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Review of the ecological and economic significance of forest Hepialidae (Insecta: Lepidoptera)

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ABSTRACT

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The Hepialidae are primitive moths found throughout much of the world in habitats ranging from grasslands to forests. The forest-inhabiting species are best known from South America, the Orient and the western Pacific. Damage to forest trees occurs when larval tunneling and feeding cause wood defects in stems, branches, and roots and provides entry sites for decay or pathogenic micro-organisms. Hosts include a wide range of species from Angiospermae and Gymnospermae although individual species of Hepialidae range from generalist to specialist (monophage) feeders. The Hepialidae generally have a low economic and ecological profile. A few species of forest Hepialidae are recognized pests, but control procedures are limited or non-existent. The recent discovery of high-density populations of *Korscheltellus gracilis* (Grote) in areas of forest decline in North America suggests that the prevalence and impact of Hepialidae can go undetected until a critical forestry issue focuses attention on their secluded feeding habits.

INTRODUCTION

Most pest Lepidoptera of forests feed on foliage, fine twigs, flowers or seeds of trees (Johnson and Lyon, 1988) and are members of the suborder Ditrysia which includes over 98% of all Lepidoptera species (Kristensen, 1984). The remaining 2% of Lepidoptera are divided among four suborders and about 23 families (Nielsen, 1985) and include well-known pest species that feed on leaves (miners, skeletonizers) or twigs (borers). The Hepialidae are members of the suborder Glossata (Nielsen, 1985) and among the most poorly known forest Lepidoptera although they comprise the largest non-ditrysian

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family. Hepialidae comprise about 500 known species (Kristensen, 1984) distributed in forests, shrublands, moss bogs, and grasslands throughout much of the world (Tindale, 1938). Knowledge of the Hepialidae is fragmentary although a number of recent studies have reviewed aspects of ecology and taxonomy (Kristensen, 1978, 1984; Nielsen and Robinson, 1983; Mallet, 1984; Nielsen and Scoble, 1986; Wagner, 1988; Grehan, 1989; Wagner and Rosovsky, 1991).

Adult Hepialidae have non-functional mouth parts, but larvae feed on a wide range of species and host-plant tissues (Grehan, 1989). Many Hepialidae feed on the foliage of ground herbs or grasses and some are major pests of improved pasture (Hill, 1929; Tindale, 1938; Madge, 1954; Hardy, 1974; Ferro, 1976; Elder, 1978; French and Pearson, 1981). Species feeding on leaf litter or foliage of ground herbs and grasses in the forest do not constitute a forest pest problem. Other species, however, feed on roots or bore into trunks and branches of trees and shrubs of economic or environmental importance in forestry.

The main features of hepialid feeding and its significance for forest management is described in reference to forestry in the broad sense including managed and unmanaged forests, forest plantations, and individual tree species. Damage by Hepialidae to trees of economic importance is generally recognized only for some timber-boring species in India (Nair, 1986, 1987), southeast Asia and Japan (Matsuzawa et al., 1963; Dhanarajan, 1976; Yasuda and Abe, 1986), Australia (Kile et al., 1979) and New Zealand (Grehan, 1989). Many Hepialidae live in the soil (Nielsen, 1985) and are less likely to be recognized in association with the health condition of their hosts. The secluded larval feeding is not immediately obvious compared with foliage and twig-feeding Lepidoptera where damage and impact are directly observable. The low species diversity of forest Hepialidae in North America and Europe may also lead to a general underappreciation of hepialid impact in forest ecosystems. This review will highlight the feeding biology of forest Hepialidae and the short-term and long-term consequences for forest growth and management.

GENERAL BIOLOGY

The female does not select oviposition sites on the host plant, but deposits eggs on the ground during flight or at rest. Contact with the host plant is initiated by the enclosed larva. Forest species feed on leaf litter, mosses, ferns or higher plants (conifers and angiosperms). Most forest hepialids are subterranean feeders either specializing on fern rhizomes and leaf petiole bases (McCabe and Wagner, 1989), or including ferns in a diet of higher plants (Tobi et al., 1989). Many fern-feeding species such as *Phymatopus hecta* (Linn.) may inhabit forests, but their habitats have not been precisely documented (Buckler, 1887; Barrett, 1895; South, 1908). Root feeders consume xylem, phloem, or callus tissue. Some borers such as *Leto venus* (Stoll) and *Hepialus californicus* (Bdv.) (Duke and Taylor, 1964; Wagner, 1985; Grehan, 1987a) feed principally on xylem tissue, but most arboreal species (those inhabiting trunks and branches — *Aenetus, Endoclita, Sahyadrassus, Trichophassus*) tunnel into the wood and feed primarily on callus tissue (Grehan, 1987a,b).

Many of the best known lepidopteran pests are phytophagous throughout larval development, but the young instars of some Hepialidae are mycophagous, feeding on detritus or fungi before transferring to vascular plants for most of their development. The transition in stem-boring species involves migration of larvae between physically distinct parts of the forest ecosystem and in *Aenetus* there is temporary morphological change where sclerotized pinacula fuse and darken during the molt preceding transfer. Larvae return to their former appearance in the molt immediately following establishment in a host tree (Grehan, 1981).

ROOT INJURY

Reductions in fine and woody root tissues by Hepialidae could reduce water and nutrient assimilation, and result in a host susceptibility to root pathogens entering through wounds which are well known as infection sites (French, 1988; Manion, 1991). However, there are few records of hepialid injury to woody roots of trees and shrubs — possibly due to the lack of visible damage. In Australia three genera are known to damage tree roots: *Trictena* in *Eucalyptus*, and *Abantiades* and *Oxycanus* in *Acacia* and *Eucalyptus* (Grehan, 1989). Kile et al. (1979) described damage by *Abantiades latipennis* on the roots of *Eucalyptus obliqua* L'Héritier and *Eucalyptus regnana* F. von Mueller. Larvae construct nearly vertical tunnels extending 12–35 cm into the soil. The tunnels come into contact with tree roots 5–20 cm below the soil surface. Larvae feed on callus tissue causing lesions may girdle the roots and sometimes stimulate local rhizomorph development by facilitating access of fungi to internal root tissues. Localized root deformities with internal discoloration and decay are sometimes associated with lesions. Root-rot fungi (*Armillaria* sp. and *Poria medulloris* Grey) have been identified at some feeding wounds. Kile et al. (1979) suggested that reduction in root size or establishment of decay organisms could reduce the vigor and competitive ability of young trees, but no visual effects were discerned in the crowns of heavily infested hosts. Kile et al. (1979) noted that the limited historical *A. latipennis* records could be attributed to the insect being rare or a lack of collecting from favored habitats.

Species of the North American genus *Sthenopis* have attracted attention for their damage to tree roots in forest plantations (Furniss and Carolin, 1977;

Vallée and Béique, 1979; Gross and Syme, 1981). Larval feeding includes both roots and stems and provides a behavioral transition between the specialized root or stem feeding occurring in most other Hepialidae (Grehan, 1989). Larvae of *Sthenopis quadriguttatus* Grote feed on roots and stems of aspen, cottonwood and willow (Furniss and Carolin, 1977), but commercial impact is confined to occasional serious damage to regenerating stands of *Populus tremuloides* Michx. and plantations of *Populus balsamifera* Duroi (Vallée and Béique, 1979). Wood staining was found in all larval tunnels and nearly half the tunnels contained wood rot, but no rot species could be isolated (Gross and Syme, 1981). In a forest plantation of 12 poplar species and hybrids Vallée and Béique (1979) reported a 24% infestation in hybrids and a 20–100% infestation in clones. The genus *Sthenopis* is present in Eurasia but it has not been recorded as a forest pest. The early larval biology of the related *Zenophassus shamyl* (Chz.) in forests of the Caucasus Mountains was described by Slashchevskii (1929), but the impact of larval damage and significance for forestry was not identified.

Damage by the North American root-feeding species *Korscheltellus gracilis* (Grote) represents a potentially significant mortality factor for spruce and fir in North America (Grehan et al., 1992) but until recently it was overlooked apart from occasional capture dates, locality and host records (Packard, 1865, 1895; Engelhardt, 1920; Forbes, 1923; Prentice, 1965; Hooper, 1981). The impact of *K. gracilis* attracted attention in the 1980s when its association with regional forest decline was recognized (Tobi et al., 1989). Investigations at the University of Vermont Entomology Research Laboratory (Tobi et al., 1992a,b) revealed high densities of *K. gracilis* larvae in the upper humus–soil horizons of the mid-montane forest (880–1230 m) which is dominated by red spruce and balsam fir (zonation from Siccama et al, 1982). Studies on *K. gracilis* populations in New Hampshire, Vermont and New York have recorded average larval densities of up to about 40 larvae m^2 at elevations of 900–1100 m (Leonard et al., 1991; Wagner et al., 1991). These densities are comparable with recognized pasture pests (Leonard et al., 1991) and suggest a widespread feeding impact on host trees such as red spruce and balsam fir (Wagner et al., 1987; Tobi et al., 1989, 1992b).

Red spruce regeneration is scarce in severely declining sites (Whitney, 1988) and a 75% decrease in seedlings was recorded between 1965 and 1986 on Camel's Hump, Vermont (Vogelmann et al., 1988). Field and laboratory studies have shown that a single larva can kill a seedling or cause significant reductions in its growth (Tobi et al., 1989; Leonard et al., 1991; Grehan et al., 1992), but the proportion of seedling mortality in the field population caused by *K. gracilis* is unknown. Larval feeding may also have a long-term impact on forest health through the cumulative exposure of inner root tissues to soil-inhabiting pathogens. Pathogenic and wood decay fungi such as *Armillaria mellea* are known to enter white spruce roots through wounds similar to those caused by feeding of *K. gracilis* (Whitney, 1961) and decay and pathogenic fungi have been isolated from wood discoloration surrounding *K. gracilis* feeding wounds (J.R. Grehan and D.R. Bergdahl, unpublished data, 1991).

STEM-BORING HEPIALIDAE

Stem borers have attracted most attention because their tunnels are more accessible to observation and they affect timber quality through direct physical damage and from wood decay or staining resulting from fungi entering the tunnels. Larvae construct a single main tunnel from the surface into the stem and then along the wood grain, either going up or down the stem or branch for several centimeters. Some hepialid tunnels may exceed a meter in length (Grehan, 1989). Stem borers have attracted the greatest economic interest in India, southeast Asia, and Japan for species of *Endoclita (Phassus)* (Kondo, 1961; Matsuzawa et al., 1963, Yasuda and Abe, 1986) and *Sahyadrassus* (Nair, 1986, 1987; Devasahayam et al., 1987). In Japan *Endoclita excrescens* (Butler) and *Endoclita signifer* (Walker) feed on a wide range of woody ornamental and forest species including *Populus, Salix, Alnus, Castanea* and *Quercus*, but these hosts are not of major significance in forestry (Kondo, 1961; Matsuzawa et al., 1963). Young larvae of *Endoclita signifer* feed in the stems of annual and perennial grasses and Kondo (1961) found that they can be controlled by eliminating these grasses in forests and nurseries.

Endoclita gmelina (Tind.) and *Endoclita sericeus* (Swinhoe) are major pests of teak, an economically important timber species in Malaysia and Indonesia (Kalshoven, 1965; Dhanarajan, 1976). Dhanarajan (1976) suggested that *Endoclita gmelina* infestations in teak plantations could be reduced by eliminating alternate hosts. Damage from *Endoclita hosei* (Tindale) has been observed in plantations of introduced *Eucalyptus* in Malaysia, but their economic significance has not been assessed (Yasuda and Abe, 1986). *Endoclita hosei* is a major pest of planted cocoa (Conway, 1971).

Scientists at the Kerala Forest Research Institute (India) studied the ecology and pest status of the sapling borer *Sahyadrassus malabaricus* (Moore) (Nair, 1986, 1987). It is reported from 50 species of woody shrubs and trees, including economically important species such as pear, clove, sandalwood, teak, and *Eucalyptus* (Devasahayam et al., 1987). The economic impact in teak and *Eucalyptus* plantations is believed to be significant (Nair, 1982). The number of infested teak saplings was found to range from 6 to 61% and larval feeding resulted in stems being broken at the tunnel site, ring-barked by larval feeding, or damaged by woodpeckers searching for larvae (Nair, 1987). Control procedures developed by Nair (1986) require removal of the feeding cover and brushing insecticide over the feeding surface. Five insecticides were tested and quinalphos (BSI, ISO. 0,0-diethyl 0-2-quinoxalinyl phosphorothioate) was most effective. The method is labor intensive, but considered less cumbersome than injection of pesticide into the tunnel or plugging the tunnel entrance with tar (Nair, 1986).

Several South American tree species may have stem-boring larvae, but only one is known to be a forestry problem (Grehan, 1989). *Eucalyptus* plantations established in southern Brazil were attacked by larvae of *Trichophassus giganteus* (Viette). This problem prompted a description of damage and life history (Briquelot, 1956), but no further published studies could be found.

The genus *Aenetus* includes a number of species which have an impact on forestry in Australia and New Zealand (Grehan, 1987a). Several species tunnel into *Eucalyptus* in Australia, but they have a relatively low pest status (Grehan, 1984), possibly because tunnels are often in smaller terminal branches and population densities may be low compared with other timber borers. The most significant effect occurs when larvae tunnel into the main stem of regenerating saplings (Tindale, 1953). The related *Zelotypia stacyi* (Scott) also bores into *Eucalyptus* stems, but is geographically restricted in central–eastern Australia and has a negligible economic impact (Chadwick, 1989; Grehan, 1989). The New Zealand species, *Aenetus virescens* (Doubleday), feeds in several tree species and the tunnels may provide significant sites for entry and establishment of wood rot and pathogenic fungi, possibly vectored by secondary inhabitants of vacated tunnels (Milligan, 1974). Larvae sometimes attack *Eucalyptus* but do not thrive and are only a minor nuisance (Grehan, 1984, 1987a). The economic impact of *Aenetus virescens* is low either because hosts are not major commercial species, or significant commercial logging of host plants occurs outside the insect's geographic range.

DISCUSSION

Control procedures are virtually non-existent and damage by the root-feeding species may go unnoticed. Apart from work on *K. gracilis*, specific knowledge on the impact assessment of root-feeding Hepialidae is sparse. Very little is known about the composition and impact of organisms affecting populations of forest Hepialidae. Recognized biological agents include species of Ichneumonidae (Hymenoptera), Tachinidae (Diptera) (Wagner et al., 1989), and a few bacterial and fungal pathogens (Grehan and Wigley, 1984; Nair, 1987; Wagner et al., 1989). Woodpeckers and parrots have been observed extracting larvae of timber-boring species, but this results in additional damage to the host tree (Tindale, 1953; Nair, 1987). Fungal pathogens such as *Verticillium* are being developed for commercial control of forest pests in the soil (Skinner et al., 1991) and this approach may be effective against young instars of Hepialidae while they are present in the litter and upper soil layers.

Two management strategies have been found to be effective for controlling timber borers: (1) removal of alternate hosts, particularly undergrowth around host trees; (2) removal of plant detritus, especially decaying wood. Both methods are labor intensive and may have a negative impact on forestry values such as recreation and aesthetics. These impacts may not be problematic for plantations where timber production is the only concern, but they also may have an effect on ecological processes such as nutrient cycling and soil desiccation. Incineration of leaf litter has been successfully employed against larvae of the forest pest *Paraclemensia acerifoliella* (Fitch) (Lepidoptera: Incurvariidae) when they are present in the litter and upper soil (Simmons et al., 1977) and could have a similar impact on the populations of forest Hepialidae during the litter feeding stages. Loss of understory and litter from frequent burning within *Eucalyptus* forests may be responsible for the low densities observed (J.R. Grehan, unpublished data, 1982) for *Aenetus* in Australia. Vallée and Béique (1979) proposed management for *Sthenopis quadriguttatus* by selection of poplar clones resistant to larval attack. Tree improvement activities are time consuming, but may be appropriate for fast-growing hosts such as poplar.

Few species of Hepialidae are recognized as chronic pests, but their impact on forest ecosystems may be grossly underestimated. The process of dietary transition suggests a complex ecological role with respect to host plant and food web relationships. The biomass of young *Aenetus virescens* larvae on dead wood and fungal sporophytes, for example, may exceed that of any other macro-invertebrate mycophages. Host fungi include wood rots and pathogens (e.g. *Heterobasidion*) (Grehan, 1984), and transferring larvae could vector spores into the new host tree although this relationship has not been confirmed.

New perceptions in forest management and environmental issues represent a major development in understanding the ecological impact of forest Hepialidae. The efficacy of ecological models describing ecosystem processes are contingent upon specific knowledge of the composition and interrelationships of organisms. For example, the widespread decline of mid- to high-elevation spruce–fir forests is widely correlated with the effects of atmospheric pollution such as acid deposition and ozone (Klein and Perkins, 1988), but conclusive experimental evidence for the impact of acidic deposition on species such as red spruce has been problematic (Mattson et al., 1990). Recently DeHayes et al. (1991) found a negative impact on red spruce seedling cold tolerance from exposure to ambient acidic cloud deposition and suggest that if a reduction of this nature could be demonstrated consistently it would implicate pollution as a predisposing factor in foliar winter injury. However, experimental evidence for the negative impact of *K. gracilis* feeding on red spruce suggests that any effect from acidic deposition is contingent upon the impacts from other active biological processes that also influence tree growth.

Studies of aboveground insects record a general feeding preference for ozone-treated foliage; Hiltbrunner and Flückiger (1992) and Hain (1987) suggest that there is reasonable correlative evidence to suggest that air pollutants influence the outbreak patterns of forest insect species. The recent recognition of *K. gracilis* as one of the most abundant macro-invertebrates in the soil–litter horizon of upper elevation spruce–fir forests represents a significant finding in a region with a century of entomological research on forest ecosystems. However, the interrelationships between damage by insects such as *K. gracilis* and ecological trends in forest structure and composition are poorly understood. The root-feeding activities of *K. gracilis* suggest several possibilities for interactions with host plants and the ambient physical and chemical environment. The larvae feed on both regeneration and mature trees. Each of these interactions may be affected by atmospheric impacts on a four-way co-contingent relationship between the host plant, the insect, root rots and pathogens, and root mycorrhizae. At present specific knowledge on this relationship does not exist, and understanding of atmospheric impacts on forest components such as the rhizosphere is fragmentary (Reddy et al., 1991). The significance of acidic deposition or ozone for insect feeding is also contingent upon their effect on life-history patterns (Hiltbrunner and Flückiger, 1992), and for *K. gracilis* there may be a dynamic relationship with forest decline if changes in forest structure also affect the insect's distribution and abundance through reproductive behavior and larval survival.

The potential interrelationships represented by the feeding biology of *K. gracilis* illustrate both the potential long-term impacts of forest insects such as the Hepialidae and the ecological limitations of ecosystems models in general. The structure and predictive power of ecological models is contingent upon the inclusion of recognized ecosystem components, but the inter-organism relationships associated with hepialid feeding have yet to be incorporated into long-term models for forest decline. The potential significance of *K. gracilis* illustrates the need for recognizing and understanding the ecological role of forest Hepialidae as they may affect environmental or commercial management of forest ecosystems.

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