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# Exploitation of the xylem stream by parasitic organisms

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## SUMMARY

A taxonomically diverse group of angiosperms and certain homopteran insects derive water, inorganic and organic solutes from angiosperm xylem sap. Parasitic angiosperms are connected to their host(s) by a specialized organ (the haustorium) and form close cellular contacts with host xylem tissue, while insects tap xylem vessels by means of stylets. Adaptations to phytophagy are discussed with respect to gaining access to xylem tissue and the nutrition of sap feeders. Parasitic angiosperm–host interactions are examined in relation to recent advances in our understanding of root-to-shoot communication via the xylem (the influence of host-sourced signals on the parasite) and the functional significance of high rates of transpiration in parasitic angiosperms.

## 1. INTRODUCTION

Moving goods from A to B is always a risky business, and for plants it's no different. Some organisms are able to gain access to the contents of xylem or phloem by mechanical probing (*sensu* Fitter & Hay 1987), and obtain part or all of their resources from the sap. The two major life forms which use xylem sap in this fashion are the parasitic angiosperms and certain homopteran insects.

More than 3000 species of angiosperm (about 1% of the total) are at least partly parasitic. Approximately half of these are mistletoes (Loranthaceae and Viscaceae), with the rest being classified into approximately 15 families. Parasitic angiosperms are attached to their host by at least one haustorium, which is located either above- (stem parasite) or below- (root parasite) ground. The organisms are further classified according to the presence (hemiparasite) or absence (holoparasite) of chlorophyll.

Among the Homoptera, spittlebugs (Cercopidae) and cicadas (Cicadidae) are the most noticeable xylem feeders. Buckton (1890) found himself to be 'quite inconvenienced by the large drops of clear liquid shed, by hundreds of Aphrophorae, upon my paper, whilst sketching under elm trees', and the spittles of nymphal Cercopidae can be readily observed on many species of herbaceous plants in late spring and early summer. There is little evidence to support claims that other families of Homoptera, Auchenorrhyncha and in certain circumstances some Sternorrhyncha, are xylem feeders. Apart from Cercopidae and Cicadidae there is, however, good evidence for xylem feeding by members of the family Tetigellinae, in which it appears to be the norm, and in some euscelid species where it is common, but not obligatory (otherwise phloem or parenchyma feeders). Most other Auchenorrhyncha appear to be phloem (Deltocephalinae) or mesophyll (Typhlocybini) feeders, whereas the Sternorrhyncha (aphids, psyllids, coccids) are normally phloem feeders.

Many studies of parasitic angiosperms have focused on species of importance as agricultural weeds, such as the genera *Striga* (Scrophulariaceae) and *Orobanche* (Orobanchaceae) (see, for example, Musselman 1980), or as silvicultural pests (see, for example, Hawksworth 1983). Xylem-feeding insects can also influence plant productivity. They may perturb plant water relations, can cause extensive wilting, and are capable of transmitting xylem-borne pathogens, such as the bacteria which cause Pierce's disease in grapes (Purcell 1985). Since the publication of J. A. Raven's (Raven 1983) scholarly and stimulating review a decade ago on phytophages of xylem and phloem (animal and plant sap-feeders), there have been important advances in our understanding of xylem feeders in natural and semi-natural ecosystems, particularly the mistletoes and West Australian woody root hemiparasites. Our knowledge of animal xylem feeders has lagged behind somewhat, and this is reflected in the bias towards plant feeders in this review. We examine recent advances in our understanding of both plant and animal xylem feeders, and discuss their interaction with the transpiration stream.

## 2. ACCESS TO THE XYLEM STREAM

### (*a*) *Plant feeders*

Seed dormancy in many holoparasites and some

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hemiparasites is broken by a specific host-derived chemical signal (for example, see Logan & Stewart 1991, 1992). After germination (albeit months later in some instances, see below) the switch from the 'free-living' to parasitic mode is also triggered by a host-derived chemical signal in many genera (see, for example, Lynn *et al.* 1981; Lynn & Chang 1990), although (as with germination) the requirement for an externally derived signal may not be ubiquitous (Ben-Hod *et al.* 1991). Additional signals may also be concerned with host selection. It has also been proposed, but not substantiated, that in the stem parasite *Cuscuta subinclusa* (Convolvulaceae) flavonoids on host tissue allow the parasite to discriminate between host species prior to haustorial initiation (Kelly 1990).

Haustorial development has been described for a number of species, for example, *Striga asiatica* (Visser & Dorr 1987; Smith *et al.* 1990) and *Viscum album* (Viscaceae) (Sallé 1983). It is supposed that penetration of host tissue involves both mechanical and enzymic action, although our understanding of these processes is still at a rudimentary level in comparison with the more extensively studied bacterial and fungal pathogens.

Transfer of water and solutes across the haustorium was originally thought to take place through direct xylem-to-xylem contacts at the host–parasite interface, which were considered to be ubiquitous (see discussion in Kuijt 1977). Although such contacts have been demonstrated in many species, most contacts with host xylem tissue are often through parenchyma cells. For example, Pate *et al.* (1991*a*) report direct xylem-to-xylem contact in approximately 3% of the parasite cells at the interface between *Amyema linophyllum* (Loranthaceae) and *Casuarina obesa*. Haustoria differ greatly in both size and structure between species (Kuijt & Toth 1985), and many species may have even fewer direct xylem-to-xylem contacts than those reported by Pate *et al.* (1991*a*). In a detailed study of *Olax phyllanthi* (Olacaceae) parasitizing different hosts, the total number of parasite cells impinging on the interface between the haustorium and the host xylem ranged from 8110 to 44 230, of which between 0.2 and 1.2% were xylem elements (Pate *et al.* 1990*a*). The numbers of direct xylem-to-xylem contacts were an order of magnitude lower, and ranged from 0.02 to 0.11% of the total number of parasite cell contacts. Where direct xylem-to-xylem contact was made, luminal continuity was rarely observed (Pate *et al.* 1990*a*; see also Fineran 1987). There are also species for which no xylem-to-xylem contact can be demonstrated (Lamont 1983), and in some of these cases no xylem at all is formed in the haustorium (Alosi & Calvin 1985). Thus the vast majority of cellular contacts at the haustorial interface with host xylem in *O. phyllanthi* and many other parasitic angiosperms is with parenchyma cells (Fineran 1987; Kuo *et al.* 1989; see also Heide-Jørgenson & Kuijt 1993).

Tracer studies using lanthanum or uranyl ions and calcofluor white have demonstrated that host xylem sap is transported apoplastically, along both vascular and non-vascular pathways (Kuo *et al.* 1989; Fineran 1987; Coetzee & Fineran 1987, 1989). Plasmodesmatal connections have not been observed at the host–parasite interface, and transport is not thought to occur in the symplasm (Coetzee & Fineran 1987). Specialized parenchyma cells (the transfer cells of Pate & Gunning (1972)), characterized by numerous large mitochondria, may then play a part in loading the parasite tracheary elements with host xylem sap (Fineran 1987; Visser & Dorr 1987). Contact between host and parasite phloem exists in some holoparasitic associations (Kuijt & Toth 1976), although movement of solutes from host to parasite is still apoplastic. Such phloem proximity does not occur in all holoparasitic associations, and is presumed to be absent from hemiparasitic haustoria, despite the difficulties of detecting phloem tissue.

### (*b*) *Animal feeders*

The presence of a large cibarial pump, to overcome diurnal tension in the xylem, may be a *sine qua non* of xylem feeding, according to the calculations of Raven (1983). This may restrict xylem feeding to those Homoptera with a porrect cephalic swelling (Cobben 1988); namely those groups discussed above and perhaps certain fulgoroid families and some cicadellids. Xylem feeders also need to be able to excrete ingested sap at a high rate, and may exceed the excretion rates of phloem feeders by two orders of magnitude. For example, *Philaenus spumarius*, a known xylem feeder, has a mean excretory rate of approximately 500 to 1000 mg $\text{mg}^{-1}$ 24 $\text{h}^{-1}$ (Wiegert 1964; Horsfield 1977); these compare with excretion of a phloem-feeding aphid of 10.6 mg $\text{mg}^{-1}$ 24 $\text{h}^{-1}$ for *Tuberolachnus salignus* (Auclair 1963) and 2.4 mg $\text{mg}^{-1}$ 24 $\text{h}^{-1}$ for a phloem feeding psyllid (Hodkinson 1973).

Production of large quantities of liquid is readily understood if the insects are tapping xylem vessels, and this does indeed appear to be the case. A number of histological studies have established that the stylets of such insects do generally (88–90% of cases) penetrate xylem (Withycombe 1926; Wiegert 1964; Carle & Montous 1965; Hagley & Blackman 1966; Horsfield 1977). There are clear anatomical features of both the stylet apparatus and the gut which lend further support to this conclusion. Prominent in these xylem feeders is a very distinctive cibarial pump and precibaria which are broad to give less resistance to fluid flow, and heavily sclerotized to provide a strong structure against which enlarged dilator muscles can pull (Backus 1985). Unlike many phloem feeders (e.g. aphids) which have very fine flexible stylets and which penetrate sieve tubes by secreting digestive enzymes, most xylem feeders appear to penetrate the xylem wall mechanically and in order to do so have strong, rather inflexible stylets (figure 1).

Even for those 10% or so of Homoptera species which are obligatory xylem feeders, there is no permanent attachment to the host and feeding positions may be changed frequently. Detection of xylem vessels may require specialised anatomical and sensory equipment. Xylem-feeding leafhoppers (Cicadellidae) usually have widely spaced distal sensillae on a broad precibaria whereas phloem-feeders have paired or

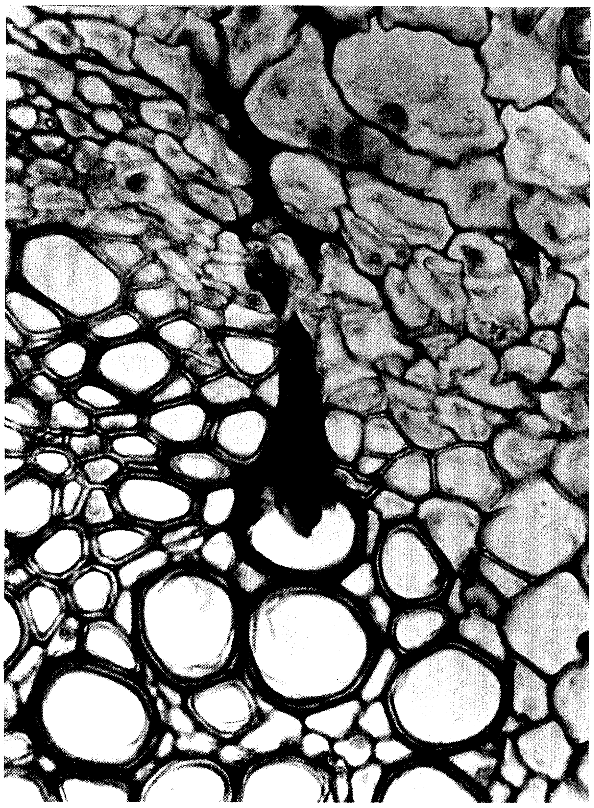

Figure 1. Transverse section of the stem of *Pisum sativum* with the terminal part of the salivary sheath of an instar 3 nymph of *Philaenus spumarius* extending through the wall of a xylem vessel. ×400. By kind permission of D. Horsfield.

single-file sensillae on a very narrow precibaria (Backus & MacLean 1983). In *Graphocephala atropunctata*, severing the nerves to these sensillae prevents them from distinguishing between leaves which differ markedly in nutritional quality. Internal mechanical cues are detected by movements of the stylets as they probe and chemical cues by drawing fluids up the stylets. Feeding action can be monitored by using the insect as a contact breaker in a low voltage circuit completed through the plant (McLean & Kinsey 1964). In such a system xylem feeding produces a pattern which is different from that of phloem feeders (Port 1978), probably because xylem sap has higher conductivity than phloem sap.

Also associated with xylem feeding is poor development of the oesophageal valve between the oesophagus and mid-gut, which is usually well defined in other Homoptera. In contrast, the filter chamber is well developed, presumably to enable the insect to dispose of surplus water by passing it directly to the hind-gut (El-Desouky 1985). This structure was noted by Buckton (1890) in Cercopidae where it reaches its most complex state.

Raven (1983) has calculated that overcoming the tension (negative pressure), supposed to be the diurnal norm in xylem, could just be achieved by the combination of stylet anatomy and cibarial pump mechanics which Cercopidae and Cicadidae possess. Although recent direct measurements demonstrate negative pressures in xylem, they were not the norm and neutral or positive pressures were more frequently recorded (Balling & Zimmermann 1990). It is possible that xylem feeders actually require a negative pressure to feed effectively, since Horsfield (1977) showed that applying pressure to the xylem resulted in a reduction of feeding rate by *Philaenus spumarius* (figure 2). However a more likely explanation is that at greater pressure the xylem sap was more concentrated (see below), so that the insects did not need to extract sap at such a high rate.

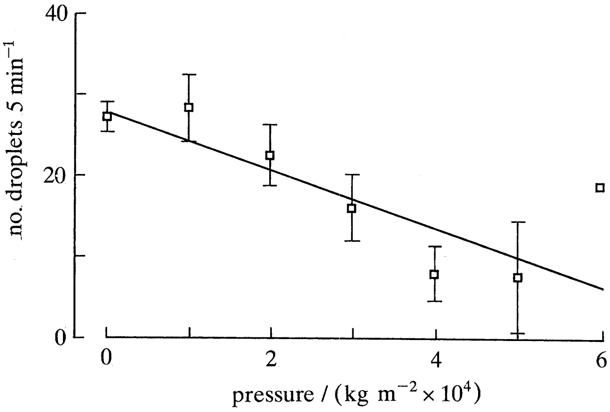

Figure 2. The effect of pressure applied to the roots of *Vicia faba* on the mean (±s.d.) number of droplets of excreta of adult *Philaenus spumarius*. There was no replication at the highest pressure. Data provided by D. Horsfield.

## 3. MATERIALS TRANSFERRED

### (*a*) *Nutrition of plant feeders*

The xylem stream is the major route for transport of water and ions from the soil solution to the shoots of 'free-living' plants, and similarly from the haustorium to the shoots of parasitic plants. In addition to ions (see, for example, Raven (1983) for representative concentrations), xylem sap also contains organic solutes, including amino and organic acids, low molecular mass carbohydrates and plant growth substances.

The dependency of the parasite on transfer of materials from the host(s) varies enormously. Some root hemiparasites are facultative; the perennial *Olax phyllanthi* may survive for several months before making haustorial connections with host plant(s) (Pate *et al.* 1990*b*), and annual root hemiparasites from the Scrophulariaceae can complete their lifecycle in the absence of a host (e.g. ter Borg 1985). Attachment greatly stimulates growth (e.g. Atsatt & Strong 1970; Seel *et al.* 1993), although the extent to which such stimulation occurs depends on the nature of the host, with hemiparasites often, but not always, performing better on nitrogen-fixing legumes (Gibson & Watkinson 1989; Press *et al.* 1993; Seel *et al.* 1993). The balance between host-derived and soil-derived water and ions is rarely quantified, but the former is likely to predominate in the hemiparasitic Scrophulariaceae, which have vestigial, non-mycorrhizal roots, and in some cases no root hairs (see references in Press 1989).

Assimilation of inorganic ions may limit autotrophy to a greater extent than uptake. Nitrogen fertilization studies and assays of nitrogen assimilating enzymes suggest that some of these plants have only little, if any, capacity to assimilate inorganic ions, but that they are able to assimilate organic solutes in host sap (see Stewart & Press 1990). At the opposite end of the parasitic continuum, shoot hemiparasites and holoparasites are obligate heterotrophs for water and inorganic solutes.

Holoparasites are heterotrophic for carbon, but some hemiparasites are also in receipt of significant amounts of host carbon from xylem sap. In the obligate root hemiparasite *Striga hermonthica* (Scrophulariaceae) parasitising sorghum, parasite photosynthetic activity is low, and is a function of the concentration of nitrogen supplied to the host, and was found to range from approximately 4 to 8 μmol $m^{-2} s^{-1}$ (Cechin & Press 1993). Models based on growth and gas exchange measurements suggest that *S. hermonthica* may be unable to maintain any appreciable positive carbon balance in the absence of carbon from the host (Graves *et al.* 1989, 1990, 1992). A combination of foliar stable carbon isotope ($\delta^{13}C$ values) and gas exchange measurements allows quantification of carbon transfer from the $C_4$ host to the $C_3$ parasite (Press *et al.* 1987*a*; Cechin & Press 1993; but see Press *et al.* 1991). The proportion of heterotrophic carbon in mature leaves of *S. hermonthica* was negatively correlated with parasite photosynthetic activity, and ranged from 6 to 27% (Cechin & Press 1993).

By using this approach, Marshall *et al.* (1993) demonstrated that in eight Australian mistletoe associations, between 5 and 21% of parasite carbon was host-derived. Combining measurements of the concentration of carbon in xylem sap with measurements of parasite transpiration rates, Richter & Popp (1992) suggested that between 23 and 43% of the carbon in *Viscum album* was host-derived. In *Phoradendron juniperinum* (Loranthaceae) parasitising *Juniperus ostersperma*, 62% of parasite carbon was estimated to be host derived, using both the sap analysis-transpiration and $\delta^{13}C$-gas exchange approach (Marshall & Ehleringer 1990). Similarly, high proportions of host-derived carbon were estimated for mistletoes growing in the Namib desert (Schulze *et al.* 1991). It seems likely that the flux of amino and organic acids in the xylem would be insufficient to account for high levels of heterotrophy, and some of the mistletoes might also be in receipt of significant amounts of carbohydrate (Schulze *et al.* 1991). Pate and co-workers have shown this to be the case in root hemiparasites, and that the form in which carbon is transferred is host dependent: in an elegant study of the root hemiparasite *Odontites verna* (Scrophulariaceae), Govier *et al.* (1967, 1968) demonstrated that the parasite received more than 90% of its carbon in the form of nitrogenous substances when the host was a legume, compared with an almost nitrogen free mixture of monosaccharides and organic acids with non-leguminous hosts. Diversion of carbon from the host accounts at least in part for the lower productivity of infected plants compared with uninfected individuals (Press *et al.* 1990; Seel *et al.* 1992). Our understanding of factors controlling carbon partitioning in parasitic angiosperm associations is rudimentary in comparison to those involving microbial organisms, and it would be of interest to know whether alterations in host carbon metabolism (see e.g. Press *et al.* 1990) result from passive processes (sink demand by the parasite) or active intervention.

### (*b*) *Solute specificity of plant feeders*

The extent to which parasitic angiosperms control the nature of solutes received from the host is uncertain. Several studies suggest a lack of specificity, for example: the accumulation of host specific polyols in *Viscum album* parasitizing different hosts (Richter & Popp 1992); the accumulation of host specific alkaloids in *Castilleja sulphurea* (Scrophulariaceae) parasitizing *Lupinus argenteus* (Arslanian *et al.* 1990); and the accumulation of sulphur, manganese or sodium in *Dendrophtoe falcata* (Loranthaceae) parasitizing hosts which accumulate these elements (Glatzel 1987*a*). In many instances the diversity and concentration range of solutes which parasitic taxa encounter is remarkable, and probably exceed those of many 'free-living' angiosperms. Quantitative differences between host and parasite tissues and sap suggest, in contrast, that there may be some selective uptake across the haustorium (see, for example, Lamont & Southall 1982; Lamont 1983; Glatzel 1983; Goldstein *et al.* 1989; Pate *et al.* 1991*b*). Comparisons between solutes are difficult because they do not take into account factors which could alter the ratio of solutes in host and parasite, such as the magnitude of the flux between host and parasite, recycling within the parasite, foliar leaching and leaf abscission (J. S. Pate, personal communication). However, studies by Pate and co-workers (Govier *et al.* 1967, 1968; Pate *et al.* 1991*b*), suggest that in some root hemiparasites at least, certain host xylem solutes (both inorganic and organic) are transferred directly to the parasite xylem, while others are either not transferred or are metabolized within the haustorium. Studies on the haustorium of *S. hermonthica* using low and high molecular mass dyes as tracers, together with enzyme histochemistry, support an active role of the haustorium in metabolizing some solutes obtained from the host (P. S. Mallaburn 1992).

### (*c*) *Xylem sap signals*

It seems likely that abscisic acid (ABA) plays an important role in root-to-shoot communication, signalling the effects of soil drying (Zhang *et al.* 1987; Zhang & Davies 1989; Davies *et al.* 1990; Davies & Zhang 1991). In intact leaves of *Striga hermonthica*, stomatal aperture is relatively unresponsive to ABA (Shah *et al.* 1987), in contrast to the situation observed in epidermal strips (Smith & Stewart 1990). This anomaly may be explained at least in part by the modulatory effects of high foliar concentrations of potassium ions, the most important cation involved in altering guard cell turgor (MacRobbie 1991), since responses to ABA in epidermal strips were damped in the presence of high concentration of this ion. Accumulation of potassium ions is a consistent feature of hemiparasitic angiosperms. Concentrations can exceed those in the host by a factor of more than twenty (Lamont 1983), and potassium enrichment is greater than that seen for most, if not all, other inorganic ions. It is, however, perhaps rather simplistic to interpret stomatal behaviour in intact *Striga* leaves solely with respect to potassium ions, since other ions, particularly calcium, can play an important regulatory role (Mansfield *et al.* 1990).

In some circumstances stomatal closure is observed in *Striga*, for example, in response to severe soil drying. Stomatal closure in the parasite always occurs after that in the host, with parasite recovering before host following rewatering (M. C. Press, unpublished results). Root-sourced ABA can induce stomatal closure in 'free-living' plants, and since *Striga* has only a vestigial root system, it has yet to be determined whether stomatal closure results from ABA synthesized in the parasite (root or shoot) or the host. High concentrations of xylem sap ABA have been measured in *S. hermonthica* parasitizing sorghum, from both well watered (100–160 $\mu$mol m$^{-3}$ ABA) and water-deprived (290–470 $\mu$mol m$^{-3}$ ABA) plants (I. Cechin, W. E. Seel, W. J. Davies & M. C. Press, unpublished results). These exceeded host xylem sap ABA concentrations by an order of magnitude. Stomatal sensitivity to ABA varies both between species, and within species, in response to factors including water status (Tardieu & Davies 1992), nutritional status (Schurr *et al.* 1992) and the concentration of cytokinins (Fußeder *et al.* 1992). These factors may influence guard cells directly (e.g. through changes in flexibility (Kondo & Maruta 1987)) or indirectly via sequestration (e.g. in the chloroplast, (Davies *et al.* 1990)). Bulk leaf ABA concentrations in *S. hermonthica* were also high (*ca.* 2500 nmol g$^{-1}$ dry mass). It could be that release of sequestered ABA (at lower water potentials) accounts for increases in xylem sap ABA concentration and stomatal closure in the hemiparasite. The whole question of parasite responses to signals generated within the host plant is intriguing. Further information on the dynamics of abscisic acid in these plants would be desirable especially in the light of differences between parasite and host nutrient and water relations.

Movement of other plant growth regulators has been demonstrated from host to parasite. Giberellins are readily translocated, as demonstrated by the rapid elongation of *Orthocarpus purpurascens* (Scrophulariaceae) internodes following application of giberellic acid to cut stems of the host (Atsatt 1983). Closer relationships between the types and concentrations of cytokinins in the xylem sap of mistletoes and their hosts have been reported in mimicking compared with non-mimicking situations (Hall *et al.* 1987). Convergent leaf morphology may be attributable to 'genetic selection for hormonal compatibility during the process of adaptation to (the) host' (Atsatt 1983). However, *Dendrophthoe glabrascens* (Loranthaceae) will parasitize numerous host species (mainly in the genera *Eucalyptus* and *Melaleuca*), and sometimes with a strong pattern of convergence between mistletoe and host leaf form (Atsatt 1983), which may be attributable to the movement of plant growth regulators from the host.

Root hemiparasites from the Scrophulariaceae keep their stomata partly open at night (Press *et al.* 1987*b*, 1988, 1993). Greater nocturnal stomatal closure is observed in the green leafy mistletoes (Ullmann *et al.* 1985). It is of interest that this pattern of stomatal behaviour is not reversed in mistletoes parasitic on hosts performing Crassulacean acid metabolism (CAM) (Schulze *et al.* 1991), in which the metabolic pathways mediating diurnal opening and nocturnal closing of stomata are either lost or inhibited (Lee & Assmann 1992). The lack of synchrony between host and parasite behaviour suggests some independence from metabolic signalling within the host. Electrical signalling has been shown to be responsible for the systemic induction of proteinase inhibitors in wounded tomato (Wildon *et al.* 1992). If such signals are propagated symplastically via plasmodesmata, as suggested by Wildon and co-workers, then the apparent absence of symplastic continuity between host and parasite might isolate the parasite from such signals. Systemic changes in surface electrical potentials have also been identified in response to wounding, and may result from hydraulic signals (Malone & Stanković 1991; Malone 1992). Such signals would move apoplastically and thus a critical feature determining their perception by the parasitic angiosperm might be the resistance of the haustorium.

### (*d*) *Nutrition of animal feeders*

It has been suggested that for some Homoptera, xylem feeding provides a source of water rather than nutrients and is engaged in only when water balance is disturbed (Raven 1983). A number of Cicadellidae (other than the Tetigellinae and the euscelids discussed above) do appear to be facultative xylem feeders (e.g. *Orosius argentatus* (Day *et al.* 1952), *Empoasca flavescens*, (Carle & Moutous 1965), *Empoasca fabae*, *Macropsis trimaculata* (Putman 1941), *Nephotettix* (Khan & Saxena 1984)) together with some Delphacidae (*Niliparvata lugens* (Sogawa 1970); *Dicranotropis hamata* (Hill 1976)). The case of *Nephotettix virescens* is particularly interesting because biochemical evidence suggests that it is a xylem feeder on resistant varieties of its principal food plant rice, but a phloem feeder on susceptible varieties (Auclair *et al.* 1982). This was confirmed by Khan & Saxena (1984) using safranine dye translocated in xylem vessels and reappearing in the insect excreta.

Facultative xylem feeding may not be confined to the Auchenorrhyncha. Spiller *et al.* (1990) have reported evidence from electrical recording of plant penetration by aphids (*Aphis fabae*) which may be consistent with xylem feeding following dehydration. Cull & van Emden (1977) predicted that aphids feeding on phloem sap by day may suffer osmotic stress, but suggested that this may be alleviated by feeding on the less concentrated xylem sap at night. If

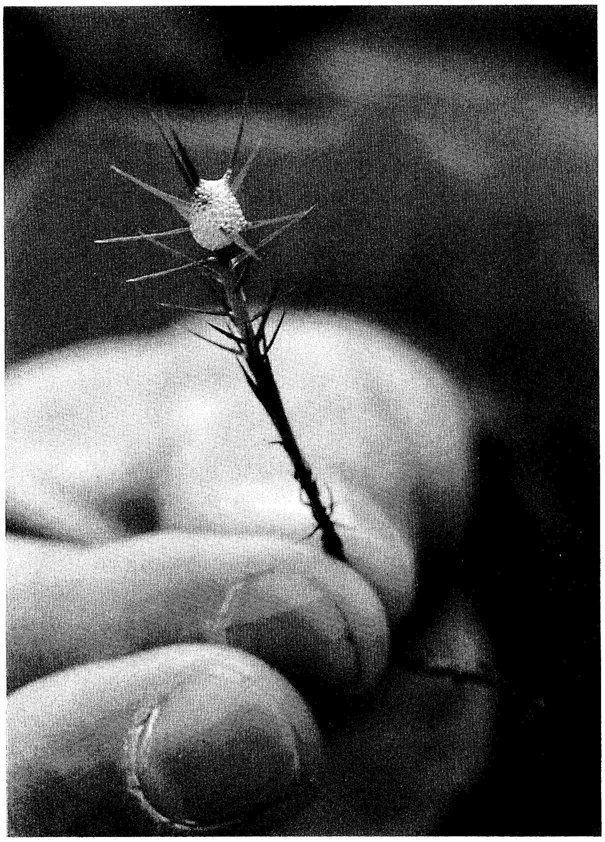

Figure 3. Spittle produced by *Neophilaenus lineatus* nymph feeding on *Polytrichum commune* on 30 June.

they, and perhaps some Auchenorrhyncha, do restore water balance by feeding on xylem it would be expected that, in the absence of a strong cibarial pump, they could do this only at night when xylem sap was under reduced tension or even positive pressure (but see above).

As yet, no studies of diel rhythms in feeding rates of xylem feeders such as *Philaenus spumarius*, or facultative feeders such as aphids and Auchenorrhyncha lacking cibarial pumps, have been published. They would be instructive both in view of the expected diel changes in xylem sap tension (Raven 1983) and diel changes in the chemistry of xylem exudate reported by Andersen & Brodbeck (1989).

Most of the xylem feeding Homoptera for which food plants are known are polyphagous. *Philaenus spumarius*, predominantly but not exclusively a dicotyledon feeder, is highly polyphagous. Weaver & King (1954) recorded 384 host species to which many more may now be added (e.g. Halkka *et al.* 1967). *Neophilaenus lineatus*, although largely restricted to monocotyledons can feed on a number of species of grasses and rushes. Other British Cercopidae are recorded from a number of food plants (le Quesne 1965), though none feeds so widely as do *P. spumarius* and *N. lineatus*. Similarly, nymphs of *Magicicada septendecim* (Cicadidae) were shown by Lloyd & White (1987) to be capable of feeding on almost any small rootlet, whether gymnosperm, angiosperm, monocotyledon or dicotyledon.

The tettigellid *Homalodisca coagulata* is highly polyphagous (Brodbeck *et al.* 1990), though, like *P. spumarius*, there is a distinct seasonal preference for different hosts, hoppers moving from plant to plant during the season in concert with changes in amino acid concentrations. Feeding may take place from shoots (even at several metres height in trees) or from roots despite Raven's (1983) demonstration that it is easier to remove xylem sap from roots than from shoot apices. Root xylem sap has a higher organic content than most shoot xylem sap and there is a smaller tension to be overcome to extract it (Raven 1983). There appears in practice to be a trade-off between the advantages of enriched sap and the physical problems of penetrating xylem vessels, which may be further from the external surface and protected by trichomes and perhaps root hairs (Hoffmann & McEvoy 1985). Experiments in which concentrations of amino acid in xylem sap were manipulated (Horsfield 1977; Brodbeck *et al.* 1990) strongly suggest that host selection and rates of development and survival are positively correlated with amino acid concentrations. Feeding sites of Cercopidae may also be influenced by the need for nymphs to feed at sufficient rate to replenish evaporating spittle so as to avoid desiccation and exposure to predators (Whittaker 1970). Evaporative rates will depend in turn on the microclimate within the vegetation, which may differ markedly over short distances within the canopy (Whittaker 1970). It is thus extremely interesting to record the presence of well-formed spittles on the top 1 cm of *Polytrichum commune* in June, demonstrating that the vascular bundles and chemical composition of 'xylem' sap in this moss were adequate for feeding by *Neophilaenus lineatus*, a cercopid which normally feeds on grasses, sedges and rushes (figure 3).

## 4. THE TRANSPIRATION STREAM IN PLANT PARASITES

Transpiration rates have been measured for many hemiparasitic species from a large number of ecosystems, and are characteristically high in comparison to those recorded for associated 'free-living' plants. For example, transpiration rates for the Mediterranean species *Bartsia trixago* (Scrophulariaceae) and *Parentucellia viscosa* (Scrophulariaceae) ranged from 10 to 25 mmol $m^{-2} s^{-1}$, compared with rates of between 7 and 12 mmol $m^{-2} s^{-1}$ for six putative host species (Press *et al.* 1993). Similarly, high rates have been measured in other hemiparasites from the Scrophulariaceae (for examples, see Press *et al.* 1988, 1989; references cited in Govier *et al.* 1968). Large differences in transpiration rates have been found between mistletoes and their hosts; for 18 different associations in Australia, the quotient of host/parasite transpiration ranged from 1.5 to 7.9 (Ullmann *et al.* 1985). These high rates of water loss in mistletoes are associated with high diurnal stomatal conductances. At night, the hemiparasitic Scrophulariaceae differ from the mistletoes and 'free-living' plants (with the notable exception of CAM species) in maintaining high rates of stomatal conductance (see above), although rates of water loss will be much smaller than those recorded during the day because of higher atmospheric relative humidities and smaller vapour pressure deficits between the leaf and the atmosphere.

Elucidating the functional significance of high transpiration rates in hemiparasitic angiosperms has attracted some interest, particularly in the mistletoes. High transpiration rates will maintain a strong water potential gradient between parasite and host, and they have therefore been interpreted as an important mechanism for acquiring water and solutes from the host sap (see Fisher 1983; Stewart & Press 1990). In particular, they may be necessary to generate the water potential gradients required to allow transport of solutes across the haustorium (assuming such movement is passive or largely so). There have been few measurements of haustorial hydraulic resistance, but Glatzel (1987*b*) estimates it to be 'fairly large' in *Loranthus europaeus* (Loranthaceae), between two and four times that of the parasite shoot.

The water economy of mistletoes has been interpreted specifically with respect to the supply of nitrogen from the host (Schulze & Ehleringer 1984; Schulze *et al.* 1984; Ehleringer *et al.* 1985). Using $\delta^{13}$C values to assess water use efficiency (WUE), the photosynthesis/transpiration quotient, of a wide range of mistletoes growing on nitrogen-fixing and non-fixing hosts, it has been found that the mistletoes had a WUE closer to that of their host when a more concentrated source of nitrogen was available in host xylem sap. This has been interpreted as indicating that regulation of water use occurs in response to the concentration of nitrogen in the xylem stream (Ehleringer *et al.* 1985).

Nitrogen is an important component of photosynthetic machinery, and positive correlations between foliar nitrogen concentration and light saturated rates of photosynthesis have been reported in both 'free-living' and parasitic angiosperms (Field & Mooney 1986; Evans 1989; Cechin & Press 1993; Press *et al.* 1993). It is thus important to determine the extent to which the components of WUE (photosynthesis and transpiration) change, as differences could be accounted for by either higher rates of photosynthesis or lower rates of transpiration. Measurements of instantaneous WUE for *B. trixago* growing under field conditions in Mallorca on different hosts, show a positive linear correlation between light saturated rates of photosynthesis and foliar nitrogen concentration (Press *et al.* 1993). There was no clear relationship between the latter and either stomatal conductance or transpiration, although there was a positive (but non-significant) association between foliar nitrogen concentration and WUE, and this was dictated by higher rates of carbon dioxide fixation as opposed to lower rates of water loss. Differences between host and parasite WUE could not be determined in this study, since the parasites were supported by a number of different host species, a common situation for some root hemiparasites.

Givnish (1986) has further questioned the interpretation of the Ehleringer–Schulze hypothesis. Nitrogen fixation in the hosts of the Ehleringer *et al.* (1985) study had no significant effect on the $\delta^{13}$C value and inferred WUE of the parasite. The primary effect on the difference between host and parasite WUE was largely accounted for by differences in WUE between nitrogen fixing and non-fixing hosts. The relative constancy of $\delta^{13}$C in mistletoes on the two host types suggests that their high rates of water use may be set largely by the economics of water, not nitrogen, acquisition (Givnish 1986). In addition, the use of stable carbon isotope ratios to assess integrated water use efficiency (Farquhar *et al.* 1982) may be inappropriate here because of the likely contribution of at least some heterotrophic carbon from the host plant. Thus the $\delta^{13}$C value of parasite leaf tissue will not only reflect the substomatal/ambient partial pressure of carbon dioxide of the parasite, but also that of the host. Moreover, any relationship between parasite WUE and heterotrophic nitrogen supply can not be separated from WUE and heterotrophic carbon supply, because of some common sources of these two elements in xylem sap solutes. Thus the economics of water use may be driven by requirements for host carbon as well as, or instead of, nitrogen.

High rates of transpiration may not necessarily result in greater fluxes of solutes to the shoot. In the humid tropics, plants grow at extremely high humidities and growth and foliar ion acquisition are not depressed, despite low rates of transpiration (see Grubb 1977). In laboratory experiments, no differences in growth rate or foliar element concentrations were observed in maize grown under different relative humidities, despite up to a three fold difference in transpiration (Tanner & Beevers 1990). This may be explained by the inverse correlation between transpiration rate and the concentration of solutes in the xylem sap (Smith 1991): Shaner & Boyer (1976*a*,*b*) demonstrated that the flux of nitrate to barley leaves was virtually constant over a two fold range of transpiration rates, and Schulze & Bloom (1984) found net ammonium and nitrate influx to radish and tomato leaves to be independent of transpiration rate.

The flux of xylem solutes to the leaf is a function of both the concentration of solutes in xylem sap and transpiration rate. These variables will be species dependent, and may in turn be a function of relative growth rate (see Porter & Lawlor 1991). Thus the water economy of the parasite may be determined by the growth rate of the host. This may account for the similarity in growth and photosynthesis between certain hemiparasitic Scrophulariaceae parasitizing nitrogen fixing legumes and some fast growing grasses (W. E. Seel & M. C. Press, unpublished results). Control of stomatal conductance in hemiparasites may be mediated at least in part by foliar potassium ion concentrations. Those factors which determine the foliar potassium ion concentration (see above) could account for high stomatal conductances in hemiparasites. Water use above a certain threshold may therefore confer no benefit on the hemiparasite and may instead be an inevitable consequence of a partially heterotrophic lifestyle.

## 5. CONCLUDING REMARKS

Xylem feeders possess many features which distinguish them from non-xylem feeders at the anatomical, physiological, biochemical and molecular level (see references cited in Press *et al.* 1991). Similarities may be drawn between the functional significance of such adaptations in animal and plant feeders, for example, high feeding rates and high transpiration rates (Anderson *et al.* 1989; Stewart & Press 1990). There are also important differences between the two groups, for example, the permanency of plant associations compared to insect associations. Many of the questions posed by Raven (1983) are still pertinent today, for example, regulation of the interaction between host plant and xylem feeder, and a deeper understanding of the transpiration stream in plants should stimulate research on the biology of both plant and animal xylem-feeding organisms. In addition the converse is also true, and xylem feeding organisms may be used as model systems to probe the function of the transpiration stream.

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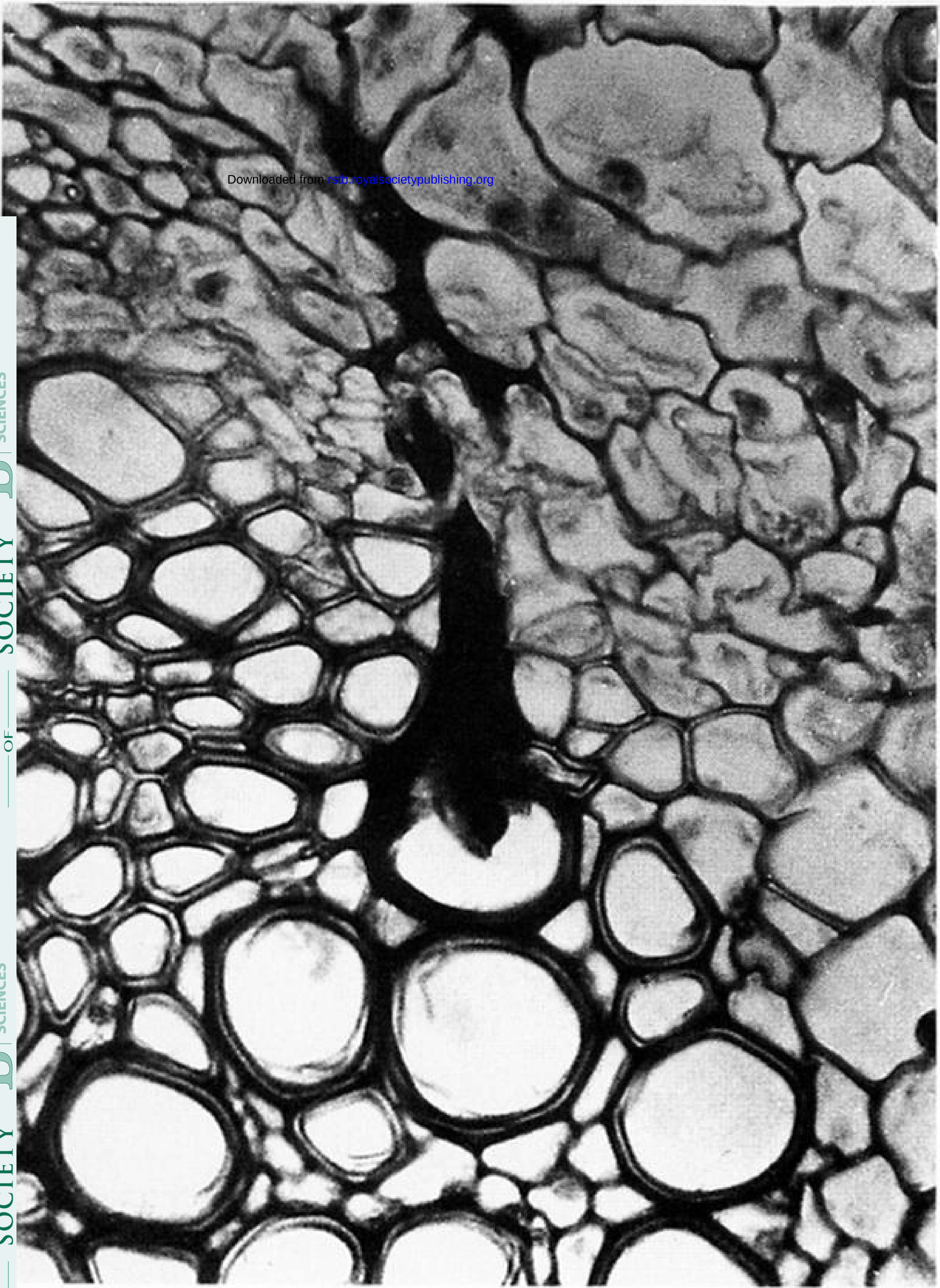

gure 1. Transverse section of the stem of *Pisum sativum* with e terminal part of the salivary sheath of an instar 3 nymph *Philaenus spumarius* extending through the wall of a xylem ssel. × 400. By kind permission of D. Horsfield.

gure 3. Spittle produced by *Neophilaenus lineatus* nymph feeding on *Polytrichum commune* on 30 June.