THE XYLEM AS A TARGET FOR HEMIPTERAN HERBIVORES

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The aim of this presentation is to describe the main physiological features of the xylem transport system, highlighting those aspects that affect the interaction with sap feeding hemipeterans. Plants, like animals, have a well developed and sophisticated transport system. Unlike the simple low pressure system in animals, the plant circulation system is comprised of a high pressure phloem integrated with a low and high pressure xylem. The anatomy, composition, biochemistry and biophysics of both xylem and phloem dominate interaction with those herbivores who would exploit the particular plant resource. The adaptations possessed by herbivores that access and feed from the xylem will be discussed in relation to the physiology of the xylem.

Structural features

Mature xylem consists of strong lignified/subersised tubes that form large open conduits for efficient transport of water and dissolved components. Such lignifications provide a mechanical barrier for any herbivore that exploits this conduit. The structure if the stylets appears more robust and the mechanism of feeding site location appears less sophisticated in exclusive xylem feeders compared to herbivores that mainly feed from the phloem.

Diet composition

Unlike the phloem individual xylem tubes are dead and have no direct membrane to regulate composition. Classically xylem is thought to transport sap of low concentration, with little or no organic content and particularly low in reduced nitrogen making it a poor diet for herbivores. Despite the direct association with a membrane, xylem composition can be tightly regulated. The casparian strip in the root endodermis necessitates the membrane passage of water and solutes entering the stele and so the xylem, thus providing a potential point of regulation for the plant. Once in the xylem, composition of sap moving up to the leaves is altered by active uptake into parenchyma and mesophyll cells. In addition the concentration of solute in xylem sap can vary by two orders of magnitude diurnally. However overall the dogma is that the xylem provides diet of low in carbon and nitrogen. Feeding studies indicate that xylem herbivores process large volumes of sap and are able to efficiently extract organic solutes.

Negative pressure

While flow in the sieve tubes is under the driven by high pressure generated osmotically, flow in the xylem during the day is driven by evaporation from open stomatal pores generating a negative tension in leaf cell wall water that is transpired by the cohesion of water into the xylem vessels and ultimately the root. This combination of cohesion and tension can generate huge negative pressure within the xylem fluid which can amount to minus 2-3 MPa. Overcoming this negative pressure requires adaptations from any herbivore that

can generate at least an equivalent negative pressure adding an additional energetic cost to xylem feeding during the day. The specific structure of the cibaral pump allows generation of sting 'suction' necessary for xylem feeding.
The negative pressure in the xylem represents and additional hurdle for a putative xylem feeding herbivore. Water under tension is under a meta stable state and xylem sap columns can snap cavitating the xylem and stopping transport. Cavitation is a serious problem for plants and can limit their distribution in xeric or freezing environments. It presents a serious problem for the xylem herbivore attempting to feed since introduction of feeding stylets would be expected to induce cavitation. However, current data suggests that many hemipteran are able to feed from xylem under tension, the mechanism by which they avoid cavitation have not yet been determined.

A variable food source?

At night or under low evaporative demand stomata shut and xylem pressures rise. During the night solutes are actively transported across the endodermis into the stele generating high osmotic pressure and therefore turgor. Under these conditions xylem pressures can reach 2 or 3 MPa positive pressure with sap containing many solutes. Under these conditions xylem sap represents a more favourable food source. However data on the diurnal feeding behaviour of xylem herbivores is not extensive. However it is clear that xylem feeding during the day under low pressure low concentration conditions is clearly undertaken.

Hemipteran osmoregulation

There are clearly hemiptera that have adapted to feed perhaps exclusively in the difficult environment of the xylem. However, detailed examination of the feeding behaviour of apparently exclusively phloem feeding hemipterans such as the aphids reveals that not only do they feed from the high pressure, low water potential environment of the sieve tube but also access the physically and chemically very different xylem. Indeed, the need for osmoregulation imposed by the high osmotic pressure of the phloem may require some rehydration from the xylem. The need for in apparently exclusively phloem feeding aphids explains why aphicides such as thiomethoxan (TMX) that are transported in the xylem can reduce aphid performance and open the possibility that novel control strategies could focus on herbivore osmoregulation mechanisms.