

North-South Variation in the Response of the Pine Engraver (Coleoptera: Scolytidae) to Lanierone and Ipsdienol in Eastern North America'

D. R. Miller,¹ K. F. Raffa,³ M. J. Dalusky⁴ and C. W. Berisford⁴

U.S.D.A. Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602-2044 USA

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Abstract Lindgren multiple-funnel traps were used to evaluate the response of the pine engraver, *Ips pini* (Say), to the pheromones lanierone and ipsdienol, in Wisconsin and in southern Appalachia (western North Carolina and northern Georgia). As in Wisconsin, the attraction of *I. pini* to ipsdienol-baited traps in southern Appalachia was strongly synergised by lanierone. In Wisconsin, *I. pini* demonstrated a strong dose-response to both lanierone and ipsdienol, preferring traps releasing lanierone and ipsdienol at the highest rates. *Ips pini* in northern Georgia exhibited dose response to ipsdienol, preferring traps with lures releasing ipsdienol at the highest rate, but little in the way of a dose response to lanierone across the range of release rates tested. In Georgia, the sympatric species *I. avulsus* preferred traps with lures releasing ipsdienol and lanierone at the highest rates.

Key Words *Ips pini*, *Ips avulsus*, Scolytidae, *Pinus strobus*, *Pinus resinosa*, ipsdienol, lanierone, dose response

The pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), occurs throughout North America, breeding in the phloem tissue of dead, dying or downed pines, including lodgepole (*Pinus contorta* var. *latifolia* Engelman), ponderosa (*P. ponderosa* Lawson ex Lawson), red (*P. resinosa* Aiton), jack (*P. banksiana* Lamb.), and eastern white pine (*P. strobus* L.) (Furniss and Carolin 1980, USDA Forest Service 1985). At times, population levels of *I. pinican* increase dramatically during drought conditions or following disturbance events such as logging, fire, windthrow or epidemics of primary bark beetles (Furniss and Carolin 1980). The combination of large populations of *I. pini* and decreased availability of susceptible hosts can result in attacks on live trees, resulting in significant levels of tree mortality (Sartwell et al. 1971, Geiszler et al. 1984, Amman and Ryan 1991).

Ips pini uses both (+)- and (-)-ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) (Birch et al. 1980, Lanier et al. 1980) as well as lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale et al. 1991) as pheromones to facilitate aggregations on suitable host material (Borden 1982). However, there is considerable geo-

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^{*}Address for offprint requests (dmiller03@fs.fed.us).

¹Department of Entomology, University of Wisconsin, Madison, WI 53706.

⁴Department of Entomology, The University of Georgia, Athens, GA 30602.

graphic variation across North America with respect to preferred pheromone blends by *I. pini* (Miller et al. 1996, 1997).

Populations of *I. pini* in New York show a preference for racemic ipsdienol (a 50:50 mix of (+)- and (-)-ipsdienol) (Lanier et al. 1980, Teale and Lanier 1991); whereas, populations in California prefer (-)-ipsdienol (Birch et al. 1980). Populations in British Columbia respond to ipsdienol over a broad range of enantiomeric compositions (20:80 to 80:20) (Miller et al. 1996). Populations in Wisconsin prefer ipsdienol with an enantiomeric composition ranging from (50:50) to (75:25) (Raffa and Klepzig 1989, Aukema et al. 2000 a,b). The attraction of *I. pini* to racemic ipsdienol is strongly synergised by lanierone in Wisconsin (Miller et al. 1997, Aukema and Raffa 2000) and New York (Teale et al. 1991, Miller et al. 1997). In contrast, lanierone is not synergistic with (-)-ipsdienol in attracting *I. pini* in California (Seybold et al. 1992, Miller et al. 1997) and only moderately synergistic with racemic ipsdienol in Montana and south-central British Columbia and (-)-ipsdienol in southeastern British Columbia (Miller et al. 1997).

The geographic range of *I. pini* in eastern North America extends from the edge of the Great Plains to the Atlantic Ocean in the North, and along the Appalachian Mountains into northern Georgia in the South. Previous pheromone studies in eastern North America have focused on populations of *I. pini* in New York and Wisconsin (Teale et al. 1991, Miller et al. 1997, Aukema et al. 2000 a,b, Aukema and Raffa 2000, Erbilgin and Raffa 2000 a,b, 2001). Geographic variation may exist between northern and southern populations in eastern North America, in addition to the well-described longitudinal variation (Birch et al. 1980, Lanier et al. 1980, Seybold et al. 1992, Miller et al. 1997). Using subtractive field assays, Birgersson et al. (1995) found that *I. pini* in northern Georgia require both lanierone and ipsdienol for maximal attraction to traps baited with the beetle-produced compounds ipsdienol, lanierone, cis-verbenol and 2-methyl-3-buten-2-ol.

Our objectives were to: (1) verify the synergistic activity of lanierone in the southern Appalachian region; and (2) compare the effect of racemic ipsdienol and lanierone, over a broad range of release rates, on the attraction of *I. pini* in both north-central and southeastern United States. Our expectation was that catches of *I. pini* in both Wisconsin and Georgia would be highest in traps with lures releasing ipsdienol and lanierone at the highest rates.

Materials and Methods

Semiochemical-releasing devices. Phero Tech Inc. (Delta, British Columbia) supplied the following types of polyvinyl, bubble-cap lures: (1) racemic ipsdienol (chemical purity, 98%) in solution with 1,3-butanediol; and (2) lanierone (chemical purity, 98%) in solution with 1,3-butanediol. Each type of lure was formulated with different concentrations of ipsdienol or lanierone resulting in devices releasing ipsdienol or lanierone at rates of 0.2-200 µg/d (Phero Tech Inc.). 1,3-Butanediol, used in the formulations to reduce the risk of polymerization, is not attractive to *I. pini* (Miller 1991).

Experimental procedures. In 2002, Experiment 1 was conducted to verify the activity of lanierone in the southern Appalachia using the same design and methodology as Miller et al. (1997) in 1992. Twenty eight-unit Lindgren multiple-funnel traps (Lindgren 1983) (Phero Tech Inc.) were set in five blocks of four traps per block at each of two sites dominated by eastern white pine in the Blue Valley Experimental

Forest, Nantahala National Forest, NC, for a total of 40 traps. Each block of four traps constituted a replicate. Blocks and traps within blocks were spaced 10 m apart, with no trap within 3 m of any tree. Each trap was suspended from a pole such that the bottom funnel of each trap was 0.5 m above ground level. The following treatments were randomly assigned within each replicate: (1) blank control; (2) lanierone; (3) ipsdienol; and (4) lanierone and ipsdienol. Bubblecap lures, as in Miller et al. (1997), released lanierone and ipsdienol at approximately 20 and 200 $\mu\text{g/d}$, respectively, at 24°C. The experiment was conducted from 30 May to 8 August with beetles collected at intervals of 10 to 14 d.

In 1992, two sets of concurrent experiments were conducted near Spring Green, WI, and Clayton, GA (within 20 km of the site in the Blue Valley Experimental Forest used in 2002 for Experiment 1). In both regions, 20 Lindgren multiple-funnel traps were set in five parallel lines of four traps per line at each of two sites for a total of 40 traps per region. Each line of four traps constituted a replicate. Traps and trap lines were spaced 15 to 20 m apart. Eight-unit funnel traps were used in Wisconsin, and 12-unit funnel traps were used in Georgia. Each trap was suspended by rope such that the bottom funnel of each trap was 0.5 to 1.0 m above ground level. No trap was within 2 m of any tree. Traps were set in stands of red pine in Wisconsin and of eastern white pine in northern Georgia, with beetles collected at intervals of 10 to 14 d.

Experiment 2 evaluated the effect of ipsdienol, released at different rates, on the attraction of *I. pini* to lanierone-baited traps. All traps were baited with bubble-cap lures releasing lanierone at a rate of approximately 200 $\mu\text{g/d}$ at 24°C. The four treatments consisted of the addition of bubble-cap lures releasing ipsdienol at the following rates: (1) 0.2 $\mu\text{g/d}$; (2) 2 $\mu\text{g/d}$; (3) 20 $\mu\text{g/d}$; and (4) 200 $\mu\text{g/d}$. Experiment 2 was conducted from 2 to 23 July, 1992 in Wisconsin and 7 July to 3 August 1992 in northern Georgia.

Experiment 3 tested the converse relationship. All traps were baited with bubble-cap lures releasing ipsdienol at a rate of approximately 200 $\mu\text{g/d}$ at 24°C. The four treatments consisted of the addition of bubble-cap lures releasing lanierone at the following rates: (1) 0.2 $\mu\text{g/d}$; (2) 2 $\mu\text{g/d}$; (3) 20 $\mu\text{g/d}$; and (4) 200 $\mu\text{g/d}$. Experiment 3 was conducted from 23 July to 20 August, 1992 in Wisconsin and 3 August to 10 September, 1992 in Georgia.

Statistical analyses. Data were analyzed using the SYSTAT statistical package version 9.01 (SPSS 1999). In all experiments statistical analyses were conducted on total numbers of beetles caught per trap, transformed by $\ln(y + 1)$ or $\ln(y)$ to remove heteroscedasticity. Data in Experiment 1 were subjected to two-way full-factorial analysis of variance (ANOVA) using the following model terms: lanierone, ipsdienol, and lanierone $\times$ ipsdienol. The interaction term (lanierone $\times$ ipsdienol) was used to determine synergy between lanierone and ipsdienol (as in Miller et al. 1997). Data in Experiments 2 and 3 were subjected to separate regression analyses, excluding data for the lowest rate when examination of residuals suggested non-linearity, as well as two-way full-factorial ANOVA when comparing data for Wisconsin and southern Appalachia using the following model terms: dose, region, and dose $\times$ region. The interaction term (dose $\times$ region) was used to determine variation between Wisconsin and southern Appalachia. Data in all experiments were also subjected to one-way ANOVA, followed by Fisher's least significant difference pair-wise multiple comparison test when $P < 0.05$. Voucher specimens were deposited at the Entomology Museum, Pacific Forestry Center, Victoria, British Columbia.

Results and Discussion

Trap catches of *I. pini* were significantly affected by treatments in Experiment 1 ($F = 157.10$; $df = 3,36$; $P < 0.001$) with the highest catches in traps baited with ipsdienol and lanierone (Fig. 1). *Ips pini* was clearly attracted to ($\pm$)-ipsdienol in southern Appalachia ($F = 404.25$; $df = 1,36$; $P < 0.001$). As in Wisconsin and New York (Miller et al. 1997), lanierone was not attractive by itself but strongly synergised attraction of *I. pini* to ipsdienol ($F = 35.72$; $df = 1, 36$; $P < 0.001$) (Fig. 1), resulting in a 9-fold increase in trap catch. These results are consistent with those of Birgersson et al. (1995) for the same site in north Georgia, obtained in 1991. Male *I. pini* represented 49.1% (SE = 2%) of all *I. pini* caught in our study.

There was a strong dose response exhibited by *I. pini* to ipsdienol in northern Georgia ($F = 76.72$; $df = 1,28$; $P < 0.001$) and Wisconsin ($F = 76.72$; $df = 1,28$; $P < 0.001$) with catches directly proportional to the release rate of ipsdienol (Fig. 2) and no differences between the two regions ($F = 2.05$; $df = 1,58$; $P = 0.157$). More than 70% of the variation in catches of beetles to lanierone-baited traps was explained by the release rate of ipsdienol. In both locations, traps with baits releasing ipsdienol at the highest rates caught significantly more beetles than traps with baits releasing ipsdienol at the remaining rates (LSD multiple comparison test, $P = 0.05$). Traps with the three lowest rates of ipsdienol release caught relatively few beetles.

Ips pini demonstrated a strong dose response to lanierone in ipsdienol-baited traps in Wisconsin ($F = 80.56$; $df = 1,38$; $P < 0.001$). Trap catches were directly proportional to the release rate of lanierone (Fig. 3). More than 67% of the variation in trap catches was explained by the release rate of lanierone. Traps with baits releasing lanierone at the highest rates caught significantly more beetles than traps with baits releasing

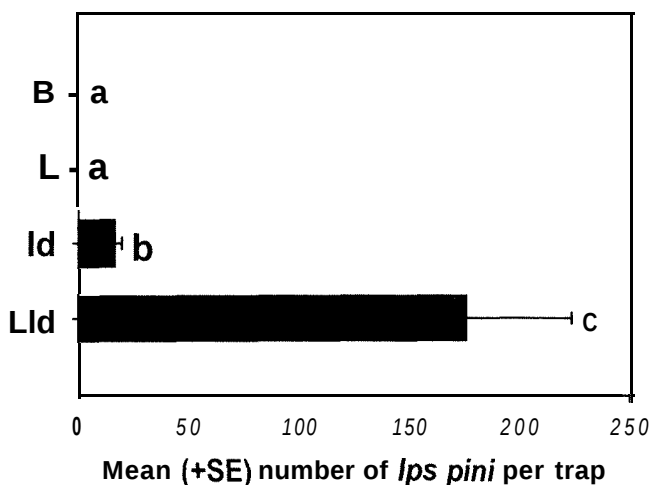


Fig. 1. Effects of ipsdienol (Id), lanierone (L) and the combination of ipsdienol and lanierone (LId) on the attraction of *Ips pini*, compared to a blank control (B), in western Northern Carolina ($n = 10$). Means followed by different letters are significantly different at $P = 0.05$ (LSD multiple comparison test).

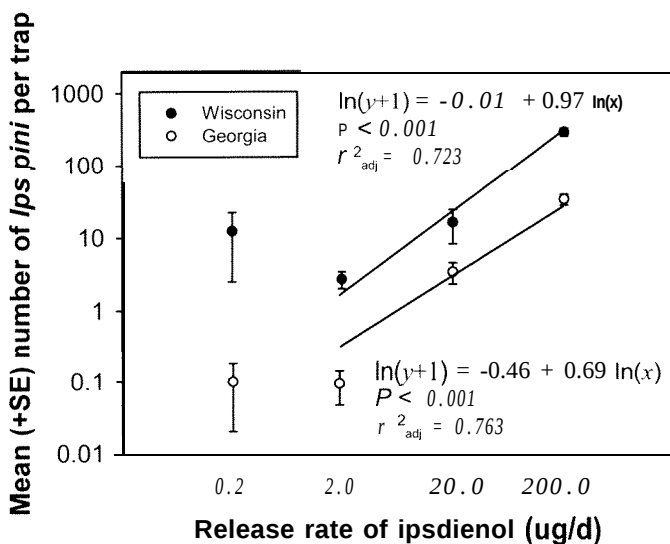


Fig. 2. Effects of ipsdienol, released at rates of 0.2-200.0 $\mu\text{g/d}$, on the attraction of *Ips pini* to lanierone-baited multiple-funnel traps in Wisconsin and northern Georgia ($n = 10$). Slopes of regression lines are significantly different from zero (t test, $P < 0.05$).

lanierone at the remaining rates (LSD multiple comparison test, $P = 0.05$). These results are consistent with previous studies showing lanierone synergizes the attraction of *I. pini* to ipsdienol in Wisconsin (Miller et al. 1997), and that the magnitude of this response increases with increasing release rates of lanierone (Aukema and Raffa 2000).

The responses of *I. pini* to lanierone doses differed significantly between Wisconsin and northern Georgia ($F = 6.31$; $df = 1, 17$; $P = 0.015$). In contrast to Wisconsin populations, *I. pini* in northern Georgia did not exhibit a strong dose-dependent response to lanierone across the range of release rates tested ($F = 3.82$; $df = 1, 34$; $P = 0.059$) (Fig. 3). Less than 8% of the variation in response was explained by the release rate of lanierone ($r^2_{adj} = 0.075$).

Our results demonstrate north-south geographic variation in the use of pheromones by eastern populations of *I. pini* in a fashion different from that between eastern and western populations. The difference is based on the dose of lanierone rather than simply its occurrence. Lanierone is strongly synergistic for eastern populations, moderate for northwestern populations and non-existent for Californian populations (Miller et al. 1997). Populations in Wisconsin exhibited a strong dose response to lanierone whereas a population in southern Appalachia did not (Fig. 3).

Various theories have been suggested to explain geographic variation in the use of pheromones by *I. pini*. It is possible that the current distributions of pheromone biotypes are the result of post-glaciation dispersal of beetles and their hosts from different refugia (Miller 1991, Seybold et al. 1992). A second and nonexclusive theory suggests that predation pressure has influenced pheromone synthesis and prefer-

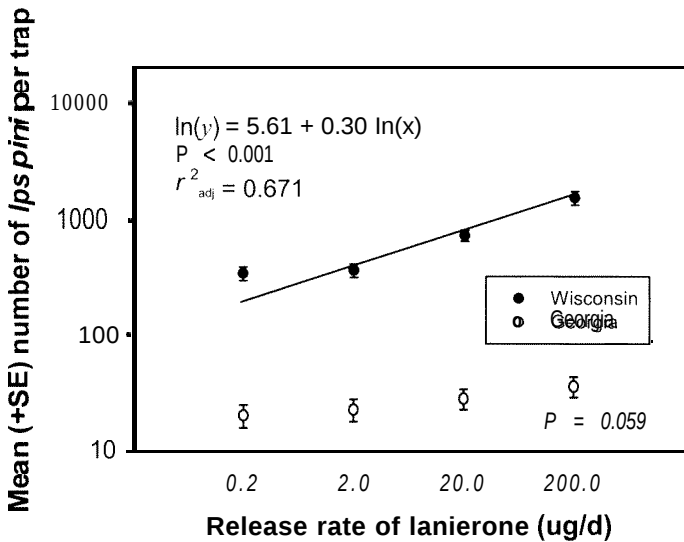


Fig. 3. Effects of lanierone, released at rates of 0.2-200.0 $\mu\text{g/d}$, on the attraction of *Ips pini* to ipsdienol-baited multiple-funnel traps in Wisconsin and northern Georgia ($n = 10$). The slope of the regression line is significantly different from zero (t test, $P < 0.05$).

ences by 1. *pini* (Raffa and Klepzig 1989, Raffa and Dahlsten 1995). A third and likewise nonexclusive possibility may be that selection pressures from competing species have shaped the use of pheromone blends across North America (Miller 1991, Seybold et al. 1992). For example, in California, *I. pini* uses (-)-ipsdienol whereas the sympatric species, *I. paraconfusus*, uses (+)-ipsdienol (Light and Birch 1979, Birch et al. 1980). In Montana, *I. pini* uses ipsdienol and lanierone whereas the sympatric species, *I. integer*, uses lanierone with attraction interrupted by ipsdienol (Miller et al. 1997).

In northern Georgia, traps caught substantially more of the sympatric four-spined southern pine engraver, *I. avulsus* (Eichhoff). *Ips avulsus* showed a clear dose dependent response to both ipsdienol in the presence of lanierone ($F = 105.92$; $\text{df} = 1,38$; $P < 0.001$) and lanierone in the presence of ipsdienol ($F = 22.19$; $\text{df} = 1,25$; $P < 0.001$), with catches directly proportional to the release rate of each compound (Fig. 4). Approximately 73% of the variation in responses to lanierone-baited traps was explained by the release rate of ipsdienol; 45% of the variation to ipsdienol-baited traps was explained by the release rate of lanierone. Traps with baits releasing lanierone and ipsdienol at the highest rates caught significantly more *I. avulsus* than traps with baits releasing lanierone and ipsdienol at the remaining rates (LSD multiple comparison test, $P = 0.05$). Our results are consistent with Birgersson et al. (1995) who demonstrated that both ipsdienol and lanierone are required for maximal attraction of *I. avulsus* to a blend of beetle-produced compounds.

The area of sympatry between *I. pini* and *I. avulsus* is generally limited to pine stands in southern Appalachia (USDA Forest Service 1985). *Ips avulsus* is common

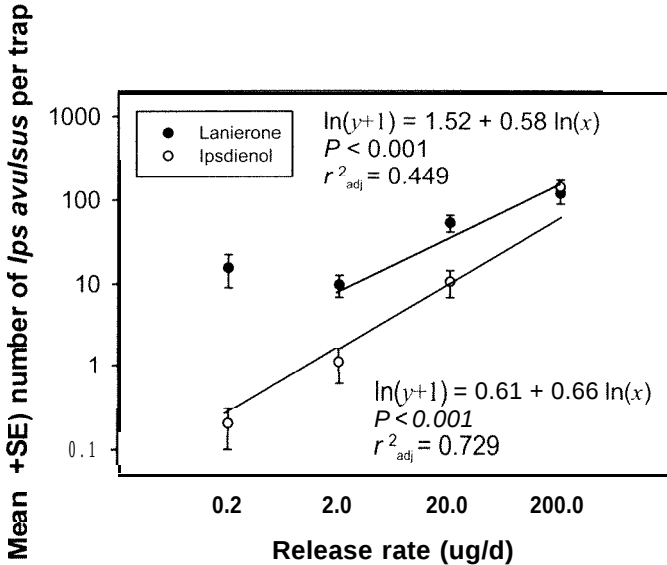


Fig. 4. Effects of lanierone and ipsdienol, released at rates of 0.2-200.0 $\mu\text{g/d}$, on the attraction of *Ips avulsus* to ipsdienol- and lanierone-baited multiple-funnel traps, respectively, in northern Georgia ($n = 10$). Slopes of regression lines are significantly different from zero (t test, $P < 0.05$).

throughout the southern states, extending to Texas, Florida and southern Pennsylvania. The distribution of *I. pini* does not extend farther south than northern Georgia. Separation of breeding sites may rely on the relative amount of lanierone produced by beetles in this limited area of sympatry. In addition the species may separate within trees as well. *Ips pini* tends to occur on trunks and large branches whereas *I. avulsus* tends to attack smaller branches, particularly within crowns of pines (USDA Forest Service 1985). We caught less than 20 *I. avulsus* in Experiment 1, with stands consisting mainly of eastern white pine and oaks, with little in the way of recent or active disturbances. The site in northern Georgia was the same as the one used by Birgersson et al (1995) in 1991 and consisted of a mix of eastern white pine, shortleaf pine (*P. echinata* Mill.) and pitch pine (*P. rigida* Mill.), with active logging in the stand to remove shortleaf and pitch pines, leaving only eastern white pine. The southern pines such as shortleaf and pitch pine are some of the preferred hosts for *I. avulsus*, but not *I. pini* (USDA Forest Service 1985) and selective use of logging slash likely provided a population explosion of *I. avulsus*.

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