E, ethanol.

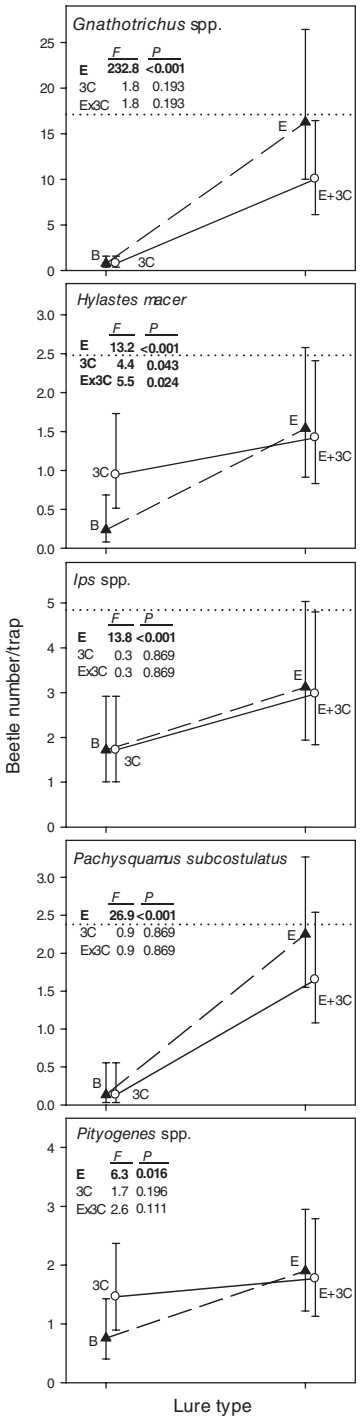

Figure 2 Mean number of beetles trapped by lure type ($n = 15$) for the five species or genera with a trap catch by ethanol + 3-carene lures lower than the summed trap catch of the separate ethanol and 3-carene lures (horizontal dotted line), in a ponderosa pine forest near La Pine, Oregon from 23 April until 11 June, 2015. Symbols are back-transformed geometric means and 95% confidence interval (CI), offset horizontally to eliminate CI overlap. The results of the analysis of variance shown in bold indicate statistical significance (d.f. = 1,42 for all species). The solid line connects traps with 3-carene lures present, and the dashed line connects traps without 3-carene. Lure type: B, blank; 3C, 3-carene; E, ethanol.

than those by ethanol lures. All taxa in this group were attracted to lures with ethanol, although only *Hylastes macer* responded to lures with 3-carene in statistically higher numbers than lures without it (Fig. 2). *Hylastes macer* also expressed an interaction between ethanol and 3-carene lures but, unlike species in the first group, it was an inhibitory antagonism or interruption.

Discussion

Ethanol lures alone did attract *D. valens*, although traps with 3-carene lures captured 2.1-fold more beetles. The ethanol + 3-carene lures attracted the most beetles and, although just 1.3-fold greater than the sums from traps with individual ethanol and 3-carene lures, the response was synergistic. This synergism is especially relevant to pioneering *D. valens* host selection and colonization of fire-injured ponderosa pine that accumulate ethanol in response to sublethal heat stress (Kelsey & Westlind, 2017a, b) because 3-carene is the most abundant compound in approximately 22 of the 60 common xylem resin types of ponderosa pine identified across its geographical range, and the second major resin constituent in approximately 20 additional resin types (Smith, 2000). Ethanol concentrations in the phloem and sapwood sampled 2 cm above *D. valens* gallery entrances in fire stressed ponderosa pine were 3.2- to 35.2-fold greater than those on the opposite bole side with no gallery entrance or in an adjacent unattacked tree with similar fire injury (Kelsey & Westlind, 2017b). This is also consistent with *D. valens* responding in greater numbers to ethanol lures with high release rates over those with low release rates when both were combined with the same (1 : 1, α-pinene : β-pinene) lures (Joseph *et al*., 2001). *Hylurgops reticulatus* and *H. nigrinus* responded similar to *D. valens* to the four lures, including synergistic responses to ethanol + 3-carene. *Hylurgops porosus* responses mimicked the three species above, although the higher trap catches with ethanol + 3-carene lures were not confirmed statistically as a synergistic response because just a few traps with this lure caught a high proportion of the beetles.

A second group of five taxa, mostly in low numbers except for the *Gnathotrichus* spp., responded in greater numbers to ethanol than 3-carene or their combination. One possible explanation is they may prefer α-pinene or β-pinene over 3-carene or some combination of all three. All of these taxa but the *Pityogenes* spp. were previously captured in traps with ethanol + (1 : 1) α-pinene : β-pinene lures (Joseph *et al*., 2001).

Ethanol lures attracted *D. valens* and eight other Scolytinae taxa. This attraction is consistent with the host selection of these nonaggressive, secondary beetles that typically colonize stressed, dying or recently dead trees, as well as fresh slash, logs or stumps (Furniss & Carolin, 1977). Many of these woody materials, such as the burned trees mentioned above, may synthesize and accumulate ethanol when stressed by pathogen infection (Kelsey *et al*., 2013, 2016), drought (Manter & Kelsey, 2008; Kelsey *et al*., 2014), flooding (Joseph & Kelsey, 1997; Kreuzwieser *et al*., 2000) or severed stems in the case of logs (Kelsey, 1994a, b) and stumps (von Sydow & Birgersson, 1997; Kelsey & Joseph, 1999). Furthermore, seven of the species here, plus *Ips pini* and *Gnathotrichus retusus*, responded in greater numbers as the ethanol release rates increased (Joseph *et al*.,

Table 1 Total number of each beetle species captured by each lure type in a ponderosa pine forest near La Pine, Oregon from 23 April until 11 June, 2015

Species	Blank	Ethanol	3-Carene	Ethanol + 3-carene	Total
Dendroctonus valens	69	196	412	807	**1484**
Gnathotrichus spp.	16	329	16	203	**564**
Hylastes gracilis	1	4	8	13	26
Hylastes longicollis Swaine	0	1	0	3	4
Hylastes macer	4	26	16	24	**70**
Hylastes nigrinus	48	105	78	296	**527**
Hylastes ruber Swaine	1	2	0	10	13
Hylurgops porosus	123	419	746	2272	**3560**
Hylurgops reticulatus	321	977	1955	4089	**7342**
Hylurgops rugipennis (Mannerheim 1843)	0	1	0	0	1
Ips spp.	33	60	33	57	**183**
Pachysquamus subcostulatus (Mannerheim 1853)	2	34	2	5	**63**
Pityogenes spp.	12	30	23	28	**93**
Trypodendron spp.	3	3	1	2	9
Totals	633	2187	3290	7829	13 939

All are known to vector spores of *Leptographium wageneri*, except *Gnathotrichus* spp., *H. ruber*, *H. rugipennis*, *Pityogenes* spp. and *Trypodendron* spp. (Witcosky *et al*., 1986; Schweigkofler *et al*., 2005). The *P. subcostulatus* was previously *Hylurgops subcostulatus* (Mercado-Vélez & Negrón, 2014). Totals indicated in bold were analyzed statistically (Figs 1 and 2).

2001). This ability enhances their likelihood of finding the most stressed trees with compromised chemical defences (Raffa *et al*., 2005), allowing successful colonization by small numbers of beetles, especially when local population densities are low. It may also direct them to hosts with a higher nitrogen content and better nutritional quality (Ayres *et al*., 2000) because trees with high nitrogen produce substantially greater quantities of ethanol than those with low nitrogen, when stressed similarly (Kelsey *et al*., 1998a).

The influence of ethanol on host selection of these beetles has implications for maintaining and spreading infections of some tree pathogens. Nine of the species captured in the present study, including *D. valens*, may vector spores of *Leptographium wageneri* (W.B. Kendr.) M.J, which is the pathogen causing black stain root disease (Witcosky *et al*., 1986; Owen *et al*., 1987, 2005; Schweigkofler *et al*., 2005). In the case of *D. valens* and fire-injured ponderosa pine, ethanol in the presence of 3-carene or other oleoresin monoterpenes attracts and induces attacks by pioneering beetles (Kelsey & Westlind, 2017b), with some portion carrying spores of *L. wageneri* (Owen *et al*., 1987; Schweigkofler *et al*., 2005). Many of these infested trees remain alive because this beetle does not contribute substantially to post-fire mortality (Fettig *et al*., 2008; Owen *et al*., 2010; Fettig & McKelvey, 2014) and some of the surviving trees will become infected with the vectored fungus. As these trees recover from fire injury, ethanol concentrations associated with heat stress will decline (Kelsey & Joseph, 2003), although those tissues now stressed by *L. wageneri* infection may begin to synthesize and accumulate ethanol, as shown for infected ponderosa pine and Douglas-fir (Kelsey & Joseph, 1998; Kelsey *et al*., 1998b). These diseased trees may attract more *D. valens* (Goheen *et al*., 1985) or other species that respond to ethanol + monoterpene mixtures, vectoring additional pathogen spores into the tissues (Owen *et al*., 2005). Ponderosa pine mortality from *L. wageneri* can occur within 2 years, whereas others slowly decline over multiple years before death, and others survive the infections (Owen *et al*., 2005). Diseased trees actively producing ethanol will likely remain suitable hosts for most of the taxa in the present study, and function as redistribution centres when emerging beetle offspring carry spores to surrounding trees. Thus, the life cycles of *D. valens* and some of the other species here are linked to the life cycle of *L. wageneri* by stress-induced ethanol mixed with tissue monoterpenes, especially 3-carene in ponderosa pine.

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