Hemlock Woolly Adelgid (Homoptera: Adelgidae): Stylet Bundle Insertion and Feeding Sites

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ABSTRACT Stylet bundle insertion site, path traveled, and feeding site were examined for the hemlock woolly adelgid, *Adelges tsugae* Annand, on needles from current and previous years of eastern hemlock, *Tsuga canadensis* Carriere. The stylet bundle is composed of 4 individual stylets—2 outer mandibular stylets and 2 inner maxillary stylets. *A. tsugae* inserts its stylet bundle on the adaxial side of eastern hemlock needles, proximal to the twig with respect to the leaf abscission layer. Insertions are primarily intracellular through epidermal cells. Once inserted, the stylet bundle then follows a mixed intracellular and intercellular pathway, the latter predominating, when penetrating the plant tissue to the feeding site, the xylem ray parenchyma cells. We observed evidence of salivary secretions, tracks, and sheaths produced by *A. tsugae* in the plant similar to those produced by aphids and other adelgids in their host plants. Unlike other adelgids studied, which feed on cortical parenchyma cells and on solutes from phloem of their spruce hosts, *A. tsugae* appears to feed only on storage cells, the parenchyma cells which comprise the xylem rays. This suggests that the intense effect of *A. tsugae* on eastern hemlock may be caused by factors other than its food consumption, that is, a possible toxin effect, or altered host plant response to environmental conditions.

KEY WORDS *Adelges tsugae*, hemlock woolly adelgid, stylet bundle

THE HEMLOCK WOOLLY adelgid, *Adelges tsugae* Annand, is thought to be native to Japan (McClure 1992a). It was first found in North America in British Columbia in 1924 (Annand 1924) and later in Oregon in 1928 (Annand 1928). On the West Coast it now occurs from northern California to southern Alaska and on the east coast from Virginia to Massachusetts. Its effect on western hemlock, *Tsuga heterophylla* Sargent, has not been great (McClure 1989), but damage to eastern hemlock, *T. canadensis* Carriere, has been extensive (McClure 1992a, Paca 1993). Infested eastern hemlocks often die within 4 yr (McClure 1991).

The life cycle of *A. tsugae* has been documented by McClure (1987, 1989, 1991, 1992a). It has 2 parthenogenetic generations on hemlock per year, the 1st hatching in May and the 2nd in late June. In addition, during the 2nd generation, a migratory form develops that disperses to spruce (*Picea* spp.), but there is no evidence of its survival on this host (McClure 1989). For many adelgid species, spruce is the primary host plant and other conifers serve as secondary hosts (Carter 1971, Rohfritsch 1990). In the case of *A. tsugae*, a suitable spruce host may not exist.

Little is known about how *A. tsugae* feeds on and kills its host plant. Studies to date have concentrated on the life cycle, dispersal, ecology, and chemical control of the insect (McClure 1987, 1990, 1991, 1992a, b; Paca 1993). The objectives of our study were to determine the method and site of stylet bundle insertion in the plant, to describe the path taken by the stylets through the plant tissue, and to observe on what tissues the adelgid feeds. We also wanted to determine if *A. tsugae* produces saliva in the plant as McClure (1991) suggested.

Materials and Methods

At 2-wk intervals from late May to late July 1993, twigs of adelgid-infested current year growth and previous year growth were removed from a *T. canadensis* tree on the grounds of the U.S. Forest Service Northeastern Forest Experiment Station in Hamden, CT. At each time interval, twigs were clipped from each of 4 quadrants on the tree, and at heights ranging from ground level to ≈2.5 m. Samples taken between 19 May and 2 June, when current year needles were available and when the 1st generation of adelgids had just established, were compared with samples taken between 14

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July and 30 July, when the 2nd generation of adelgids had established and been feeding for a month. For convenience, the former period is termed early summer and the latter is termed late summer.

In addition, healthy potted *T. canadensis* seedlings were infested with *A. tsugae* by clipping branches from naturally infested eastern hemlocks and placing them on the potted trees during the period when crawlers were active. Twigs were clipped from 6 potted trees during the early summer period and compared with twigs taken from the naturally infested *T. canadensis*.

For scanning electron microscopy (SEM), all plant and insect material was immediately fixed in 3% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.0, postfixed in 2% osmium tetroxide in the same buffer, and dehydrated with ethanol. Specimens were critical point dried, mounted, coated with gold in a sputter coater, and examined with an ETEC Autoscan scanning electron microscope (ETEC, Hayward, CA) at an accelerating voltage of 20 kV.

Stylet insertion sites were determined by examining both fresh and formol-acetic-alcohol fixed material with a stereo microscope. The distance between the insertion site and the abscission layer of the needle was measured, and whether the site was proximal or distal to the abscission layer was recorded. The length of the stylet remaining outside the plant tissues was measured. The body length of all insects also was measured but no attempt was made to differentiate among instars. *t*-Tests were performed to determine significant differences ($P < 0.05$) among samples.

For light microscopy, samples were trimmed and fixed in-formol-acetic-alcohol, dehydrated through a tertiary-butyl alcohol series, and embedded in Paraplast-Plus (Oxford Labware, St. Louis, MO). Specimens were serially sectioned, both transversely and longitudinally, at 5–10 μm. Sections were routinely stained with Safranin O and counterstained either with Fast Green or with Auramine O and Methylene Blue (Berlyn and Miksche 1976). Some sections were stained with napthol yellow-S to test for the presence of protein in the saliva (Berlyn and Miksche 1976).

To examine the morphology of the stylets, adelgids were gently teased off the plant stems with insect pins and fine brushes, then fixed and processed for SEM. The length of the stylet bundle was measured on live adelgids of 3 life stages—established crawlers, nymphs, and adults. Adelgids were teased off the plant and their stylet bundles were measured immediately under a stereo microscope equipped with an ocular micrometer. Insects were then mounted and examined with a light microscope at 400× to ensure that only intact stylets were included in the data set.

Voucher specimens have been deposited in the collection of the Systematic Entomology Laboratory, USDA–ARS, Beltsville, MD.

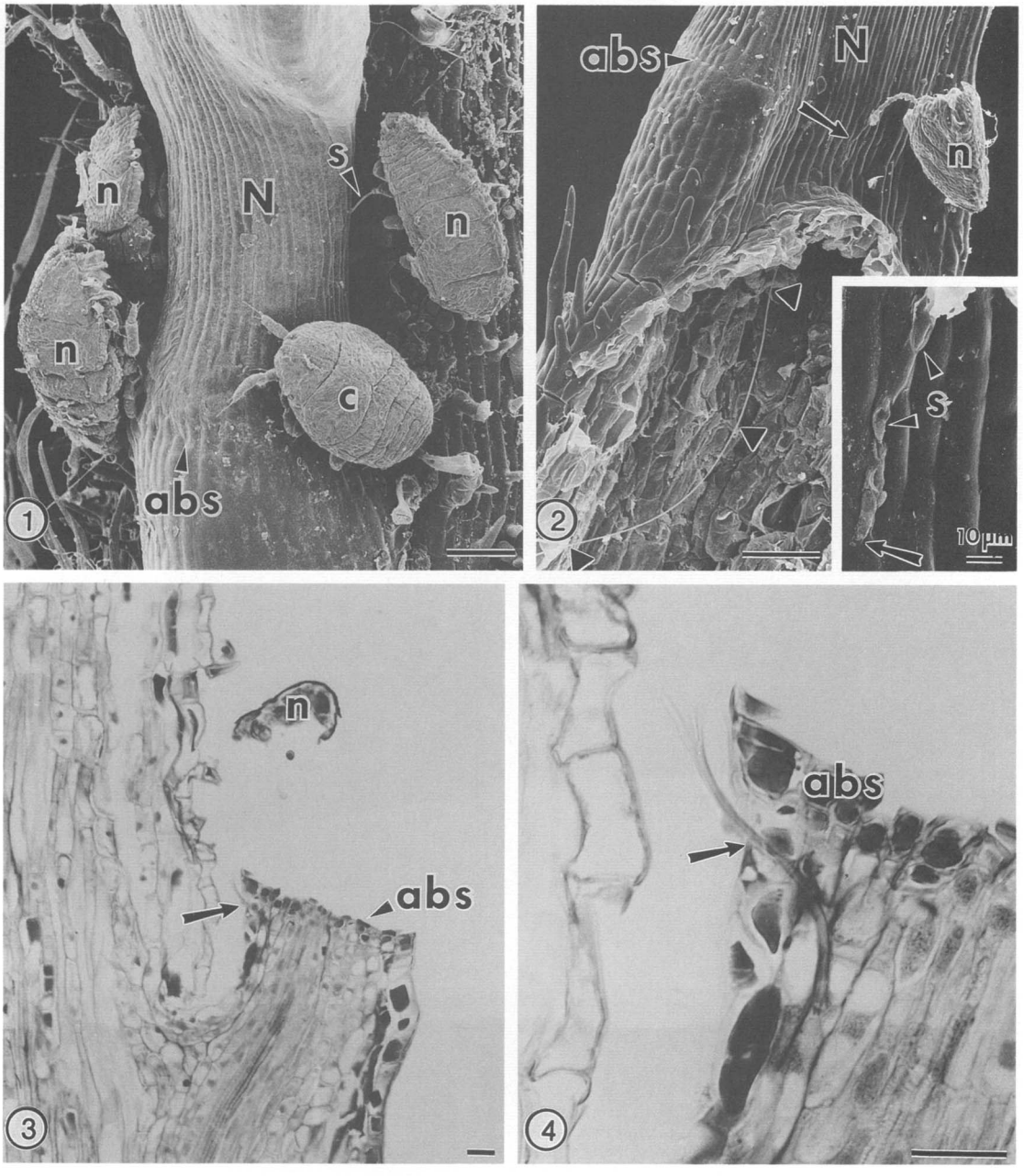
Results

All observations of adelgid establishment, stylet bundle insertion, and initial pathway were similar for all trees. However, too few adelgids became established on the potted trees to permit extensive sampling, and observations reported here are limited to the naturally infested tree.

Establishment and Stylet Bundle Insertion. Fig. 1 shows a mobile crawler and nymphs of the early summer generation at the base of a hemlock needle. Insects settled at the base of needles on new twig growth, typically with 1 crawler per needle. As eggs continued to hatch, some of the new crawlers established at the base of the needles where other adelgids already were feeding. After the early summer generation had established, there generally were 1–2 adelgids on each side of the petiole of each needle. When the late summer generation had settled, we observed as many as 3 nymphs on each side of a needle petiole, suggesting an increase in the population.

Adelgids were located distal to the abscission layer of the needle (Figs. 1–4), but the actual site of stylet bundle insertion was some distance away. The insertion site was almost always proximal to the abscission layer, on the adaxial side of the needle, closest to the xylem of the vascular bundle (Fig. 2). None of the 76 adelgids examined on previous year needles had its stylets inserted distal to the abscission layer; only 10 of 77 adelgids (13%) examined on current year needles had inserted their stylets distal to the abscission layer. The entire length of the stylet was not inserted into the needle, and there was no difference in the length of the portion remaining outside of the plant in current year needles (0.183 ± 0.065 mm; $n = 77$) and previous year needles (0.162 ± 0.065 mm; $n = 76$; $P = 0.061$). However, there was a significant difference between the distance of the insertion site from the abscission layer in current year needles (0.059 ± 0.088 mm) and in previous year needles (0.103 ± 0.067 mm; $P < 0.001$). There was also a significant difference between the body length of nymphs established on current year needles (0.322 ± 0.017 mm) and previous year needles (0.347 ± 0.044 mm; $P < 0.001$), perhaps reflecting a difference in instars.

Histological studies indicated that stylet bundle insertion was almost always intracellular through the epidermal cells, near the center of the adaxial side of the needle and proximal to the abscission layer, but distal to the juncture of needle and stem tissues (Figs. 3–5). Of the 44 insertions observed (both cross sections and longitudinal sections), 41 were intracellular and 3 were intercellular. At insertion, the stylet bundle sometimes traveled between the cell walls of the epidermal cells before actually penetrating the cell interior (Fig. 2, inset). Stereo microscope observations indicated that the adelgids always inserted their stylets into the needle petiole distal to the point of



Figs. 1–4. Establishment and stylet bundle insertion. (1) crawler and nymphs of the early summer generation of *A. tsugae* on current year needles of eastern hemlock. (2) Nymph with stylet bundle inserted on the adaxial side of a needle, proximal to the stem with respect to the leaf abscission layer; the needle was pulled off a stem to expose the stylet insertion site (arrow); arrow heads point to stylet bundle; inset, stylet insertion site showing stylet bundle penetrating and traveling within the cuticle of the plant (arrow heads) before actually penetrating the plant cells (arrow). (3) Insertion site of stylet bundle (arrow) below abscission layer, showing nymph position on the needle and the actual site of stylet insertion. (4) Higher magnification of insertion site showing intracellular penetration of an epidermal cell (arrow). abs, abscission layer; c, crawler; n, nymph; N, needle; s, stylet bundle. Scale, 100 μm.

attachment to the stem, but in histological sections where 2 or more adelgids were feeding on the same needle, insertions proximal to this attachment site sometimes were observed. This region contains a vascular bundle with secondary xylem and rays consisting predominately of ray parenchyma, although marginal ray tracheids may also be present (Fig. 5).

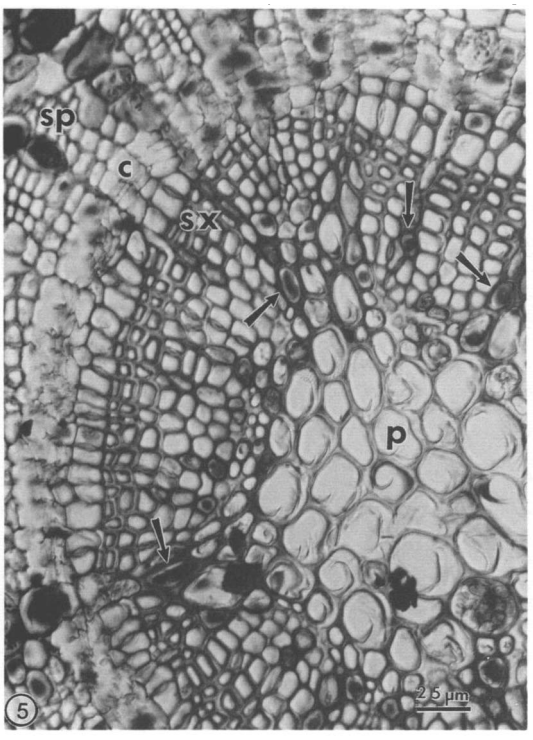


Fig. 5. Cross section of the base of previous year hemlock needle proximal to its abscission zone showing (centripetally) pith, secondary xylem with numerous rays (arrows), a cambial zone with several rows of differentiating cells, and considerable secondary phloem with radial rows of sieve cells. p, pith; sx, secondary xylem; c, cambial zone; sp, secondary phloem.

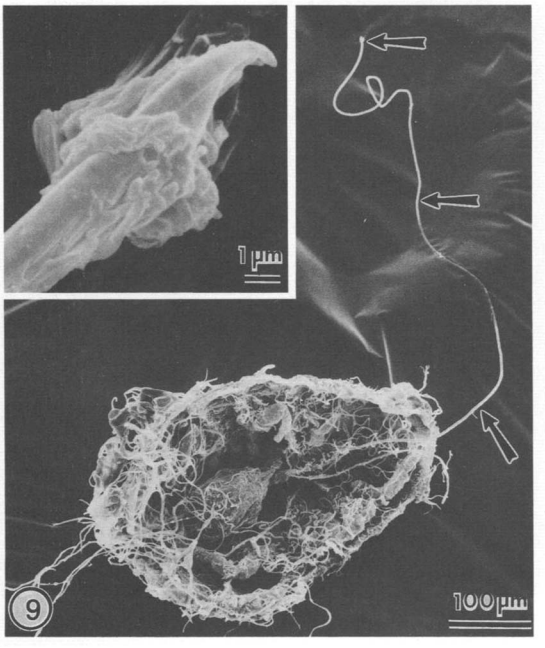
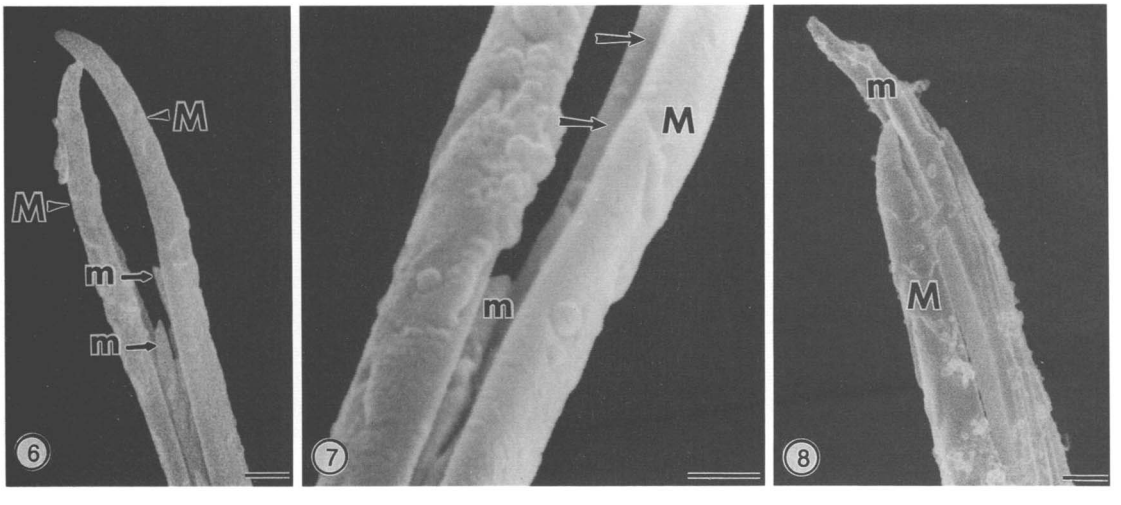
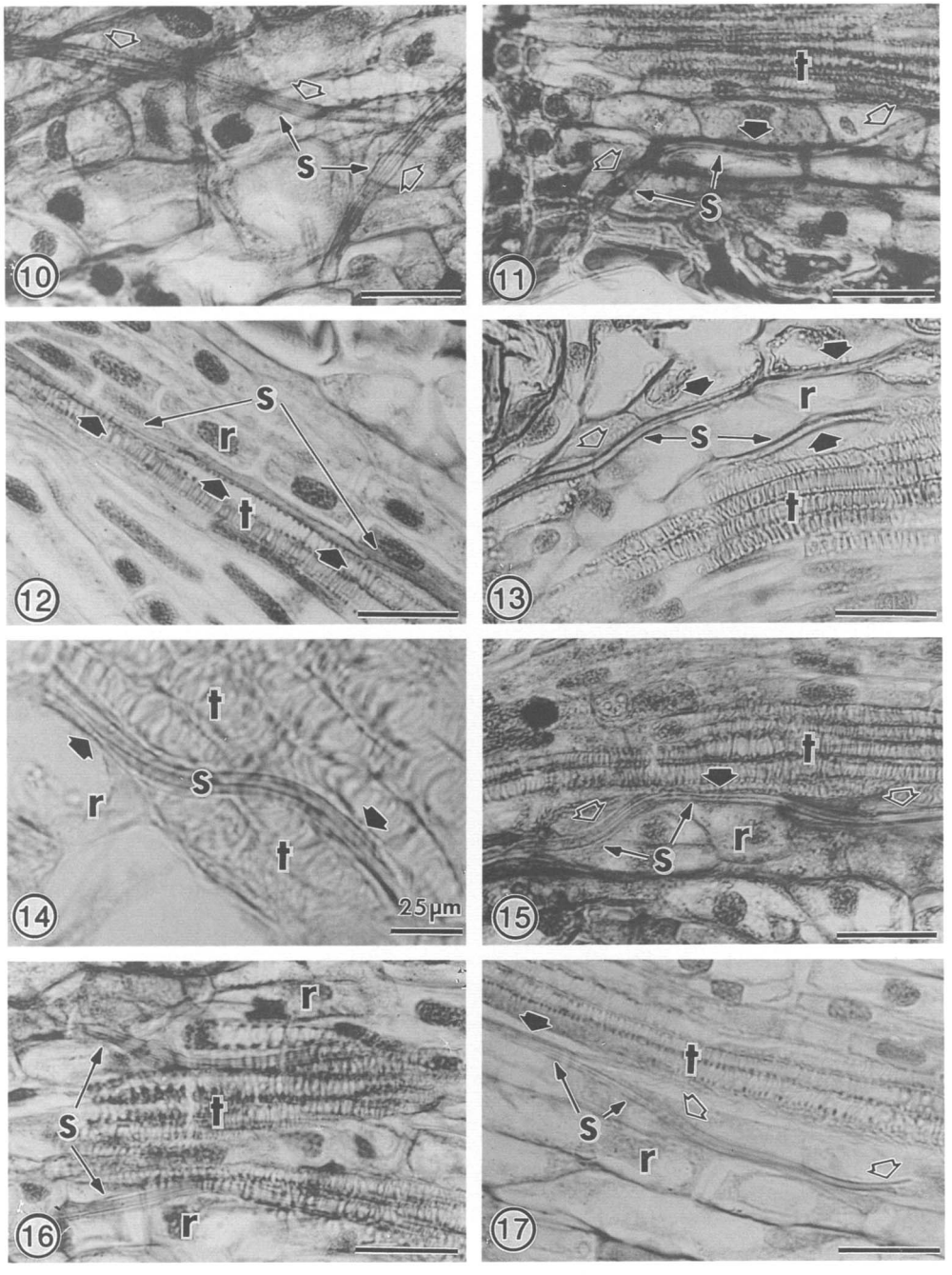


Fig. 9. Exuviae of *A. tsugae* showing molted stylet bundle cuticle (arrows); inset shows tip of molted stylet bundle.

Stylet Bundle Structure. The hemlock woolly adelgid stylet bundle is composed of 4 stylets, 2 outer mandibular stylets and 2 inner maxillary stylets (Fig. 6). The mandibular stylets have deep grooves in which the maxillary stylets lie (Fig. 7); these maxillary stylets can be extended from and retracted within the mandibular stylets (Fig. 8). The maxillary stylets are grooved, but SEM micrographs did not indicate the presence of separate



Figs. 6–8. Stylet bundle structure. (6) Tip of stylet bundle showing 2 outer mandibular stylets with 2 inner maxillary stylets retracted. (7) Groove in mandibular stylets (arrows) in which maxillary stylets lay. (8) Tip of stylet bundle with maxillary stylets extended. M, mandibular stylets; m, maxillary stylets. Scale, 1.0 μm.



Figs. 10–17. Stylet bundle path. (10) Predominantly intracellular initial path of stylet bundles. (11) Mixed intracellular and intercellular initial path. (12) Intercellular travel between tracheids and xylem ray parenchyma cells. (13) Two stylet bundles in plant, 1 penetrating ray parenchyma cells both intracellularly and intercellularly, and one traveling intercellularly between tracheids and rays. (14) Intercellular travel both between tracheids and ray parenchyma cells and between tracheids and tracheids. (15) Stylet bundle following vascular bundle with both intracellular and intercellular penetrations. (16) Two stylets following tracheids on opposite sides of vascular bundle. (17) Stylet bundle traveling intracellularly through a xylem ray parenchyma cell toward end of path. r, xylem ray parenchyma cell, s, stylet bundle, t, tracheid. Open arrow head indicates intracellular penetration; closed arrow head indicates intercellular penetration. Scale, 100 μm.

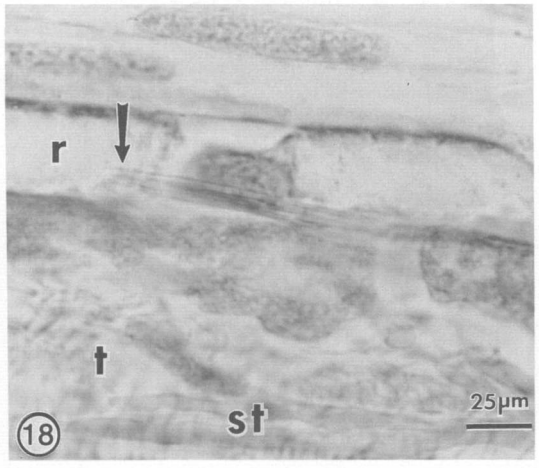


Fig. 18. Stylet bundle ending intracellularly in xylem ray parenchyma cell (arrow). r, xylem ray parenchyma cell; st, salivary tracks; t, tracheid.

food and salivary canals. At each molt, the stylet bundle was retracted from the plant and stylet cuticle shed, as both stereo microscope observations and SEM data showed (Fig. 9). We found no instances of isolated stylets or stylet cuticle within plant tissues. Exuviae were found only in the immediate proximity of established nymphs, where 1 or more exuviae, with stylet bundle cuticle attached, often were attached to the waxy secretions.

Mean stylet lengths and stylet length to body ratios were as follows: established crawlers, 1.04 ± 0.04 mm and 3.25 (n = 14); established nymphs, 1.11 ± 0.06 mm and 3.17 (n = 20); established adults, 1.27 ± 0.06 mm, and 1.15 (n = 10).

Stylet Bundle Path. The entire stylet path, from the point of insertion to the actual feeding site, was both intracellular and intercellular (Figs. 10–17). The initial short path from the insertion site to the vascular bundle was predominantly intracellular (Fig. 10). We did observe some examples, however, of mixed intracellular and intercellular initial pathways (Fig. 11). Once the stylet bundle had reached the vascular tissue, it followed a predominantly intercellular path along the vascular bundle in the xylem, generally between tracheids and ray parenchyma cells proximal to the center of the stem (Fig. 12). Stylet bundles also were observed between ray parenchyma cells (Fig. 13), between tracheids (Fig. 14), or following a combination of paths (Fig. 15). When 2 insects fed on the same petiole, 1 stylet bundle often followed the tracheids proximal to the stem axis while the other followed the tracheids distally, then later crossed the tracheids to feed on the ray parenchyma cells. In some cases, 2 stylet bundles traveled proximal to the stem axis but followed the tracheids on opposite sides of the vascular bundle (Fig. 16). At the end of the path, the stylet bundle often traveled intracellularly through 1 or several xylem ray parenchyma cells to its final feeding site (Fig. 17). Insects feeding on current year growth that was collected in early summer appeared to exhibit the greatest variation and the least directness in the path traveled by their stylets.

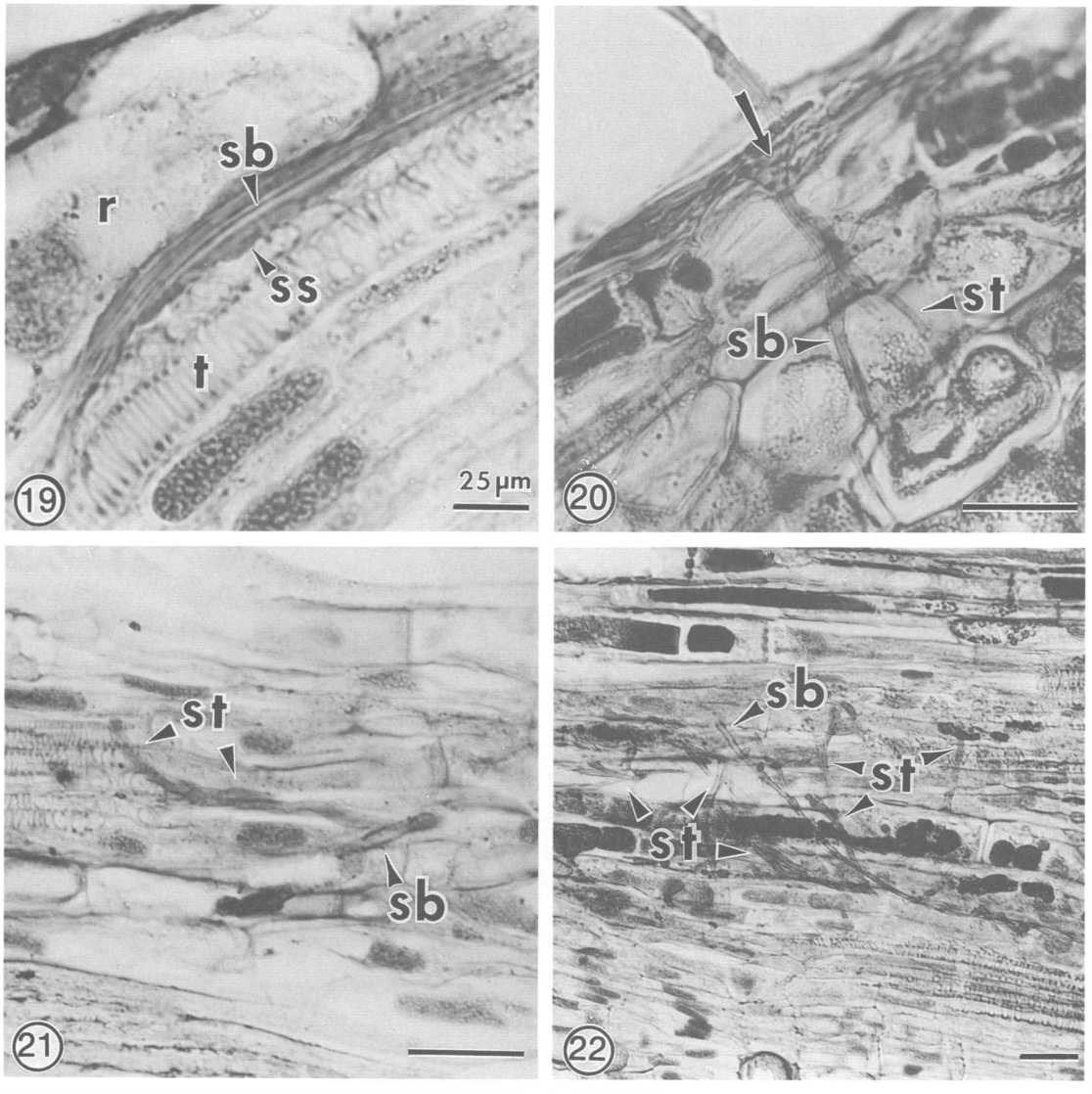
Stylet Bundle Destination. The tips of stylet bundles were difficult to discriminate in cross sections. Although the exact endpoint of the stylets could not always be determined, most appeared to end in xylem ray tissue (16 of 18). From longitudinal sections, where the endpoints of stylets could readily be observed, we determined that 21 out of 24 stylets ended intracellularly in xylem ray parenchyma cells (Fig. 18). Of the remaining 3 stylets observed, 1 appeared to terminate intercellularly between a tracheid and a ray, 1 ended intracellularly in a cortical parenchyma cell, and 1 ended intracellularly in a phloem ray cell.

Salivary Secretions. In all samples, we observed evidence of salivary tracks and sheaths similar to those produced by other aphid and adelgid species (Pollard 1973, Rohfritsch 1990, Bing et al. 1991) (Figs. 19–22). These tracks and sheaths stained red with Safranin O. Saliva stained yellow with Napthol yellow-S, indicating the presence of protein.

The salivary sheath varied in thickness along its path (Fig. 19); it was usually very thin until it approached the feeding site, where it appeared thicker and darker. Salivary tracks were most evident near the feeding site, where they were often dark red and globular. Tracks were sometimes present near the insertion site (Fig. 20), although these usually did not stain as intensely as those near the feeding site. Tracks were much more numerous in previous year growth collected in early or late summer and in current year growth collected in late summer than in current year growth collected in early summer (Figs. 21–22). The incidence of salivary tracks within the plant probably reflected a developing population of adelgids. In early summer, current year growth had tracks only from the developing 1st generation, whereas in late summer, current year growth had tracks from all the instars of the 1st generation, plus tracks from the developing 2nd generation.

Discussion

Adelgids tend to have much greater stylet length to body length ratios than do aphids (Rohfritsch 1990). Stylet bundle lengths of nymphs of *A. piceae* may be up to 5 times the body length, but there is no successive increase in stylet length concurrent with increase in body length (Balch 1952 in Pollard 1973). In this study, the hemlock woolly adelgid, too, shows no significant increase in stylet length proportionate to increases in body length. The length of adelgid stylets may be adapted not just to their feeding biology but also to a need for anchorage on the stems on which they feed (Pollard 1973).



Figs. 19–22. Salivary secretions. (19) Stylet bundle located intercellularly between tracheids and rays with salivary sheath visible. (20) Intracellular insertion (arrow) of stylet bundle with salivary track visible. (21) Salivary track near feeding site in current year growth, sampled in early summer. (22) Salivary tracks near feeding site in current year growth, sampled in late summer. sb, stylet bundle; ss, salivary sheath; st, salivary track; r, xylem ray parenchyma cell; t, tracheid. Scale, 100 μm.

The results of our stylet insertion site studies indicate that *A. tsugae* inserts its stylet bundle primarily intracellularly, and almost always proximal to the plant with respect to the needle abscission layer. All 4 of the distal insertions observed occurred on current year growth and on twigs where there were ≥4 adelgids inserted on 1 needle, and so distal insertion may be a result of competition for a feeding position. The fact that no living or dead adelgids were found with stylets inserted distal to the needle abscission layer on previous year growth suggests that distal insertions on current year growth may result in needle abscission, or in the insect withdrawing its stylet bundle. Perhaps the distal position is too far away from the preferred tissues for feeding to occur; perhaps the abscission zone is difficult for stylet bundles to traverse; or perhaps attempted penetration of the abscission zone triggers needle abscission.

The intracellular insertion of the stylet bundle indicates that the adelgid is either using mechanical pressure or some sort of sawing motion of the individual stylets to pierce the epidermal cells as was suggested by Pollard (1973) for aphids. In ear-

ly summer, stylet bundle insertion sites were primarily on the current year needles, perhaps reflecting a preference for settling at the base of a needle where no crawler has previously settled, or a preference for immature tissue. When plant tissue is young, the middle lamellae of the cell walls consist mainly of pectin. As the tissue matures, lignin is deposited in the walls, and at maturity the middle lamellae are 60–90% lignin (Berlyn 1964, 1969; Berlyn and Mark 1965). Because lignin is difficult to metabolize, adelgids would most probably avoid lignified tissue. It is not known if *A. tsugae* can detect its initial penetration site and pathway in young tissues for reinsertion after molting; perhaps the salivary sheath deposited in the plant aids in reinsertion.

According to Miles (1990), most aphids and adelgids avoid mature tissues and prefer new growth; he suggests that this preference may be caused by the lower nutrient content and higher allelochemical content of older plant tissues. *A. tsugae* preference for new plant growth may be a mechanism of avoiding plant chemical defenses. Miles (1987, 1990) has proposed that the salivary sheaths of aphids and adelgids may serve to prevent wound responses of damaged plant cells along the stylet path by sealing off cell ruptures. The sheath also absorbs phenolic compounds in vitro (Miles 1990), and so may slow or prevent plant defenses by absorbing allelochemicals before surrounding undamaged cells can be signaled. The salivary sheath secreted by *A. tsugae* may allow it to continue to feed on hemlock throughout the season as the tissues mature, and to reinsert its stylet bundle after molting, by suppressing plant chemical defenses.

The stylet insertion site on previous year needles was more proximal to the plant with respect to the abscission layer than in current year needles. This difference might be caused by the greater density of insects feeding on previous year growth than on current growth. After the 2nd generation of adelgids had hatched and settled on the plant, there were up to 5 or 6 adelgids feeding on a petiole, 2 or 3 on each side. It seems likely that the later settling insects would have to adjust their site of insertion around those insects already established.

After inserting intracellularly, *A. tsugae* stylets traveled through the plant both inter- and intracellularly, although the intercellular route predominated. According to a number of reports (McAllan and Adams 1961, Miles 1987, Bing et al. 1991), aphids with pectinase in their saliva generally penetrate tissue intercellularly, and aphids without pectinase penetrate only intracellularly. Pectinase hydrolyzes the pectin in the middle lamellae and thus allows the stylet bundle to travel through the middle lamellae between cells (Forbes and Mullick 1970, Bing et al. 1991). Histological studies of *Rhopalosiphum maidis* (Fitch) on *Zea mays* L., however, showed many intercellular pathways (Bing et al. 1991), even though previous studies on the saliva and salivary glands of this aphid had found no evidence of pectinase (McAllan and Adams 1961, Ma et al. 1990). The predominantly intercellular pathway of the hemlock woolly adelgid stylets once within the plant tissue, and the positive staining results with napthol yellow-S, suggest that the insect saliva contains enzymes, possibly pectinase, but does not confirm it.

Adelges tsugae appears to probe for a feeding site, as well as feed in several locations within the xylem ray tissue. Salivary tracks were observed near insertion sites and near feeding sites; those near the feeding site were darker and more numerous than those near insertion. *A. tsugae* may make initial probes to locate the vascular bundle along which the stylet bundle travels down the plant, and once the stylet bundle is fully inserted it may again probe to find its food source, the xylem ray parenchyma cells. The darker, globular tracks often seen near the feeding site may be evidence of previous feeding or of sealed-up cells that proved to be unsatisfactory feeding sites; many aphids, when probing for a feeding site, leave such globular deposits to seal up damaged cells (Pollard 1973).

During the course of this study, the tissue on which *A. tsugae* fed was almost always the xylem ray parenchyma. Although most aphids feed on the phloem sieve cells in plants, most adelgid species are parenchyma feeders (Rohfritsch 1990). Holocyclic adelgids, which migrate between a primary spruce host and a nonspruce secondary host, produce characteristic galls on spruce (Carter 1971) and have minimal effect on the secondary conifer (Rohfritsch 1990). While on spruce, these adelgids feed on cortical parenchyma cells; they modify these cells to make them better conductors of solutes from the phloem and, in so doing, induce gall formation (Rohfritsch 1990). *A. tsugae* also is a parenchyma feeder, but it does not induce gall formation. It feeds not on the cortical parenchyma of eastern hemlock, but on xylem ray parenchyma cells. These cells transfer and store nutrients in the plant. The parenchyma cells of the rays form a continuous network of living cells, connecting the phloem to the xylem and the pith (Zimmermann and Brown 1971).

Future studies will focus on the physiological effects of *A. tsugae* feeding on eastern hemlock to determine what responses it may induce in the host plant. It is possible that the intense impact of the hemlock woolly adelgid on eastern hemlock may not be caused entirely by a direct depletion of plant photosynthate, as it is not feeding on plant sap but on storage cells. Perhaps *A. tsugae* saliva contains a toxin, or perhaps heavy infestations of *A. tsugae* result in an otherwise neutral salivary component having toxic effects on the tree. Perhaps hemlock woolly adelgid feeding and resultant depletion of storage cells weakens the host plant, rendering it more susceptible to other environmental stresses.

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