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ASPECTS OF THE FEEDING BEHAVIOR OF *SCOLYTUS*
MULTISTRATUS (MARSHAM) (SCOLYTIDAE: COLEOPTERA)
AND IMPLICATIONS FOR CONTROL¹

H. Riedl and J. W. Butcher²

Successful protection of elm trees can only be accomplished by means of thorough understanding of the feeding behavior of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham). Wolfenbarger and Buchanan (1939) and Whitten (1958) noted that most feeding occurred in the outer portion of the upper crown region, but offered no quantitative data. Therefore, this study was initiated to investigate the regional distribution of feeding injuries along a vertical and horizontal gradient in native American elm, *Ulmus americana* L.

Another objective of this study concerned a detailed analysis of feeding scars in order to correlate specific physical characteristics of twig crotches with feeding injuries. Chemical aspects of feeding stimulation have received considerable attention (Baker and Norris, 1967), but the importance of physical characteristics of the twig crotch of the feeding process was not fully researched. Information of this kind could be valuable in the selection of elms with twig crotch characteristics which would not induce feeding attack. However, as Heybroek (1969) pointed out, an elm resistant to feeding by *multistriatus* could still be attacked by other vectors.

MATERIALS AND METHODS

Six elm trees henceforth designated A to F were sampled at three height levels: 5, 10 and 15 meters. The elms were park trees and had not been sprayed at any time during the previous five years. In this respect the natural feeding pattern was not disturbed. Tree height ranged from 15 to 18 meters. Random samples of 50-70 twig crotches were taken from five points in each height level (from four compass points and the interior of the crown). A light-weight aluminum pole pruner, extendable to 16 m was used to sample elm twigs. The total number of twig crotches and the number of feeding injuries were recorded from each sample. The number of scars in places other than twig crotches (mainly in leaf axils) was not included in the figure for total attack. The average feeding attack for each height level was computed from the percentage feeding at the five sample points (Table 1). Also, the position of the sample branches at the three height levels was recorded as: (a) pointing upwards, (b) projecting horizontally, and (c) pointing downwards.

For a study of feeding preference for vertical quarters, each sample tree was subdivided into five sections: N (north), S (south), E (east), W (west), and C (center). In order to demonstrate the consistency of the horizontal feeding pattern over the three height levels, the twig-crotch injury data for each tree was subjected to Friedman's ANOVA according to rank (Siegel, 1956, p. 166). Tree A was deleted from this analysis because of the low attack rate at all levels.

In order to study the association of certain morphological features of twig crotches to feeding, 300 samples from tree B and 400 samples from tree D were analyzed. The following characteristics were recorded:

1. Angle between the two lateral members of crotch. This was measured by placing the twig crotch on polar coordinate graph paper (accurate to 5°).
2. Crotch base: either rounded or acute (Fig. 1).
3. Injuries by vector feeding.
4. Position of feeding scar; either lateral or central (Fig. 1).

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Table 1. Feeding attack in three height levels of six mature elm trees.

Tree		Height level (m)		
		5	10	15
A	a)	0	2.9 ± 1.3	4.5 ± 1.5
	b)	0	0	0
B	a)	9.3 ± 1.4	34.8 ± 4.8	62.1 ± 5.7
	b)	0	0	0
C	a)	24.0 ± 7.8	84.2 ± 1.8	92.6 ± 2.3
	b)	0	11	32
D	a)	17.8 ± 4.2	81.7 ± 9.2	83.0 ± 9.6
	b)	0	0	6
E	a)	27.2 ± 8.9	65.2 ± 14.0	81.7 ± 5.1
	b)	0	6	3
F	a)	0.4 ± 0.4	27.8 ± 6.6	63.0 ± 9.0
	b)	0	3	0

a) Average per cent attack, ± SE.
 b) Total no. attacked leaf axils.

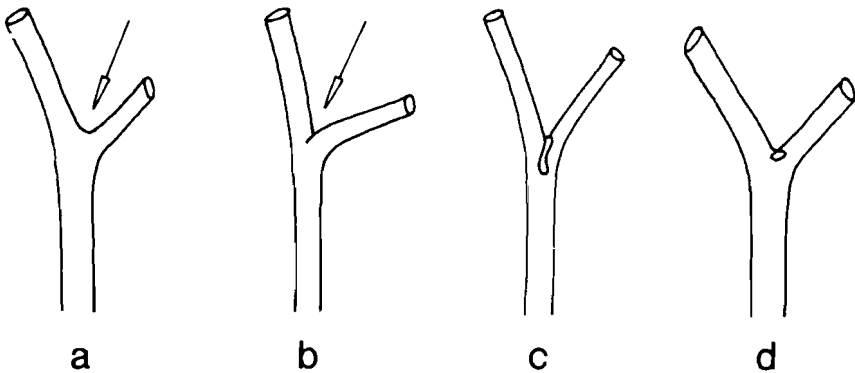


Fig. 1. Type of twig crotch base: (a) rounded, (b) acute and type of feeding: (c) lateral, (d) central.

Several t-tests were performed on the angle data of attacked and unattacked twig crotches to test if *multistriatus* had a preference for twig crotches with certain angles. No t-value was calculated for tree B at the lowest height level because the numbers of attacked crotches was too small.

Combinations of type of twig crotch base and type of feeding were tested for their independence in a 2 × 2 contingency table. The combinations were round-lateral, round-central, acute-lateral and acute-central.

RESULTS AND DISCUSSION

REGIONAL DISTRIBUTION OF FEEDING INJURIES ALONG A VERTICAL GRADIENT.— The relationship between height level and amount of feeding (Table 1) appeared to be linear for low and high vector pressure (Fig. 2). It appears that as most available twig crotches in the top level become attacked, newly arriving vectors have difficulty finding suitable feeding sites and move down into the middle level of the crown region. This explains the departure from the linear relationship between elevation and feeding in trees C and D.

In trees where the attack rate exceeded 80%, the beetle vectors occasionally resorted to feeding in leaf axils. This was especially noticeable on trees C, D, and E, but feeding wounds of this kind were also present on tree F where the average attack at height level 2 was lower (27.8%). The importance of feeding in leaf axils with regard to effective disease transmission is not known. Twig crotches were sometimes attacked more than once, particularly in samples with a great number of feeding injuries.

The amount of feeding was not correlated with branch position. Location of the feeding wound, in respect to upper or bottom side of the twig showed no pattern regardless of the position of the branch. Morphological variation of twig characteristics among the six sampled elms was considerable. Some elms had long slender twigs which were very flexible. These also had few crotches (tree E and F) while others had many crotches and were more sturdy in appearance.

REGIONAL DISTRIBUTION OF FEEDING INJURIES ALONG A HORIZONTAL GRADIENT.—Using Friedman's ANOVA by rank only trees B and E had greater differences in feeding attack between the five sample points consistently over all three height levels (Table 2). In tree B the percentage of feeding injuries was lowest in the S sector, but considerably higher in the N and E sectors. Tree E had the least feeding in the W sector and the highest number of injuries in the E sector.

Initially it was suspected that the central sector at the lower height levels 2 and 3 would be the region with the fewest number of feeding scars, because of a reported

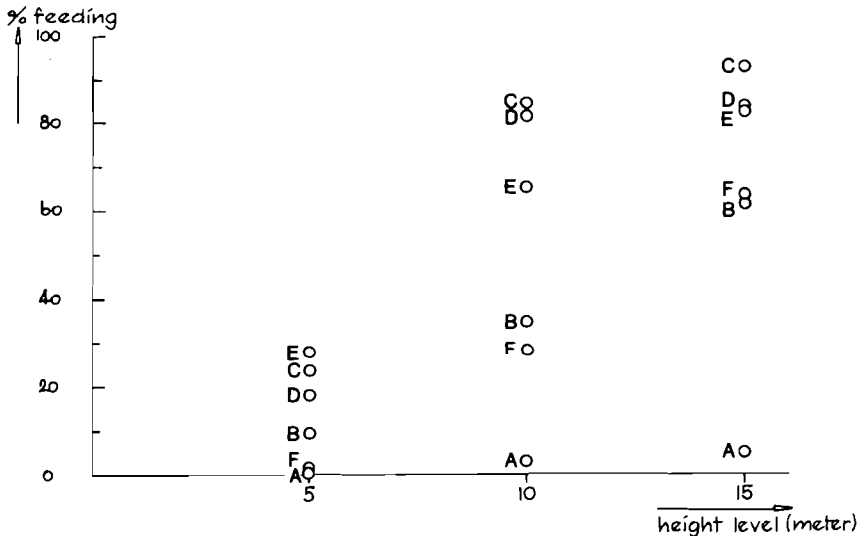


Fig. 2. Relationship between feeding by *S. multistriatus* and height level on six untreated elms (A to F).

Table 2. Comparison of feeding attack in four cardinal quarters and center section of elm trees using Friedman's ANOVA.

Tree	X_r^2	Significance	Highest feeding in quarter of tree
B	7.47	0.20	N, E
C	3.67	n.s.	—
D	3.00	n.s.	—
E	7.47	0.20	E
F	6.50	0.20	—

$X_r^2 = 7.78$ ($\alpha = 0.10$, $df = 4$)
 $X_r^2 = 5.99$ ($\alpha = 0.20$, $df = 4$)

vector preference for the periphery of the crown (Wolfenbarger and Buchanan, 1939). However, this was not the case in this study.

Uneven distribution of feeding wounds in the 5 vertical sections of the tree (N, S, E, W, C) was probably not the result of preferential feeding in any one of the five regions. Rather, the proximity of a beetle-producing elm tree to a particular quarter of the above sample trees might have caused this difference in attack.

The question of a possible difference in the overall feeding pattern on elm trees in a closed stand and on road-side elms was also raised. Sample trees A, B, C and D were in closed stands, together with other tree species, while trees E and F were part of a road-side planting. The vertical and horizontal distribution of feeding injuries in these two groups of trees did not seem to be different. However, both road-side elms showed differences in the number of feeding injuries in the five sectors of the tree. Whether this is a general trend among road-side trees can only be speculated upon since the sample was too small. These findings suggest that the whole upper tree region requires particular attention during spraying operations. Differential hazard regions for fungus infection must be considered as well. Fungal infections originating from feeding wounds in the lower part of an elm tree are more likely to cause quicker mortality because of the shorter distance the fungus has to travel to the main trunk (Zentmyer *et al.*, 1946). As a consequence, spray application methods should be judged in respect to their performance on the whole tree.

ASSOCIATION OF PHYSICAL TWIG CROTCH CHARACTERISTICS WITH FEEDING.—No relation was observed between crotch angle and feeding (Table 3). Of interest is the fact that the angle means of the height level samples for tree B, with 87.3°, 83.0° and 84.5° were considerably higher than the means for tree D, with 64.6°, 66.8° and 69.1°. The great difference in angle means between these two trees is an example of the morphological variability one can find among elm trees.

Ouelette (1962) noted that lateral feeding resulted in a higher infection rate than did central feeding. Presumably during lateral feeding the beetle vector with the spores attached to its body exterior establishes better contact with the conductive tissue.

The contingency table (Table 4) suggested that twig crotches with a rounded base are more likely to induce lateral rather than central feeding responses. Therefore, the probability of fungal infection is higher on trees with a greater proportion of twig crotches with a rounded base because of the preferred lateral type of feeding.

SUMMARY

Extensive sampling of untreated elm trees revealed that *Scolytus multistriatus* feed preferentially in the whole upper tree region. Feeding attack rate increased linearly from the bottom to the top. This behavior must be considered for the proper choice and evaluation of a spray application method in order to achieve maximum protection. Differences in attack in vertical sections of a tree were observed but were believed to be more directly related to the close proximity of a beetle-producing tree than to a particular

Table 3. T-comparisons of angle means of attacked and unattacked twig crotches.

Tree	Height level (m)		n	Mean angle	s _x	t _{calc}
	Att.	Unatt.				
B	5	Att.	5	85.0	3.16	not calc
		Unatt.	95	87.3	.85	
	10	Att.	32	84.1	2.63	.575
		Unatt.	68	82.4	1.50	
	15	Att.	32	81.7	3.12	1.11
		Unatt.	68	85.7	2.01	
D	5	Att.	18	63.9	2.72	.299
		Unatt.	82	64.7	1.28	
	10	Att.	120	66.5	.94	.364
		Unatt.	30	67.3	2.15	
	15	Att.	118	68.5	1.04	1.277
		Unatt.	32	71.4	2.01	

t = 1.980 (a = .05, df = 98)

t = 1.960 (a = .05, df = 148)

Table 4. Association between type of feeding and type of twig crotch base.

Type of feeding	Twig crotch base		Total
	Round	Acute	
Lateral	124	60	184
Central	83	72	155
Total	207	132	399

X² calc = 6.78

X² tab = 3.84

(a = 0.05, df = 1)

quarter of a sample tree. Several physical twig crotch characteristics were investigated with respect to their association with vector feeding. The size of the angle between the main and lateral member of a twig crotch had no influence on feeding. However, there was a significant relation between a more rounded twig crotch base and lateral feeding. Lateral feeding reportedly results in more successful inoculations than does central feeding. These findings pointed out a possible resistance mechanism against feeding by *multistriatus*.

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