Red Turpentine Beetle: Innocuous Native Becomes Invasive Tree Killer in China

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Abstract

The red turpentine beetle (RTB), *Dendroctonus valens* LeConte (Coleoptera: Curculionidae: Scolytinae), is a secondary pest of pines in its native range in North and Central America. Outbreaks and tree mortality attributed to RTB alone are rare in its native range. RTB was introduced into China in the early 1980s and spread rapidly from Shanxi Province to four adjacent provinces; it has infested over 500,000 ha of pine forest and has caused extensive tree mortality since 1999. We provide a historical background on RTB outbreaks, explanations for its invasive success, management options, and economic impacts of RTB in China. Genetic variation in RTB fungal associates, interactions between RTB and its associated fungi, behavioral differences in Chinese RTB, and other factors favoring RTB outbreaks are considered in an effort to explain the invasiveness of RTB in China. The promise of semiochemicals as a management tool is also discussed.

INTRODUCTION

RTB: red turpentine beetle

Haplotype: a segment of DNA containing closely linked gene variations that are inherited as a unit

The red turpentine beetle (RTB), *Dendroctonus valens* LeConte (Coleoptera: Curculionidae, Scolytinae), commonly infests pines in its native range in North America (Canada, the United States, and Mexico) and parts of Central America (Guatemala and Honduras) (16, 71, 89, 109). In this geographic range, RTB is considered a secondary pest, often predisposing trees to attack by more aggressive bark beetles and only occasionally killing healthy trees (71). Outbreaks and tree mortality attributed to RTB alone are rare in its native range (11, 71, 89). In the early 1980s, RTB appeared for the first time outside its native range in China, where it is thought to have been introduced on unprocessed logs imported from the west coast of the United States (114). After 1999, RTB spread rapidly from Shanxi Province to the adjacent provinces of Hebei, Henan, Shaanxi, and Beijing and infested over 500,000 ha of pine forest, causing extensive tree mortality (74, 114, 115). It is estimated that RTB has killed more than 10 million *Pinus tabuliformis* as well as other pine species, including the possibly endangered *P. bungeana* (19, 68, 114, 122).

The invasion of RTB into China is worrisome because extensive loss of forest cover can result in dramatic changes to ecosystems, with concurrent losses of biodiversity and carbon sequestration capacity (48, 114). Moreover, pines are key reforestation species in China, and *P. tabuliformis* is widely planted across large areas of the country. Several conditions may have contributed to the success of RTB in China, including an abundance of naïve hosts, a lack of natural enemies, and mutualistic symbioses with microorganisms. Increasing global temperatures are also expected to contribute to RTB success by broadening its latitudinal range. The behavior of RTB in its native range is clearly different from that in China, and appropriate management options will be required for it there. Careful monitoring and new research, aimed at understanding RTB's novel biology in its new environment, will be required to inform management options and avoid further economic and ecological damage.

MECHANISMS OF INVASION

Genetic Variation

Until recently, few studies have been conducted to assess genetic variation in RTB populations, undoubtedly because its pest status is a new phenomenon. Genetic variation in a number of other damaging *Dendroctonus* species in North America has, however, been extensively studied (3, 7, 41). Only recently have studies begun to reveal the genetic architecture of RTB, and these were intended as source estimation studies to trace the origin of Chinese RTB populations (10, 12).

The comparative genetic structure of native and nonnative RTB was first studied by estimating phylogenetic and genetic frequencies using partial sequences of mitochondrial cytochrome oxidase subunit I (COI) of individuals sampled from multiple locations in North America and China (12). Overall, high haplotype diversity was found, and Chinese beetles shared haplotypes with beetles from the Pacific Northwest (PNW) of North America, supporting the hypothesis that the introduction of *D. valens* into China was recent and originated from the PNW of North America (12). However, the high haplotype diversity within populations and the high genetic similarity among populations produced many unresolved relationships between haplotypes and populations (12). This issue was addressed by Cai et al. (10), who also used a partial sequence of COI but included individuals from more sites in China, larger sample sizes, and paleoclimatic and geological data.

Cai et al. (10) showed that the Chinese beetle-to-haplotype ratio was more than double that for the PNW of North America, suggesting a genetic bottleneck of some degree in the early stages after the introduction of RTB into China, followed by a relatively rapid population buildup

(10). Loss of rare alleles or haplotypes is expected as a result of founder effects and bottlenecks during colonization by invasive pests, and these consequences are even more intense when the introduced populations are small (5). High levels of genetic diversity can be maintained, however, if the population expands (79).

The earliest major split for RTB that gave rise to the North American and Central American lineages most likely occurred during the late Pliocene, before the beginning of the most recent ice age (10). It is no surprise that glacial and postglacial events affected the phylogeography of RTB, and in fact these geological factors had an important role in the generation of lineages in many other taxa, including some pine species (90). The marked genetic differences between eastern and western North American populations, and between Mexican/Guatemalan and US populations (10), call for more extensive molecular phylogeographic studies, especially with the eastern populations, in order to better understand the genetic relationships of RTB globally.

Distinct Characteristics of Chinese Red Turpentine Beetle

Developmental and behavioral characteristics of RTB were initially presumed to be similar in North America and China (114). However, Chinese beetles have distinct adaptations, which likely developed in response to different conditions in the new ecosystem. The most striking characteristic of Chinese RTB is its ability to colonize, kill, and reproduce in healthy *P. tabuliformis*, resulting in multiple outbreaks with no parallel in its native region. In North America, RTB initiates attack on trees near ground level, and beetles colonize a short distance both upward along the bole and downward to the upper roots (71, 89). In China, RTB extensively colonizes and overwinters in roots (9, 112). RTB cannot overwinter in the tree bole above the root crown when the temperature is below −18°C (112). Roots provide better thermal insulation than the lower bole, and low temperatures probably favored beetles that could survive in roots (68, 80). During the early years of RTB colonization of China, winter temperatures below −18°C were common, presumably limiting rapid range expansion by RTB (114). In recent years, however, temperatures have seldom dropped below −18°C, expanding the range of suitable overwintering sites for the beetles. The increase in overwintering niches may have resulted in a buildup of RTB populations and concomitant dispersal to adjacent regions. The effects of climate change on range expansion of other North American bark beetles have been well summarized (6), and similar consequences can be anticipated for RTB in China.

RTB preferentially colonizes pines growing on south-facing hillsides, those growing in valleys rather than at midslope or on ridgetops, and large-diameter trees (55). Studies in the United States have demonstrated RTB attraction to host volatiles released during harvesting operations (22), and research in China has shown that RTB exploits specific concentrations of host monoterpenes to locate hosts of a size for optimal larval survival (54). In cold regions, the beetles complete only one generation per year or even one generation every two years, whereas in warmer climates they are reported to have up to three generations per year (80, 89, 122).

RTB has excellent dispersal abilities. Its flight distance was shown to exceed 16 km in North America (89), and in China flight distances of up to 35 km have been documented (122). Long-distance flight capability enables the beetle to migrate over large areas, including such barriers as extensive gaps in forest cover. In China, RTB has overcome the Lüliang and Taihang mountain ranges, which, barring human-assisted transport, shows remarkable long-distance and altitudinal migrating ability (122).

The detection of host tree volatiles by beetles is also important in RTB biology and may have contributed to its successful establishment in China (83). Volatiles from frass expelled from female nuptial chambers are apparently used by males to locate these chambers (56). In China, RTB

Pheromone: a semiochemical that mediates intraspecific interactions

Kairomone: a semiochemical that mediates interspecific interactions to the benefit of the receiver but not the emitter

Semiochemical: a chemical emitted by one organism that affects the behavior of another organism, either between or within species

Allelochemical: a semiochemical that mediates interspecific interactions

has been shown to harbor *trans*-verbenol, *cis*-verbenol, myrtenol, myrtenal, and verbenone in its hindgut (83). These volatiles are known pheromone components in other species of *Dendroctonus* (97). *Trans*-verbenol, myrtenol, and myrtenal are detected by antennal receptors and elicit attraction in RTB (120). In field tests, both *trans*-verbenol and myrtenol significantly increased catches of beetles in traps baited with host kairomone (120). Newly emerged females and males have only minute amounts of these compounds, but the quantity of volatiles from female adults increases after feeding (83). Male adults produce larger quantities of volatiles after they join females in galleries, which could be a means for RTB males to accelerate mass colonization of host trees (83). Zhang et al. (121) reported that verbenone functions as a multipurpose pheromone for RTB—attractive at very low concentrations but repellent at high concentrations. This phenomenon has been reported in other species of *Dendroctonus*, but for practical purposes, the primary function of verbenone for all species of *Dendroctonus* tested is as an interruptant to host or mate location (78).

In North America, large-group extracts also showed trace quantities of the bicyclic acetal frontalin in females but not in males. Small groups of juvenile hormone III (JH III)–treated or *Pinus radiata*–fed females also produced frontalin (64). Groups of males did not produce frontalin, irrespective of treatment. Both sexes, in this experiment, also produced *cis*-verbenol, *trans*-verbenol, and verbenone, with females producing more *cis*- and *trans*-verbenol and males generally producing more verbenone (64). Myrtenol and myrtenal may be new compounds produced by RTB in China, but this hypothesis has not been explored in US populations. These two oxidized monoterpenes have been proposed as attractants for trapping RTB in China (95).

Rapid production of aggregation semiochemicals could expedite host location and thereby reduce exposure of beetles to predation and other mortality factors. Shi & Sun (83) found that *cis*-verbenol, *trans*-verbenol, myrtenal, myrtenol, and verbenone were not synthesized de novo by the beetles; instead, they were synthesized through oxidation of the host monoterpene, α-pinene. Oxidation of α-pinene is a relatively simple chemical conversion and hence may involve lower metabolic costs and provide faster mobilization and release of attractant semiochemicals.

Complex Biological Interactions

Bark beetles are well-known vectors of fungi, particularly species of Ophiostomataceae (Ascomycota), several of which are important pathogens of conifers (38, 42, 73, 85, 88). Similarly, numerous species of ophiostomatoid fungi and particularly *Grosmannia* spp. are well-known associates of RTB in its native range (87, 108). Unlike some other species of *Dendroctonus*, such as *D. frontalis*, RTB has no known specific cuticular adaptation to carry fungi; rather, adult beetles simply carry inoculum in pits and on setae on their body surfaces (73). An earlier study by Klepzig et al. (44) clearly showed that host tree allelochemicals induced by beetle-vectored fungal infestation could inhibit fungal germination and growth and in some cases were also repellent to scolytine beetles, including RTB.

An intriguing question regarding RTB in China relates to the fungi associated with the beetle in its new environment and whether these might, at least in part, account for its unusual behavior there. Various studies have been undertaken to compare the fungal associates of RTB in China and North America (60–63) (**Table 1**). Interestingly, of all the fungi isolated from North American and Chinese beetles, only two shared species, *Leptographium procerum* and *Ophiostoma ips*, have been found (60). Of these, *L. procerum* is the most consistently isolated from RTB in China (60). Oddly, however, *L. procerum* and *L. terebrantis* are the most frequently recorded associates of RTB in North America (43, 86, 108), yet despite relatively intensive collections, *L. terebrantis* has never been found associated with the insect in China.

Table 1 Fungi reported from red turpentine beetle

Species	Host(s)	Origin	Reference(s)
Ceratocystis collifera	*Pinus teocote*	Mexico	65
Graphium sp.	*Pinus ponderosa*	United States	70
Grosmannia clavigera	Not known	United States	86
Grosmannia europhioides	Not known	North America	110
Grosmannia piceaperda	Not known	North America	81
Hyalorhinocladiella pinicola	*Pinus tabuliformis*	China	60
Leptographium alethinum	*Pinus tabuliformis*	China	62
Leptographium koreanum	*Pinus tabuliformis*	China	62
Leptographium pini-densiflorae	*Pinus tabuliformis*	China	60, 100
Leptographium procerum	*Pinus sylvestris*, *Pinus resinosa*, *Pinus banksiana*, *Pinus strobus*	United States	36, 43, 108
	Pinus tabuliformis, *Pinus bungeana*	China	60–62, 100
Leptographium sinoprocerum	*Pinus tabuliformis*, *Pinus bungeana*	China	60, 61, 100
Leptographium terebrantis	*Pinus ponderosa*, *Pinus sylvestris*, *Pinus resinosa*, *Pinus banksiana*	United States	32, 43, 70, 86, 108
Leptographium truncatum	*Pinus tabuliformis*	China	60, 62, 100
Leptographium wageneri	*Pinus ponderosa*	United States	27
Leptographium wageneri var. *ponderosum*	*Pinus ponderosa*, *Pinus jeffreyi*	United States	82
Leptographium wingfieldii	*Pinus resinosa*, *Pinus strobus*	United States	36
Ophiostoma sp.	*Pinus tabuliformis*	China	60
Ophiostoma abietinum	*Pinus tabuliformis*	China	60
Ophiostoma floccosum	*Pinus tabuliformis*	China	60, 100
Ophiostoma ips	*Pinus tabuliformis*	China	60
	Pinus ponderosa, *Pinus resinosa*	United States	43, 70
Ophiostoma minus	*Pinus tabuliformis*	China	60, 100
Ophiostoma piceae	*Pinus tabuliformis*	China	60
Ophiostoma piliferum	Not known	North America	75
Pesotum aureum	*Pinus tabuliformis*	China	62
Pesotum pini	*Pinus tabuliformis*	China	62

It is unclear whether *L. procerum* was introduced into China along with RTB, although the fungus is a frequent RTB associate in eastern and central North America and this seems the most likely case. A recent study by Lu et al. (59) provides some evidence that the fungus was introduced with RTB into China. There are, however, puzzling contradictions in this regard. For example, although *L. procerum* has never been reported from western North America, this is the area thought to be the source of the Chinese introduction (10, 12). Recent intensive collections in the western United States have confirmed the absence of *L. procerum* associated with RTB in that region (24), so there is clearly a need for a more in-depth comparison of RTB's fungal associates in its native and introduced ranges.

L. procerum is not known to be a primary pathogen in North America, although it has been associated with tree decline syndromes and with other scolytines that feed on living conifers (108). On the other hand, strains of *L. procerum* collected from exotic RTB in China were much more virulent in pathogenicity tests on *P. tabuliformis* than a strain from the beetle in North America (58).

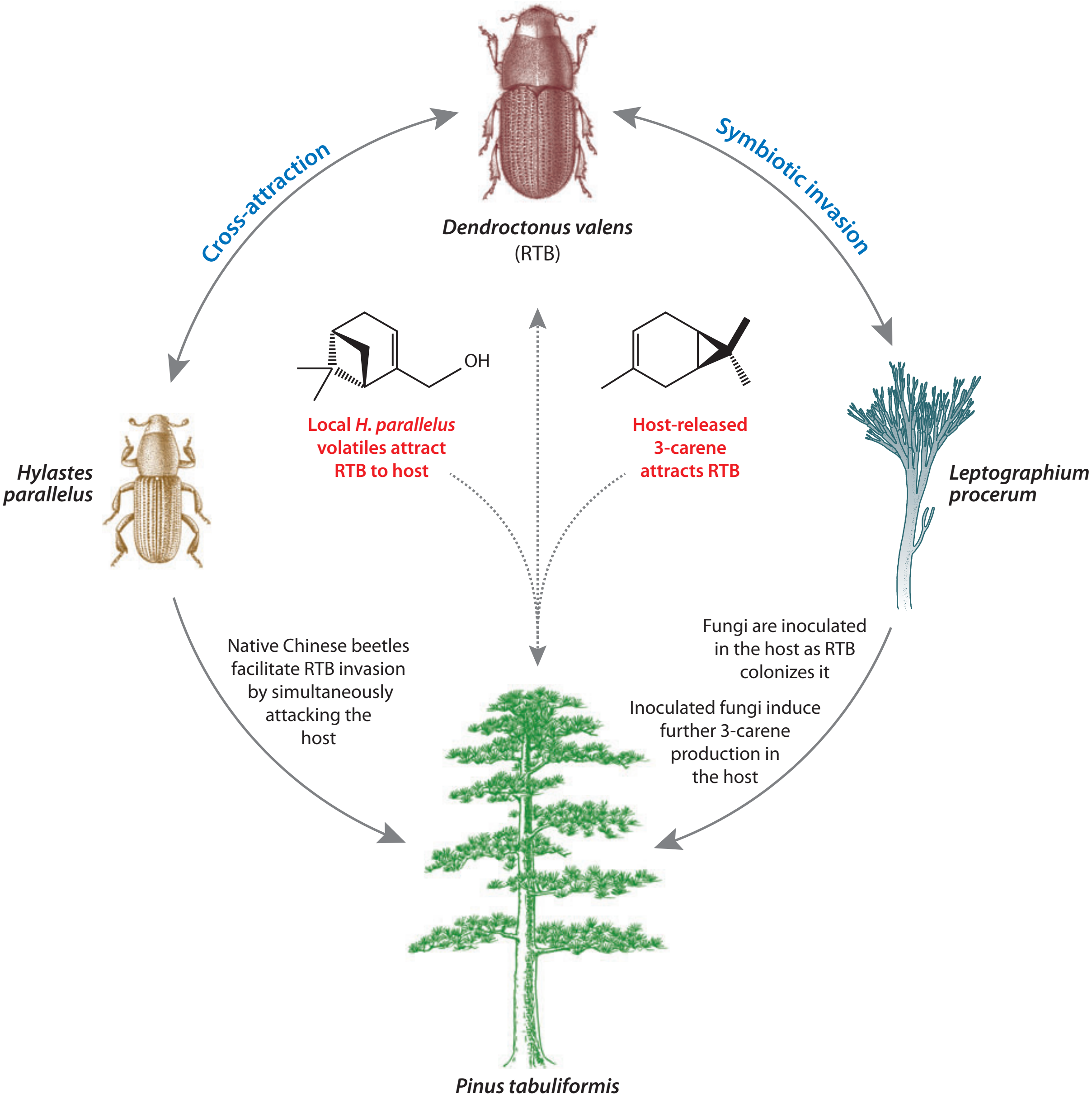

Figure 1

Symbiotic invasion of the red turpentine beetle (RTB) and its associated fungi in China.

Multitrophic interaction: interaction occurring between more than two trophic levels

Intriguingly, these Chinese strains also increased tree production of 3-carene, the most attractive host volatile for RTB, in inoculated pine seedlings. Although these results are of a preliminary nature, Lu et al. (58, 59) suggest that this multitrophic, semiochemical interaction could be an important factor involved in the RTB invasion in China (**Figure 1**). Elevated 3-carene levels have been associated with insect and disease defense in other conifers in Pinaceae (18), and the isolation

INVASIVE BEETLE–FUNGUS SYMBIOSES: BAD NEWS FOR FORESTS

A disturbing new phenomenon has arisen worldwide: the sudden emergence of previously unnoticed or unknown tree-killing beetle–fungus symbioses. In some cases, such as that of *Xyleborus glabratus* vectoring laurel wilt disease, the symbiosis is longstanding, and beetle and fungus were apparently introduced simultaneously to North America from Asia. In the case of the red turpentine beetle and *Leptographium procerum*, the fungus has a long association with the beetle in its native region, but new, aggressive fungal genotypes arose after the symbiosis was introduced into China. In the case of *Platypus quercivorus* vectoring the oak wilt pathogen *Raffaelea quercivora* in Japan, the association appears to have resulted from an encounter between a native beetle and an introduced fungus. And in the case of thousand cankers disease and the walnut twig beetle *Pityophthorus juglandis*, the association is apparently longstanding, but other factors, possibly including climate change, have extended the beetle's range and increased tree mortality from the symbiosis. In the past, we were ill-prepared to identify even native fungal associates of scolytine beetles because fungal taxonomic methods were so challenging. Now, with molecular methods for their study, we should intensify investigation of these symbioses so that we can rapidly and appropriately respond to new introductions.

of 3-carene synthase cDNA should facilitate mechanistic testing of the function of 3-carene in the chemical ecology of RTB and its fungal associates in their pine hosts. The phenomenon of aggressive new beetle–fungal associations is reported with increasing frequency and raises serious phytosanitary concerns (24, 31, 33, 35, 36, 37, 47) (see sidebar, Invasive Beetle–Fungus Symbioses: Bad News for Forests).

The assemblage of fungi associated with RTB in China is remarkably different from that known of the insect in its native range (**Table 1**). There is clear evidence that in China the insect has established a unique community of associates (24, 60, 61), including the new species *L. sinoprocerum* collected in Shanxi Province (61). The implications of this novel assemblage of fungi associated with RTB in China and the novel beetle–fungal interactions with a new Chinese host tree are not entirely understood. It should also be noted that interactions between RTB and fungi can be either beneficial or detrimental to the beetles, as has been suggested from in vitro experiments with Chinese RTB. In these experiments, larvae fed on an artificial diet including *O. minus* exhibited a decreased rate of weight gain compared with those fed on *L. procerum* and *L. terebrantis* (101). The immunocompetence of RTB stimulated by the fungi has been inferred to be the underlying mechanism for the antagonism (84). However, RTB larvae seem to be able to control this negative effect by producing a suite of volatiles (verbenol, myrtenol, and myrtenal) that inhibit growth of *O. minus* (101).

Two well-known insect pathogenic fungi, *Beauveria bassiana* and *Metarhizium anisopliae*, infect RTB larvae, pupae, and adults in China (104, 112, 122). Laboratory tests demonstrated that some strains of *B. bassiana* caused 100% mortality of RTB adults in concentrations of 1×10^7 conidia ml^{-1} (118). This result is consistent with other studies using *B. bassiana* as a biocontrol agent of beetles (15, 46, 77).

Many species of bacteria have been isolated from RTB in the United States and Mexico. The bacterial gut community of RTB from Mexico was characterized and included species of *Lactococcus*, *Acinetobacter*, *Pantoea*, *Rahnella*, *Stenotrophomonas*, *Erwinia*, *Enterobacter*, *Serratia*, *Janibacter*, *Leifsonia*, *Cellulomonas*, and *Cellulosimicrobium* (69). This study revealed a relatively low species diversity (17 species) compared with communities in other insects (>100 species in termites, cockroaches, and scarab beetles) (69). A possible explanation for this low level of diversity is that bark beetle guts contain toxic host compounds that could limit the number of bacterial species (69).

Bacterial symbionts of RTB, like those of other bark beetles, play a role in nutrition, detoxification of host volatiles, and regulation of fungal symbiont populations (2). Bark beetle guts typically harbor a few to more than a dozen bacterial species, but relatively few shared bacterial species among bark beetles have been investigated for the presence of these organisms. For example, RTB and *Ips pini* shared only three bacterial genera (14, 69), suggesting a relatively tightly evolved relationship between bark beetle species and bacteria. The bacterial gut community of RTB reported from Mexico included 17 species (69), whereas widespread sampling in the United States revealed 19 operational taxonomic units (1), with little overlap among taxa between the two sites. Indeed, Adams et al. (1) found significant differences in the bacterial compositions even between the sites in the United States. Nevertheless, all bark beetles studied to date share the genera *Stenotrophomonas* and *Pantoea* (69), which hints at an essential and ancient symbiotic relationship. These types of relationships are very complex and could have evolved as RTB defensive mechanisms against pathogens. The understanding of these multipartite symbioses may reveal unexpected opportunities in bark beetle pest management (76).

In the United States, RTB is known to be associated with conditions leading to tree stress such as wildfire scorching, disease, or infestation by other forest insect and disease pests (71). Common insect associates of RTB include *Ips* spp., *Hylurgops* spp., *Hylastes* spp., *Dendroctonus brevicomis*, *D. jeffreyi*, and *D. ponderosae* (71), and fungi associated with attack by RTB in the United States include *Leptographium wageneri*, *L. terebrantis* (western and central United States only), and *L. procerum* (eastern and central United States only) (43, 72). In China, an important semiochemical relationship exists between RTB and the root-feeding scolytine *Hylastes parallelus* (57). Both species can infest trees simultaneously, with RTB infesting the lower trunks and upper roots and *H. parallelus* infesting the lower roots and both insects contributing to the success of the overall infestation (112). This synergistic relationship appears to be mediated through cross-attraction via chemical cues (57) (**Figure 1**).

In the United States, several generalist predators of *Dendroctonus* spp. bark beetles are presumed to prey on RTB, including *Temnochila chlorodia* (Coleoptera: Trogissitidae), *Thanasimus dubius* and *Enoclerus* spp. (Coleoptera: Cleridae), and *Lasconotus* spp. (Coleoptera: Colydiidae) (23). Studies that conclusively demonstrate such predation, however, have not been conducted, probably because of the nonpest status of RTB in the United States. Massey (66) makes oblique reference to a nematode parasite species of North American RTB that reaches 9 mm in length, but does not identify it taxonomically. Rose (80) reports finding two nematode species, *Rhabditis* sp. and *Ditylenchus* sp., in RTB galleries in central Mexico but did not define their roles with respect to RTB.

Several field surveys in China have revealed the occurrence of various natural invertebrate predators of RTB, which occur in low numbers. These include *Agulla xiyue*, *Camponotus japonicus*, *Dendrocopos major*, *Formica sinensis*, *Labidura riparia*, *Platysoma attenuata*, *Raphidia sinica*, *Tetramorium guineense*, and *Thanasimus formicarius* (104, 122). *P. attenuata* has shown some potential for the control of RTB (104), and an unidentified species of Tenebrionidae (Coleoptera) was a highly effective predator in laboratory experiments (112). *Rhizophagus grandis* Gyllenhal, a predator of the closely related *Dendroctonus micans* (Kugelann) in Europe, has excellent prey-search abilities and high fecundity and has been used successfully to control *D. micans* in several European countries (8, 45). Gregoire et al. (28) identified several oxygenated monoterpenes in the frass of RTB larvae that collectively functioned as oviposition stimulants for *R. grandis*, indicating promise for its use as a biocontrol agent for RTB. In 2000, *R. grandis* was first introduced into China where mass-rearing techniques had been developed for its use (107), but it was able to establish and attack RTB with only moderate efficacy, so its role as a biocontrol agent has been somewhat limited (126).

Factors Favoring Red Turpentine Beetle Outbreaks

Favorable climate and abundant hosts have undoubtedly contributed to RTB establishment in northern China. However, high levels of humidity arising from frequent rainfall disrupt egg hatch and larval development (68). *Pinus tabuliformis* forests occur in four climatic regions (111) and these likely also differentially affect RTB outbreaks. They are (*a*) a warm/dry region, (*b*) a warm/moist region, (*c*) a warm/wet region, and (*d*) a subtropical/wet region. The outbreak of RTB in northern China has occurred in the warm/dry region, which has one-half to one-third the precipitation of the other regions, especially from October to May (94); its mean relative humidity is the lowest of the four climatic regions and it has the longest mean daylength (111). Several consecutive years of severe drought in northern China may have stressed *P. tabuliformis* and made it more susceptible to RTB damage (49, 93), and an unusually dry spring in 1997 has been suggested as an important trigger for the first outbreak in 1998 (102). Elevated temperatures in Shanxi Province from 1997 to 2000 probably also favored RTB survival (68). Winter temperatures since the early 1980s, in particular, have been warmer than in the previous 10 years and appear to be critical for beetle survival (49, 113). Felling of RTB-attacked trees at the initial outbreak stage without treating stumps to prevent development of RTB may have been another major contributing factor because these stumps release volatiles that attract more beetles and then serve as a source of new attacking beetles (71).

In North America, RTB attacks all species of pine within its range, and occasionally spruce and larch (11, 23). In western North America, *Pinus ponderosa*, *P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. monticola*, and *P. radiata* are preferred hosts (89), whereas in China the primary host is *P. tabuliformis* (49, 68). Occasionally, RTB may be found infesting *P. armandii*, *P. bungeana*, and *Picea meyeri*, but there have been no confirmed reports of mortality in these hosts (114, 122). *P. sylvestris*, a rare nonnative species in China's Shanxi Province, has occasionally been attacked by RTB (114), and global warming may increase this trend by reducing cold-induced beetle mortality in this region. Indeed, *P. sylvestris* is more or less continuously distributed across northern Eurasia (13) and is quite high in 3-carene (99), so this species has the potential to serve as a corridor for the spread of RTB into Western Europe.

P. tabuliformis is one of the most widely distributed pines in China. It grows over a vast area in northern and north-central China, from 31°N to 44°N latitude and from 101°30′E to 124°25′E longitude (111). This wide distribution provides abundant habitat ecotypes for RTB. Of these ecotypes, seven are recognized RTB-infested areas. Those in central and southern Shanxi, western Hebei, and northeastern Henan provinces belong to the middle ecotype, and the infested areas of Shaanxi Province belong to the middle west ecotype. The midwest and southern ecotypes of *P. tabuliformis* may suffer cold-related damage (northern Shaanxi and Henan provinces) (113), which may make *P. tabuliformis* vulnerable to RTB attack in the spring. The fact that most *P. tabuliformis* stands in these areas are monocultures, thus providing a concentrated food source, elevates the probability of RTB infestation. Consequently, northern Shaanxi Province should be viewed as an area at high risk of future RTB outbreaks (9, 114).

MANAGEMENT OPTIONS

Prior to 1999, RTB was not considered a forest pest in China. However, its pest status escalated as the beetle continued to spread and levels of damage increased. The Chinese State Forestry Administration now ranks RTB as the second most important forest pest nationwide, and a National Management Project was initiated for RTB in 2000. Promising management options for controlling RTB, as with any bark beetle pest, include regulatory, silvicultural, insecticidal, and semiochemical tactics; all these approaches have been implemented in China as integrated pest management programs to mitigate RTB damage. Biological control has not been effective to date but remains a promising avenue for future research (69). Approximately 30% of the 85,300 ha of pine forest in eastern Shanxi Province has been infested, with approximately 7% mortality of *P. tabuliformis* just in 2001. RTB infestations extended into Henan Province, but an end to the drought combined with a rapid response including physical, chemical, and regulatory control by the State Forestry Administration appears to have kept damage to a minimum in 2002 (114). Data provided by the Shanxi Forestry Bureau indicate that the RTB-infested area within Shanxi Province has decreased from 256,668 ha in 1999 to 29,913 ha in 2010. Over a 12-year period (1999–2010), the average acreage of control projects was 38,981 ha, with a peak of 79,333 ha in 2001.

Regulatory Tactics

As the risk from RTB became apparent in China, the potential distribution and risk assessments for range expansion were modeled using data from 305 weather stations (98, 103). The potential risk of RTB in China was analyzed by the risk analysis software @RISK. The sensitivity analysis of conditional influencing factors showed that for all the evaluation indices, the risk of further RTB outbreaks and range expansions in China was extremely high (98). These assessments were used regionally to regulate transport of potentially infested wood materials in order to limit human-assisted RTB spread. According to the model, suitable areas with a higher likelihood of drought are located north of the presently infested area, so if RTB were to spread to this area the damage would likely increase greatly. Analyses of host volatiles that serve as beetle attractants (monoterpenes) show that *Pinus bungeana* and *Picea asperata*, which grow in this region, may be more susceptible to RTB attack than other hosts in the infested area (103), and global warming may increase their susceptibility.

Human-mediated movement appears to be the predominant means of spread where pine stands are widely separated, so monitoring and regulatory enforcement are essential to prevent or slow the spread of RTB in China (114). Any pine material with intact bark could potentially harbor RTB, and harvesting of dying, infested trees might facilitate RTB spread through the movement of infested logs. Restrictions on unauthorized tree harvesting and the movement of infested material (logs, wood blocks, and wood boxes with bark) are therefore strictly enforced. The Forest Pest Control Station system that was established in China facilitated enforcement of quarantine regulations from the central government to the provincial, city, and county levels. Strict quarantine regulations are enforced at ports and along highways and railways.

Silvicultural Tactics

Several silvicultural methods are advised to minimize the risk of RTB attack, among them (*a*) preventing tree wounds, (*b*) eliminating chip piles or other sources of attractive host volatiles, (*c*) carefully timing thinning, pruning, and soil ripping to avoid periods when trees might be drought-stressed and dispersing beetles high in number (22, 71), and (*d*) reducing stand density to minimize stress resulting from competition (51). Avoidance of monocultures is also frequently recommended to minimize resource concentration that might favor pest population increases (4, 51, 52). In China, where the outbreak demands more coordinated and systematic action, RTB status has been monitored annually since 1999, primarily using baited traps combined with summer and fall plot inspections for signs of attack such as pitch tubes and frass on stems. Plots with one or more trees with these signs are noted as positive for the pest, and then four forest management measures are applied to infested stands: ceasing turpentine collection from living trees, reducing stand density, removing infested trees, and increasing tree species diversity (51).

Insecticidal Tactics

In North America, fenitrothion (30), carbaryl, and permethrin (96) have all shown efficacy for individual tree protection from RTB attack, but application must be made before beetles attack. Methods effective in China for killing 80–100% of beetles include fumigating boles with aluminum phosphide under plastic cover (67), injecting dichlorvos or omethoate into newly initiated galleries, and spraying insecticides (e.g., phorate, monocrotophos, cypermethrin, phoxim) onto boles (40, 92, 105, 106, 123). Fumigation and injection with insecticides can be conducted throughout the year, but the optimal timing is early June to October, when pupation and development of new larvae occur (114).

Fenitrothion: *O*,*O*-dimethyl *O*-(3-methyl-4-nitrophenyl) phosphorothioate, a phosphorothioate (organophosphate) insecticide

Carbaryl: 1-naphthyl methylcarbamate, a chemical in the carbamate family used chiefly as an insecticide

Permethrin: a synthetic pyrethroid widely used as an insecticide, acaricide, and insect repellent

Semiochemical Tactics

Chemical control with insecticides is the most effective treatment, but semiochemical tactics such as application of antiattractants, trap-out of beetles with attractants, or combinations thereof are more environmentally friendly and less labor-intensive (25, 119). Promising semiochemicals include attractant kairomones produced by hosts and conspecific beetles, sex attractant pheromones, aggregation pheromones, and antiattractants.

RTB earned its common name because of its well-known attraction to turpentine, a variable mix of resins. The first specific resin components demonstrated to attract RTB were (−)-β-pinene and secondarily (+)-α-pinene and (+)-3-carene (34), with (−)-β-pinene attracting five to ten times as many beetles as the other components. The antipode (−)-α-pinene interrupted response to (+)-α-pinene in the first reported example of chiral specificity of kairomones (34). Subsequent work in China showed that (+)-3-carene was the best RTB attractant in the invaded region (91), leading to the supposition that founder effects had yielded an invasive RTB population with semiochemical responses different from those of native populations (12, 114). A large follow-up study, however, showed that when identical study protocols were applied globally, all populations in China and North America, including Mexico, responded most strongly to (+)-3-carene (17). Release rates differed vastly in the two studies, which may explain the different results. Because of its superior performance, (+)-3-carene was subsequently used in a series of successful trapping projects in China (50, 53, 95, 116).

RTB has also shown kairomonal responses to semiochemicals other than host volatiles. Lu et al. (57) showed both antennal and behavioral responses by RTB to volatiles produced by a native Chinese root beetle, *H. parallelus*, in a study revealing the first reported kairomonal interactions between native and introduced insects. Joseph et al. (39) reported increased attraction of RTB by kairomones with the addition of ethanol, but Fettig et al. (20) found an insignificant increase with ethanol, suggesting that it may not function consistently enough to be useful in operational trapping programs. The potential for combining effective semiochemicals in binary and ternary blends for enhanced trapping merits further exploration.

RTB was long suspected not to have an aggregation pheromone (20, 124), and aggregations are not typical in the native range. In addition, the death of the host, which is more assured when beetles aggregate, is presumably not necessary for RTB reproduction (73), but this supposition remains to be tested empirically. By contrast, the North American *Dendroctonus* species that are considered tree killers aggregate in large numbers and must do so quickly to overcome tree resin defenses. Recent work, however, has overturned the misconception that RTB lacks aggregation pheromones. Hall (29) reported attraction of RTB to trees baited with the aggregation pheromone of *D. brevicomis*, which also attacks pines in the native range of RTB, but he concluded that host volatiles were responsible for the attraction. Later, Zhang & Sun (120) demonstrated significant attraction of the *Dendroctonus* pheromone components, *trans*-verbenol, myrtenol, and myrtenal, in walking bioassays of RTB behavioral response and these pheromones were later isolated from RTB, confirming their pheromonal role for RTB. Luxova et al. (64) reported evidence that frontalin serves as a sex pheromone for RTB.

Nonhost volatiles: chemicals emitted by nonhosts that often serve as antiattractants to host-seeking beetles

Antiaggregation or interruptant semiochemicals can also be exploited to protect trees from RTB attack (25). Verbenone was shown to interrupt the response of RTB to baited traps and trees (78), and Gillette et al. (26) assisted in the development of verbenone-releasing plastic flakes that, when applied to the trunks, reduced RTB attack rates to zero. These dispersible pheromone flakes can also be applied by aircraft (25), so they may also have application for RTB mitigation. Fettig et al. (20) demonstrated reduction of RTB response to kairomone-baited traps by exo-brevicomin, a component of the aggregation pheromone of *D. brevicomis*, but frontalin, another component of the *D. brevicomis* pheromone blend, is probably responsible for the commonly noted attraction of RTB to *D. brevicomis*–infested trees. The *Ips* spp. pheromones ipsenol, ipsdienol, and *cis*-verbenol also disrupt attraction of RTB to attractant-baited trees (21), so these too may have promise for tree protection. Zhang et al. (117) also demonstrated antiattractant activity for RTB of three nonhost volatiles, 1-octen-3-ol, (*Z*)-3-hexen-1-ol, and (*E*)-2-hexen-1-ol, with reductions in response to attractants of 69.5%, 68.3%, and 66.0%, respectively. These antiattractants might provide even more effective control if applied in multiple-component blends (125).

SUMMARY POINTS

1. RTB populations occur in a variety of habitats and use many different hosts in vast areas of RTB's native range. In China, where it is invasive, RTB has rapidly expanded its range but is currently more or less restricted to *P. tabuliformis*, an important reforestation species of pine. Variation in RTB populations inhabiting these areas has been summarized and discussed. Many factors account for the differences between RTB infestations in its native and introduced ranges. Key differences between RTB's behavior in the two areas most likely reflect adaptations to a new environment.
2. Factors that may explain RTB's successful colonization and establishment in China include more aggressive attack behavior, high dispersal capability, an abundance of naïve hosts, lack of predators and pathogens, positive interactions with native bark beetles, an effective symbiosis with new fungal associates, and favorable climate patterns.
3. Monitoring and detection programs were initiated in 1999 in areas where RTB has caused severe damage in China. The potential distribution of RTB has been forecast and the potential risk has been evaluated. Strict quarantine regulations have been applied and enforced at ports and along highways and railways within infested areas, and forest management measures to control the pest have been studied. Fumigation during the flight period is a direct control method that is effective at killing beetles on a large scale. Trapping beetles with semiochemicals lures (host volatiles) has been tested as a promising labor-saving and environmentally friendly method for RTB management.

FUTURE ISSUES

1. Comparative studies of RTB biology in China and North America have already enhanced our understanding of its potential spread and impact in China. These studies should clearly continue and include, in particular, extended population genetic comparisons of beetles as well as monitoring the spread of RTB beyond China.
2. Genomic studies of RTB and some of its microbial associates have been initiated. Information from this work, together with studies of transcriptomes and metabolomes, will clearly enhance the base of knowledge about not only this important bark beetle but conifer-infesting bark beetles and their microbial symbionts in general.
3. The relevance of multitrophic interactions between RTB and pines, fungi, bacteria, mites, and other beetles remains unclear. A comprehensive understanding of these ecological interactions is crucial to understanding the biology of RTB and other invasive beetle–fungus mutualisms.
4. Planting strategies (mixed-species stands and mixed-age stands) should be designed to reduce outbreak potential. Improved lures, including host volatiles and pheromones, and improved trapping techniques will enhance monitoring, detection, interruption, and trap-out. Similarly, epidemiological models for RTB in urban, managed, and natural forests will benefit from refinement.

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57. Describes interspecific facilitation and mechanism of invasion by RTB.

58. Describes symbiotic invasion of the RTB-fungus complex.

59. Shows how novel fungal genotypes assisted the invasion of China by the RTB-fungus complex and posits risk of reinvasion.

60. Excellent summary of RTB-associated fungi in China.

63. Comprehensive review of the relationship between RTB and its associated fungi, with particular relevance to the Chinese literature.

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