

Colonization patterns of the red turpentine beetle, *Dendroctonus valens* (Coleoptera: Curculionidae), in the Luliang Mountains, China

Zhudong Liu¹, Longwa Zhang², Zhanghong Shi¹, Bo Wang¹, Wan Qiang Tao³, and Jiang-hua Sun¹

¹The State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, ²Anhui Agricultural University, Hefei, ³Beijing Forest Pest Control Station, Beijing, China

Abstract The alien red turpentine beetle (RTB), *Dendroctonus valens* LeConte, is one of the most economically destructive forest pests in China, having killed more than 6 million pines in recent years. There is a need to understand the basic biology and ecology of the beetle in order to develop an effective monitoring and management strategy. In this study, the effects of hillside exposure (south- and north-facing), host-tree locations according to relief (valley, mid-slope, and ridge-top) and tree diameters on RTB colonization were investigated in one valley (3 sites). The results showed that (i) RTB clearly preferred colonizing pines growing on south-facing hillsides, especially in the valley; (ii) RTB preferred to colonize the pines growing at the valley rather than pines growing at mid-slope or on ridge-top; (iii) RTB preferred to colonize trees with large diameter over small and medium-sized pines; (iv) the attack density of RTBs (measured by pitch tubes/pine) was obviously higher on larger trees standing in the valley than other trees standing at other places. We conclude from RTB colonization patterns, that RTB prefers to attack large trees in the valley, which may be useful in developing a pest-management strategy.

Key words colonization patterns, *Dendroctonus valens*, *Pinus tabulaeformis*, tree diameter, tree exposure, tree location according to relief

Introduction

The red turpentine beetle (RTB), *Dendroctonus valens* LeConte (Coleoptera: Curculionidae, Scolytinae), is a widespread pest of pines in North America (Eaton & Lara, 1967; Owen, 2003). It has been recorded on at least 40 species of conifers. In North America, attacks by RTB are typically not considered to be a significant threat to tree health (Smith, 1971; Cibrián-Tovar *et al.*, 1995). However, the North American native beetle was introduced into China in the early 1980s when unprocessed logs were imported from the west coast of the United

States (Song *et al.*, 2000) and has spread rapidly since its first outbreak in 1999 from Shanxi Province to three other adjacent provinces of Hebei, Henan and Shaanxi (Miao, 2002). It has infested over half a million ha of pine stands and is causing severe tree mortality (Li *et al.*, 2001; Miao *et al.*, 2003). With pines as a major reforestation species in China, and *Pinus tabulaeformis* Carr widely planted across a large portion of the country, the potential for this exotic beetle to cause damages is great (Li *et al.*, 2001; Sun *et al.*, 2003). A better understanding of its basic biology and ecology is important for developing an effective management strategy.

As RTB is a secondary pest in North America and a serious alien species in China, knowledge of the biology and ecology of RTB is still limited (Smith, 1971; Cibrián-Tovar *et al.*, 1995; Zhang *et al.*, 2002; Gao *et al.*, 2003; Sun *et al.*, 2003; Liu *et al.*, 2006; Zhang & Sun, 2006; Zhang *et al.*, 2007). In addition, when an exotic herbivore invades

Correspondence: Jiang-hua Sun, Institute of Zoology, Chinese Academy of Sciences, Datun Road, Chaoyang District, Beijing 100101, China. Tel: +86 10 64807121; fax: +86 10 64807099; email: sunjh@ioz.ac.cn

and colonizes a new habitat, it is typically confronted with new hosts, competitors and natural enemies, which have caused some trait change in adapting to new habitats (Erbilgin *et al.*, 2007). To better understand the invasion biology of the beetle and develop an efficient management strategy to suppress or prevent future outbreaks, certain basic questions related to its biology need to be answered. One of these questions concerns the colonization patterns of the beetle.

Based on field observations, large trees in the valley seem to have a higher chance of being infected by RTB and each tree may host several adults. Based on these observations, several questions were raised, such as (i) does hillside orientation affect RTB attack; (ii) do RTBs prefer to attack trees standing in the valley than at mid-slope or ridge-top; (iii) do RTBs prefer larger pines over smaller ones; and (iv) do pine tree location and tree diameter influence the density of RTBs (measured as pitch tubes per tree), and how? Colonization patterns are very important for the development of semiochemical methods to control RTB. In this study, field experiments were carried out with the aim of answering some of the above questions.

Materials and methods

Field investigation site of RTB and the symptoms of RTB attack

Field investigations were conducted in September 2004 in a natural stand of *P. tabulaeformis* at Beishe Mountain at the foot of the Luliang Mountains (37° 48' N, 111° 57' E, average elevation 1400 m), west of Gujiao, Shanxi Province, China. This stand is about 30 years old and had the first *D. valens* outbreak in 1999. The terrain of these mountains is diverse and it is difficult to find different valleys with the same orientation and elevation. The stand was chosen because of its high population of RTB. Both hillsides along the valley were investigated for the RTB attack: one south-facing, one north-facing (Fig. 1).

Attacks are distinguished by the presence of large, light-pink to reddish-brown pitch tubes, about 1–2 inches in diameter around the base of the tree, and/or piles of pink or white dust at the base of the tree and in bark crevices (Smith, 1971) (Fig. 2). These two characteristics were used to determine if RTB attack had occurred, and the number of pitch tubes was also recorded as attack density.

The relationships among RTB attack, tree exposure, tree location according to relief and tree diameter

On this mountain, most pines can be divided into three

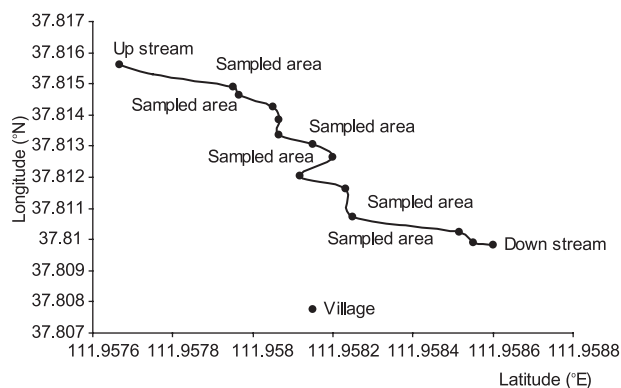


Fig. 1 Global positioning system location of investigated valley in Luliang Mountains of China. The line shows the pathway of the sampled valley to show the orientation. Investigation sites were located on both hillsides along the pathway.



Fig. 2 Pitch tubes and piles of pink or white dust made by red turpentine beetles boring at the base of the tree (photograph by Z. D. Liu). The arrows show a pitch tube (up) and pink dust (down).

groups according to age that is, younger than 20 years, between 20 to 30 years, and older than 30 years, respectively. These three groups were recognized using the diameter at breast height (DBH) under the help of local workers, that is, DBH < 15 cm, DBH 15–20 cm and DBH > 20 cm. Along the pathway of the valley from low to high elevation, three sites were selected and hillsides south-facing and north-facing were investigated at each site. Both hillsides rise to about 200 m elevation above the valley. Three investigating locations were taken along each hillside of the valley: valley floor, mid-slope (at 100 m above the valley), and

ridge-top, respectively. At each location, 50 pines were randomly chosen (approximately 17 trees for each size group). A total of 900 trees were randomly chosen for this study (6 locations for both hillsides at each site and 3 sites in the valley). RTB attack, attack density (pitch tube number per tree), hillside orientation, tree location, and tree diameter were recorded for each sampling tree. For attack density, pitch tubes were counted from ground to 2m high, although most were concentrated parting the low area. Old and fresh pitch tubes were included.

Statistical analysis

Attack rate (%) was obtained from counting and arcsine was transformed before analysis. For both RTB attack rate and attack density data, univariate of the general linear model (GLM) (SPSS, 1999) was used to reveal the relationship between tree exposure, tree location and tree diameter. Simple one-way ANOVA followed by a multiple comparison was carried out to analyze for attack rate and density with tree size and location. Chi-square test was applied separately (SAS, 1998) to reveal the effects of hillside exposure on RTB attack.

Results

The results (Table 1) of the GLM revealed that the extent of RTB attack was significantly associated with hillside exposure, tree locations on the hillsides, tree diameter, and location-diameter combined effects. In comparison, attack density was affected significantly by tree location and tree diameter.

Hillside exposure and RTBs attacks

The data from three sites in the investigated valley were used to estimate the relationship between hillside orientation (Fig. 1) and RTB attacks. The results (Table 2) indicated that RTBs showed a decided preference for colonizing pines growing on south-facing hillsides, especially in the valley ($\chi^2 = 12.9187, P = 0.0003$), confirming our observation when RTB collection was carried out in the field. In this Table, we can see 101 of 450 investigated pines were attacked on a south-facing hillside, whereas only 60 of 450 pines were attacked on north-facing hillsides.

Table 1 Results from GLM for attack rate (%) by RTB and attack density.

Source	Attack rate (%) by RTB				Attack density (pitch tubes per tree)			
	Sum of squares	df	F	P	Sum of squares	df	F	P
Model	10 374.757	17	25.093	< 0.000 1	492.438	17	2.332	0.016
Hillside	901.764	1	37.079	< 0.000 1*	2.756 × 10 ⁻²	1	0.002	0.963
Location	5 113.188	2	52.935	< 0.000 1*	102.213	2	4.114	0.025*
Diameter	2 574.744	2	52.935	< 0.000 1*	247.453	2	9.959	< 0.000 1*
Hillside × Location	122.852	2	2.526	0.094 0	14.375	2	0.578	0.566
Hillside × Diameter	56.692	2	1.166	0.323 0	26.278	2	1.058	0.358
Location × Diameter	1 517.386	4	15.598	< 0.000 1*	83.239	4	1.675	0.117
Hillside × Location × Diameter	88.531	4	0.906	0.471 0	18.870	4	0.380	0.882

GLM, general linear model; RTB, red turpentine beetle. Percentage data were arcsine transformed before GLM analysis. * significant ($P < 0.05$).

Table 2 Relationship between *Dendroctonus valens* attack (number of attacked trees) and hillside exposure.

Tree diameter	Valley			Halfway			Top			Total		
	SFH	NFH	χ^2	SFH	NFH	χ^2	SFH	NFH	χ^2	SFH	NFH	χ^2
DBH < 15 cm	12	3	6.352 9*	5	2	1.382 5	5	2	1.382 5	22	7	7.759**
DBH 15–20 cm	25	17	2.627 3	2	0	2.040 8	1	1	0	28	18	2.174
DBH > 20 cm	33	20	6.784 4**	9	10	0.065 0	9	5	1.328 9	51	35	2.977
Total	70	40	12.918 7**	16	16	0.630 3	15	8	2.307 3	101	60	10.441**

* means that pine infestation had significant differences at $P < 0.05$, ** means that pine infestation had significant differences at $P < 0.001$ (Chi-square test, SAS). DBH, diameter at breast height; SFH, south-facing hillside, NFH, north-facing hillside.

The relationships between RTB attack and tree location

Our investigation proved that tree location (at the valley, mid-slope, and on the ridge-top) influenced RTBs attack. In total, pines growing in the valley were preferred most by RTBs: 34% of pines in the valley were attacked by RTB whereas only 9% and 7% of pines on the mid-slope and at the ridge-top, respectively, were attacked (Table 3) ($F = 62.611$; $df = 2,51$; $P < 0.001$). However, there was some variance according to pine size. Among small pines (DBH < 15 cm), there were no significant differences regardless of tree location ($F = 1.675$; $df = 2,15$; $P = 0.220$). Among medium-sized pines (DBH 15–20 cm), attack rate in the valley was highest, which was significantly higher than those on medium-sized pines located at the mid-slope and on the ridge-top ($F = 54.818$; $df = 2,15$; $P < 0.001$), whereas no marked differences were found between trees located at mid-slope and on the ridge-top. For large trees (DBH > 20 cm), RTBs significantly preferred to attack them at the valley, compared to the large pines at mid-slope and on the ridge-top ($F = 27.575$; $df = 2,15$; $P < 0.001$); moreover preferences did differ significantly between large trees growing at the mid-slope and on the ridge-top ($F = 6.369$, $df = 1,10$, $P = 0.030$).

The relationships between RTB attack and tree diameter

The RTBs preferentially attacked large pines. On average, 27% of the large pines were attacked by RTB whereas only 11% and 9% of the medium-sized and the small-sized trees, respectively, were infested (Table 3) ($F = 7.568$; $df = 2,51$; $P = 0.001$). The beetle's preference for large pines varied with trees locations on the hillside. In the valley, RTBs significantly preferred large and medium-sized pines, 49% and 39% of investigated pines, respectively, over small trees (14%) ($F = 17.069$; $df = 2,15$; $P < 0.001$). At the mid-slope and on the ridge-top, only large pines incurred more attack by RTBs than did medium-sized and small pines ($F = 20.272$; $df = 2,15$; $P < 0.001$ for pines at the mid-slope and $F = 8.495$, $df = 2,15$; $P < 0.003$ for pines on the ridge-top).

The relationships among RTB attack density, tree location and tree diameter

Tree location significantly affected RTB attack density, about 7, 5 and 4 pitch tubes per tree, respectively, for pines in the valley, at the mid-slope, and on the ridge-top (Table 4) ($F = 3.112$; $df = 2,51$; $P = 0.053$). For tree size, the attack density was significantly higher on large trees

Table 3 Relationship between attack rate (%) by RTB, tree location and tree diameter.

	Valley	Halfway	Top	Total
DBH < 15 cm	13.89 ± 3.99 aB	6.48 ± 1.71 aB	7.41 ± 2.32 aB	9.26 ± 1.27 B
DBH 15–20 cm	38.89 ± 3.51 aA	1.85 ± 1.17 bB	1.85 ± 1.17 bAB	11.20 ± 4.41 B
DBH > 20 cm	49.07 ± 5.63 aA	20.37 ± 1.85 bA	12.96 ± 2.34 cA	27.47 ± 4.27 A
Total	33.95 ± 4.33 a	9.56 ± 2.10 b	7.41 ± 1.56 b	

The data shown as mean ± SE. Percentage data were arcsine transformed before analysis and original data were shown.

Same small letters following the data in the same line mean no significant differences between locations in RTB attack at $P < 0.05$ (Scheffé's test). Different caption letters following the data in the same column mean significant differences between tree diameters in RTB attack at $P < 0.05$ (Scheffé's test). DBH, diameter at breast height; RTB, red turpentine beetle.

Table 4 The relationship between RTB attack density (pitch tubes per tree), and tree location and diameter.

	Valley	Halfway	Top	Total
DBH < 15 cm	3.28 ± 0.88 (15) aB	5.17 ± 1.19 (7) aA	3.25 ± 0.85 (7) aA	3.57 ± 0.90 B
DBH 15–20 cm	6.72 ± 1.12 (42) aAB	2.17 ± 1.64 (2) bA	1.83 ± 1.17 (2) bA	3.90 ± 0.58 B
DBH > 20 cm	10.72 ± 1.44 (53) aA	8.56 ± 2.30 (19) aA	5.53 ± 1.14 (13) aA	8.26 ± 1.06 A
Total	6.91 ± 0.97 a	5.30 ± 1.15 b	3.54 ± 0.68 b	

The data shown as mean ± SE, value in parenthesis is pine number trees attacked by RTBs.

Same small letters following the data in the same line mean no significant differences between locations in attack density at $P < 0.05$ (Scheffé's test), different caption letters following the data in the same column mean significant difference between tree diameters in attack density at $P < 0.05$ (Scheffé's test). DBH, diameter at breast height; RTB, red turpentine beetle.

than on medium and small-sized trees ($F = 9.116$; $df = 2,51$; $P < 0.0001$). It was more obvious in the valley (10 pitch tubes / pine) than at other locations ($F = 10.128$; $df = 2,15$; $P = 0.002$).

Discussion

The results confirmed that the extent of RTB attack was associated with hillside exposure, tree locations and tree diameter. RTBs prefer to attack the large pines in the valley and the attack density obviously varied according to tree diameter in the valley: large pines were most frequently attacked, followed by medium-sized and then small pines.

As the terrains of Luliang Mountains are well complicated, we could not find the same kind of valley as that which we investigated. In this paper, we only investigated two hillsides along the valley; although three sites were selected in this valley, the results cannot be extrapolated too broadly. Since RTB is an invasive species and only occurs in local forests, results here do contain new information that is potentially useful to forest managers.

Given the colonization patterns, the question arises: why are these the colonization patterns? RTBs may find their preferred location using heat as a cue, or using the volatiles released by pines caused by sunlight, or both. During the day, the south-facing hillside has more time to absorb sunlight, which can change the levels of volatile compounds released that may attract RTBs. This hypothesis merits further investigation. However, the south-facing hillside is always much warmer than the north-facing hillside, and the valley is always warmer than the mid-slope and the top because of the interaction between sunlight and elevation. RTB probably are thermotropic. RTB attacking behavior experiments showed they needed about 20 hours to bore into the pine and the peak took place in the early morning and evening (Liu *et al.*, 2006). The low temperatures ($\approx 5\text{--}10^\circ\text{C}$ degree) prevalent in the mountains in the morning may limit RTB activity.

The RTBs prefer to attack large pine trees at any location on hillsides. In other scolytidae, some bark beetles also showed a decided preference for colonizing large-diameter trees (Preisler & Mitchell, 1993; Fettig *et al.*, 2007) due to host susceptibility. According to local plantation histories, a pine with DBH > 20 cm is about 30 years old (pers. comm. local forest workers) and is preferred by RTBs. In general, the large (DBH > 20 cm) and small (DHB < 15 cm) trees were thought to be the least vigorous, the medium-sized pines (15–20 cm DBH), the strongest. Further, an important link is stand density, which has been illustrated by Larsson *et al.* (1983) and Fettig *et al.* (2007). In the

investigated valley, there are more pines standing per area in the valley than at the mid-slope or on the ridge-top, which is perhaps the main reason for decreasing host vigor. Also, when pines were stressed, more host volatiles may be released, which attract more RTBs and they attack more effectively, which was proven by Owen (2005).

The effects of diameter on RTB attack density did not differ significantly among the three sizes of pines at other locations except for the valley, and RTBs are more likely to attack large trees. Burnell (1977) suggested that beetles attack trees randomly, and that large trees are killed most often because they present beetles with the largest landing targets. In that case, the attack density (pitch tubes per surface area) would be constant, which was not supported by our results here, because the attacking density of big trees was 3-fold on that of small trees (Table 4). However, the surface area of big trees was about less than 2-fold that of small trees, although the diameter of each tree was not exactly measured. Regarding the mechanisms limiting RTB attack density, two factors probably act together: population density and RTBs' attacking behavior. This can explain the density differences between tree sizes and locations. RTB population density is higher in the valley than at other locations because of the high attack rate there caused by host susceptibility and other unknown reasons. Differences in population density mediate RTB choice of large trees over small and medium-sized trees among valleys, half-slopes, and ridge-tops. RTBs prefer to attack large trees, so large trees in the valley incur the most damage. Last, RTB attack behavior also plays a critical role in determining population density in attacked pines. When a pine is successfully colonized by a pioneer RTB beetle, many other beetles are attracted to it (Liu *et al.*, 2006).

Red turpentine beetles remain a significant problem in China and this seems to be spreading to adjacent other provinces, such as Inner Mongolia Autonomous Region and Henan (pers. comm. local workers involved in forest protection). Currently, the main method of control is traps with semiochemicals. Our results can make RTB management more efficient. Given RTB population density and colonization patterns, these traps, the baited 8-funnel Lindgren traps (Phero Tech, Delta, BC, Canada), should be hung on the large pine trees in the valleys, where they have the chance to monitor and trap the majority of RTBs. Cutting some old pines to set as natural traps along the valleys to attract adults and then kill the insects using chemical methods is also suggested. Moreover, some new management strategies could be considered, such as the sterile insect technique (SIT) based on the insect's special colonization patterns (Liu *et al.*, 2006).

Acknowledgments

This study was funded by the National Natural Science Foundation of China (Project 30525009 and 30621003) and Beijing Science and Technology Commission (D0705002040391). Workers at Chakou Forest Farm, Gujiao, Shanxi Province, provided technical assistance in the field. We thank Emily Wheeler for editorial assistance.

References

- Burnell, D.G. (1977) A dispersal-aggregation model for mountain pine beetle in lodgepole pine stands. *Researches on Population Ecology*, 19, 99–106.
- Cibrián-Tovar, D., Mendez, J.T., Montiel, C.R., Yate, H.O. III and Lara, J.E. (1995) *Forest Insects of Mexico*. Universidad Autónoma Chapingo, Chapingo, Mexico. 453 pp.
- Eaton, B., Lara and R.R. (1967) Red turpentine beetle, *Dendroctonus valens* LeConte. *Important Forest Insects and Diseases of mutual Concern to Canada, the United States and Mexico* (ed. A. G. Davidson & R.M. Prentice), pp. 21–24. Canadian Department of Forestry and Rural Development, Ottawa, Ontario.
- Erbilgin, N., Morr, S.R., Sun, J.H., Stein, J.D., Owen, D.R., Merrill, L.D., Campos Bolanos, R., Raffa, K.F., Mendez Montiel, T., Wood, D.L. and Gillette, N.E. (2007) Response to host volatiles by native and introduced populations of *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytidae) in north America and China. *Journal of Chemical Ecology*, 33, 131–146.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negrón, J.F. and Nowak, J.T. (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *Forest Ecology and Management*, 238, 24–53.
- Gao, B.J., Xin, J.N., Guan, H.Y., Li, S.L., Wang, L.F., Liu, Z.Q., Qiao, L.H. and Li, X.H. (2003) The generation and damage of red turpentine beetle. *Chinese Journal of Zoology*, 38, 71–73. (in Chinese)
- Larsson, S., Oren, R., Waring, R.H. and Barrett, J.W. (1983) Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. *Forest Science*, 29, 395–402.
- Li, J.S., Chang, G.B., Song, Y.S., Wang, Y.W. and Chang, B.S. (2001) Management of the red turpentine beetle. *Forest Pest and Disease*, 20 (4), 41–44. (in Chinese)
- Liu, Z.D., Zhang, L.W. and Sun, J.H. (2006) Attacking behavior and behavioral responses to dust volatiles from holes bored by the red turpentine beetle, *Dendroctonus valens* (Coleoptera: Scolytidae). *Environmental Entomology*, 35 (4), 1030–1039.
- Miao, Z.W. (2002) Space distribution of entering tree holes of *Dendroctonus valens* image. *Shanxi Forestry Science and Technology*, (3), 7–9. (in Chinese)
- Miao, Z.W., Zhao, W.M., Wang, L.Z., Pei, H.C., Di, J.M. and Sun, J.H. (2003) Application of semiochemicals in monitoring the red turpentine beetle, *Dendroctonus valens*. *Entomological Knowledge*, 40 (4), 346–350. (in Chinese)
- Owen, D.R. (2003) The red turpentine beetles. *Tree Notes*. Californian Department of Forestry and Fire Protection, Num. 9, 4 pp.
- Owen, D.R., Wood, D.L. and Parmeter, J.R. (2005) Association between *Dendroctonus valens* and black stain root disease on ponderosa pine in the Sierra Nevada of California. *Canada Entomologist*, 137, 367–375.
- Preisler, H.K. and Mitchell, R.G. (1993) Colonization patterns of the mountain pine beetle in thinned and unthinned lodgepole pine stands. *Forest Science*, 39, 528–545.
- SAS Institute (1998) *The SAS System for Windows*. SAS Institute. Cary, NC.
- Smith, R.H. (1971) *Red Turpentine Beetle*. USDA Forest Pest Leaflet 55, 9 pp.
- Song, Y.S., Yang, A.L. and He, L.J. (2000) Pest risk analysis of red turpentine beetle (*Dendroctonus valens*). *Forest Pest and Disease*, 19, 34–37. (in Chinese)
- SPSS Inc. (1999) *The Basics: SPSS for Windows 10.0*. SPSS Inc. Chicago, IL.
- Sun, J.H., Gillette, N.E., Miao, Z.W., Kang, L., Zhang, Z.N., Owen, D.R. and Stein, J.D. (2003) Verbenone interrupts attraction to host volatiles and reduces attack on *Pinus tabulaeformis* (Pinaceae) by *Dendroctonus valens* (Coleoptera: Scolytidae) in the People's Republic of China. *Canada Entomologist*, 135, 721–732.
- Zhang, L.W., Gillette, N.E. and Sun, J.H. (2007) Electrophysiological and behavioral responses of *Dendroctonus valens* to non-host volatiles. *Annals of Forest Science*, 64, 267–273.
- Zhang, L.W. and Sun, J.H. (2006) Electrophysiological and behavioral responses of *Dendroctonus valens* (Coleoptera: Curculionidae: Scolytinae) to candidate pheromone components identified in hindgut extracts. *Environmental Entomology*, 35, 1232–1237.
- Zhang, L.Y., Chen, Q.C. and Zhang, X.B. (2002) Studies on the morphological characteristics and bionomics of *Dendroctonus Valens* LeConte. *Science Silvae Sinicae*, 38 (4), 95–99.

Accepted May 6, 2008