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Influence of bark thickness, trunk diameter and height on reproduction of the longhorned beetle, *Monochamus sutor* (Col., Cerambycidae) in burned larch and pine

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Abstract

The small white-marmorated longicorn, Monochamus sutor L., is one of the most prevalent steminfesting insects in burned areas of the Great Xing An Mountains, China. Burned trees of larch (Larix dahurica) and pine (Pinus sylvestris var. mongolica) are suitable for reproduction by M. sutor from the trunk base to within an average of 3.3 and 4.6 m from the top, respectively, for trees from 13–23 m in height. The emergence of M. sutor gradually declines with height, and ceases at a bark thickness of less than 0.3 cm in both species. Emergence increased in a logarithmic relationship with either bark thickness or trunk diameter in both tree species. Two linear regression equations, Y = 2.01 + 0.426Xand Y = 0.07 + 0.771X, were derived in order to predict the average density of M. sutor emergence per 0.1 m² bark area (Y) for the trunk based on an observed density (X) at breast height position (1.5 m) for larch and pine, respectively. The total number emerging from a tree can be predicted by multiplying the average density estimate by the expected reproduction bark area. Reproduction of cerambycids is discussed with respect to selection of host trees, interactions with guild species, effects of bark thickness, and forest fire dynamics.

1 Introduction

The extensive forest fire of the Great Xing An Mountains that occurred in 1987 not only brought about tremendous losses of forest resources but also caused serious destruction of ecological environments (L1U et al. 1989). A great number of scorched trees that were dying as well as weakened trees that resulted from the fire provided abundant food resources and suitable reproductive habitat for bark beetles, Ips cembrae = subelongatus (Col., Scolytidae), and longhorned beetles, Monochamus sutor L. (Col., Cerambycidae) (ZHANG et al. 1989, 1990). Within 3 years after the fire most trees were infested with these and other stem insects. The small (15-24 mm long) white-marmorated longicorn, M. sutor, became widely distributed and severely attacked the burned trees. The population of longhorned beetles increased to such proportions that nearly all burned trees were infested (CHU et al. 1990). The outbreak not only killed the scorched and weakened trees but also reduced wood quality, both in strength and coloration. Therefore, the outbreak of stem insects in this region was popularly referred to in China as a 'non-smoking forest fire' compared with the real forest fire in 1987. In order to develop a method for calculation of the population density of this pest on burned trees and estimate the potential for timber loss, we sampled bark in burned stands of larch and pine from June to August 1989 in the Great Xing An Mountains.

2 Materials and methods

Twenty-three burned trees of *Larix dahurica* and nine of *Pinus sylvestris* var. mongolia attacked by M. sutor were sampled. A range of trees were selected which varied in their height and diameter and were

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attacked by the beetle. The trees (80 to 150 years old) were felled just after M. sutor adults had emerged (28 June-2 August 1989), and the trunks were sawn into 2 m lengths except for the base which was divided into two, 1 m long logs. The emergence holes of the beetle were counted in 0.1 m² bark areas (20 × 50 cm) in the middle of each section. The diameters and bark thicknesses (outer corky bark plus the phloem/cambium) at both ends of each log section were measured to obtain an average diameter and bark thickness at each of the bark samples. Curvilinear least squares regressions were performed on the data to determine the relationships between (a) trunk diameter and bark thickness, (b) trunk diameter and emergence density, and (c) bark thickness and emergence density. The general pattern of emergence was revealed by adjusting the emergence from each log section as a percentage of the total emergence from the tree and by adjusting the height as a percentage of the total length of the trunk infestation. Linear regression equations for the average emergence of the longhorned beetle per 0.1 m^2 bark area of the tree (Y) were calculated based on the emergence density at the 1.5 or 3 mheights (X). The infested trunk surface area was calculated precisely from the individual log sections as well as approximately using the tree height, average height of infestations below the top, and the diameter at the base of the tree. Since the two estimates of the bark surface area were similar, the approximate calculation for area can be multiplied by the average emergence density to yield the total expected emergence from the tree.

3 Results

3.1 Emergence density patterns along the trunk

The emergence of *M. sutor* from larch (*Larix daburica*) and Scots pine (*Pinus sylvestris* var. *mongolica*) trunk sections at various diameters and bark thickness are summarized in tables 1 and 2, respectively. It can be seen that the average emergence from the 23 larch trees increased with height, was highest at the 2-4 m section, and then decreased with height. This pattern was also evident for pine. Linear or curvilinear regression of emergence

Table 1. Trunk diameter, bark thickness, and emergence hole density along the trunk of Larix dahurica

Height along trunk (m)	n	Mean trunk diameter (cm)	Mean bark thickness (cm)	Mean emergence (holes/0.1 m ²)
0–1	23	28.9 ± 3.1	2.58 ± 0.32	2.91 ± 0.82
1-2	23	25.2 ± 2.7	1.74 ± 0.25	4.09 ± 1.04
2-4	23	22.5 ± 2.5	1.33 ± 0.18	5.00 ± 0.9
4-6	23	20.3 ± 2.4	1.03 ± 0.14	4.87 ± 1.03
6-8	23	18.2 ± 2.4	0.82 ± 0.11	4.00 ± 0.87
8-10	23	15.8 ± 2.4	0.63 ± 0.09	3.57 ± 0.74
10–12	23	13.2 ± 2.3	0.48 ± 0.09	2.78 ± 0.71
12-14	23	10.8 ± 2.2	0.35 ± 0.07	1.65 ± 0.58
14-16	21	9.0 ± 2.0	0.25 ± 0.06	1.18 ± 0.54
16-18	18	7.3 ± 1.6	0.19 ± 0.05	0.72 ± 0.59
18-20	12	6.3 ± 1.3	0.16 ± 0.05	0.42 ± 0.74
20-22	5	5.9 ± 2.7	0.17 ± 0.08	0.20 ± 0.56
22–24	2	5.0	0.18 ± 0.4	0

 $(n = 23 \text{ trees}; \pm 95\% \text{ confidence interval})$

density with height for larch or pine was not strongly correlated (r = 0.5 to 0.55), which is probably due in large part to the different colonization densities as well as the different total heights and diameters of the trees. A better regression can be obtained by standardizing both the sampling heights as a percentage of the uppermost emergence height and the emergence from each sampled section as a percentage of the total sampled emergence. For larch (fig. 1), the best-fitting curvilinear regression was quadratic ($Y = -0.00277X^2 +$ 0.208X + 10.7, r = 0.56, n = 203). A similar pattern is seen in fig. 1 for the emergence from Scots pine ($Y = -0.00169X^2 - 0.042X + 17.4$, r = 0.70, n = 66).

Height along trunk (m)	n	Mean trunk diameter (cm)	Mean bark thickness (cm)	Mean emergence (holes/0.1 m ²)
0–1	9	26.8 ± 4.6	2.06 ± 0.50	4.33 ± 1.39
1-2	9	24.1 ± 4.8	1.52 ± 0.54	5.00 ± 1.09
2-4	9	21.9 ± 5.2	1.20 ± 0.52	5.44 ± 1.49
4-6	9	19.8 ± 5.6	0.91 ± 0.48	4.44 ± 1.39
6-8	9	17.2 ± 6.0	0.62 ± 0.34	2.89 ± 0.90
8-10	9	14.7 ± 6.1	0.41 ± 0.22	2.11 ± 1.12
10-12	9	12.2 ± 5.9	0.31 ± 0.18	1.56 ± 1.85
12-14	9	9.7 ± 5.5	0.22 ± 0.13	1.00 ± 1.39
14–16	7	9.3 ± 5.9	0.18 ± 0.12	1.29 ± 2.76
1618	3	11.5 ± 11.8	0.22 ± 0.31	1.33 ± 5.74
18-20	3	7.8 ± 6.8	0.16 ± 0.20	0.67 ± 2.87
20–22	3	6.0 ± 4.3	0.13 ± 0.14	0

Table 2. Trunk diameter, bark thickness, and emergence hole density along the trunk of Pinus sylvestris var. mongolica
(n = 9 trees; ± 95 % confidence interval)

3.2 Relationship between trunk diameter and emergence density

The emergence density increases in a logarithmic relationship as the diameter of the trunk increases (fig. 2). For larch the best fitting logarithmic equation is $Y = 2.005 \ln X - 2.31$ (r = 0.50, n = 226, fig. 2), while the best curve for pine is $Y = 2.719 \ln X - 4.14$ (r = 0.65, n = 75, fig. 2). The two curves are remarkably similar for the two tree species. The smallest



Fig. 1. Pattern of relative emergence of *Monochamus sutor* along the trunk that was infested in larch, *Larix dahurica* (n = 23), and Scots pine, *Pinus sylvestris* var. *mongolia* (n = 9) in the burned region of the Great Xing An Mountains, China (July-August 1989)



Fig. 2. Relationship between trunk diameters of larch, Larix dahurica, (n = 23) and Scots pine, Pinus sylvestris var. mongolia, (n = 9) and emergence density of Monochamus sutor per 0.1 m² bark area in the burned region of the Great Xing An Mountains, China (July-August 1989)

average diameter that was suitable for reproduction in larch was 7.9 ± 1.1 cm (± 95 % C.I.) and 10.5 ± 4.1 cm for pine. The relationship between trunk diameter and bark thickness was best fit by a geometric curve (fig. 3). For larch the equation was $Y = 0.0114X^{1.495}$ (r = 0.92, n = 226, fig. 3) and for pine it was $Y = 0.007X^{1.596}$ (r = 0.93, n = 75, fig. 3).

3.3 Relationship between bark thickness and emergence density

The relationship between bark thickness and emergence (fig. 4) follows a logarithmic function. The best fitting equation for larch was $Y = 1.134 \ln X + 3.6$ (r = 0.46, n = 226, fig. 4) and that for pine was $Y = 1.578 \ln X + 4.25$ (r = 0.65, n = 75, fig. 4). The average bark thickness at which emergence ceased along the trunk was nearly identical for both species, 0.307 ± 0.065 cm (± 95 % C.I.) for larch and 0.306 ± 0.154 cm for pine.

3.4 Estimation of the emergence from a tree based on density at breast height

The total expected emergence of M. sutor from a tree can be calculated precisely from the emergence at each sample and bark surface area of the respective trunk section. The average emergence density per 0.1 m² is then the total expected emergence divided by the calculated area. A linear regression of the emergence at 1.5 m (1-2 m section) with the average emergence density gave the following equation for *Larix*:

$$Y = 2.01 + 0.426X; r = 0.69$$
(1a)

where Y is the average density of emergence per bark area from the tree (emergence holes/ 0.1 m^2) and X is the emergence density per bark area (0.1 m²) at breast height. When trees



Fig. 3. Relationship between trunk diameter and bark thickness of larch, Larix dahurica, (n = 23) and Scots pine, Pinus sylvestris var. mongolia, (n = 9) in the burned region of the Great Xing An Mountains, China (July-August 1989)



Fig. 4. Relationship between bark thickness of larch, Larix dahurica, (n = 23) and Scots pine, Pinus sylvestris var. mongolia, (n = 9) and emergence density of Monochamus sutor per 0.1 m² bark area in the burned region of the Great Xing An Mountains, China (July-August 1989)

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can be sampled after felling the regression equation at 3 m height gives a somewhat better correlation, Y = 0.66 + 0.619X (r = 0.82). These equations were tested with data from 10 other infested trees and the observed densities differed by only about 15% from the equation estimates.

The appropriate equation at 1.5 m height for Scots pine was:

$$Y = 0.07 + 0.771X; r = 0.87$$
(1b)

or at 3 m height: (Y = 0.76 + 0.58X; r = 0.91).

The larch trees had an average height of $18.96 \pm 1.19 \text{ m} (\pm 95 \% \text{ C.I.})$. *M. sutor* infestations ceased at an average height of $15.65 \pm 1.19 \text{ m}$, or 3.31 m less than the top of the tree. Pine trees had an average height of $17.28 \pm 2.84 \text{ m}$ and emergence ceased at $12.66 \pm 2.66 \text{ m}$, or 4.62 m below the top. The infestation area, as described above, can be calculated precisely from the diameters of the individual trunk sections according to the formula:

$$\sum_{s=1}^{n} \frac{L_s + U_s}{2} \pi H_s$$
 (2)

where L is the diameter of the lower part of a log section und U is the upper diameter, s is the trunk section, from 1 to n (the number of the section), and H is the length of each section (1 or 2 m). The infestation area also can be calculated approximately from:

$$\frac{\frac{3.31}{H}D + D}{2}\pi (H - 3.31)$$
(3)

where D is the diameter of the tree's base, H is the height of the tree, and 3.31 is the average length of a tree that is uninfested, as in the case of larch above (or 4.62 for pine). Comparison of the two methods for calculating area of larch (n=23) showed that the average infested area was 8.61 m² and 9.14 m² for the precise and approximate methods, respectively. For pine (n=9) the areas were 7.46 and 7.65 m² for the two methods, respectively. Since the two methods only differed by about 5% in both species, the approximate method can be used on a practical basis.

Thus to estimate the total emergence of the beetle from a larch tree, the emergence in a 0.1 m² area at 1.5 m height is sampled. The regression equation (1a) then is used to obtain the expected average emergence density. This is multiplied by the expected infested area, found from the diameter of the tree at the base and the height with equation (3). Using the regression equations and approximate areas for larch trees the expected within-tree emergence ranged from 102 to 549 (mean = 294 ± 57 , ± 95 % C.I.), while the range for pine was from 108 to 852 (mean = 278 ± 184 , ± 95 % C.I.). These estimates of emergence can be compared to more precise estimates, using sample data and section areas, that ranged from 73 to 809 (mean = 327 ± 82) for larch and from 158 to 1118 (mean = 318 ± 236) for pine.

4 Discussion

Many wood-boring Coleoptera were found infesting the fire-damaged larch and pine compared to more healthy trees. Insect selection of stressed trees is the result of either a specific attraction over relatively long-range (several meters) or that oviposition and reproduction are successful in these low resistant trees, or both. Forest insects that feed on trees must locate their host through a combination of visual and olfactory cues (LANIER 1983; BYERS 1989). 'Primary attraction' occurs when an insect orients toward a source releasing chemical volatiles, characteristic of an appropriate host condition. Flatheaded borers (Buprestidae), roundheaded borers (Cerambycidae) and bark beetles (Scolytidae) often utilize plant compounds to find their host. These insect herbivores seem to prefer hosts that are 'stressed' by drought, disease, or fire. Lightning strikes and heat injury from fires can cause resin exudation and release of monoterpenes. Cerambycids and some scolytids are attracted to monoterpenes, probably not only from abiotic injuries but also from boring activities of their own or associated species. For example, the cerambycids, *M. carolinensis* and *M. titillator*, were attracted to turpentine (mostly α -pinene and β -pinene) released at from 0.2–5 g/day (FATZINGER 1985; PHILLIPS et al. 1988). CHÉNIER and PHILOGÈNE (1989) found four cerambycid species, including *M. scutellatus*, were significantly attracted to a monoterpene blend of which α -pinene was the most attractive component (released at about 0.4 g/day). Buprestids are generally not attracted by monoterpenes (CHÉNIER and PHILOGÈNE 1989).

Ethanol is known to be produced by stressed plants (KIMMERER and KOZLOWSKI 1982) and by suspected microorganisms in the tree during its death and decay (GRAHAM 1968). Saprophytic beetles, termed 'secondary colonizers', are often attracted to ethanol (c.f. CHÉNIER and PHILOGÈNE 1989). MONTGOMERY and WARGO (1983) compared traps baited with water or ethanol (2 g/day release) and found that ethanol alone is attractive to cerambycids (species numbers undetermined) but not to buprestids. Of the cerambycids, *Aegoschema modesta* and *Graphisurus fasciatus* were not attracted to ethanol, while *Analeptura lineda*, *Clytus ruricola*, *Elaphididionides villosus*, and *Urgleptes querci* were strongly attracted to ethanol. In another study, at least eight species of cerambycid were captured with ethanol baited traps (55 g/day) more so than with water (DUNN et al. 1986). Ethanol and monoterpenes are weakly synergistic in eliciting attraction for some cerambycids such as *M. scutellatus* and *M. titillator* but apparently not for others, e.g. *M. carolinensis* (CHÉNIER and PHILOGÈNE 1989; PHILLIPS et al. 1988). It is not known if *M. sutor* is attracted to either or both monoterpenes and ethanol, but it is not unlikely.

Several species of cerambycid have been shown to use a sex pheromone. In most cases the male is attracted to a female-released pheromone that functions at a range of some centimeters (c. f. WANG et al. 1991). Chemical components have not been identified. In Xylotrechus pyrrhoderus, however, the male releases a pheromone, composed of (2S,3S)octanediol and (2S)-hydroxy-3-octanone, that is attractive to females over a distance of 1-1.5 m (IWABUCHI et al. 1985). M. sutor, like other cerambycids, probably has a shortrange sex pheromone that operates over several cm while the beetle walks on the host tree, but the pheromone may not aid the insect in finding the host during flight. Other scolytid beetles such as I. cembrae that compete for the bark areas with M. sutor (ZHANG et al. 1990, 1992; LIU et al. 1991, however, do use an aggregation pheromone (STOAKLEY et al. 1978; KOHNLE et al. 1988) to locate the host. Cross-attraction of M. titillator to pheromones of competing Ips bark beetle species of the southern U.S.A. was reported by BILLINGS and CAMERON (1984). Also M. clamator in North America is attracted to ipsdienol, the major pheromone component of I. pini (MILLER and BORDEN 1990). The cerambycids probably improve their chances of finding suitable hosts by responding to already infested trees of their cohabiting guild species.

In general, larvae of species of *Monochamus* begin feeding in the phloem/cambium layers under the corky bark. Severe competition between cerambycids and bark beetles within the two-dimensional food resource has been reported, with bark beetles the losers due to their being eaten (COULSON et al. 1976, 1980). The spatial distribution and density of the bark beetle, *Dendroctonus frontalis*, was altered by the presence of foraging *M. titillator* (COULSON et al. 1976, 1980). The area foraged by *M. titillator* peaked at a height of about 60% of the infested trunk, and in this area bark beetle mortality was highest (up to 70%). In a later study, however, it was stressed that competition and mortality from *M. titillator* was largely avoided by bark beetle evasion strategies (FLAMM et al. 1989). *Ips* larvae avoided competition in a general sense by developing more rapidly than cerambycids and emerging from the tree before the latter would forage extensively. The slower developing *D. frontalis* escaped cerambycid foraging by boring into the outer corky bark,

where they fed during the later instars and pupated. *M. titillator* appears to forage at random, sometimes encountering and eating a scolytid larva (FLAMM et al. 1989). Undoubtely, *I. cembrae* suffers competition by *M. sutor* (ZHANG et al. 1990, 1992; LIU et al. 1991) but the former may attempt to minimize interactions by early colonization of the host and rapid development and emergence. *M. sutor*, like *M. titillator*, may benefit from association with *Ips* species and their symbiotic fungi that paralyze the resin system of the tree so that it is unable to defend itself. Conversely, *Ips* species may benefit from cerambycid colonization since the bark beetles' natural enemies may be eaten during the latter stages of foraging (MILLER 1985).

As the larvae of Monochamus continue to develop they burrow into the xylem tissue, which is less nutritious as food but being three-dimensional is less limiting. We found that thicker bark is positively related with M. sutor reproduction and emergence as would be expected based on competition for food. However, the correlation is not high since (1) phloem thickness is not perfectly correlated with bark thickness and (2) the larvae only spend part of their development time in the bark and then penetrate the xylem. The sapwood, although related in volume to the bark thickness, would be less constricting spatially on larval growth than the two-dimensional bark. In other words, bark beetles that feed in the phloem exclusively would be expected to exhibit a higher correlation in emergence with bark thickness than would cerambycids. I. calligraphus reared in logs with phloem thicker than their body width had higher fat content, could fly twice as long, and produced more progeny per female than those reared in phloem thinner than body width (SLANSKY and HAACK 1986; HAACK et al. 1987). Thus, in both bark beetles and M. sutor, there should be a bark thickness near the top of the trunk that is too small to support larval growth, probably since the larvae must feed too much in the xylem and corky outer bark when excavating feeding galleries that optimally should remain largely in the phloem.

In the short run our methods will allow estimates of M. sutor populations. However, prediction of future outbreaks requires knowledge of area-wide stand structure and resistance levels, as well as knowledge about natural enemies, *I. cembrae* cohabitants, and fire-stand dynamics. The tree and its stem-feeding herbivores (Scolytidae, Cerambycidae) have evolved under the influence of periodic fires into a stable forest structure of high diversity (SCHOWALTER et al. 1981; GEISZLER et al. 1984). A period without fires allows buildup of aged and susceptible hosts for beetles, resulting eventually in an outbreak, leaving fuel for fires, which soon burn and maintain the community. Trees that survive a fire may not be attacked for many years, although fire scars are eventually infected by fungi, leading to beetle attack, death of the tree, more fuel and then another fire (GEISZLER et al. 1984).

Acknowledgement

We would like to thank CHU DONG for assistance in sampling of the burned trees.

Zusammenfassung

Bedeutung von Rindendicke, Stammdurchmesser und Stammhöhe für die Fortpflanzung des Langhornbocks, Monochamus sutor (Col., Cerambycidae) in verbrannten Lärchen und Kiefern

Der kleine weiß-marmorierte Langhornbock, Monochamus sutor L. ist einer der weit verbreiteten, in Stämmen lebenden Insekten in durch Waldbrand geschädigten Gebieten der Great Xing An Mountains in China. M. sutor kann sich in verbrannten 13–23 m hohen Lärchen (Larix dahurica) und Kiefern (Pinus sylvestris var. monogolica) vom Stammfuß bis durchschnittlich 3,3 bzw. 4,6 m unterhalb der Spitze fortpflanzen. Das Schlüpfen von M. sutor nimmt allmählich mit der Höhe ab und hört bei einer Rindendicke von weniger als 0,3 cm bei beiden Baumarten auf. Das Schlüpfen nahm bei beiden Baumarten logarithmisch entweder mit Rindendicke oder Stammdurchmesser ab. Zwei lineare Regressionsgleichungen Y = 2.01 + 0.426X bzw. Y = 0.07 + 0.771X wurden abgeleitet, um bei Lärchen und Kiefern die Durchschnittsdichte von schlüpfenden M. sutor pro 0,1 m² Rindenfläche (Y) aus der beobachteten Dichte (X) in Brusthöhe (1.5 m) vorauszusagen. Die geschätzte Durchschnittsdichte kann mit der erwarteten Reproduktionsrindenfläche multipliziert werden, um dadurch die Gesamtschlüpfzahl vorauszusagen. Die Fortpflanzung der Cerambyciden wurde unter Berücksichtigung der Wirtsbaumwahl, der Wechselwirkungen zwischen den zusammenlebenden Arten, der Bedeutung der Rindendicke und dem Verlauf von Waldbränden diskutiert.

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