

Improved Population Monitoring of Bark Beetles and Predators by Incorporating Disparate Behavioral Responses to Semiochemicals

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ABSTRACT Estimating populations of both pest and natural enemy species is important in the planning and implementation of biological control. For example, synthetic pheromone lures are used to sample bark beetles, and sometimes their predators, in forest ecosystems. However, insect attraction to natural pheromone sources may differ from attraction to synthetic pheromone lures. Moreover, these differences may vary systematically between the target pest and some important natural enemies. Thus, the accuracy of both absolute and relative abundances of bark beetles and predators could vary with lure selection. We evaluated a series of synthetic lures to determine which lure gave the closest approximation to actual numbers of *Ips pini* (Say) and predators arriving at hosts infested with *I. pini* in Wisconsin. We deployed synthetic lures containing various ratios of the (+) and (-) enantiomers of the principal *I. pini* pheromone component, ipsdienol, with or without an additional component, lanierone. *I. pini* showed strong preferences for specific enantiomeric ratios of ipsdienol, and these responses were synergized by lanierone. Predators showed equally strong attraction to ipsdienol, but preferred different ratios of the stereoisomers. The addition of lanierone had no effect on predators. The most abundant predator, *Thanasimus dubius* (F.), showed greater preference for host material infested with *I. pini* than any synthetic lure. These disparities in responses, combined with strong disparities in seasonal flight patterns, provided estimates of pest to predator ratios that varied by as little as 12% to as much as 12 times, from pest:predator ratios arriving at host material infested with *I. pini*. These results suggest that variation between herbivores and their natural enemies in their phenology, preferred pheromone blends, and infested host material should be considered when developing estimates of relative pest and predator densities for subsequent management options.

KEY WORDS *Ips pini*, *Thanasimus dubius*, *Platysoma*, pheromones, biological control, population monitoring

BARK BEETLES (COLEOPTERA: Scolytidae) comprise the most damaging insect group affecting North American conifers under both natural conditions and in commercial plantations (Coulson and Stark 1982, Waters et al. 1985). These include both native species, such as the spruce beetle, *Dendroctonus rufipennis* Kirby (Reynolds and Holsten 1994, 1996), and invasive species such as *Scolytus multistriatus* Marsham, vector of the Dutch elm disease pathogen (Lanier 1989), and more recently, the pine shoot beetle, *Tomicus piniperda* (L.) (Haack and Lawrence 1995, Haack et al. 1997).

Bark beetles have complex semiochemical systems that govern mass attacks on selected hosts (Wood 1982). Adult beetles bore into the subcortical tissue of trees and emit aggregation pheromones that are synergized by or derived from host monoterpenes (Hughes 1974, Hendry et al. 1980, Byers and Birgersson 1990, Miller and Borden 1990, Seybold et al. 1995). The resulting mass attack may exhaust host resistance within a few days, usually causing tree death (Raffa

and Berryman 1983). Adults mate and establish brood galleries in the phloem. The progeny feed in the phloem, pupate in the inner or outer bark, and emerge as adults to seek new hosts (Wood 1972).

Management strategies for reducing the impact of bark beetles include insecticide application (McCullough et al. 1998), silviculture (Coulson 1979, Berryman 1982, Stark 1982), sanitation (Borden et al. 1992), and behavior modifying semiochemical treatments (Bakke 1989; Gray and Borden 1989; Payne and Billings 1989; Shea et al. 1992; Borden et al. 1993; Bertram and Paine 1994a, 1994b; Hayes and Strom 1994; Ross and Daterman 1995; Salom and Hobson 1995). Each of these control tactics has various advantages and disadvantages. However, all rely on the ability to forecast and rapidly detect incipient outbreak populations (Stephen and Taha 1976, 1979).

Despite these strategies, bark beetles continue to cause high economic losses in forests and plantations (Waters et al. 1985, Preisler and Mitchell 1993, Reynolds and Holsten 1996). This is due in part to difficulties in predicting scales and onsets of outbreaks. Monitoring programs that incorporate estimates of both bark beetle and natural enemies populations can improve such forecast models (Billings et al. 1985, Billings 1988). Numerous studies have shown that natural

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enemies can play an important role in scolytid population regulation (Thatcher and Pickard 1966; Dahlsten and Stephen 1974; Amman and Cole 1983; Kulhavy and Miller 1989; Turchin et al. 1991, 1999; Weslien 1992, 1994; Weslien and Regnander 1992; Raffa 1995; Reeve et al. 1995; Reeve 1997).

The easiest method for sampling bark beetles, and one that holds promise for predicting population dynamics, is to deploy traps baited with synthetic pheromones. Natural enemies of bark beetles exploit beetle pheromones as kairomones to locate prey (Wood 1982), and so can be sampled in these traps also. However, bark beetles and their major predators may differ in their relative preferences for optical isomers and other components of scolytid pheromones (Payne et al. 1984, Raffa and Klepzig 1989, Herms et al. 1991, Seybold et al. 1992, Raffa 1995, Raffa and Dahlsten 1995). Additional differences in seasonal variation and dispersal behavior may add to these disparities (Raffa 1991). It has been proposed that relatively subtle nuances of pheromone chemistry and ecology, such as stereochemistry, potentiators of insect and plant origin, dispersal behavior, and seasonal variation may provide bark beetles with viable options for partial escape from predators while retaining intraspecific functionality (Raffa 1995). Thus, a deeper understanding of the chemical and ecological interactions among bark beetles and predators could improve sampling estimates important for pest management decisions (Billings et al. 1985, Billings 1988, Raffa and Klepzig 1989, Herms et al. 1991, Grégoire et al. 1992). Currently, it is not known, for example, how catches in traps baited with synthetic lures reflect either the absolute or relative numbers of bark beetles and predators arriving at infested trees.

Our test model consisted of the pine engraver, *Ips pini* (Say) and its major predators, *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae) (Raffa and Klepzig 1989, Raffa and Dahlsten 1995), in Wisconsin. *I. pini* cause chronic problems during harvest operations throughout western North America (Miller et al. 1997) and to stressed pines in plantations in the Great Lakes region (Klepzig et al. 1991). *I. pini* males produce ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol), which occurs in both (+) and (-) enantiomers (Wood 1982). *I. pini* response to ipsdienol is synergized by a second component, lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale et al. 1991). Responses by *I. pini* and its major predators show strong inter-regional variation to varying ratios of (+) to (-) ipsdienol, and to lanierone (Lanier et al. 1972; Birch et al. 1980a, 1980b; Lanier et al. 1980; Seybold et al. 1992; Seybold 1993; Miller et al. 1997). Responses by *I. pini* and predators to infested hosts is less understood, especially in the Great Lakes region. Erbilgin and Raffa (2000) observed *I. pini*-predator arrival ratios of 0.97 to red pine (*Pinus resinosa* Aiton), 1.03 to samples of red, white (*Pinus strobus* L.), and jack (*Pinus banksiana* Lamb) pines, and no significant difference among tree species. The goal of this work was to determine which synthetic lures most accu-

rately represent the actual arrival of *I. pini* and its major predators responding to host trees infested with *I. pini* in Wisconsin.

Materials and Methods

The experiment was conducted in the field as a behavioral choice assay. The treatments consisted of six combinations of synthetic pheromones, a screened log infested with *I. pini* males, a screened blank control log of similar dimensions, and a blank control trap. Polyvinyl bubble cap lures (Pherotech, Delta, BC) contained three ratios of (+) to (-) synthetic ipsdienol, with or without lanierone: 75(+)/25(-), 50(+)/50(-), and 03(+)/97(-). The lures contained 20 mg active ingredient in a 1,3-butanediol carrier solvent that is unattractive to *I. pini* (Miller 1990). The release rates were 110 and 100 μg per day of ipsdienol and lanierone, respectively, at 25°C (Pherotech).

The *I. pini* males used for the infested-log treatment were obtained from a laboratory colony maintained using the methods of Raffa and Dahlsten (1995). This colony was derived from local beetles and periodically infused with additional field insects caught locally. Vigorous males between 5 and 14 d old were established on red pine logs ≈ 15 cm in diameter and 30 cm long. Twenty evenly spaced 1.25-cm-diameter holes were drilled into the phloem, and one male was inserted into each hole. Gel caps were fastened over each hole with masking tape. Males were allowed to tunnel for 24 h. Immediately before the logs were taken to the field, the gel caps were removed. Any males that had not entered the log were replaced with new vigorous males. The logs were enclosed in 18 by 16-mesh 0.28-mm (0.011-inch)-diameter aluminum mesh screening (Phifer Wire Products, Tuscaloosa, AL) to prevent beetle escape.

Experimental Design and Field Sites. The study site was located in a 40- to 50-yr-old red pine plantation near Dellwood in Sauk County, WI (latitude N 43° 33.42', longitude W 89° 50.61'). Twelve-funnel Lindgren traps (Lindgren 1983) were deployed in three lines spaced 100 m apart. Each line consisted of nine traps, with each trap containing one randomly assigned treatment. Treatments were rerandomized within each line every 4 d for six sample periods so that no treatment could systematically influence another. The traps within each line were spaced 10 m apart and were suspended from ropes stretched between two trees, such that the trap's cup was at least 50 cm from the ground and the trap was at least 50 cm from the nearest tree. Synthetic pheromone lures were attached to the middle funnels of the traps. Logs were attached to the ropes with eye hooks, and the traps were suspended underneath from screw hooks. At each randomization, new logs and insects were brought to the field. A 3 by 3-cm time-released 20% organophosphate insecticide strip (Pest STRIP, Loveland Industries, Greeley, CO) was placed inside each trap cup to prevent destruction of trap contents by attracted predators.

Table 1. *I. pini* and associates caught in response to various attractant sources during 1997 and 1998 in Wisconsin, USA

| Insect | Family | 1997 | | 1998 | | Total (624) |
|---|---------------|--------------|--------------|--------------|--------------|-------------|
| | | Spring (160) | Summer (144) | Spring (161) | Summer (159) | |
| Herbivores (88.4%): | | | | | | |
| <i>Ips pini</i> (Say) | Scolytidae | 17.71 | 15.66 | 14.40 | 20.79 | 10,714 |
| <i>Ips grandicollis</i> (Eichhoff) | Scolytidae | 0.02 | 0.02 | 0.11 | 0.10 | 39 |
| <i>Ips perroti</i> Swaine | Scolytidae | 0.04 | 0.22 | 0.14 | 0.02 | 62 |
| <i>Ips calligraphus</i> Germar | Scolytidae | 0.00 | 0.00 | 0.00 | 0.01 | 1 |
| <i>Dendroctonus valens</i> LeConte | Scolytidae | 0.09 | 0.03 | 0.15 | 0.08 | 55 |
| <i>Orthotomicus caelatus</i> (Eichhoff) | Scolytidae | 0.00 | 0.01 | 0.05 | 0.01 | 12 |
| <i>Hylastes</i> spp. | Scolytidae | 0.04 | 0.01 | 0.01 | 0.01 | 10 |
| Metallic wood borers ^a | Buprestidae | — | — | 0.06 | 0.01 | 11 |
| Long horned beetles ^b | Cerambycidae | 0.14 | 0.09 | 0.07 | 0.06 | 55 |
| Total Herbivores: | | | | | | 10,959 |
| Parasitoid (0.3%): | | | | | | |
| <i>Tomicobia tibialis</i> Ashmead | Pteromalidae | 0.06 | 0.03 | 0.01 | 0.15 | 40 |
| Predators (11.3%): | | | | | | |
| <i>Thanasimus dubius</i> (F.) | Cleridae | 1.81 | 0.56 | 1.18 | 0.38 | 621 |
| <i>Enoclerus nigripes</i> Say | Cleridae | 0.10 | 0.01 | 0.34 | 0.05 | 79 |
| <i>Enoclerus spegeus</i> (F.) | Cleridae | 0.10 | 0.03 | 0.42 | 0.07 | 98 |
| <i>Enoclerus nigrifrons</i> (Say) | Cleridae | 0.00 | 0.31 | 0.01 | 0.66 | 152 |
| <i>Phlogistosternus dislocatus</i> (Say) ^{a,c} | Cleridae | — | — | 0.01 | 0.06 | 11 |
| <i>Zenodosus sanguineus</i> (Say) ^a | Cleridae | — | — | 0.04 | 0.03 | 10 |
| <i>Platysoma cylindrica</i> (Paykull) | Histeridae | 0.94 | 0.08 | 0.86 | 0.19 | 329 |
| <i>Platysoma parallelum</i> (Say) | Histeridae | 0.07 | 0.01 | 0.15 | 0.00 | 37 |
| <i>Corticus parallelus</i> (Melsheimer) | Tenebrionidae | 0.16 | 0.01 | 0.10 | 0.02 | 46 |
| <i>Grynocharis quadrilineata</i> (Melsheimer) | Trogoidea | 0.08 | 0.00 | 0.07 | 0.00 | 23 |
| <i>Tenebroides</i> spp. ^d | Trogoidea | 0.19 | 0.02 | 0.18 | 0.08 | 74 |
| Total Predators: | | | | | | 1,480 |
| Total Insects: | | | | | | 12,479 |

Average numbers of insects obtained per 4-d collection period per trap in field trials are shown for each species. Figures in parentheses indicate number of samples. Total shows sum of all replications.

^a Not tabulated for 1997.

^b Primarily *Monochamus carolinensis* Olivier and *Monochamus titillator* (F.).

^c Natural history undetermined. Likely a predator (Cleridae).

^d *Tenebroides* nr. *collaris* Sturm and another.

The experiment was conducted four times, twice each in 1997 and 1998. Sampling was timed to correspond with the major periods of flight by predators and *I. pini* in Wisconsin (Raffa 1991). In 1997, sampling was conducted from 21 June to 11 July and 4 to 24 August. In 1998, trapping was conducted from 29 May to 22 June and 14 July to 3 August. The first and second experiments of each year are referred to as the "spring" and "summer" trials. Some data from the 20–24 August 1997 period were lost because of incorrect treatment randomization in the field. In the spring of 1998, one extra sample period was performed (18–22 June) to replace the collection of 2–6 June, which had very low numbers because of cold weather. Trap catches were tabulated for herbivores, predators, and *Tomicobia tibialis* Ashmead (Hymenoptera: Pteromalidae), a parasitoid of *I. pini* (Senger and Roitberg 1992).

Statistical Analyses. The numbers of each species of arriving insect were analyzed using analysis of variance (ANOVA) (PROC MIXED, SAS Institute 1996). Data were transformed by square root (\sqrt{y}) to reduce heteroscedascity. Potential sources of variation included treatment, line, sample period, replication across years, and all interactions. An analysis of correlated variances was performed using Mauchley's test for sphericity. Sphericity proved positive ($P > 0.05$), so variances are not correlated. Therefore, analysis

was conducted as a mixed effects split-plot model with period, line, and the interaction as blocking factors in the whole plot, and treatment and sample period and the treatment-sample period interaction in the subplot. Line, line*treatment, and the interaction across replications were considered random effects. Least squared means were used to adjust for all terms in the model.

Replications were pooled across seasons (by year) and across years (by season) to examine both season and year effects as well as their treatment interactions. The data were pooled across both years by season when treatment-by-year interactions were not significant. Where significant ($P < 0.05$) treatment effects occurred, least squared means were separated using pairwise *t*-tests. For data presentation and calculations of pest to predator ratios, raw means are shown. Standard errors were calculated from the insect numbers averaged across the sampling times, which were considered subsamples.

We conducted statistical analyses on all species for which a minimum of 45 specimens over 2 yr were obtained. Insects were retained in subsequent analyses if they exhibited a treatment effect in either 1997 or 1998 and the effect was significant when both years were pooled. Only insects that responded to both the log and synthetic lures were analyzed. We grouped

Table 2. Sources of variation caused by seasonal phenology and year in numbers of *I. pini* and associates caught in response to various attractive sources in Wisconsin

| Term | <i>Ips</i> | <i>I. pini</i> | <i>T. dubius</i> | <i>E. nigripes</i> | <i>E. nigrifrons</i> | <i>Platysoma</i> | Predators | |
|----------------------------------|------------|----------------|------------------|--------------------|----------------------|------------------|---------------------|---------------------|
| | | | | | | | Spring ^a | Summer ^b |
| Seasonal differences within year | | | | | | | | |
| Season (1997): | | | | | | | | |
| <i>F</i> | 0.73 | 0.63 | 17.71 | 7.25 | 17.50 | 36.68 | 60.23 | 41.86 |
| <i>df</i> | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 |
| <i>P</i> | 0.4818 | 0.5095 | 0.0001 | 0.1146 | 0.0527 | 0.0262 | 0.0162 | 0.0231 |
| Season (1998): | | | | | | | | |
| <i>F</i> | 16.70 | 15.06 | 12.46 | 22.64 | 13.35 | 32.92 | 103.24 | 16.29 |
| <i>df</i> | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 | 1, 2 |
| <i>P</i> | 0.0550 | 0.0604 | 0.0717 | 0.0414 | 0.0674 | 0.0291 | 0.0095 | 0.0562 |
| Trt * Season (1997): | | | | | | | | |
| <i>F</i> | 3.35 | 3.32 | 1.93 | 1.34 | 1.45 | 4.08 | 2.14 | 1.73 |
| <i>df</i> | 8,32 | 8,32 | 8,32 | 8,32 | 8,32 | 8,32 | 8,32 | 8,32 |
| <i>P</i> | 0.0067 | 0.0071 | 0.0898 | 0.2581 | 0.2148 | 0.0019 | 0.0610 | 0.1290 |
| Trt * Season (1998): | | | | | | | | |
| <i>F</i> | 3.40 | 3.46 | 2.99 | 1.48 | 4.72 | 2.21 | 4.23 | 3.02 |
| <i>df</i> | 8, 32 | 8, 32 | 8, 32 | 8, 32 | 8, 32 | 8, 32 | 8, 32 | 8, 32 |
| <i>P</i> | 0.0061 | 0.0056 | 0.0127 | 0.2044 | 0.0007 | 0.534 | 0.0015 | 0.0122 |
| Annual differences within season | | | | | | | | |
| Year (spring): | | | | | | | | |
| <i>F</i> | 1.05 | 1.03 | 4.28 | 15.67 | NA | 0.01 | 0.01 | NA |
| <i>df</i> | 1, 2 | 1, 2 | 1, 2 | 1, 2 | NA | 1, 2 | 1, 2 | NA |
| <i>P</i> | 0.4137 | 0.4175 | 0.1745 | 0.0583 | NA | 0.9410 | 0.9495 | NA |
| Year (summer): | | | | | | | | |
| <i>F</i> | 0.11 | 0.09 | 0.03 | NA | 5.66 | 3.39 | NA | 7.23 |
| <i>df</i> | 1, 2 | 1, 2 | 1, 2 | NA | 1, 2 | 1, 2 | NA | 1, 2 |
| <i>P</i> | 0.7703 | 0.7873 | 0.8777 | NA | 0.1404 | 0.2069 | NA | 0.1149 |
| Treatment * Year (spring): | | | | | | | | |
| <i>F</i> | 0.75 | 0.73 | 0.20 | 1.11 | NA | 0.94 | 0.26 | NA |
| <i>df</i> | 8, 32 | 8, 32 | 8, 32 | 8, 32 | NA | 8, 32 | 8, 32 | NA |
| <i>P</i> | 0.6467 | 0.6605 | 0.9889 | 0.3823 | NA | 0.5004 | 0.9730 | NA |
| Treatment * Year (summer): | | | | | | | | |
| <i>F</i> | 10.03 | 10.24 | 0.20 | NA | 1.69 | 1.52 | NA | 1.82 |
| <i>df</i> | 8, 32 | 8, 32 | 8, 32 | NA | 8, 32 | 8, 32 | NA | 8, 32 |
| <i>P</i> | 0.0001 | 0.0001 | 0.9889 | NA | 0.1383 | 0.1910 | NA | 0.1103 |

Terms denoted by a season in parentheses are pooled over 1997 and 1998 replications. Terms denoted by a year in parentheses are pooled over spring and summer replications.

^a Spring predators include *T. dubius*, *E. nigripes*, and *Platysoma*.

^b Summer predators include *T. dubius*, *E. nigrifrons*, and *Platysoma*.

Platysoma parallelum (Say) (Coleoptera: Histeridae) with *P. cylindrica* as '*Platysoma* spp.' for analysis purposes, because these species exhibit similar responses to *I. pini* semiochemicals (K.F.R., unpublished data). Although *Ips perroti* Swaine (Coleoptera: Scolytidae) responded to pheromones in the summer of 1998, we excluded this species from the analysis as it comprised <1% of the total *Ips* spp. caught.

Results

Twenty-one species of insects were obtained (Table 1). The most prevalent bark beetle responding to these treatments was *I. pini*. Other subcortical herbivores were collected in relatively small numbers. The most prevalent predators were *T. dubius* and *P. cylindrica*. Most of the other responding predators were additional species of Cleridae, Histeridae, and Trogositidae. With the exception of the parasitoid *T. tibi-*

alis, all insects responding to these treatments were coleopterans.

Response by *I. pini* and Associates. Numbers of *I. pini* were relatively constant during the spring and summer trials. However, the numbers of major predators trapped displayed high seasonal variance. Seventy-seven per cent of *T. dubius*, 88.6% of *Enoclerus nigripes* (Say) (Coleoptera: Cleridae), and 88.3% of *Platysoma* were caught in the spring. Overall, 72.4% of all predators were caught in the spring during both years. The only exception was *Enoclerus nigrifrons* (Say) (Coleoptera: Cleridae), of which 97.9% were obtained in the summer. Because of the significant seasonal effects and season by treatment interactions for *I. pini* and its predators (Table 2), data were analyzed separately for spring and summer. Year-to-year variation was not significant for any insect, so seasons were pooled across years. Treatment response shifted between years in the summer for *I. pini*, so these data

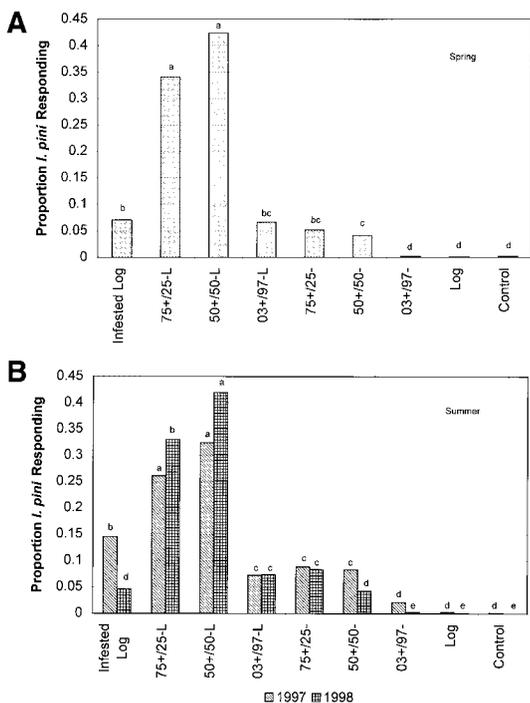


Fig. 1. Proportion of *I. pini* responding to various natural and synthetic sources of odor as assessed by field studies in Wisconsin. Proportions are developed from mean responses to each treatment per sample period. Different letters indicate treatments are significantly different within a species at $P < 0.05$. (A) Spring; pooled data from 1997 and 1998. (B) Summer; shown separately for 1997 and 1998 based on interaction effects in Table 2.

were analyzed separately for 1997 and 1998. Treatment response did not shift between years for any other insect (Table 2).

Responses by *I. pini* during the spring and summer trials are shown in Fig. 1A and B, respectively. Summer results are shown separately for 1997 and 1998 because a significant treatment by year interaction (Table 2). *I. pini* showed strong preferences for specific chiralities of ipsdienol, and lanierone synergized their responses (Table 3). Pine engravers responded in highest numbers to racemic ipsdienol and 75(+)/25(-) ipsdienol, each in the presence of lanierone (Fig. 1). Responses to the preferred blends of synthetic pheromones were much higher than to the infested host material. *I. pini* were more attracted to the infested logs than to the controls, but uninfested logs were not attractive. *I. pini* were not attracted to 3(+)/97(-) ipsdienol in the absence of lanierone. Overall, the proportion (where all treatments are summed to 1.0) of *I. pini* arriving at the infested logs was best approximated by 75(+)/25(-) ipsdienol without lanierone, 50(+)/50(-) ipsdienol lure without lanierone, and, surprisingly, 03(+)/97(-) ipsdienol in the presence of lanierone (Fig. 1A and B).

The highest catches of *T. dubius* in traps baited with synthetic lures in the spring occurred with the two

75(+)/25(-) ipsdienol treatments, followed by the two 50(+)/50(-) ipsdienol treatments (Fig. 2). Their responses were not enhanced by lanierone. *T. dubius* were not attracted to lures containing 3(+)/97(-) ipsdienol, relative to the controls. *T. dubius* responded to the infested log treatment in numbers ≈ 3 times higher than to any of the synthetic lures (Fig. 2). They were not attracted to uninfested logs. During the summer sampling periods, *T. dubius* did not show significant variation in responses to various chiralities of ipsdienol, a result that is likely because of insufficient numbers of insects for statistical differences (Tables 1 and 3).

Similar to *T. dubius*, *Platysoma* spp. preferred specific enantiomers of ipsdienol in the spring when they were abundant, and the presence of lanierone did not enhance their responses (Table 3). Highest numbers were caught using 03(+)/97(-) ipsdienol lures (Fig. 3). Racemic ipsdienol also attracted more *Platysoma* spp. than did the controls. Response to the infested log was best emulated with traps baited with 50(+)/50(-) or 75(+)/25(-) ipsdienol in the spring (Fig. 3). Uninfested logs did not attract *Platysoma* spp. In the summer, *Platysoma* spp. did not vary significantly between the infested log and controls, probably because of low numbers present at this time (Tables 1 and 3).

The clerid *E. nigripes* was only caught in sufficient numbers for analysis in the spring (Table 1). It was the only predator that did not show a preference for specific stereoisomers of ipsdienol, nor did it show a preference for lures with versus without lanierone (Table 3). *E. nigripes* responded in similar numbers to the synthetic lures and the infested log. In contrast, *E. nigrifrons*, which was trapped in high numbers in the summer, responded in highest numbers to $\leq 50(+)$ ipsdienol ratios (Tables 1 and 3). It was not affected by lanierone. Its response to the infested log was similar to its response to the 75(+)/25(-) ipsdienol lure.

When all predator data were pooled, there was a significant treatment effect, and a significant attraction of insects to infested logs versus uninfested logs, but there was no overall preference for any stereoisomer of ipsdienol, because the differing behaviors of *T. dubius* and *Platysoma* species negated each other. Predators as a group were not responsive to the addition of lanierone to ipsdienol (Table 3). Collectively, in the spring, the predators were more attracted to infested logs than to any synthetic lure.

Both *Dendroctonus valens* LeConte (Coleoptera: Scolytidae) and *Corticicus parallelus* (Melsheimer) (Coleoptera: Tenebrionidae) were present in sufficient numbers in the spring to be included in the analysis. These species preferred the infested log to any synthetic lure. When all treatments were included, both insects showed statistically significant treatment effects ($F = 22.65$; $df = 8, 32$; $P = 0.0001$ and $F = 7.23$; $df = 8, 32$; $P = 0.0001$ respectively). However, when the infested log treatment was removed from the analysis, their responses to the synthetic pheromone lures and controls were nonsignificant (D).

Table 3. Effect of overall treatment, and specific effects of varying chirality and lanierone, on responses of *I. pini* and associates

| Term | <i>Ips</i> | <i>I. pini</i> | <i>T. dubius</i> | <i>E. nigripes</i> | <i>E. nigrifrons</i> | <i>Platysoma</i> | Predators | |
|-------------------|------------|----------------|------------------|--------------------|----------------------|------------------|---------------------|---------------------|
| | | | | | | | Spring ^a | Summer ^b |
| Spring | | | | | | | | |
| Treatment effect: | | | | | | | | |
| <i>F</i> | 122.41 | 122.55 | 21.73 | 2.78 | NA | 14.60 | 23.64 | NA |
| df | 8, 32 | 8, 32 | 8, 32 | 8, 32 | NA | 8, 32 | 8, 32 | NA |
| <i>P</i> | 0.0001 | 0.0001 | 0.0001 | 0.0187 | NA | 0.0001 | 0.0001 | NA |
| Chirality effect: | | | | | | | | |
| <i>F</i> | 29.86 | 29.84 | 24.93 | 0.43 | NA | 7.12 | 1.19 | NA |
| df | 2, 8 | 2, 8 | 2, 8 | 2, 8 | NA | 2, 8 | 2, 8 | NA |
| <i>P</i> | 0.0002 | 0.0002 | 0.0004 | 0.6622 | NA | 0.0167 | 0.3533 | NA |
| Lanierone effect: | | | | | | | | |
| <i>F</i> | 402.95 | 403.58 | 0.02 | 0.47 | NA | 1.84 | 0.39 | NA |
| df | 1, 32 | 1, 32 | 1, 32 | 1, 32 | NA | 1, 32 | 1, 32 | NA |
| <i>P</i> | 0.0001 | 0.0001 | 0.8787 | 0.4992 | NA | 0.1847 | 0.5372 | NA |
| Summer | | | | | | | | |
| Treatment effect: | | | | | | | | |
| <i>F</i> | 174.86 | 172.46 | 8.82 | NA | 4.53 | 2.25 | NA | 9.95 |
| df | 8, 32 | 8, 32 | 8, 32 | NA | 8, 32 | 8, 32 | NA | 8, 32 |
| <i>P</i> | 0.0001 | 0.0001 | 0.0001 | NA | 0.0009 | 0.0491 | NA | 0.0001 |
| Chirality effect: | | | | | | | | |
| <i>F</i> | 30.94 | 31.11 | 4.26 | NA | 1.74 | 4.37 | NA | 1.25 |
| df | 2, 8 | 2, 8 | 2, 8 | NA | 2, 8 | 2, 8 | NA | 2, 8 |
| <i>P</i> | 0.0002 | 0.0002 | 0.0549 | NA | 0.2359 | 0.0521 | NA | 0.3365 |
| Lanierone effect: | | | | | | | | |
| <i>F</i> | 442.56 | 442.51 | 0.95 | NA | 2.85 | 0.06 | NA | 2.98 |
| df | 1, 32 | 1, 32 | 1, 32 | NA | 1, 32 | 1, 32 | NA | 1, 32 |
| <i>P</i> | 0.0001 | 0.0001 | 0.3372 | NA | 0.1012 | 0.8075 | NA | 0.0942 |

Overall treatment effect refers to all combinations of ipsdienol enantiomers in the presence or absence of lanierone, plus infested logs and controls. Chirality effect refers to significance in a one-way ANOVA of synthetic lures grouped by three ipsdienol chiralities. Lanierone effect is a contrast of synthetic ipsdienol lures with versus without lanierone. Data are from field studies in Wisconsin, pooled over 1997 and 1998 replications.

^a Spring predators include *T. dubius*, *E. nigripes*, and *Platysoma*.
^b Summer predators include *T. dubius*, *E. nigrifrons*, and *Platysoma*.

valens, $F = 1.76$; $df = 8, 28$; $P = 0.1363$; *C. parallelus*, $F = 1.59$; $df = 7, 28$; $P = 0.1809$). Thus, no comparison among the treatments for population monitoring purposes could be made.

Effects of Various Odors on Estimates of Pest:Predator Ratios. Table 4 shows the ratios of *I. pini* to predators that would be estimated for a local population

based on the use of each synthetic lure, and how these estimated ratios compare with that in infested host material. The chemical composition of the lure greatly affected these estimates. Because predator numbers varied between spring and summer, and because *I. pini* behavior varied between the summers of 1997 and 1998, summer ratios were developed separately in-

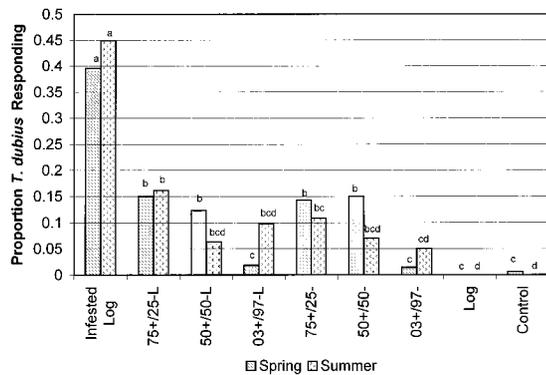


Fig. 2. Proportion of *T. dubius* responding to various natural and synthetic sources of odor in Wisconsin, 1997 and 1998. Proportions are developed from mean responses to each treatment per sample period. Different letters indicate treatments (within a season) are significantly different at $P < 0.05$.

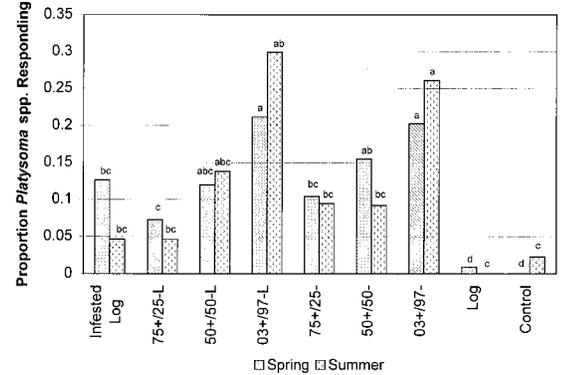


Fig. 3. Proportion of *Platysoma* spp. responding to various natural and synthetic sources of odor in Wisconsin, 1997 and 1998. Proportions are developed from mean responses to each treatment per sample period. Different letters indicate treatments (within a season) are significantly different at $P < 0.05$.

Table 4. Variable estimates of relative numbers of *I. pini* and predator populations in Wisconsin red pine plantations generated by using different synthetic lures

| Insects | Infested Log | Lanierone | | | No lanierone | | |
|-------------------------------|--------------|-------------|-------------|-------------|--------------|-------------|-------------|
| | | 75(+)/25(-) | 50(+)/50(-) | 03(+)/97(-) | 75(+)/25(-) | 50(+)/50(-) | 03(+)/97(-) |
| Spring (1997 and 1998) | | | | | | | |
| Predators ^a | 1.49 | 17.65 | 19.39 | 4.02 | 2.38 | 1.66 | 0.16 |
| <i>T. dubius</i> | 1.89 | 24.37 | 36.85 | 38.44 | 3.87 | 2.97 | 2.00 |
| <i>Platysoma</i> | 8.90 | 75.22 | 56.69 | 5.01 | 7.97 | 4.31 | 0.21 |
| Summer | | | | | | | |
| Predators ^b (1997) | 6.98 | 32.72 | 81.22 | 7.09 | 18.18 | 12.53 | 3.20 |
| Predators ^b (1998) | 5.43 | 42.23 | 42.27 | 6.42 | 13.10 | 10.29 | 0.25 |

Values shown are ratios of *I. pini* to predators. Ratios are shown separately for spring and summer because of phenological shifts in predator abundance, and separately for summer predators in 1997 and 1998 because of significant annual differences. Ratios are shown for all predators and separately for the major species in spring when predators are abundant because of differing insect behaviors.

^a Spring predators include *T. dubius*, *E. nigripes*, and *Platysoma*.

^b Summer predators include *T. dubius*, *E. nigrifrons*, and *Platysoma*.

stead of pooled across years as for the spring. The infested log always attracted more *I. pini* than predators. Synthetic lures that attracted high numbers of *I. pini*, i.e., those with lanierone, generated ratios that were much higher. For example, using 50(+):50(-) with lanierone in the spring would yield an estimate of pests to predators of 19.4, when the actual value in infested logs was 1.5. This error would be even greater in years when *Platysoma* spp. were the most abundant predators. Only one lure, 03(+)/97(-) ipsdienol without lanierone, attracted more predators than *I. pini*, thereby generating a ratio that was <1.

Ratios of *I. pini* to predators were much higher in the summer than in the spring. Meaningful pairwise comparisons were not possible between ratios because of the large number of zero values, which comprise up to 90% of the values for predators in the summers over the two seasons. Similar to insect responses obtained in the spring, lures containing lanierone generated relatively high pest:predator ratios in the summer. Almost all summer ratios were smaller in 1998 because of the higher number of predators than 1997 (Table 1).

Absolute Sampling Efficiency of *I. pini* and Predators. Although useful, the estimates of relative numbers of *I. pini* to its major predators provided in Table 4 are inadequate by themselves, because absolute pest density forms the baseline for most action thresholds. In the case of plantation pines in Wisconsin, several species of *Ips* can be important, and several species of *Enoclerus*, in addition to the predators we emphasized in our behavioral studies, can be important (Table 1). Therefore, the absolute numbers of all *Ips* pooled and all predators pooled are provided in Fig. 4, and are further delineated by treatment, season, and where necessary, by year.

Discussion

These results demonstrate that behavioral disparities between herbivores and predators responding to the herbivore's pheromones can affect estimates of their relative abundances when synthetic lures are used. From the perspective of population monitoring, the ideal synthetic lure would be one that is efficient

in sampling both the pest and its major predator species, yields estimates of relative pest and predator densities that reflect actual proportions arriving at host plants, and provides useful population information soon enough to deploy control tactics effectively. This possibility is confounded, however, by our observations that *I. pini* and its predators show different preferences for various enantiomers of ipsdienol, different responses to lanierone, different responses to natural versus synthetic sources of semiochemicals, and different patterns of seasonal abundance (Figs. 1-4; Table 1). Such disparities have important implications for bark beetle population dynamics, predator-prey coevolution, and semiochemically based trap-out tactics, but they also can pose significant challenges to population monitoring and our ability to forecast outbreaks.

The extent and direction of deviations in relative population estimates from actual arrival rates at infested host material, that would be incurred using each synthetic lure, are shown in Fig. 5. As an example, the appropriateness of using the 75(+)/25(-) ipsdienol lure with lanierone for pooled predators in the spring can be evaluated by dividing the pest:predator ratio for that lure (49.43 *I. pini*/2.80 predators = 17.65 [Table 4]), by the actual arrival ratio at the infested log, (10.17 *I. pini*/6.83 predators = 1.49 [Table 4]). Thus, that lure gave an overestimate of 17.65/1.49 = 11.85X (Fig. 5). A ratio of 1 gives a perfect approximation between the synthetic lure and actual arrival ratio of the infested log. The estimates of natural arrival ratios in the spring differed by as little as 11.54%, using 50(+)/50(-) ipsdienol without lanierone, to >12 times higher than the infested log using 50(+)/50(-) ipsdienol with lanierone (Fig. 5). The greatest overestimates were generated consistently by lures that contained lanierone, which synergizes the responses of *I. pini* but not the predators *T. dubius* or *Platysoma* spp. (Figs. 2 and 3). The major underestimates occurred when high proportions of (-) ipsdienol were present, because this enantiomer is attractive to *Platysoma* spp. but not *I. pini* in Wisconsin (Fig. 1).

In the spring, when predators are most abundant, racemic ipsdienol lures without lanierone give the most accurate estimates of pest:predator ratios, for *T.*

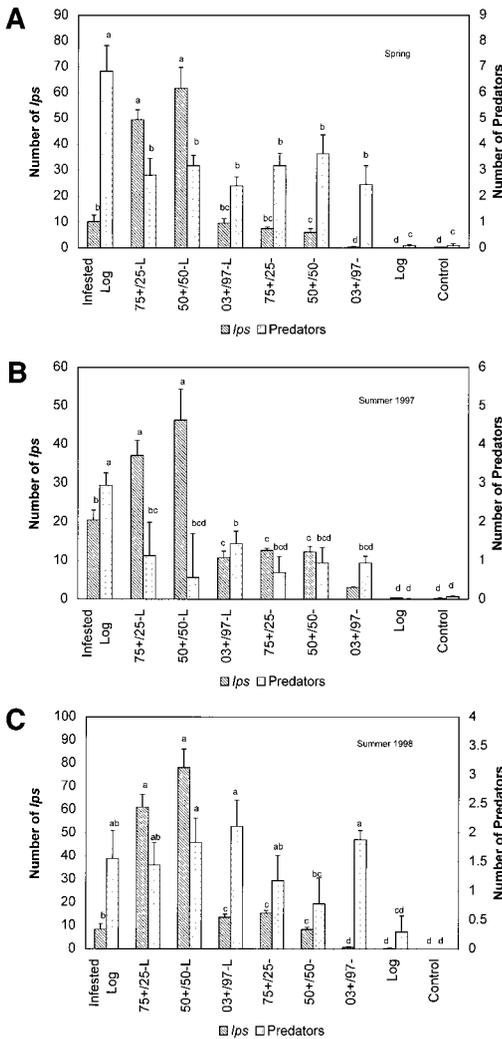


Fig. 4. Mean numbers of *Ips* and their principal predators responding to various natural and synthetic sources of odor per four day sample period in field studies in Wisconsin, 1997 and 1998. *Ips* are graphed on the left y-axis; predators are graphed on the right. Different letters indicate treatments are significantly different within a species at $P < 0.05$. (A) Spring 1997 and 1998, predators include *T. dubius*, *E. nigripes*, and *Platysoma* spp. (B) Summer 1997. Summer predators include *T. dubius*, *E. nigrifrons*, and *Platysoma* spp. (C) Summer 1998.

dubius, *Platysoma* spp., and all predators grouped (Fig. 5A). In terms of absolute sampling efficiency, however, racemic ipsdienol without lanierone is relatively inefficient for *I. pini*, efficient for *T. dubius*, and moderately efficient for *Platysoma* spp. (Fig. 4). Use of chiralities and pheromone blends that *I. pini* prefer introduced errors of >10 times for all predators, and almost 20 times for *T. dubius*. Because predator numbers varied between spring and summer, and because *I. pini* behavior varied somewhat between the summers of 1997 and 1998, we calculated these errors separately for the two summers (Fig. 5B). In the summer, the closest approximation of pest:predator ratios

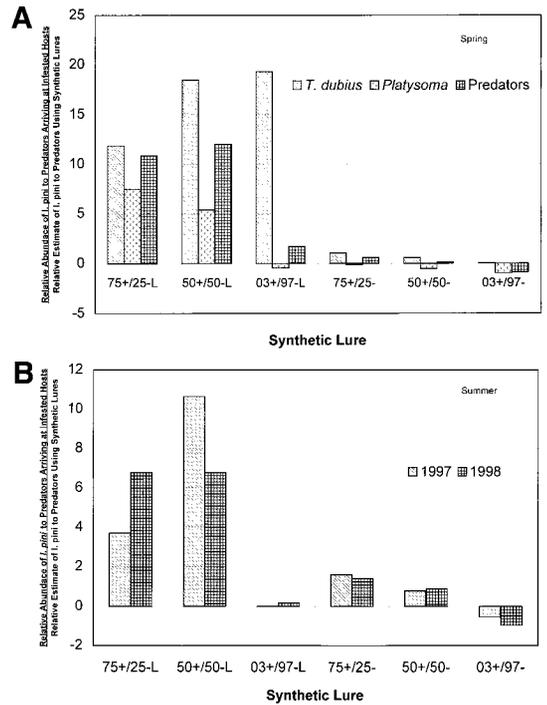


Fig. 5. Relative over- or underestimate of the pest:predator arrival ratio generated by each synthetic lure. Each estimate is calculated by dividing the arrival ratio at the given lure by the actual arrival ratio (i.e., the infested log). (A) Spring data are pooled over 1997 and 1998. *T. dubius*, *Platysoma* spp., and grouped predators (*T. dubius*, *E. nigripes*, and *Platysoma* spp.). (B) Summer predators (*T. dubius*, *E. nigrifrons*, and *Platysoma* spp.), 1997 and 1998.

in natural infestations was given by a 03(+)/97(-) ipsdienol lure with lanierone. In terms of absolute sampling efficiency, however, 03(+)/97(-) ipsdienol with lanierone is inefficient for sampling *I. pini*, inefficient for sampling *T. dubius*, and efficient only for sampling *Platysoma* species (Fig. 4).

In general, the estimates of relative pest to predator abundance are most reliable (based on comparisons between infested logs versus synthetic lures) in the spring, because fewer predators are present in the summer (Raffa 1991). This is encouraging, because early detection is crucial to effective management of bark beetles (Borden et al. 1993). Responses by *I. pini* over the 2 yr shifted slightly from 75(+)/25(-) to 50(+)/50(-) ipsdienol (Fig. 1). Plasticity in response patterns to ipsdienol has been noted by Herms et al. (1991), and may in part reflect coevolution between predators and prey (Raffa and Klepzig 1989, Raffa 1995).

Although estimates of ratios of pests to predators are useful for determining relative abundance, absolute numbers are needed to calculate population thresholds, predator functional and numerical impacts, and economic injury thresholds. Our results suggest that several types of lures may be needed to provide both. For example, an action threshold based solely on the

absolute abundance of *Ips* in the spring should be based on 50(+)/50(-) ipsdienol with lanierone (Fig. 4A). However, the most accurate way to incorporate the numbers of predators (all species) into a response threshold might be to use data based on 50(+)/50(-) ipsdienol without lanierone (Table 4). The alternative, using a single type of lure and then correcting for behavioral differences among species, might be simpler and less expensive. However, this would also be sensitive to population fluctuations between *T. dubius* and *Platysoma* spp. (Table 4).

Although our results demonstrate the feasibility of incorporating behavioral disparities among bark beetles and predators to improve overall monitoring, some practical challenges remain before implementation. For example, our overall estimates of pest to predator ratios are sensitive to the species of predator that is most abundant, which can vary between years and throughout seasons (Table 1; Figs. 4 and 5). Thus, we need additional information on which predators have greatest impact on *I. pini* populations, and how their population densities vary.

A potential weakness to any behavioral choice assay involves interactions among the various choices. For example, lures that are most attractive to *I. pini* could theoretically attract beetles away from the infested log treatment, thus creating artificially low estimates of natural ratios of *I. pini* to predators in host tissue. However, randomizing the positions of our nine treatments should preclude any systematic error. Further, the ratio of *I. pini* to predators arriving at our infested logs (1.49, Table 4) was similar to that reported by Erbilgin and Raffa (2000), 1.03, during the same periods in a neighboring plantation in Sauk County, WI (latitude N 43° 11.78', longitude W 90° 11.15'). Such ratios obviously vary among stands, but the available data suggest that our estimates of ratios of *I. pini* to predators are not deflated by neighboring lures, and may actually lead to conservative estimates in Fig. 5.

The predator *T. dubius* was much more strongly attracted to host tissue colonized by *I. pini* than to any mixture of synthetic pheromones. *T. dubius* also was more attracted to infested logs, relative to synthetic pheromone, than was *I. pini* to its own sources of odors (Fig. 1). It is possible that *I. pini* in infested logs emit more ipsdienol or lanierone than do the synthetic lures, but this seems unlikely because other responding species, such as *I. pini* and *Platysoma* spp., showed greater responses to the synthetic lures than the logs. Based on data from Lanier et al. (1980) and Teale et al. (1991), our synthetic lures released approximately the same amount of ipsdienol as *I. pini* in the log, but much more lanierone. Higher release rates of lanierone attract more *I. pini* (Teale et al. 1991), especially males, but predators' responses are not enhanced (Miller et al. 1997, Aukema and Raffa 2000). A more likely explanation is that volatiles from the infested logs are exploited as kairomones by *T. dubius* (Mizell et al. 1984, Chénier and Philogène 1989, Miller and Borden 1990). Host volatiles alone are unlikely to generate the high responses by *T. dubius* to infested tissue seen in Fig. 1, as Erbilgin and Raffa (2000)

detected no synergism using combined releases of monoterpenes and pheromones. Dahlsten (1992) proposed that parasitoids may use metabolites from fungal associates to locate bark beetles. Similar responses could occur in some predators. For example, microorganisms associated with bark beetles (Whitney 1982, Paine et al. 1997) are known to aid in pheromone production (Brand et al. 1976), and to synthesize compounds such as monoterpenes, sesquiterpenes, alcohols, acetates, and ketones (Lanza and Palmer 1977, Mironov et al. 1982, Hanssen 1993) that can affect insect behavior. Some microorganisms establish rapidly in colonized trees (Paine et al. 1997). *T. dubius* arrive synchronously with bark beetles during mass attack, but arrival persists up to day 11 after attack, long after pheromone production has ceased (Camors and Payne 1973, Dixon and Payne 1979). Some predators of bark beetle eggs and early instars, such as *C. parallelus*, also feed on *Ophiostoma minus* (Hedgecock) (Clemens 1919, Goyer and Smith 1981, Triplehorn 1990), a common bark beetle gallery fungus (Paine et al. 1997).

If kairomonal action of host tree compounds or brood gallery volatiles could be further characterized, such chemicals could be used to improve sampling of both bark beetles and predators. The general trends observed here may also provide a basis for improved population monitoring in other production systems in which predators and parasitoids use host and habitat cues in host finding (Beevers et al. 1981).

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