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Gallery Characteristics and Life History of the Ambrosia Beetle *Trypodendron betulae* (Coleoptera: Curculionidae: Scolytinae) in Birch

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Abstract

Trypodendron betulae Swaine distributed attack entrance holes uniformly over the surface of standing stressed sub-canopy birch trees. Male and female pairs constructed galleries consisting of an entrance tunnel about 20 mm in length and then primary and secondary lateral tunnels averaging between 16 and 23 mm in length into the sapwood. Egg niches were constructed in the lateral tunnels after the symbiotic fungus was established in the galleries. Larvae enlarged the niches into cradles. Pupae and eventually teneral adults developed in the cradles. The sex ratio of resulting progeny adults was approximately one to one, and they emerged from galleries in September to overwinter in the litter.

Trypodendron betulae Swaine (Coleoptera: Curculionidae: Scolytinae) was described by Swaine (1911) and further defined by Wood (1957). Dodge (1938) and Leech et al. (1940) briefly described the beetle's habits in Minnesota. The hosts of the beetle include all Betula species and Alnus viridis subsp. sinuata (Regel) with the distribution of T. betulae following the natural distribution of Betula spp. in North America (Wood 1957, Wood 1982, and Atkinson 2015). Kuhnholz (1994) found the aggregation pheromone of T. betulae was composed of the ESR and ZRR stereoisomers of titalol while other Trypodendron species used the pheromone (+)-lineatin and suggested that conophthorin was an active kariomone. The fungal transmitting structure of T. betulae was described as a pair of prothoracic tubular mycangia and was similar in structure to that found in other Trypodendron (Abrahamson et al. 1967). The purpose of this paper is to describe the attack pattern on birch and the nature of the beetle's constructed gallery and life history.

Materials and Methods

Collection Sites and *T. betulae* Attacked Host Trees. Trees were sampled at the following locations: 1) Fish Creek, Door Co., Wisconsin. 45° 07' 34" N, 87° 14' 36" W. Twenty-six white birches, *Betula papyrifera* Marshall were sampled in 1982-1985; 2) Alamado Rd., Midland Co. Michigan. 43° 43' 15" N, 84° 31' 28" W. Thirty-two white birches were sampled in 1989-1990; 3) Buelah, Benzie Co., Michigan. 44° 41' 05" N, 86° 06' 55" W. Two yellow birches, *Butela alleghaniensis* Britt. were sampled in 2013; 4) Chippewa Township, Isabella Co., Michigan. 43° 33' 40" N, 84° 37' 12" W. Twelve white birches were sampled in 2014.

Beetle colonized trees were felled between early May and early September during the sampling years at each site and brought to the laboratory for further dissection and study. Tree diameters at breast height were measured, foliage

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characteristics were observed, and the position of the tree within the canopy of the stand was recorded. In early June 1990 two white birches colonized by *T.betulae* in Midland Co. were felled and cut into meter sections. Basal diameters of the two trees were 12.5 cm and 17.3 cm. The circumference at each end of the meter sections was measured and surface area calculated. Each attack entrance hole of *T. betulae* was labeled and counted to determine the density of attack entrance holes per square meter. Distances between entrance holes were also measured to study the spacing pattern of attacks on the surface of the bark. The Clark and Evans (1954) test for nearest neighbor distribution characteristics was used to analyze for uniformity of distribution of the entrance holes.

For all tree sections sampled, two three-inch disks were cut and galleries were exposed using wood chisels. Measurements of galleries were made in millimeters using flexible plastic rulers and life stages of the beetle were recorded. A total of 163 galleries were studied.

Results and Discussion

Geographic Distribution. These collections of *Trypodendron betulae* Swaine represent new county records in Michigan: Isabella Co. and Benzie Co. and a second recorded location from Wisconsin based on Wood (1982), Cognato et al. (2009), and Atkinson (2015).

Nature of Host Tree. Kuhnholz (1994) suggested that T. betulae attacked and colonized healthy birches. A second hypothesis is that the attacked host trees were stressed by sub-canopy shading. The mean (\pm SE) diameter at breast height of attacked sub-canopy birch hosts examined in our study was 17.4 ± 3.7 cm (N = 61) and ranged from 11.6 to 27.2 cm. It was observed that attacks by T. betulae occurred on standing trees with foliage that was yellowed and wilted. Since the collections for this study began in mid–May each year, we cannot determine that the host trees were either previously stressed by shade conditions within the stands or that the earlier attack by T. betulae caused the stressed appearance. If trees lacked foliage, it was assumed that they had been dead more than one year; these were never found to have been actively attacked.

Nature of Attacks on Surface of Bark. When a male-female pair of beetles constructed the gallery system, they initiated boring through the branch scars or lenticels on the bark surface. The female was always found deeper in the gallery system than the male. Typically, the male was found near the entrance hole and appeared to be responsible for the ejection of the boring frass. The diameters of the entrance holes averaged $1.55 \pm .03$ mm (N = 130). The boring frass of T. betulae builds up as a conical mound surrounding the entrance hole. This conical feature of the frass mounds can be used to differentiate attacks by T. betulae from those of Xyloterinus politus (Say) (Coleoptera: Curculionidae: Scolytinae) which can also colonize birches. X. politus produced a cylindrical tube of frass that holds together for about an inch in length extending from the entrance hole. The sawdust-like frass of T. betulae was at first white, but darkened to a light brownish color due to the growth of the beetle's symbiotic fungus that produces a reddish brown pigment.

Leach et al. (1940) and Furniss and Kegley (2006) observed that most of the attack entrance holes of *T. betulae* were found in the basal portion of the tree. While this pattern was generally found in our study, a more uniform distribution of entrance holes was observed on two birches studied over their entire bole length (Table 1).

In the first tree the density of attacks per square meter was found to be relatively constant with 80 to 120 entrance holes per square meter to a height of 5 m. In the second tree the density of entrance holes was not as great and showed a slight variation in the pattern of entrance holes. The highest number

Table 1. Distribution of entrance holes of T. betulae along the length of two standing white birches felled in early June 1990 in Midland Co., Michigan.

Weter	Tr	${ m Tree} \ 1^1$	Tre	${ m Tree}~2^{2}$
section numbered from base	No. of entrance holes per square meter	Mean (± SE) distance between entrance holes (mm)	No. of entrance holes per square meter	Mean (± SE) distance between entrance holes (mm)
1	120	50.0±3.8	24	73.1±6.9
2	117	51.4 ± 4.8	48	51.9 ± 4.8
3	76	63.0±8.9	53	58.2±8.9
4	103	60.5±7.9	37	62.3±7.9
5	80	74.4±9.3	18	74.4±9.3
9	10	190.0 ± 15.8	35	95.5±10.5
7	0	0.0	32	60.7±7.4
∞			21	61.0±8.7
6			27	65.5±7.8
10			15	96.6±10.8
11			12	89.9±10.1
12			21	552.5±0.0
13			0	0.0

 $^{^{1}}$ basal diameter = 12.2 cm. 2 basal diameter = 17.3 cm.

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of attacks was found in the second through the fourth meter sections. The densities of attacks were then relatively constant to the ninth meter height section.

When the distances between entrance holes were measured for each meter section on both trees, it appeared that the beetles were uniformly spacing their entrance holes on the surface of the bole (Table 1). The Clark and Evans (1954) test concluded that the entrance holes were significantly uniformly distributed on the surface of the bark (tree 1: R =1.141, P < 0.005; tree 2: R = 1.165, P < 0.001). This uniform distribution may minimize competition between galleries within the sapwood. We observed only two of 163 galleries of T. betulae fusing within the sapwood.

Entrance Tunnels. The beetles bored an entrance tunnel perpendicular to the surface of the bark and into the sapwood. The mean ($\pm SE$) length of entrance tunnels with developed lateral tunnels was 21.2 ± 0.98 mm and ranged from 7 to 54 mm (N=163). None the constructed tunnels varied up or down in the axis of the bole, and thus they could be easily dissected, exposed and measured.

Lateral Tunnels. Lateral tunnels were bored at right angles from the end of the entrance tunnel. A primary lateral tunnel was bored in one direction and then the beetles returned to the entrance tunnel and constructed a second primary lateral tunnel in the opposite direction. The lateral tunnels did not appear to follow a growth ring of the xylem but tended to curve deeper into the sapwood. In only four galleries was it observed that a lateral tunnel curved back outward towards the bark. The entrance tunnels or lateral tunnels never extended into the heartwood. The primary lateral tunnels originating from the entrance had a mean length of 23.3 ± 0.6 mm and ranged from 4 to 63 mm (N = 222). In 33% of the galleries, along the primary lateral tunnels, the beetles constructed secondary lateral tunnels that curved outward or inwards into the sapwood. These secondary lateral tunnels had a mean length of 16.1 ± 3.5 mm and ranged from 2 to 60 mm (N = 37). All of the newly constructed lateral tunnels were observed to show a darkening from the growth of the beetle's symbiotic fungus assumed to be originating from the female's mycangia.

Larval Cradles and Progeny. As soon as fungal growth was visible on the tunnel walls, the female constructed shallow niches in the upper or lower side of the tunnel of the longitudinal axis of the bole's sapwood. An egg was laid into each niche. These niches were only found in primary and secondary laterals and never in the entrance tunnels. After the eggs hatched the resulting larvae began to enlarge the egg niches into cradles. The larvae ingested both sapwood and fungus, and thus should be considered to be xylomycetophagous. The distance between cradles averaged 3.6 ± 0.5 mm and ranged from 0.5 to 7.4 mm (N=79).

In early to mid-July, full-length larval cradles had been constructed and pupae were observed. The full-length cradles averaged 3.5 ± 0.09 mm in length(N = 122) and were assumed to represent the fully successful development of the progeny. The average width of the cradles was measured to be 1.4 ± 0.05 mm, (N = 117). Eighty—two percent of the cradles (N = 1097 of a total 1337) were fully developed in length based on galleries studied in late July to early August. The average number of fully developed cradles per gallery was 9.7 ± 1.1 (N = 1097) and ranged from 1 to 30 cradles per gallery. The remaining cradles were incomplete in length and lacked progeny, thus indicating larval mortality during some stage of their development. The teneral adults were first observed in mid-July. The sex ratio of males to females in mature galleries after the end of July was approximately one to one (345 males to 327 females).

Dodge (1938) observed that after the beetles had constructed their initial set of primary and secondary lateral tunnels and oviposited in these lateral tunnels, they would return and extend the entrance tunnel deeper into the sapwood. Eventually they would develop a second set of primary laterals which the female would inoculate with fungus and oviposit. In only three galleries after

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late July did we observe this type of behavior. By early September the number of progeny adults began to decrease in the gallery system, suggesting that progeny adults were leaving the gallery system and emerging from the trees. Like other *Trypodendron* species it is assumed that progeny adults overwinter in the litter to fly and attack new hosts during the following spring (Borden 1988).

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