

RESEARCH ARTICLE

Oviposition preferences of *Monochamus alternatus* and their relationship with host plant volatiles

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Monochamus alternatus is a major forestry quarantine pest and the primary vector of pine wilt disease. This study aimed to identify plant-derived compounds that mediated the oviposition behavior of *Monochamus alternatus* and provide a theoretical basis for the development of environmentally friendly control strategies by utilizing both no-choice and choice oviposition assays under laboratory conditions to evaluate the oviposition preferences of *M. alternatus* for three host species of *Pinus massoniana* Lamb. (Masson pine), *Pinus tabulaeformis* Carrière (Chinese pine), and *Larix kaempferi* (Japanese larch). Simultaneously, dynamic headspace adsorption coupled with gas chromatography-mass spectrometry (GC-MS) was employed to characterize the volatile compounds emitted from the trunks of these respective host plants. The results of oviposition trials revealed a statistically significant preference hierarchy with *M. alternatus* exhibiting the strongest ovipositional response to Masson pine, an intermediate response to Chinese pine, and the weakest response to Japanese larch ($P < 0.05$). Analysis of host volatiles demonstrated that the emitted compounds were predominantly composed of terpenes, esters, and alcohols with aldehydes and alkanes detected to a lesser extent. Notably, seven compounds including α -pinene, β -pinene, and ethanol were emitted in significantly greater quantities from Masson pine relative to the other two species ($P < 0.05$). In contrast, ten compounds such as terpinolene, nonanal, and decanal were found at higher relative abundances in Chinese pine ($P < 0.05$), whereas six compounds including myrcene, β -caryophyllene, and 3-carene were more characteristic of Japanese larch volatiles ($P < 0.05$). The results indicated that α -pinene, β -pinene, and ethanol exerted significantly attractive effects on *M. alternatus*. Consequently, it was inferred that these key plant-derived compounds likely function as principal oviposition attractants for this beetle species.

Keywords: *Monochamus alternatus*; oviposition; host plants; volatiles.

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Introduction

Monochamus alternatus (Coleoptera: Cerambycidae), commonly known as the Japanese pine sawyer, is one of the most destructive wood-boring pests infesting pine trees. In China, its geographic distribution is

primarily concentrated in the provinces of Anhui, Henan, Zhejiang, Jiangsu, and Fujian [1]. This species colonizes a range of host trees including *Pinus tabulaeformis*, *Pinus massoniana*, *Pinus thunbergii*, and *Larix kaempferi* and has also been documented to attack other conifers like *Taxodium rich*, *Abies*, and *Picea asperata* Mast

[2]. Crucially, *M. alternatus* is the primary insect vector of the pine wood nematode, *Bursaphelenchus xylophilus*, the pathogen responsible for pine wilt disease, which has caused catastrophic damage to pine forest ecosystems [3].

It is well established that phytophagous insects depend extensively on their olfactory sensory systems to perceive volatile chemical cues emitted by host plants, thereby enabling the location and discrimination of suitable hosts for feeding and oviposition [4, 5]. A diverse array of volatiles released from various pine species has been implicated in the attraction of *M. alternatus* and the stimulation of its feeding and reproductive behaviors [6]. However, both the types and amounts of these volatiles differ significantly among tree species, a phenomenon that is particularly pronounced under conditions of physiological decline or abiotic stress [7, 8]. Furthermore, in response to pest attack or pathogen infection, plants frequently upregulate the biosynthesis and emission of secondary metabolites. While these compounds primarily function as direct chemical defenses, they can also profoundly modulate insect behavior by deterring pests or attracting their natural enemies [9]. Previous study found that colonization by fungi vectored by bark beetles (*Scolytinae*) induced a significant accumulation of phenolic stilbene glucosides in the bark of Norway spruce (*Picea abies* (L.) H. Karst.) [10]. Similarly, herbivory by *Manduca sexta* larvae triggered the release of linalool and sesquiterpenes from *Nicotiana tabacum* L., which in turn attracted the herbivore's natural enemies, constituting an archetypal example of indirect plant defense [11]. Other studies found that *M. alternatus* exploited host plant volatile cues to identify optimal oviposition substrates, exhibiting a pronounced preference for sympatric tree species [12, 13]. Therefore, characterizing the composition and relative concentrations of host plant volatiles is essential for elucidating and predicting the infestation patterns of this pest. While prior studies have established that pine-derived volatiles can

function as attractants for cerambycid beetles [14], the specific relationship between the oviposition preferences of *M. alternatus* and the distinct volatile chemical profiles of different host species remains poorly defined, representing a critical knowledge gap that urgently needs to be addressed to advance current prevention and control strategies.

This research integrated no-choice and choice oviposition bioassays with dynamic headspace adsorption coupled to gas chromatography-mass spectrometry (GC-MS) to elucidate the host selection mechanisms and interspecific differences in oviposition behavior exhibited by gravid *M. alternatus* females toward suitable host trees. By identifying key volatile compounds that stimulated oviposition, this study provided valuable theoretical insights that could underpin the development of environmentally sustainable management strategies for *M. alternatus* populations.

Materials and methods

Insect source

Adult *M. alternatus* were field-collected from *Pinus massoniana* stands within Jigongshan National Nature Reserve, Xinyang, Henan, China (114°01' - 114°06' E, 31°46' - 31°52' N) via sweep nets. The collection site was characterized as a mixed coniferous-broadleaf forest predominantly composed of *Pinus massoniana*, *Quercus variabilis* Blume, *Taxodium distichum*, *Pinus tabulaeformis*, and *Larix kaempferi* with *Pinus massoniana* sustaining severe infestation damage attributable to *M. alternatus* attack. Under local climatic conditions, adult beetle emergence commenced in mid-April and reached peak abundance during May and June. Mating behavior was initiated approximately ten days post-emergence, and females commenced oviposition 5 to 6 days after copulation. The oviposition peak coincided with daily mean temperatures of 23 - 25°C, which typically prevailed throughout May and June in the study region.

Experimental host trees and oviposition tests

Trunk selection of *Larix kaempferi*, *Pinus massoniana*, and *Pinus tabulaeformis*, each approximately 15 years of age, were harvested from the same forest stand for laboratory oviposition experiments. Bioassays were conducted under controlled environmental conditions of 20 – 25°C and a 14 h:10 h (L:D) photoperiod. No-choice oviposition test was conducted by placing a single trunk of 35 cm long and 10 cm diameter of each tree species individually into separate wooden rearing cages with 40 cm × 40 cm × 40 cm volume of each. Each trunk was positioned in a water-filled container to prevent desiccation. Abundant one-year-old branches of the corresponding pine species were provided as a food source and replenished every three days for the duration of the trial. Choice oviposition test was performed by placing trunk segments of all three species with the matching dimensions used in the no-choice test simultaneously in a single rearing cage, together with an ample supply of one-year-old pine branches serving as a common food source. For both tests, each cage housed one sexually mature pair of *M. alternatus* (one female and one male). The experiment was replicated three times. Any mortality observed during the experimental period was immediately remediated by the introduction of a replacement adult of the corresponding sex. The experiment was initiated on May 15, 2025, and terminated on June 25, 2025. The numbers of oviposition grooves and deposited eggs on each trunk segment were recorded throughout the period.

Collection and analysis of volatile organic compounds

Volatile organic compounds (VOCs) emitted from the trunk sections of *Larix kaempferi*, *Pinus massoniana*, and *Pinus tabulaeformis* were collected using a dynamic headspace adsorption technique [15]. The trunk samples utilized for VOC collection were obtained from the same individual trees that provided the material for the oviposition experiments. Each trunk segment was enclosed within a Zhongpu Star PVF sampling bag (Zhongjian Yida Laboratory Equipment Co.,

Ltd., Guangzhou, Guangdong, China). A stainless-steel collection tube packed with Tenax-TA adsorbent (Taitong Technology (Guangzhou) Co., Ltd., Guangzhou, Guangdong, China) and an activated charcoal-filtered air inlet (Huayu Instrument & Meter Co., Ltd., Yancheng, Jiangsu, China) were inserted into the sampling bag. Teflon tubing connected the inlet and outlet ports of the bag to a QC-2A gas sampler (Beijing Ke'an Labor Protection New Technology Co., Ltd., Beijing, China), which was operated at a constant flow rate of 1.5 L/min. Volatile collection proceeded continuously for 4 h with three independent replicates per host tree species. Each volatile sample was eluted three times with 2 mL of n-hexane (500 µL per elution) and stored at –20°C pending subsequent analysis. Analysis of volatile compounds emitted from *Larix kaempferi*, *Pinus massoniana*, and *Pinus tabulaeformis* was performed using a Shimadzu QP2010 Ultra gas chromatograph–mass spectrometer (GC-MS) (Shimadzu Corporation, Shanghai, China) with Agilent 19091S-433 HP-5MS column (Agilent Technologies, Beijing, China), 1.0 µL splitless injection volume, helium as carrier gas, and the oven temperatures of initial 40°C for 2 min followed by a linear ramp of 5°C/min to a final temperature of 220°C. The mass spectrometric conditions were electron ionization source operating at 70 eV, ion source temperature of 250°C, interface temperature of 200°C, and mass scan range of 40 – 500 m/z.

Statistical analysis

SPSS version 25.0 (IBM, Armonk, New York, USA) was employed for statistical analysis of this research. One-way analysis of variance (ANOVA) was performed to evaluate significant differences among the three host tree species with respect to the numbers of oviposition grooves, deposited eggs, and relative abundance of volatile organic compounds. Post hoc mean separation was performed by using Duncan's multiple range test. *P* value less than 0.05 was defined as statistically significant difference.

Results

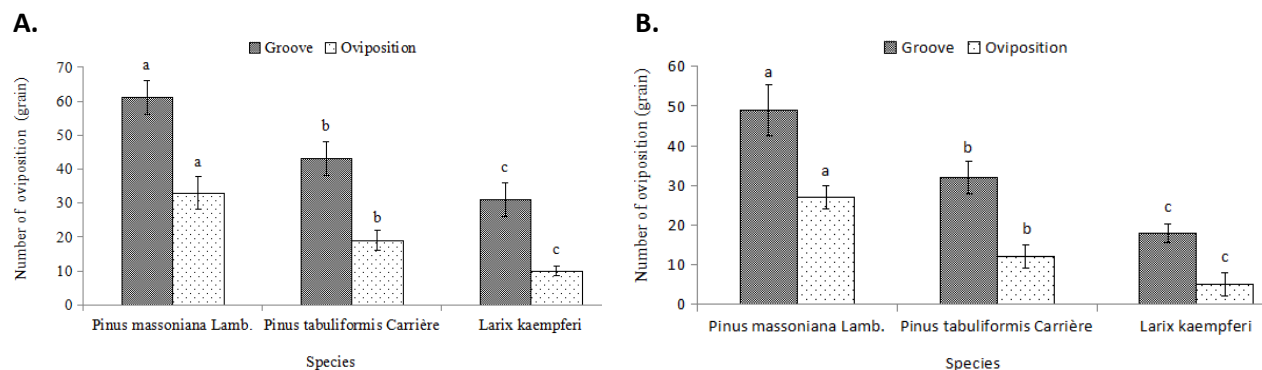


Figure 1. The results of no-choice (A) and choice (B) oviposition behaviors of *M. alternatus* adults on the three host trunks. Different Lowercase letters denoted statistically significant differences in the number of grooves and eggs laid among the three host species ($P < 0.05$).

Indoor oviposition experiments

The results of the no-choice oviposition test of *M. alternatus* detected a statistically significant difference in oviposition preference among the three host tree species ($P < 0.05$) (Figure 1A). Both the number of oviposition grooves and the number of eggs deposited were the highest on trunk sections of *Pinus massoniana*, the intermediate on *Pinus tabuliformis*, and the lowest on *Larix kaempferi*. Across all three host species, the number of oviposition grooves consistently exceeded the number of eggs deposited, and statistically significant differences were observed among all pairwise comparisons of host species for both oviposition parameters ($P < 0.05$). The results of choice oviposition test were consistent with the no-choice test, revealing a similarly significant variation in both the number of oviposition grooves and the number of eggs deposited across the three host species ($P < 0.05$) (Figure 1B). *Pinus massoniana* again recorded the highest number of oviposition grooves followed by *Pinus tabuliformis* with *Larix kaempferi* being the least utilized. Congruently, egg deposition was the highest on *Pinus massoniana*, the intermediate on *Pinus tabuliformis*, and the lowest on *Larix kaempferi*. Across all three host species, the number of oviposition grooves consistently exceeded the number of eggs deposited with statistically significant differences detected among the three hosts ($P < 0.05$).

Analysis of volatile compounds of the three host plant species

Analysis of the volatile organic compound profiles emitted from the trunk sections of the three host species revealed that terpenes, esters, and alcohols constituted the dominant chemical classes, whereas aldehydes and alkanes were present at comparatively lower relative abundances. Significant interspecific differences in the emission levels of multiple individual compounds were detected ($P < 0.05$). α -pinene, β -pinene, and longifolene exhibited the highest emission rates from *Pinus massoniana*, significantly exceeding those recorded from *Pinus tabuliformis* and *Larix kaempferi* ($P < 0.05$). Conversely, terpinolene, γ -terpinene, nonanal, and capraldehyde were the most abundant in the headspace volatiles of *Pinus tabuliformis* with concentrations significantly surpassing those detected in *Pinus massoniana* and *Larix kaempferi* ($P < 0.05$). Meanwhile, myrcene, β -caryophyllene, 3-carene, and 4-ethylbenzaldehyde were emitted in the greatest quantities by *Larix kaempferi* at the levels significantly higher than those observed in the other two species ($P < 0.05$) (Figure 2). Notably, the emission levels of α -pinene and β -pinene, the principal terpene constituents of pine trees, followed a consistent hierarchical pattern across the three host plants as *Pinus massoniana* > *Pinus tabuliformis* > *Larix kaempferi*. Phenyl formate, butyl acetate, ethanol, tetradecane, and pentadecane exhibited their highest emission

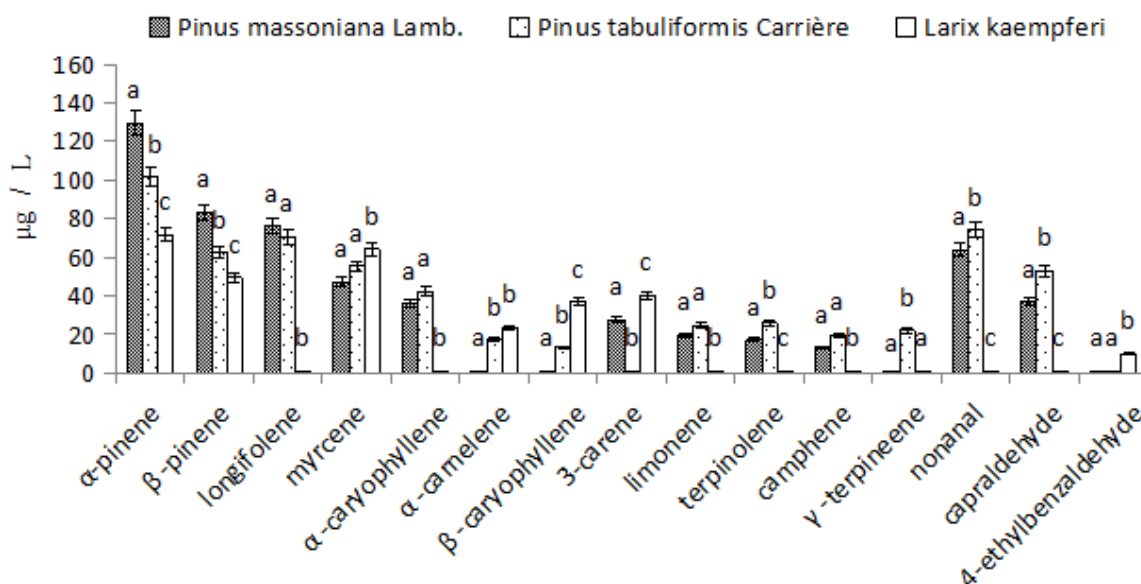


Figure 2. Emission quantities of terpene and aldehyde compounds in different host plants. Different lowercase letters for the same compound indicated significant differences in volatile emissions among host species ($P < 0.05$).

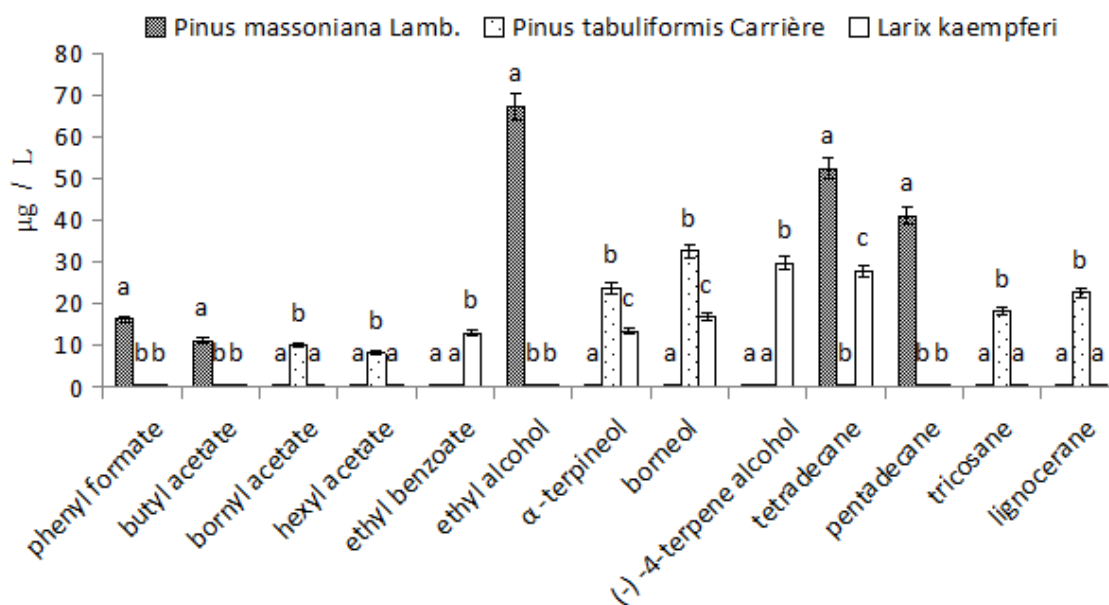


Figure 3. Emission quantities of ester and alcohol compounds in different host plants. Different lowercase letters for the same compound indicated significant differences in volatile emissions among host species ($P < 0.05$).

rates from *Pinus massoniana*, significantly exceeding those recorded from the other two host species ($P < 0.05$). Bornyl acetate, hexyl acetate, α-terpineol, borneol, tricosane, and lignoceran were most abundant in the headspace volatiles of *Pinus tabuliformis* with concentrations significantly greater than those

detected in *Pinus massoniana* and *Larix kaempferi* ($P < 0.05$). Ethyl benzoate and (-)-terpene-4-ol displayed maximum emission levels from *Larix kaempferi* at significantly higher abundance than those observed in *Pinus massoniana* and *Pinus tabuliformis* ($P < 0.05$) (Figure 3).

Discussion

The results of both no-choice and choice oviposition experiments unequivocally demonstrated that *M. alternatus* exhibited a pronounced oviposition preference hierarchy among the three host species evaluated with *Pinus massoniana* being the most preferred and supporting the highest oviposition success, while *Larix kaempferi* was the least preferred, yielding correspondingly low oviposition rates. This differential host utilization pattern aligned well with findings in other cerambycid species as reported previously that *Anoplophora glabripennis* had been shown to preferentially oviposit on *Salix babylonica* over *Melia azedarach*, *Casuarina equisetifolia* L., and *Koelreuteria bipinnata* [16]. Similarly, *Apriona germari* displayed strong host specificity in both feeding and oviposition behaviors, while feeding preferences were predominantly mediated by interspecific differences in host nutrient content, and oviposition site selection was more critically governed by the concentration of plant secondary metabolites [17]. The results of this research further revealed that, across all three host species, the number of oviposition grooves excavated by *M. alternatus* consistently exceeded the number of eggs actually deposited, indicating that groove construction did not invariably culminate in oviposition. Prior studies have identified multiple factors that jointly modulate both groove formation and the decision to oviposit including ambient temperature, female body mass, trunk diameter, and the composition of volatile organic compounds emitted by the host plant. Notably, it has been estimated that approximately 40 – 50% of oviposition grooves remain devoid of eggs [18, 19], a phenomenon consistent with the behavioral observations recorded in this study. The intricate interaction between phytophagous insects and their host plants is fundamentally shaped by ecological and evolutionary pressures, within which the qualitative and quantitative composition of host plant volatiles plays a pivotal mediating role [17, 20]. Insects rely on the volatile chemical signatures emitted by host

plants to accurately identify and locate suitable substrates for feeding and oviposition [21]. Because volatile profiles exhibit pronounced interspecific variation in both chemical composition and relative concentration, they exert differential effects on insect oviposition behavior. Some previous studies have established that pine-derived volatiles function as potent attractants for cerambycid beetles and have been effectively deployed in pest management programs to lure gravid adults during their oviposition period [14, 22]. This study demonstrated that seven volatile compounds including α -pinene, β -pinene, phenyl formate, butyl acetate, ethanol, tetradecane, and pentadecane were emitted in significantly greater quantities from *Pinus massoniana* relative to *Pinus tabuliformis* and *Larix kaempferi* ($P < 0.05$). Concordantly, oviposition tests revealed that *M. alternatus* females exhibited a pronounced preference for ovipositing on *Pinus massoniana* with both the number of oviposition grooves and the number of eggs deposited significantly exceeding those recorded on *Pinus tabuliformis* and *Larix kaempferi* ($P < 0.05$). Prior investigations have identified α -pinene, ethanol, and butyl acetate as critical mediators of female oviposition behavior in *M. alternatus*, functioning as key attractants during both the emergence and oviposition periods [15, 23, 24]. These seven compounds collectively constituted the principal volatile signature mediating the attraction of gravid *M. alternatus* females to *P. massoniana* as a preferred oviposition substrate. Moreover, ten compounds including terpinolene, γ -terpinene, nonanal, decanal, bornyl acetate, hexyl acetate, α -terpineol, borneol, tricosane, and lignoceran were detected at the highest concentrations in the headspace volatiles of *Pinus tabuliformis* ($P < 0.05$). Past studies demonstrated that nonanal, decanal, and hexyl acetate emitted by *Salix babylonica* functioned as potent attractants for ovipositing *Anoplophora glabripennis* [25]. Additionally, terpenoids such as terpinolene, γ -terpinene, α -terpineol, and borneol released by various pine species showed to modulate the feeding and oviposition behaviors of *M. alternatus* [26]. Therefore, the ten compounds

emitted in greatest abundance by *Pinus tabuliformis* might also play a fundamentally important role in mediating oviposition attraction for *M. alternatus*. In contrast, six compounds including myrcene, β -caryophyllene, 3-carene, 4-ethylbenzaldehyde, ethyl benzoate, and (-)-terpinen-4-ol were predominantly emitted by *Larix kaempferi* ($P < 0.05$), while the emission levels of α -pinene, β -pinene, ethanol, the compounds recognized for their strong attractiveness to *M. alternatus*, were the lowest in the volatile profile of *Larix kaempferi* ($P < 0.05$). Correspondingly, this host species received the fewest oviposition grooves and eggs at counts significantly lower than those recorded on both *Pinus massoniana* and *Pinus tabuliformis* ($P < 0.05$). The results suggested that certain compounds enriched in *Larix kaempferi* volatiles such as myrcene and β -caryophyllene might function as oviposition deterrents, thereby conferring a degree of inherent resistance to this host species against *M. alternatus* infestation. The findings of this research supported that volatile compounds, particularly α -pinene, β -pinene, ethanol, exerted a facilitative influence on the oviposition behavior of *M. alternatus*. The oviposition preference of this beetle was tightly correlated with both the qualitative composition and the quantitative abundance of host plant volatiles. Therefore, the composition and emission rates of plant-derived volatiles should be regarded as key indicators of host resistance in breeding programs directed toward the development of *M. alternatus* resistant pine varieties.

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References

- Shi P, Wang Z, Zeng H, Shi J. 2019. Tolerance to temperature stresses on *Monochamus alternatus* and its potential range in China. *J Northwest For Univ.* 34(4):156-161.
- Song H, Xu R. 2006. Global potential geographical distribution of *Monochamus alternatus*. *Entomol Knowledge.* 4:535-539, 589.
- Wu YX, Wickham JD, Zhao L, Sun J. 2019. CO₂ drives the pine wood nematode off its insect vector. *Curr Biol.* 29(13):R619-R620.
- Francis F, Lognay G, Haubruge E. 2004. Olfactory responses to aphid and host plant volatile releases: (E)- β -farnesene an effective kairomone for the predator *Adalia bipunctata*. *J Chem Ecol.* 30(4):741-755.
- Yao S, Wang L, Shu Q, Lin L, Wang T, Sun X, *et al.* 2011. Effect of tree species and branch age on the feeding area of *Monochamus alternatus*. *J Anhui Agric Univ.* 38(6):872-876.
- Fan J, Sun J, Shi J. 2007. Attraction of the Japanese pine sawyer, *Monochamus alternatus*, to volatiles from stressed host in China. *Ann For Sci.* 64(1):67-71.
- Zhang Y, Zhuang Y, Wei Y, Zeng G, Li X, Chen X. 2018. Analysis on volatile oil composition in pine needle of *Pinus Tabuliformis* var. *Mukdensis* and *Pinus Sylvestris* var. *Mongolica* by GC-MS. *Chin J Tradit Med Sci Technol.* 25(6):819-822, 830.
- Guo A, Wang Z, Zou L. 2014. Release variation of volatile compounds from *Pinus sylvestris* var. *mongolica* Litv. and their effects on bacteriostasis. *J Northeast For Univ.* 42(4):115-118.
- Wink M. 2006. Chapter 11 importance of plant secondary metabolites for protection against insects and microbial infections. *Adv Phytomed.* 3:251-268.
- Li SH, Nagy NE, Hammerbacher A, Krokene P, Niu X, Gershenzon J, *et al.* 2012. Localization of phenolics in phloem parenchyma cells of Norway spruce (*Picea abies*). *Chembiochem.* 13(18):2707-2713.
- Kessler A. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. *Science.* 291(5511):2141-2144.
- Zhang S, Lu G. 2000. Observation of mating and egg-laying behavior, as well as determination of the egg stage and hatching rate of the pine wood nematode. *Forest Pest and Disease.* 2000(01):34-36.
- Hao D, Zhang Y, Dai H, Wang Y. 2005. Oviposition preference of *Monochamus alternatus* Hope (*Coleoptera: Cerambycidae*) to host plants. *Acta Entomol Sin.* 48(3):460-464.
- Faccoli M, Blazenec M, Schlyter F. 2005. Feeding response of host and nonhost compounds by males and females of the spruce bark beetle *Ips typographus* in a tunnelling microassay. *J Chem Ecol.* 31:745-759.
- Fan J, Meng J, Zhao L, Sun J. 2013. The combined trapping effect of aggregated pheromones and plant-derived pheromones on the pine wood nematode. *Chin J Appl Entomol.* 50(5):1274-1279.
- Luo Y. 2013. The host choice behavior of *Anoplophora glabripenn* and the research of lure from host. Hangzhou, Zhejiang, China: Zhejiang A & F University.
- Shen J, Liao W, Luo P, Wang G. 2021. A correlation analysis of host selection of *Apriona germari* (*Coleoptera: Cerambycidae*) with content of plant nutrition component and secondary metabolites. *Acta Agric Univ Jiangxiensis.* 43(4):783-791.

18. Togashi K, Yamashita H. 2017. Effects of female body size on life-time fecundity of *Monochamus urussovii* (Coleoptera: Cerambycidae). Appl Entomol Zool. 52(1):79-87.
19. Wang L, Chen F, Dong X, Tian C, Wang Y. 2023. A study on feeding and oviposition characteristics of *Monochamus alternatus*. J Nanjing For Univ. (Natural Sciences Edition). 47(2):219-224.
20. Insects on plants: Community patterns and mechanisms. Edited by Strong DR, Lawton JH, Southwood SR. Cambridge, MA, USA: Harvard University Press. 1984.
21. Morewood WD, Neiner PR, Mcneil JR, Sellmer JC, Hoover K. 2003. Oviposition preference and larval performance of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in four eastern north American hardwood tree species. Environ Entomol. 32(5):1028-1034.
22. Fan J, Sun J. 2006. Influences of host volatiles on feeding behavior of the Japanese pine sawyer, *Monochamus alternatus*. J Appl Entomol. 130:238-244.
23. Wang B, Xu X, Huang Q. 2020. Analysis of volatile components in woody plants induced by larvae of the Pine weevil. The Farmers Consultant. 19:131, 157.
24. Morewood WD, Hein KE, Katinic PJ. 2002. Borden Jh, an improved trap for large wood-boring insects, with special reference to *Monochamus scutellatus* (Coleoptera: Cerambycidae). Can J For Res. 32:519-525.
25. Wickham JD, Xu Z, Teale SA. 2012. Evidence for a female-produced, long-range pheromone of *Anoplophora glabripennis* (Coleoptera: Cerambycidae). Insect Sci. 19(3):355-371.
26. Zhao J, Jiang P, Wu C, Sun S, Jiang L, Lin C. 2000. Studies on *Monochamus alternatus* attractant and the attractability. Forest Research. 13(3):262-267.