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THE DISTRIBUTION OF SAPERDA INORNATA AND OBEREA SCHAUMII (COLEOPTERA: CERAMBYCIDAE) WITHIN THE CROWNS OF LARGE TREMBLING ASPEN, POPULUS TREMULOIDES 1

John C. Nord² and Fred B. Knight³

The larvae of Saperda inornata Say and Oberea schaumii LeConte inhabit the stems of trembling aspen (Populus tremuloides Michaux) root suckers and the twigs of larger trees. Nord et al. (1972a, 1972b) reported the biologies of these species in Upper Michigan and northern Wisconsin. S. inornata has a one or two year life cycle, probably depending on how early the egg is laid. Most (77.5%) O. schaumii develop in three years while 5.0% require only two years and 17.5% require four years to develop.

Knight (1963) described the distribution of galleries made by S. inornata⁴ and O. schaumii in the crowns of large trembling aspen, P. tremuloides, in Upper Michigan. Similar distribution data were gathered from 180 large trembling aspen felled in a survey designed to determine the relative abundance of S. inornata and O. schaumii in stands of different site quality (Nord and Knight 1972b). The analysis of that distribution data and comparisons with that of Knight (1963) are presented here. Inter- and intra-specific competition in light of the results and other behavioral information are discussed.

METHODS

The location of the study areas and the sampling procedure used were given by Nord and Knight (1972b). Galleries of S. inornata and O. schaumii were recorded by aspect, i.e. northeast, southeast, southwest, or northwest quadrant. All galleries except those found in the top branches, where aspect could not be designated, were included in the analysis of aspect. An analysis of variance was made to test for significant differences in numbers of galleries between aspects.

The galleries were recorded by their position in the crown, i.e. upper half or lower half of the living crown. Only currently active galleries or inactive galleries with egg niches that looked as though they had been made within the past two years for S. inornata and three years for O. schaumii were considered in the analysis of crown level. Old galleries were not considered because many of them located in the lower crown at the time of sampling, were in the upper half of the crown when the eggs were laid and, therefore, the position in the crowns at the time of oviposition could not be accurately ascertained for all. The differences in the number of galleries found in each crown level were analyzed with a t-test.

RESULTS AND DISCUSSION

DISTRIBUTION OF S. INORNATA GALLS WITHIN THE CROWNS

ASPECT.—Table 1 shows the number of S. inornata galls by aspect within the crowns of large trembling aspen. An analysis of the variance showed that there were no significant differences between the number of galls found in each of the four quadrants. Knight (1963) also found no significant differences between aspects.

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³School of Forest Resources, Nutting Hall, University of Maine, Orono, Maine 04473. ⁴Knight (1963) reported the species he studied as S. moesta LeConte. It was later considered to be S. inornata when it became apparent that the separation of S. moesta and S. concolor (=S. inornata) using the shape of the egg niche was untenable (Nord and Knight, 1972a) and reared specimens from P. tremuloides in the same study areas proved to be S. inornata.

Table 1. Total* number of S. inornata galls by aspect in the crowns of 180 large trembling aspen.

Replication						
	(Site)	NE	SE	sw	NW	Sum
1	40	57	51	51	54	213
2	50	39	35	38	29	141
3	60	42	44	35	22	143
Total	_	138	130	124	105	497

^{*}All galleries (old and current) except those in the top branch where aspect was not designated.

Table 2. Current S. inornata galls by crown level in 180 large trembling aspen.

		Crow			
Area	Site	Lower Half	Upper Half	Total	
I	40	16	7	23	
	50	8	12	20	
	60	2	7	9	
II	40	6	8	14	
	50	3	3	6	
	60	2	2	4	
III	40	8		19	
	50	1	4	5	
	60	$\overline{2}$	14	16	
IV	40	1	5	6	
	50	11	7	18	
	60	5	4	9	
Total	_	65	84	149	

CROWN LEVEL.—A t-test showed that there was no significant difference between the number of S. inornata galls found in the lower and upper half of the crown (Table 2). Knight (1963) found no significant differences between crown levels either. Considering these results and that new egg niches were found only in twigs ranging from 5-15 mm in diameter, it is concluded that S. inornata females oviposit in the periphery of the living crown without "preference" to crown level or aspect.

DISTRIBUTION OF O. SCHAUMII GALLERIES WITHIN THE CROWNS

ASPECT.—Table 3 shows the number of *O. schaumii* galleries by aspect within the crowns of large trembling aspen. An analysis of variance showed that there were no significant differences between the number of galleries found in each of the four quadrants. Unlike the results of Knight (1963) there was not a significant higher number of galleries in the south half of the crown.

CROWN LEVEL.—There were over five times as many O. schaumii ovipositions in the upper half of the crown as in the lower half (Table 4). A t-test showed the differences

Table 3. Total* number of O. schaumii galleries by aspect in the crowns of 180 large trembling aspen.

Replication		Aspect				
	(Site)	NE	SE	SW	NW	Sum
1	40	19	19	19	21	78
2	50	10	14	14	15	53
3	60	13	13	15	17	58
Total	_	42	46	48	53	189

^{*}All galleries (old and current) except those in the top branch where aspect was not designated.

Table 4. Current O, schaumii galleries by crown level in 180 large trembling aspen

Area		Crown		
	Site	Lower Half	Upper Half	Total
I	40	4	24	28
	50 60	0 1	13 7	13 8
II	40	1	20	21
	50 60	3 1	8 7	11 8
III	40 50 60	3 1 3	9 7 4	12 8 7
IV	40	2	8	10
	50 60	2 2	5 11	13
Total	_	23	123	146

between the mean number of galleries in each crown level to be highly significant. Knight (1963) found no significant differences between crown levels for total counts of O. schaumii. The inclusion of old galleries may have been the reason for this finding for reasons stated above. The number of currently active galleries found by Knight (1963) was low, but most of them were found in the upper crown.

Considering the results of this analysis and that new egg niches were found only in twigs ranging from 5-13 mm in diameter, it is concluded that O. schaumii females tend to oviposit most often in the periphery of the upper crowns of large trembling aspen.

INTER- AND INTRA-SPECIFIC COMPETITION.—At first it appeared as if S. inornata and O. schaumii occupied very similar ecological niches, i.e. they both lived in the small stems of aspen suckers and in the twigs of larger trees. There was no evidence that one species oviposited more frequently on trees in a physiological state different from those that the other species "selected." In fact they were often found in the same areas and on the same individuals. Therefore, it appeared as though there might be competition for space between the two species, and it could be an important factor in

the population dynamics of the insects. Intra-specific competition was also a possibility. A comparison of life cycles, behavior, distribution of the larvae within the host and other field observations indicated that, although there may be some overlapping of their ecological niches, competition was not important.

Most of the overlap in the ecological niches of S. inornata and O. schaumii seemed to occur during the first year of life for both species, and particularly among larvae living in the sucker stands. In sucker stands, the average age and diameter of oviposition sites was about the same for both species (Table 5). In large trees, although the average age of O. schaumii oviposition sites was about two years younger than that of S. inornata, the average diameter of oviposition sites was about the same for both species. However, O. schaumii oviposted more frequently (84%) in the upper half of the crown than S. inornata (56%). Therefore the overlap of their ecological niches was apparently not as complete in larger trees as it was in sucker stands. O. schaumii may have adapted to upper crown twigs because they grow more rapidly than those in the lower crown, and thus are more apt to be large enough to accommodate the large galleries of the late instars (Nord et al. 1972a).

Table 5. Comparison of the age and diameter of trembling aspen root sucker and tree twig internodes at the time of oviposition by S. inornata and O. schaumii.

	Root Suckers				Tree Twigs			
	Age (yrs.)		Diameter (mm.)		Age (yrs.)		Diameter (mm.)	
Species	Average	Range	Average	Range	Average	Range	Average	Range
S. inornata	3.0	1-5	10	5-15	4.8	1-14	9	5-15
O. schaumii	3.0	1-6	11	5-15	2.7	<1-8	8	5-13

In natural infestations, even in the highly infested patches of aspen and plantings of aspen hybrids, no egg niche (or multiple oviposition, in the case of S. inornata) was found close enough (11-18 cm) to that of the other species to create a competitive situation. Of course the low population levels of both species in relation to the great amount of space available reduced the chance that such competition would occur (Nord and Knight, 1972b). However, the fact that oviposition sites of the two species were never found in close proximity supports the hypothesis that something other than chance was operative in preventing the females from oviposition near each other. Inter-specific competition between first-year larvae may be prevented by a behavioral characteristic of the females when "selecting" an oviposition site.

It was evident that second year larvae of S. inornata and O. schaumii did not have to compete with newly hatched larvae of the same species or of the other species. New egg niche sites of both species tended to be farther out on the twig or stem than year-old egg niche sites probably because the latter had grown too large in diameter for oviposition during the intervening year. Twigs and stems containing third-year larvae of O. schaumii were even larger and thus farther removed from new egg niche sites. Furthermore, O. schaumii always extended its gallery downward into a section of larger diameter, thus the likelihood was small that a female of either species would oviposit during the succeeding year over a vulnerable portion of the O. schaumii gallery. It could be stated in another way: eggs of either species were not likely to be laid in a place where the newly-hatching larvae would have to compete with a mid- to late instar O. schaumii larva. Not infrequently an O. schaumii egg niche was made on the upper surface of a side twig within about five cm of the sucker stem. In that case the larva bored down the twig and into the stem which was usually much too large for new ovipositions.

Competition between offspring of the same female was prevented by the tendency of females to move to another sucker or branch after oviposition (Nord, et al. 1972a, 1972b). The low populations of both species, which were apparent during this study, and

the seemingly random movement of females throughout a stand reduced the chance of competition between offspring of different females of the same species. Competition between S. inornata larvae in a multiple oviposition is possible and some evidence of that was reported by Grimble and Knight (1970). The peripheral gallery of one larva often passed under the adjoining egg niches; but whether or not there was a live individual or gallery there before that happened could not be determined because the evidence was obliterated by the invading larva.

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BOOK REVIEW

NOCTUIDAE OF NORTH AMERICA, by Augustus R. Grote. E. W. Classey Limited, London, 1971. 85 pages with 4 coloured plates. Price U.S. \$16.95, (£7, 2s. sterling) plus postage, handling and applicable sales taxes. Distributed in North America by Entomological Reprint Specialists, P.O. Box 77971, Dockweiler Station, Los Angeles, California, 90007.

Seeing the appearance of this desirable reprint of "Noctuidae of North America" by Augustus R. Grote is like finding a long-lost friend on a country collecting trip. It is full of valuable lore relating to the pursuit and description of many new noctuid species of yesteryear. The four coloured plates depicting 45 species are reproduced with remarkable fidelity when compared with the originals. The pages of descriptive notes dealing with the Walker types of North American Noctuidae contained in the British Museum readily portray the keen competition coupled with criticism that was rampant with professional entomologists of that era. The feature entitled "A Colony of Butterflies," to the memory of Thomas Say, points up the authors deep concern for the preservation of certain scarce species at that early date. A foreword was added to this reprinted edition. It is an excellent and most thorough biography of Grote by Ronald S. Wilkinson. Perhaps its greatest asset is that Dr. Wilkinson cites the reference used in compiling the biography, a practice which others should emulate. This reprint will serve as a treasured historic documentation to all students of lepidoptera, besides being a valuable addition to all entomological libraries.

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