Xylem Feeding by Periodical Cicada Nymphs on Pine and Grass Roots, With Novel Suggestions for Pest Control in Conifer Plantations and Orchards

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ABSTRACT. First-instar nymphs of periodical cicadas (Homoptera: Cicadidae: Magicicada) were introduced into a 500-cm² plot in a relatively pure stand of loblolly pines and into an 1800-cm² plot on a mowed grassy lawn to determine whether they could feed on pine and grass roots, respectively. Nymphs and their associated roots were excavated within a 2-year period after introduction. Serial root sections from both study sites showed clear evidence of cicada feeding. Cicada salivary sheaths terminated in metaxytem vessels of the grass roots and tracheids of the pine roots. In a pine-hemlock plantation where mature periodical cicada nymphs had emerged, a fiberglass resin cast of the emergence burrow and associated feeding cell was carefully excavated. The feeding rootlet was located and traced to a nearby white pine (Pinus strobus). These observations suggest that the newly hatched nymphs of periodical cicadas can feed on virtually any small rootlet, whether gymnosperm or angiosperm, dicot or monocot. Furthermore, if periodical cicadas become established in a pine plantation, they may be able to feed on pine roots for their entire lives. Two control measures are suggested: 1) prior to a periodical cicada emergence, broad-leaved woody species should be removed from a conifer plantation to prevent successful oviposition by invading cicadas; and 2) in the autumn following an emergence of periodical cicadas in an orchard, the grass cover immediately beneath the canopy of each tree should be killed with an herbicide to starve the young nymphs feeding on grass roots.

INTRODUCTION

Periodical cicadas comprise three closely-related species: (Magicicada septendecim (L.), M. cassini (Fisher), and M. septendecula Alexander and Moore) that are perfectly synchronized with one another in any one part of their range, yet out of synchrony and broken up into different “broods” in different parts of the range (Marlatt 1907, Lloyd and Dybas 1966, Simon and Lloyd 1982, Lloyd 1984). They have a 17-year life cycle in the northern part of the range and a 13-year life cycle in the southern part, where they are also broken up into various “broods”. The 13-year counterparts have been given their own species names (Alexander and Moore 1962), although there is evidence that they may differ from the 17-year cicadas by only a single gene (Lloyd et al. 1983).

The natural habitat of Magicicada spp. is the eastern deciduous forest, where they maintain much higher population densities than any other kind of cicada (Dybas and Davis 1962). This fact has been attributed to their periodicity, coupled with the very long life cycle, which permits them to satiate the available predators on every emergence (Lloyd and Dybas 1966, Karban 1984). The only synchronized biological enemy is a fungus disease, Massospora cicadina Peck, whose resting spores remain until they hatch six to eight weeks later, and the first-instar nymphs drop to the ground. Since periodical cicadas live in deciduous forests where grass is virtually absent, the nymphs obviously do not require grass roots as hosts, but may perhaps use them if available. One objective of the present study was to determine whether young periodical cicada nymphs are, in fact, capable of feeding on grass roots.

Coniferous forests are not part of the natural habitat of periodic cicadas, so one would not expect them to be pests in pine plantations. It was therefore startling to see Magicicada septendecim emerging in great abundance in a plantation of white pine (Pinus strobus) and hemlock (Tsuga canadensis) in Hocking County, Ohio, near Cantwell Cliffs State Park in 1965. Figure 1A shows the appearance of the ground at that time, with numerous emergence burrows, cast skins, and dead adults. Emergence burrows counted in 15 randomly selected square-yard quadrats averaged 33.5 ± 9.1 (SE), corresponding to between 190,000 and 610,000 cicadas per ha, with 95% confidence (White et al. 1982). The conclusion seemed inescapable that the cicada nymphs had been feeding on the roots of pine and/or hemlock, because there was little else for them to feed on in this shady plantation. To confirm this, a cast was made of the feeding cell by pouring fiberglass resin down the burrow from which the mature nymph had recently emerged. This was carefully excavated to locate, immediately beneath

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FIGURE 1. A: Periodical cicadas infesting a white pine-hemlock plantation near Cantwell Cliffs State Park, Hocking County, Ohio, 1965. This was two cicada generations after 1932, when the trees were planted among deciduous scrub where cicada eggs had been laid in 1931. Two emergence burrows have brought light-colored subsoil to the surface and penetrated through the pine litter. Notice the many cast nymphal skins and one dead adult cicada. For other photographs of the same situation, see White et al. (1982). B-D: Salivary sheaths of young periodical cicada nymphs in small rootlets, all to the same scale. B, loblolly pine (Pinus taeda); C-D, dallis grass (Paspalum dilatatum); D, section near a salivary sheath, showing two metaxylem vessels completely plugged.

the cell, the feeding rootlet which was traced to a nearby pine root. A photograph of this cast is included in the present report.

This still leaves undetermined whether newly hatched, first-instar nymphs of periodical cicadas can feed on pine roots. This was the second question addressed by the present study.

MATERIALS AND METHODS

Homopterans feed on plant fluids through a salivary sheath that is produced by sticky saliva that polymerizes on contact with plant tissues. The sheath remains in situ after the mouthparts have been withdrawn, and can be found by examining serial plant sections (Miles 1972). We used this method to search the roots of known species in our experimental plots for signs of cicada feeding. First-instar nymphs were obtained by clipping twigs laden with cicada eggs approximately one week prior to the expected time of hatching and placing these twigs directly on the ground at our study sites. When clipped at this time, the majority of eggs hatch (White 1981, White and Lloyd 1981), and first-instar nymphs enter the ground.

Eggnests placed in the pine plantation were mostly those of M. septendecim, collected on 26-27 July 1978 from Burnt Chimney, Virginia (Brood I). On 1 August 1978, we placed them on 500 cm² of ground in a closed-canopy plantation of loblolly pine (Pinus taeda L.) growing on sandy soil in Durham County, North Carolina. The introduction site contained thinly scattered seedlings of sweetgum (Liquidambar styraciflua), tulip poplar (Liriodendron tulipifera), red maple (Acer rubrum), and persimmon (Diospyros virginiana), as well as vines such as Virginia creeper (Parthenocissus quinquefolia), poison ivy (Rhus toxicodendron), and Smilax sp. These angiosperms afforded the cicada nymphs alternative feeding sites, although the vast majority of the roots available at this site were those of loblolly pines.

The second sample was entirely eggnests of M. septendecim, collected on 11 July 1980 from Lewiston, Illinois (Brood III). We placed these on a mowed, unfertilized grassy lawn in Carrboro, North Carolina on 26 July 1980. They were distributed over 1800 cm² of the lawn, which consisted of poorly drained heavy clay soil supporting only dallis grass (Paspalum dilatatum Poir.) and Japanese clover (Lespedeza striata (Thurb.) H. & A.). The nearest woody plants were bushes 9 m away.

We excavated the pine plot in July and August, 1980, when nymphs were two years old, and the lawn plot in August, 1981 when nymphs were one year old. Nymphs, the rootlet associated with each nymph, and any small rootlets in the immediate vicinity were collected from both plots and preserved in 70% ethyl alcohol. Root voucher collections (the root was traced directly to its source) were also obtained at this time. Root serial sections (15 μm) were prepared by standard plant histological techniques (Johansen 1940). Safranin was used to stain both the salivary sheaths and lignin of the xylem walls; fast green was used to counterstain plant tissues.
RESULTS AND DISCUSSION

The excavated cast of a recently vacated emergence burrow (B) which turns at a sharp angle to form a feeding cell (C) is shown in Figure 2. The photograph was taken in situ with a mirror placed underneath. It shows that the small feeding rootlet (F) beneath the feeding cell is attached directly to the large white pine (Pinus strobus L.) root in the middle of the photograph. The feeding cell of a mature nymph appears to be a relatively permanent abode, thoroughly plastered from within. From its position inside that cell, the nymph had no root other than the pine available to feed on.

A salivary sheath in a root section of loblolly pine is shown in Figure 1B. The structure is characteristic of homopteran salivary sheaths (Miles 1972) and unmistakably that of a cicada (White and Strehl 1978). Five second-instar nymphs and their associated roots were excavated from the pine forest. Four of the five roots were loblolly pine; one was Smilax, which contained two salivary sheaths (not illustrated). Three of the four pine roots showed signs of cicada feeding: seven salivary sheaths altogether.

The rootlets of loblolly pine that contained salivary sheaths were all very young. The sheaths of the young cicada nymphs have penetrated through cortex and cambium into the region of primary tissue containing five-sided xylem cells on the inside and smaller stacks of rectangular phloem cells on the outside (Chamberlin 1935). Although it appears that the sheaths go beyond the phloem cells, terminating in xylem tracheids, the two tissues are intermingled. Thus, we could not conclude that the nymphs fed only on xylem fluid. Moreover, the tracheids of pine are much narrower in diameter than the metaxylem vessels of the grass root or the secondary xylem vessels of a dicot illustrated by White and Strehl (1978). In fact, the pine tracheids appear to be of smaller diameter than the outside diameter of the salivary sheath itself; hence, the latter is not so clearly targeted on a single large vessel as it is in dicot and grass roots. In the case of pine roots, then, we cannot be certain that only xylem fluid is ingested; perhaps some nutrients from phloem tissue are also ingested.

It is possible that these salivary sheaths represent abortive, unsuccessful attempts at feeding on pine rootlets. That seems improbable, however, because these nymphs, when collected, had already been living at this site for two years. Alternative dicot roots were available in the vicinity, yet nymphs were found directly associated with pine rootlets.

Four nymphs and their associated rootlets were found in the inoculated grass plot. Two of these rootlets were completely sectioned and contained five salivary sheaths. An example in which two sheaths have been directed towards adjacent large metaxylem vessels is shown in Figure 1C. Salivary sheaths found in dicot roots with secondary growth invariably end in peripheral xylem vessels (White and Strehl 1978), whereas those found in grass roots, which have no secondary growth, always have one or more of their large metaxylem vessels penetrated. Feeding is probably much easier for the young nymphs in these large metaxylem vessels, since flow rate is proportional to the fourth power of the radius of the vessel (Zimmerman 1983).

A section only a short distance from the salivary sheath in 1C is shown in Figure 1D. This section illustrates how the polymerized, viscous saliva permanently plugged up both metaxylem vessels, presumably rendering them useless to the plant. The sections of grass root show no evidence that phloem tissue was used for feeding.

This is not the first record of young periodical cicada nymphs feeding on grass roots. We now recognize that White and Strehl (1978) showed a salivary sheath in a grass root collected from a roadside, second-growth deciduous forest. They mistakenly labeled the root as "probably Sassafras albidum."

RECOMMENDATIONS

Our preliminary observations suggest two hypotheses: 1) periodical cicada nymphs are able to survive on the roots of conifers for their entire lives; and 2) newly hatched, periodical cicada nymphs can become established on grass roots, live on them for one or two years,
and later transfer onto the roots of deciduous trees. More extensive studies will be required to measure the rates of survival and growth on conifer and grass roots versus roots of broad-leaved trees. However, even if these two hypotheses are correct only in a qualitative sense, there are practical implications that should be recognized. This is especially true for Ohio, where conifer plantations and orchards are economically important, and where major emergences of periodical cicadas are imminent (1987 in western Ohio, 1991 in the southern counties, 1999 in eastern Ohio; Fig. 3). The first implication is that weedy deciduous growth should be cleared from young conifer plantations immediately prior to an emergence of periodical cicadas. The second is that control of periodical cicadas in orchards may be achieved merely by manipulating the grass cover under the trees. These are speculative and untested ideas. However, they are discussed briefly here in the hope of stimulating further research during the coming emergences of cicadas.

**Conifer Plantations.** White et al. (1982) showed that periodical cicada eggs hatch poorly from twigs of pine or hemlock, but hatch very well from weedy deciduous species such as sassafras (*Sassafras albidum*), redbud (*Cercis canadensis*) and pin oak (*Quercus palustris*). During an emergence year, periodical cicadas will invade a young conifer plantation from any nearby deciduous forest and oviposit in small twigs. If pines and hemlocks are the only twigs available for oviposition, then relatively few periodical cicadas will become established. If, on the other hand, the conifers are interspersed with woody deciduous species, then a large population of cicadas may hatch and begin feeding on tree roots in the plantation.

The fast-growing pines and hemlocks will eventually shade out the deciduous species and eliminate them almost completely. Nevertheless, if the first hypothesis is correct, then the cicadas will be able to transfer onto the roots of the conifers and continue to feed on them for the remainder of the 17-year period. This scenario evidently did occur in the pine-hemlock plantation near Cantwell Cliffs State Park in Hocking County (Fig. 1A), and may account for the comparatively poor growth of hemlocks there (White et al. 1982). It is well known that xylem feeders severely affect plant productivity (Mattson 1980). Karban (1980) has shown this specifically for periodical cicada nymphs feeding on scrub oaks (*Quercus ilicifolia*). Additionally, young conifers should not be planted inter-spersed among deciduous species, if the latter have received cicada eggs in the previous few years.

**Orchards.** Periodical cicadas are especially serious economic pests in apple orchards (Forsythe 1976, Karban 1982). The absence of the pathogenic fungus, *Massospora cicadina*, is probably one factor permitting the extraordinary abundance of periodical cicadas in orchards (White and Lloyd 1975, 1983). On the other hand, if the second hypothesis is correct, then the cover of mowed grass that is normally found in orchards may be a second factor of equal or even greater importance than the absence of entomophagous fungi.

The mouthparts of newly hatched cicada nymphs are evidently too short to penetrate to the xylem vessels of any but the smallest rootlets. Deciduous trees routinely slough most of their smallest rootlets in early winter and grow new ones in the spring (Bode 1959, Hibbard and Sykes 1973). When its rootlet dies, the small nymph must starve until it can locate another food source. This entails energy-expensive burrowing through the soil. Grass roots, with their large metaxylem vessels, are evidently ideal feeding sites for small periodical cicada nymphs, and are not so readily sloughed as are the smallest rootlets of trees. For example, in natural prairie, grass roots turn over only about once in four years (Dahlman and Kucera 1965).

By creating an understory of mowed grass, the orchardist inadvertently creates a "supernormal" habitat for periodical cicadas. The grass provides an abundance of feeding sites for the youngest nymphs; the apple roots provide excellent feeding for the older nymphs. The repeated applications by the orchardist of non-systemic insecticides do not affect cicada nymphs, which are insulated underground in their mud feeding cells, plastered from within. Considering also that the orchard may be fertilized periodically and that the trees are uncrowded, it is actually a more favorable habitat for periodical cicadas than the natural forest. Indeed, cicadas grow larger in orchards than they do in forests (Maier 1980, White and Lloyd 1985).

Periodical cicadas in orchards are vulnerable, however, owing mainly to three circumstances: they are perfectly synchronized, so that the entire population is in a given stage at a particular time; the nymphs have very little capacity for horizontal movement (Marlatt 1908, Lloyd 1987); and grass roots can be temporarily destroyed without harming the trees.

In the year of a periodical cicada emergence, the grass directly under the orchard trees should be killed by a selective herbicide after the fruit has been harvested. In
an orchard with a 36-foot interval between trees, this would be only about half the grass cover of the orchard. This half would include, however, practically all of the grass roots on which cicada nymphs are feeding, but not the lanes between the trees needed for motorized traffic. Newly hatched nymphs are small and have little energy reserves. If they are forced to burrow through the soil again in search of a second feeding site shortly after getting established and beginning to feed on the first one, most of them would probably perish in the attempt.

Following this procedure, the grass can be seeded in again under the trees. Many of the nymphs feeding on apple rootlets might transfer onto the new grass roots when the apple rootlets are sloughed during the winter. Early the following summer, the grass under the trees could be killed a second time. We postulate that this might eliminate a large proportion of all the cicada nymphs in the orchard. Before the next harvest, the grass could be seeded in yet again, and thereafter left in place.

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LITERATURE CITED


