Red Turpentine Beetle, *Dendroctonus valens* LeConte (Coleoptera: Scolytidae), Response to Host Semiochemicals in China

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ABSTRACT The response of the introduced red turpentine beetle, *Dendroctonus valens* LeConte, to host semiochemicals in Shanxi Province, China, was distinctly different from that reported in previous studies conducted in the western part of the native range of *D. valens* in the central Sierra Nevada, CA. This finding suggests either that there is regional variation in *D. valens* response to host volatiles in North America or that the species underwent rapid adaptation after its introduction into Asia. In the Chinese population of *D. valens*, (+)-3-carene was the most attractive host monoterpene tested in studies conducted in 2002 using multiple funnel traps suspended in a *Pinus tabuliformis* stand. It attracted significantly more beetles than did any other single semiochemical or any of the ternary or quaternary blends tested, including the standard *D. valens* blend used in North America [a 1:1:1 blend of (+)-α-pinene, (−)-β-pinene, and (+)-3-carene]. (+)-α-Pinene and (−)-β-pinene, presented individually, were not significantly more attractive than controls. Adding limonene to the standard lure decreased response of *D. valens* but not significantly. A new type of semiochemical release vial was tested using a range of release rates of a 1:1:1 blend of (+)-α-pinene, (−)-β-pinene, and (+)-3-carene. The rates ranged from 150 to 210 mg/d, and these were compared with the standard North American lure, which releases ≈110 mg/d. The most attractive of these vials, which released ≈150 mg/d, captured significantly more beetles than did the standard release device; however, increasing the release rate beyond 150 mg/d did not further increase trap catch. The implications of our results for the phylogenetic geography of *D. valens* and its management as an invasive species are discussed.

KEY WORDS semiochemicals, monoterpenes, phylogenetic geography, invasive species

BARK BEETLES IN SEVERAL genera attack dead, dying, and live trees; stressed trees are especially susceptible to attack (Furniss and Carolin 1977). The red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Scolytidae), is normally a nonaggressive pest of stressed, diseased, and wounded conifers, principally in the genus *Pinus* L.; its preferred host in the western United States is *Pinus ponderosa* Douglas ex P. and C. Lawson (Smith 1961). *D. valens* is geographically widespread in North America, ranging from Canada in the north to Central America in the south, and extending the breadth of the continent in the northern part of its range (Furniss and Carolin 1977). It has a wide host range as well, attacking all pines within its geographic range (Eaton and Rodríguez Lara 1967). It does not, however, typically mass attack its host, and it is not an aggressive tree-killing species, as are many of its congeners (Smith 1961, Eaton and Rodríguez Lara 1967, Cibrian Tovar et al. 1995). In some situations in North America, however, *D. valens* does cause considerable mortality, particularly in plantation situations (Eaton and Rodríguez Lara 1967, Rappaport et al. 2001).

In China, however, *D. valens* has spread rapidly since its first large outbreak in 1999 in Shanxi Province, infesting over 500,000 ha of pine stands and causing severe mortality (Yin 2000, Miao et al. 2001). Figure 1 shows the host range, location of documented outbreaks, and location of our experimental site in China. *Pinus tabuliformis* Carrière is the most important reforestation species in China and is the principal host of *D. valens* in China (Li et al. 2001). It has a vast natural distribution in northern and north-central China, an area roughly equivalent to two-thirds of the land area of the continental United States. It was introduced into northern Korea for afforestation purposes in the 18th century (Mirov 1967), but we do not

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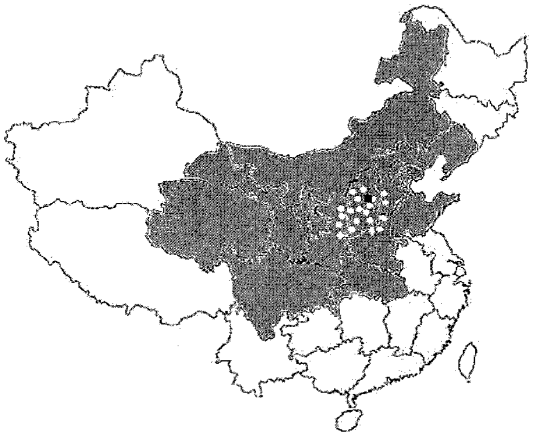

Fig. 1. Map of China showing distribution of *P. tabuliformis* (shaded), locations of documented infestations of *D. valens* (white dots), and location of 2002 experimental site (black square).

know its current distribution there. *D. valens* was first reported from China in 1983 in Shanxi Province and was presumed to have been introduced in imported, unprocessed *P. ponderosa* logs sent to Shanxi from the west coast of the United States for use in mine construction (Yin 2000). The first large outbreak was seen in Shanxi Province in 1999 (Yin 2000, Li et al. 2001) and was presumed to have resulted from several years of consecutive drought that stressed *P. tabuliformis* stands. Since the outbreak in 1999 in Shanxi Province, this exotic beetle has spread rapidly to the adjacent provinces of Hebei, Henan, and Shaanxi and has infested over 500,000 ha of Chinese pine stands, primarily those over 30 yr old, killing >4 million trees to date (J. Wu, State Forestry Administration, personal communication).

A DNA-based study is currently underway to determine the source/s of introduction of *D. valens* from North America into China, and preliminary results suggest more than one introduction, one of which is from the Pacific Northwest (A. Cognato, Texas A&M University, personal communication, and J. S., unpublished data). Multiple introductions may contribute to the successful establishment and degree of invasiveness of introduced pests because of the increased genetic diversity conferred (Barrett and Husband 1990). Other factors, such as the potential for human-assisted transport, lack of competition or natural enemies, small organism size, and high reproductive potential, are also correlated with the invasiveness of non-native species (Sakai et al. 2001), and these factors characterize *D. valens* in China. The potential damage from *D. valens* is thus catastrophic; therefore, effective measures for monitoring and controlling *D. valens* are desperately needed (Li et al. 2001, Sun et al. 2003). Insecticidal and fumigation measures to control *D. valens* have had only limited success and have undesirable environmental consequences, and silvicultural methods to reduce damage have not been effective in controlling damage (Li et al. 2001, Miao et al. 2001). The life cycle of *D. valens* in its Chinese hosts is more cryptic than in its native hosts, because in China the beetles colonize the root system more deeply than in North America, and they overwinter in the roots in their Chinese host trees (Li et al. 2001). Semiochemical control measures, therefore, are presumed to be the most promising methods for use in China.

Although much progress has been made in elucidating pheromone-mediated aggregation of bark beetles, research has shown that host volatiles, rather than aggregation pheromones, may have more promise than pheromones for management of some species (Borden 1985, Byers 1989, Wood 1982). In North America, *D. valens* is known to exploit host volatiles as kairomones in locating and selecting *P. ponderosa* (Vité and Gara 1962, Owen 1985, Erbilgin and Raffa 2000, Erbilgin et al. 2001), and volatile monoterpenes from undamaged and wounded/inoculated hosts have been shown to differentially affect the host selection behavior of *D. valens* (Klepzig et al. 1996). Hobson et al. (1993) reported attraction of *D. valens* to three chiral monoterpenes in field assays, and those results were somewhat confirmed by laboratory electroantennogram assays (White and Hobson 1993). Hobson et al. (1993) identified the principal kairomones for *D. valens* as (+)-α-pinene, (−)-β-pinene, and (+)-3-carene, with the pinenes as the principal attractants. They also presented evidence that (−)-α-pinene, the antipode of the attractant (+)-α-pinene, serves to interrupt attraction of *D. valens* to (+)-α-pinene. The semiochemical blend of (+)-α-pinene, (−)-β-pinene, and (+)-3-carene, in a 1:1:1 ratio, is now commercially available as a *D. valens* lure (Phero Tech Corp., Delta, BC, Canada). The behavioral activity of this lure in China was recently confirmed in a large field trial in Shanxi Province (Sun et al. 2003). However, recent work by Erbilgin and Raffa (2000) conducted in Wisconsin showed that both enantiomers of α-pinene were weakly attractive to *D. valens* in field tests, suggesting that the Wisconsin population may respond differently from the California population. This finding led us to re-examine *D. valens* response to host volatiles in China, on the assumption that the Chinese population might also respond differently from the California population.

Our ultimate goal is to develop more effective semiochemical tactics for monitoring and managing *D. valens* populations in China. The well-documented role of host volatiles in *D. valens* host selection (Borden 1985, Byers 1989, Joseph et al. 2001, Wood 1982) suggested that they could play an important role in this effort. Our objectives in this study were to (1) assess the roles of (+)-α-pinene, (−)-β-pinene, (+)-3-carene, and (+)-limonene in attracting or interrupting attraction of *D. valens,* including sex-specific effects; (2) assess attraction of various release rates of the commercially available kairomone blend; (3) test efficacy of a new vial releaser; and (4) quantify *D. valens* population fluctuations over time.

Table 1. Mean number of beetles ± SD responding to monoterpene-baited multiple funnel traps, Shanxi Province, 2002

Monoterpenes (release rate in mg/d)	Ratio	Mean ± SD beetles/trap/day
Monoterpene blend comparisons		
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (180)	1:1:1	23.51 ± 33.02a
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (180)	1:2:1	23.21 ± 44.60a
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (180)	1:4:1	24.92 ± 28.60a
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (180)	1:1:3	43.67 ± 47.24b
(−)-β-pinene (180)	NA	4.17 ± 6.27c
(+)-α-pinene (180)	NA	3.07 ± 6.78c
(+)-3-carene (180)	NA	71.77 ± 106.40d
(+)-α-pinene:(−)-β-pinene:(+)-3-carene:(+)-limonene (180)	1:1:1:0.5	13.25 ± 23.96a
Control (none)	NA	0.31 ± 0.69c
Monoterpene release rate comparisons		
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (110)	1:1:1	7.78 ± 13.00a
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (150)	1:1:1	35.84 ± 52.93b
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (180)	1:1:1	23.51 ± 33.02b
(+)-α-pinene:(−)-β-pinene:(+)-3-carene (210)	1:1:1	28.64 ± 38.12b
Control (none)	NA	0.31 ± 0.69c

Monoterpenes, blend released from lure, Ratio, ratio of monoterpenes in blend; all release devices were Sun devices except for the 110 mg/d treatment, which was the standard (Phero Tech) lure; *N* = 10 for each treatment.

Means in the same column followed by a different letter are significantly different at $\alpha = 0.05$ using the Bonferroni approach (multiple comparisons applied within the monoterpene blend test and the monoterpene release rate test, not across the two tests).

Materials and Methods

Study Area. The experiment was conducted in a 35-yr-old plantation of *P. tabuliformis* in the Niu Tou Mountains at the foot of the Tai Hang Mountains (N 37°28′ E 113°02′; average elevation, 1,400 m), southeast of the city of Yuci, Shanxi Province. The 167-ha stand was relatively uniform in age (35 yr), diameter at breast height (DBH; ≈17 cm), and height (15 m). The site condition was poor, with rocky soils and low rainfall, but the area was well stocked despite the harsh site and extensive *D. valens*–caused mortality. For the previous 2 yr, *D. valens*–infested stumps had been treated with insecticide fumigation and sealed in plastic to prevent beetle emergence. Nevertheless, ≈20% of standing trees were currently suffering *D. valens* attacks at the time of the study.

Experimental Materials. We assessed the effect of varying monoterpene blends by baiting 8-funnel Lindgren traps, which are recommended by the manufacturer (Phero Tech, Delta, BC, Canada) for trapping *D. valens* with the recommended *D. valens* lure, and varied the relative proportions of the three monoterpenes and added another monoterpene, limonene, as a potential interruptant. The recommended lure consisted of three host monoterpenes: (+)-α-pinene, (−)-β-pinene, and (+)-3-carene, hereafter referred to as the "standard blend." The standard blend has been used extensively over the last decade for monitoring of *D. valens* populations in North America (Erbilgin et al. 2001, Rappaport et al. 2001) and was thus intended as a standard of comparison. The monoterpenes (+)-α-pinene, (−)-β-pinene, and (+)-3-carene were also presented individually to determine whether or not the response of beetle populations in China corresponded with that of California populations in earlier tests (Hobson et al. 1993). (+)-Limonene, a presumed interruptant or repellent, was obtained from ACROS Company (Leicestershire, UK). All other chemicals were obtained from Aldrich (Milwaukee, WI); their chemical purities were as follows: (−)-β-pinene, 99%; (+)-α-pinene, 98%; (+)-3-carene, 97%; (+)-limonene, 96%. All of the lures in these assays consisted of closed 15-ml vials filled with monoterpenes to release an aggregate of 180 mg/d. Thus, for example, the treatment for (+)-3-carene contained three times the amount of (+)-3-carene as did the treatment using the standard blend. Blends of monoterpenes were assumed to release their constituents in ratios equal to their compositions, because the commercially available lure has been shown to release monoterpenes at rates very similar to their concentrations (J. P. Lafontaine, Phero Tech, personal communication).

We assessed the effect of different release rates and release vials by baiting Lindgren traps with various vial types that released the standard blend at different rates (Table 1). The standard, commercially available pheromone lures that were developed for use in North America (hereafter referred to as "standard lures") consisted of the standard blend released from a closed 15-ml polyethylene bottle at the rate of 110 mg/d (Phero Tech). This lure was used as a standard of comparison for treatments with higher release rates, which used different release devices. The new type of release bottle, hereafter referred to as the "Sun lure," was manufactured at the HongZhi Plastic Plant in Taiyuan, Shanxi Province, and was designed for three different intended release rates. Monoterpenes slowly migrated through the walls of those polyethylene bottles, with release rates adjusted by changing the wall thickness and size of the bottle. Release rates of the Sun lures were first determined gravimetrically at the laboratory of the Institute of Zoology, Chinese Academy of Sciences, at a temperature of 21°C and later during the field experiment for further confirmation. To simulate natural field conditions, an electric fan was used to generate a wind speed of ≈1.2 m^3/s. Generally, the release rates in the field were higher than in the laboratory because of high temperatures during the trapping period (mean temperature >

27°C) and strong winds. We therefore report the actual field release rate in this paper, whereas the laboratory rate was used only as reference for experimental design and manufacture of the release bottles. Three kinds of bottles, with release rates of ≈150, 180, and 210 mg/d, were eventually manufactured and used in the study. Chemical purities of components of the standard lure and the Sun lures, all of which were obtained from the same source, were as follows: (−)-β-pinene, 99%; (+)-α-pinene, >95%; and (+)-3-carene, 97%.

Experimental Design and Statistical Analysis. A total of 12 treatments with 10 replicates each were applied in the study (Table 1). We chose to use this large number of replicates rather than re-randomizing at frequent intervals, which is sometimes done to correct for overdispersed Poisson-distributed responses such as are common with scolytid trapping experiments (S. Mori, USDA Forest Service, Berkeley, CA, personal communication). To test efficacy of differing blends, 90 trees were randomly selected with trees 50 m apart in a grid; treatments were randomly assigned to each tree. The choice of semiochemical blends was based on previous work on *D. valens* and its congeners as described above (Hobson et al. 1993, White and Hobson 1993, Smith 1993, 1994, 1995, and 2000, Rappaport et al. 2001, Sun et al. 2003) and resin composition of *P. tabuliformis* (Jin et al. 1994, J. S., unpublished data). To test release rate and release device differences, 30 more trees were randomly selected at least 50 m apart and 50 m from any lure efficacy tree in a grid within the same stand. Ten traps baited with Phero Tech lures (110 mg/d) were used as a standard of comparison or positive control, whereas the baited control, releasing at the rate of 180 mg/d, from the first part of the experiment was also used as a treatment in the release rate portion of the study. Ten traps without baits were used as negative controls. In both treatments, eight-funnel Lindgren traps baited with either the standard lure (Phero Tech) or the Sun lure was suspended between trees, with the bottom of the collection cup ≈10 cm above ground level, the level at which *D. valens* attacks trees. A plastic insecticidal strip saturated with 2,2-dichlorovinyl dimethyl phosphate (Hercon Vaportape II insecticidal strips; Hercon Environmental Co., Emigsville, PA) was put in each collection cup as a killing agent. The experiment was set up on 29 April 2002, and traps were checked every 5–7 d until 20 July 2002. Beetles captured in each trap on each date were counted, sexed, and recorded. Voucher specimens were deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

Treatments were replicated 10 times in a completely randomized design (Table 1). Trap counts were analyzed with generalized linear models for overdispersed Poisson distributed responses (counts) (McCullough and Nelder 1989). Results are presented in tables as means and SD. Multiple comparisons were based on the maximum likelihood ratio test with the Bonferroni approach (experiment-wise $\alpha = 0.05$). SAS GENMOD procedures (SAS Institute 1997) were used for the analysis.

Results and Discussion

Effect of Varying the Blends of Monoterpenes. In strong contrast with previous results by Hobson et al. (1993) and White and Hobson (1993), (+)-3-carene attracted significantly more *D. valens* than any other individual compound or blend (Table 1). The next most attractive treatment was the combination of (+)-α-pinene + (−)-β-pinene + (+)-3-carene (1:1:3), followed by the standard blend, (+)-α-pinene + (−)-β-pinene + (+)-3-carene (1:1:1). The amount of (+)-3-carene, therefore, seemed to be the most important factor determining trap catch. Varying the amount of (−)-β-pinene in the standard *D. valens* semiochemical lure did not affect trap catch, nor did (+)-α-pinene or (−)-β-pinene, when presented in single-component baits, attract significantly more beetles than did the unbaited controls. This result, coupled with the fact that (+)-3-carene, when presented solo, attracted significantly more beetles than did the any of the ternary blends of (+)-α-pinene + (−)-β-pinene + (+)-3-carene, suggests that neither (+)-α-pinene nor (−)-β-pinene affects the response of *D. valens* in China. This result was surprising because previous studies (Hobson et al. 1993, White and Hobson 1993) had shown that (+)-α-pinene and (−)-β-pinene were behaviorally active at both the neural and behavioral levels. Our result indicates that (+)-3-carene is the most important primary attractant for *D. valens* in China and suggests that *D. valens,* like many other scolytids, may display regional variation in response to semiochemicals (Miller et al. 1997, Erbilgin et al. 2001). The addition of (+)-limonene reduced the trap catch by the standard blend (Table 1), but this difference was not significant. This result was not surprising because Smith (1963, 1965) had earlier demonstrated the repellency and toxicity of limonene to beetles in the genus *Dendroctonus,* and our results merely confirm his results with a congener.

Unfortunately, there has been little research into possible geographic variation in response to host volatiles by *D. valens,* but we are currently engaged in a transcontinental study to remedy that situation. Early results suggest at least some degree of variability even among sites in western North America (N. E. Gillette, unpublished observations). *P. ponderosa* needle and resin volatiles are composed principally of the three monoterpenes used in the commercial lure, with smaller amounts of myrcene and limonene (Mirov 1961, Smith 1964, Latta et al. 2000). Significant regional variation in *P. ponderosa* monoterpene composition exists, however (Smith 2000). In some northern California populations, for example, α-pinene predominates, whereas in some central California populations, 3-carene predominates. In addition, Smith (1977, 2000) showed that some *P. ponderosa* families are very high in limonene and that limonene vapors (and secondarily 3-carene vapors) are toxic to *Dendroctonus brevicomis* LeConte (Smith 1963, 1965). Although

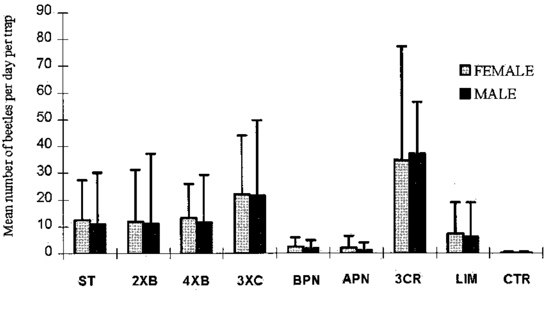

Fig. 2. Sex ratios of beetles responding to treatments, Shanxi Province, 2002 [STD, standard blend; 2XB, standard blend with twice the amount of (−)-β-pinene; 4XB, standard blend with four times the amount of (−)-β-pinene; BPN, (−)-β-pinene alone; APN, (+)-α-pinene alone; 3CR, (+)-3-carene alone; 3XC, standard blend with three times the amount of (+)-3-carene; LIM, standard blend with (+)-limonene; CTR, unbaited multiple funnel traps].

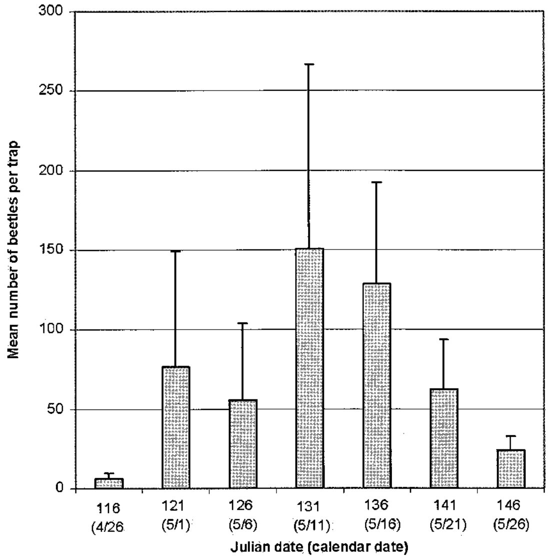

Fig. 3. Mean number of beetles/trap responding to (+)-3-carene lures from 6 May to 5 June 2002, Shanxi Province, China, by Julian date and calendar date.

there is regional variation in monoterpene composition, *P. ponderosa* is nevertheless uniquely high, among its congeners, in 3-carene, which is regarded as the "signature" monoterpene of *P. ponderosa* (Mirov 1961). The composition of needle monoterpenes of *P. tabuliformis* is reported to be similar to that of *P. ponderosa* (Jin et al. 1994, Latta et al. 2000), but a better understanding of the chemical ecology of *D. valens* and a more extensive analysis of regional variation in *P. tabuliformis* resin composition are required to fully assess the implications for *D. valens* management in China. Further studies including the behavior, neurophysiology, and genetics of *D. valens* in North America and China are needed to understand these differences in response. Based on these results, however, it is clear that (+)-3-carene has real potential for monitoring, and perhaps controlling, *D. valens* in China.

Sex-Specific Effects. There was no significant difference in response by males and females to any of the treatments (Fig. 2), which is in agreement with other reports (Hobson et al. 1993, Sun et al. 2003). Similar results were seen in a study with the closely related black turpentine beetle, *Dendroctonus terebrans* (Olivier) (Delorme and Payne 1990), and in previous studies with *D. valens* in California (N. E. Gillette, unpublished observations). Our study, however, included different monoterpenes, different combinations, and different release rates than were tested in earlier studies.

Effect of Release Rate. There was some variation in catch among the four different release rates using a fixed ratio (1:1:1) of (+)-α-pinene:(−)-β-pinene:(+)-3-carene, but only the lowest release-rate lure, which used a different type of release vial from the other three lures, was significantly different from the others. Fatzinger (1985) reported that the black turpentine beetle responded positively to increased release volumes of turpentine and ethanol, so we had expected that increasing release rates might increase attraction. Although the 110-mg release vial trapped significantly fewer beetles than did the other release rates, there was no significant difference in response at release rates of 150, 180, and 210 mg/d. Attraction of *D. valens* to vials releasing 110 mg/d was previously demonstrated in a site close to the current study site in Shanxi using Phero Tech lures, where the mean catch per trap per day was ≈12 and 14 beetles/d in two experiments (Sun et al. 2003). That is higher than the trap catch in this study, where the Phero Tech lure caught only ≈7 beetles/d. However, the infestation in that stand in 2001 was 60% higher than this site.

Adult Population Fluctuation. In the southern United States, two to three generations of *D. valens* may develop per year (Eaton and Rodríguez Lara 1967). In Shanxi Province, China, it has been suggested that after the overwintering generation emerges, a second, smaller, generation of *D. valens* may appear in late July or August (Miao et al. 2001), but the evidence supporting that conclusion is not clear. In our study, *D. valens* adults emerged in May as previously reported (Li et al. 2001, Sun et al. 2003), with the rate of emergence apparently depending on temperature. The weather was slightly warmer in most parts of northern China in 2002, which probably influenced the *D. valens* emergence date. The peak emergence occurred in late May (Fig. 3) and lasted until early June, with a slight dip in mid-May, which was probably attributable to cooler weather. After late May, there were no smaller subsequent peaks, suggesting that, in this locality, there may be only a single generation per year. Although these results do not resolve the question of voltinism of *D. valens* in China, they clearly demonstrate that the window for control in Shanxi Province should be focused on the peak in May.

Conclusions. Our results underscore the importance of site-specific testing of semiochemical blends and highlight the need for a full understanding of the phylogenetic geography of introduced pest species. The difference in response to host volatiles by Asian and North American populations suggests either that there is regional variation in *D. valens* response to behavioral chemicals in its native range or that the species adapted remarkably rapidly in its new environment. We are currently in the process of sampling *D. valens* molecular genotype and behavioral response to host volatiles across its distribution in North America and China to determine whether any population in its native range has the strong response to (+)-3-carene seen in China and whether there is corollary genetic and behavioral variation in the Chinese populations. Molecular genetic data have been used successfully to estimate sources of biological invasions (Davies et al. 1999), and behavioral chemistry has also been shown to have a geographic basis (Miller et al. 1997). A fuller understanding of such patterns of phylogenetic geography will be essential for the management of *D. valens* both in China and North America. For example, if the populations of *D. valens* in China prove to be from a single North American source, the introduced beetles may be more or less uniform in their response to host semiochemicals and a single semiochemical blend may function in the management of this introduced pest. However, if molecular genetic and semiochemical studies reveal variable genotypes and phenotypes of *D. valens* in China, its management with semiochemicals may be more challenging than had been hoped. Inasmuch as research findings in China have stimulated further study of geographic variation in the native range of *D. valens*, North American land managers may inadvertently benefit from the accidental introduction of this pest into Asia.

From a pragmatic standpoint, our results provide a new, more effective single-component lure for use in monitoring and trapping of *D. valens* in China. The information that *D. valens* in China responds most strongly to (+)-3-carene as an attractant is immensely useful for monitoring and trapping, because of the expense of pheromone-grade monoterpenes. Our findings suggest that the standard commercial lure for *D. valens* in North America may not, in fact, be optimal for all populations. This new finding is being tested in other parts of the range of *D. valens,* in part to maximize trapping efficacy in North America and in part to determine the original source/s of introduction of *D. valens* from North America to Asia. Such knowledge is often helpful in optimizing biological control and semiochemical control programs, because it incorporate factors that may vary regionally within a species.

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References Cited

Barrett, S.C.H., and B. C. Husband. 1990. The genetics of plant migration and colonization, pp. 254–277 *In* A.D.H. Brown, M. T. Clegg, A. L. Kahler, and B. S. Weir (eds.), Plant population genetics, breeding, and genetic resources. Sinauer, Sunderland, MA.

Borden, J. H. 1985. Aggregation pheromones, pp. 257–285. *In* L. I. Gilbert (ed.), Comprehensive insect physiology, biochemistry and pharmacology. Pergamon, Oxford, UK.

Byers, J. A. 1989. Chemical ecology of bark beetles. Experientia. 45: 271–283.

Cibrian Tovar, D., J. Tulio Mendez Montiel, R. Campos Bolaños, H. O. Yates III, and J. Flores Lara. 1995. Forest insects of Mexico. Universidad Autónoma Chapingo, Chapingo, México.

Davies, N., F. X. Villablanca, and G. K. Roderick. 1999. Bioinvasions of the medfly *Ceratitis capitata:* source estimation using DNA sequences at multiple intron loci. Genetics. 153: 351–360.

Delorme, J. L., and T. L. Payne. 1990. Antennal olfactory responses of black turpentine beetle, *Dendroctonus terebrans* (Olivier), to bark beetle pheromones and host terpenes. J. Chem. Ecol. 16: 1321–1329.

Eaton, B., and R. Rodríguez Lara. 1967. Red turpentine beetle, *Dendroctonus valens* LeConte, pp. 21–24. *In* A. G. Davidson and R. M. Prentice (eds.), Important forest insects and diseases of mutual concern to Canada, the United States and Mexico. Canadian Department of Forest and Rural Development, Ottawa, Canada.

Erbilgin, N., and K. F. Raffa. 2000. Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromones. J. Chem. Ecol. 26: 2527–2548.

Erbilgin, N., A. Szele, K. D. Klepzig, and K. F. Raffa. 2001. Trap type, chirality of α-pinene, and geographic region affect sampling efficiency of root and lower stem insects in pine. J. Econ. Entomol. 9: 1113–1121.

Fatzinger, C. W. 1985. Attraction of the black turpentine beetle (Coleoptera: Scolytidae) and other forest Coleoptera to turpentine-baited traps. Environ. Entomol. 14: 768–775.

Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. U.S. Dep. Agric. Forest Service, Washington, DC.

Hobson, K. R., D. L. Wood, L. G. Cool, P. R. White, T. Ohtsuka, I. Kubo, and E. Zavarin. 1993. Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. J. Chem. Ecol. 19: 1837–1846.

Jin, Y. J., J. K. Wu, F. Sun, W. H. Deng, H. J. Wang, and W. C. Sun. 1994. Terpene composition of needle oil from *Pinus tabulaeformis* and the composition with other two-needle pines. J. Beijing Forestry Univ. 16: 39–47.

Joseph, G., R. G. Kelsey, R. W. Peck, and C. G. Niwa. 2001. Response of some scolytids and their predators to ethanol and 4-allylanisole in pine forests of central Oregon. J. Chem. Ecol. 27: 697–715.

Klepzig, K. D., E. B. Smalley, and K. F. Raffa. 1996. Combined chemical defenses against an insect-fungal complex. J. Chem. Ecol. 22: 1367–1388.

Latta, R. G., Y. B. Linhart, L. Lundquist, and M. A. Snyder. 2000. Patterns of monoterpene variation within individual trees in ponderosa pine. J. Chem. Ecol. 26: 1341–1357.

Li, J. S., G. B. Chang, Y. S. Song, Y. W. Wang, and B. S. Chang. 2001. Control project on red turpentine beetle (*Dendroctonus valens*). For. Pest Dis. 4: 41–44.

McCullough, P., and J. A. Nelder. 1989. Generalized linear models. Monographs on statistics and applied probability 37. Chapman & Hall, New York.

Miao Z. W., W. M. Chou, F. Y. Huo, X. L. Wang, J. X. Fang, and M. M. Zhao. 2001. Biology of *Dendroctonus valens* in Shanxi Province. Shanxi For. Sci. Tech. 23: 34–37.

Miller, D. R., K. E. Gibson, K. F. Raffa, S. J. Seybold, S. A. Teale, and D. L. Wood. 1997. Geographic variation in response of pine engraver, *Ips pini,* and associated species to pheromone, lanierone. J. Chem. Ecol. 23: 2013–2031.

Mirov, N. T. 1961. Composition of gum turpentines of pines. U.S. Dep. Agric. Forest Service, Washington, DC.

Mirov, N. T. 1967. The genus *Pinus.* Ronald Press, New York.

Owen, D. R. 1985. The role of *Dendroctonus valens* and its vectored fungi in the mortality of ponderosa pine. Ph.D. dissertation. University of California, Berkeley, CA.

Rappaport, N. G., D. R. Owen, and J. D. Stein. 2001. Interruption of semiochemical-mediated attraction of *Dendroctonus valens* (Coleoptera: Scolytidae) and selected nontarget insects by verbenone. Environ. Entomol. 30: 837–841.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, M. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. Annu. Rev. Ecol. Syst. 32: 305–332.

SAS Institute. 1997. SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary, NC.

Smith, R. H. 1961. Red turpentine beetle. U.S. Dep. Agric. Forest Service, Washington, DC.

Smith, R. H. 1963. Toxicity of pine resin vapors to three species of *Dendroctonus* bark beetles. J. Econ. Entomol. 56: 827–831.

Smith, R. H. 1964. Perennial constancy of the monoterpene synthesis in the wood oleoresin of *Pinus ponderosa.* Nature (Lond.). 202: 107–108.

Smith, R. H. 1965. Effect of monoterpene vapors on the western pine beetle. J. Econ. Entomol. 58: 509–510.

Smith, R. H. 1977. Monoterpenes of ponderosa pine xylem resin in western United States. U.S. Dep. Agric. Forest Service Tech. Bull. 1532, Washington, DC.

Smith, R. H. 2000. *Xylem monoterpenes* of pines: distribution, variation, genetics, function. U.S. Dep. Agric. Forest Service, Berkeley, CA, PSW-GTR-177.

Sun, J. H., N. E. Gillette, Z. W. Miao, L. Kang, Z. N. Zhang, D. R. Owen, and J. D. Stein. 2003. Verbenone interrupts attraction to host volatiles and reduces attack by *Dendroctonus valens* LeConte (Coleoptera: Scolytidae) on *Pinus tabuliformis* in China. Can. Entomol. 135: 721–732.

Vité J. P., and R. Gara. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 21: 251–273.

White, P. R., and K. R. Hobson. 1993. Stereospecific antennal response by the red turpentine beetle, *Dendroctonus valens,* to chiral monoterpenes from ponderosa pine resin. J. Chem. Ecol. 19: 2193–2202.

Wood, D. L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annu. Rev. Entomol. 27: 411–446.

Yin, H. F. 2000. A synopsis of morphological and biological characters of *Dendroctonus valens* LeConte. Acta Zootaxonomica Sinica 251: 120.

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