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ECOPHYSIOLOGY OF THE SAND SEDGE, CAREX ARENARIA L. III. XYLEM TRANSLOCATION AND THE OCCURRENCE OF PATCHES OF VIGOROUS GROWTH WITHIN THE CONTINUUM OF A RHIZOMATOUS PLANT SYSTEM

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SUMMARY

The older shoots on the rhizome of the sand sedge have a lower waterpotential than the younger ones closer to the rhizome tip. The xylem translocation stream, that runs through the rhizome in accordance with the gradient in waterpotential from tip to base, could be demonstrated in translocation experiments with acid fuchsine dye and lead (EDTA) chelate.

The occurrence of patches of vigorous growth within the continuum of a sand sedge plant system can be explained by the properties of the xylem translocation system of the plant.

1. INTRODUCTION

The shoots of a sand sedge plant system are all connected by means of a rhizome through which a phloem translocation stream runs towards the rhizome tip (NOBLE 1976, TIETEMA & VROMAN 1978, TIETEMA 1980). Since the exploring growth of the rhizome tip is thus supported, the plant can be expected to invade new habitats continuously. In the field this invading growth habit has indeed been confirmed in a number of instances (VAN DIEREN 1934, TIDMARSH 1939, STEUBING 1949, NOBLE 1976). Sometimes, however, the sand sedge does not leave a distinctly localized spot in which it is growing vigorously (Kers, personal communication and own unpublished observations). Such local growth responses of a sand sedge plant system were experimentally caused by the local application of nutrients in the field (NOBLE 1976).

The present study deals with the physiology of the local reactions of a sand sedge plant system to the occurrence of favourable spots in the environment. As it is unlikely that these reactions are caused by insufficient phloem translocation towards the rhizome tip (TIETEMA 1980), an investigation was made on the distribution of water and minerals within the plant system.

2. MATERIALS AND METHODS

2.1. Plants and plant culture

Sand sedge plants were cultured in nutrient solution, as previously described (TIETEMA 1980). In the present experiments the five-shoot plant system was used as a standard plant (*fig. 1*).

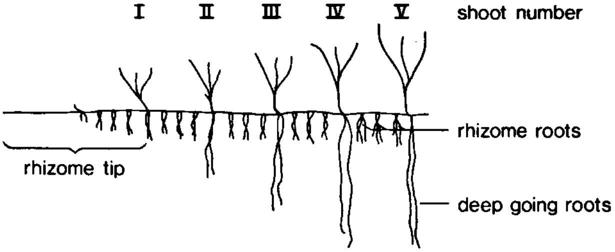

Fig. 1. The five shoot standard plant system of the sand sedge, used in these experiments. The shoots are indicated by roman numerals from young to old. The deep-going roots have the same number as the shoot at whose base they emerge. The entire plant part in front of shoot I is called the rhizome tip.

2.2. Determination of the waterpotential of the shoots

The waterpotential of the shoot (ψ_{shoot}) is the sum of the negative pressure in the xylem (P_{xyl}) and the osmotic potential of the xylem sap (π_{xyl}) (SLAVIK 1974). The negative pressure in the xylem of the shoots was determined with a pressure bomb (SCHOLANDER et al. 1965). The osmotic potential of the droplet of xylem sap, that appeared during the pressure bomb measurement, was measured with a Wescor HR-33T Dewpoint psychrometer.

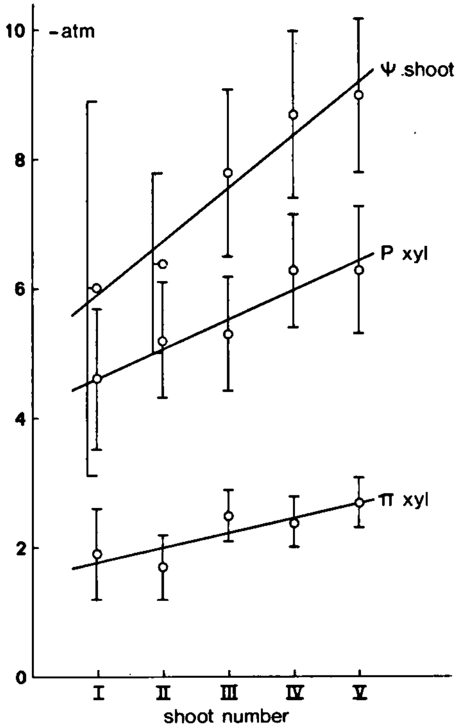

Fig. 2. The waterpotential of the shoot (ψ_{shoot}), the pressure in the xylem (P_{xyl}) and the osmotic potential of the xylem sap (π_{xyl}) in the various shoots on the rhizome. Vertical bars indicate 95 % confidence limits.

To avoid systematic errors the waterpotential was determined on 25 shoots, shoot I was in five cases the first shoot to be cut off from the plant system, in five cases the second, in five cases the third, etc.

2.3. Direct determination of xylem translocation through the rhizome with acid fuchsine dye

Since acid fuchsine does not enter the intact root, the tips of the root system to be treated were cut off under water and transferred to an aqueous solution of 2% acid fuchsine. After 24 hours the experiments were stopped; the shoots of the plant system treated were cut off and inspected on the presence of the dye visually. The procedure was repeated five times on each individual root system.

2.4. Direct determination of the xylem translocation through the rhizome with lead (EDTA) chelate

Lead (EDTA) chelate, prepared according to TANTON & CROWDY (1972) was supplied twice to the root systems I, III and V of a standard plant system. The lead chelate was supplied during 24 hours; then the plant system was divided into the separate plant parts and dried in an oven at 90°C. After determination of the dry weight, the plant parts were mineralized at 500°C during 24 hours and solubilized in 2 ml 3N HCl. Lead content was determined by atomic absorption spectrometry.

3. RESULTS

The waterpotential of the shoots (ψ_{shoot}) and its constitutive components, the negative pressure in the xylem (P_{xyl}) and the osmotic potential of the xylem sap (π_{xyl}) were all higher in younger shoots than in older ones (*fig. 2*). The lower ψ_{shoot} in older shoots implicates the possibility of xylem translocation through the rhizome towards the older shoots. The existence of such a translocation stream could be demonstrated in the translocation experiments with acid fuchsine (*fig. 3*) and in those in which lead chelate was fed to the plants (*fig. 4*).

Both kinds of experiments show the absence of xylem translocation from the roots of shoot V to the rest of the plant system (*figs. 3e* and *4c*) and the allover distribution of the xylem components absorbed by the roots of shoot I (*figs. 3a* and *4a*). Although some dye was translocated from shoot III to younger shoots (*fig. 3c*), examination showed that the export to younger shoots is quantitatively negligible (*fig. 4b*) and that xylem constituents originating from this shoot are predominantly translocated to the older shoots. Since similar results were found in both types of translocation experiments, we assume that the removal of the root tips in the acid fuchsine experiments did not seriously affect the distribution pattern of xylem translocation.

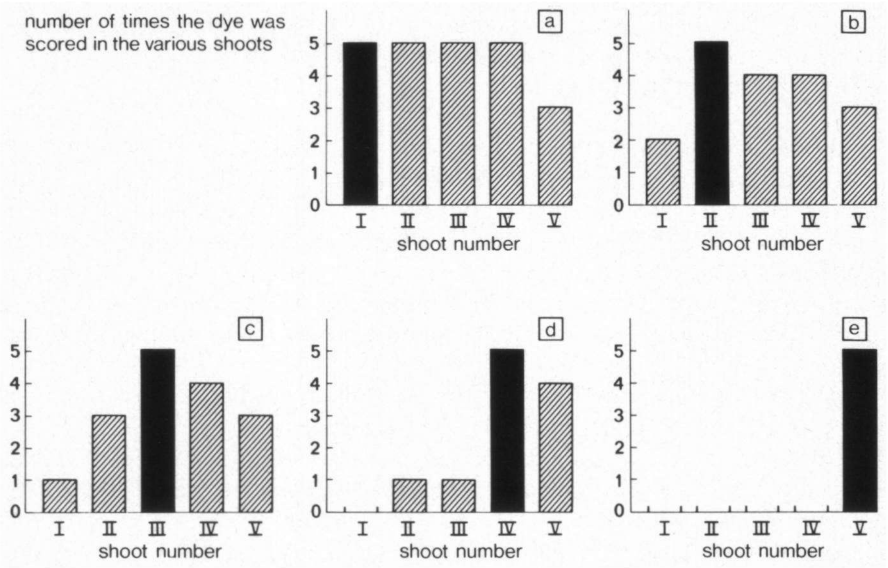

Fig. 3. The distribution of acid fuchsine dye in the various shoots after application of the dye to the roots of the successive shoots. The solid column indicates the shoot to whose roots the dye was supplied; the hatched columns indicate the number of times the presence of the dye had been scored in the various shoots.

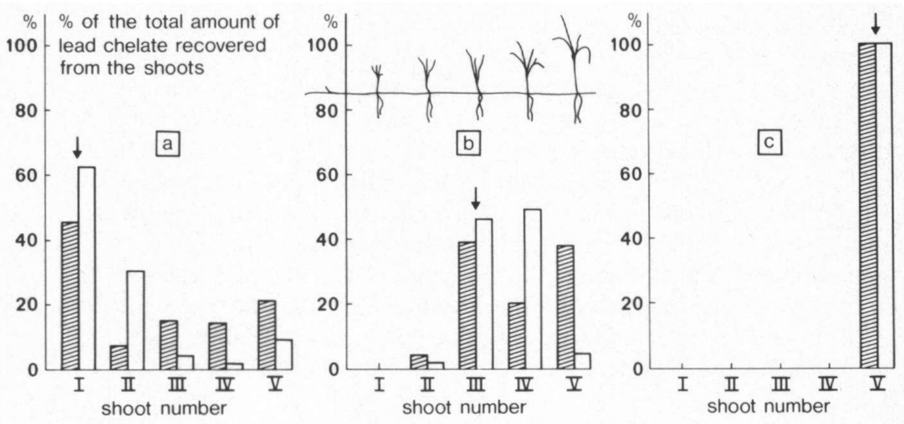

Fig. 4. The distribution of lead (EDTA) chelate in the various shoots, after application of lead chelate to the roots of shoot I (a), shoot III (b) and shoot V (c). Each series of columns corresponds with a single plant system.

4. DISCUSSION

4.1. The functional relation between the individual shoot and its root

Generally a close balance exists between the activity of shoot and root, which may be interpreted as a functional equilibrium of the plant (Brouwer 1962). In this equilibrium the shoot supplies its root with assimilates and the root supplies its shoot with water and minerals. In a rhizomatous plant such an equilibrium may well exist, as far as the whole plant system is concerned, but there is no close relationship between a single shoot and its "own" root. The presence of a xylem translocation stream through the rhizome in basal direction (*figs. 3* and *4*) implies that the root system of a single shoot not only feeds its own shoot with water and minerals, but also other ones. In addition shoots have also been reported to support more than their own roots with assimilates (Tietema 1980; Noble 1976).

4.2. The waterpotential gradient in the rhizome

The lower ψ_{shoot} in the older shoots as compared to the younger ones, results in a flow of water and solutes through the rhizome from younger to older shoots. Since transpiration is usually the driving force for solution flow in the xylem (Zimmerman 1974), this implies that the increased requirement for water by the older shoots, due to their larger leaf area is not adequately fulfilled by their "own" roots.

The roots that are assumed to be the main source of water for the shoots are the deep-going roots emerging at the base of each shoot (*fig. 1*). Each shoot has two of these deep-going practically unbranched roots. Most of the water is assumed to be absorbed by the first centimeters of the root (Robards et al. 1979). Consequently, even though the deep-going roots grow linearly in length, the absorbing surface is not concomitantly increased. The length of the water translocation pathway, from root tip to shoot, however, is five times longer in shoot V than in shoot I. Probably the resulting increase in resistance to water flow forms an additional cause for the decrease in ψ_{shoot} along the rhizome in basal direction.

This may explain comparable distributions in waterpotential reported by Slavíková (1973) for complex polycormons of several rooted "individua" of *Cynodon dactylon* (L.) Pers.

4.3. The occurrence of patches of vigorous growth within the continuum of a sand sedge plant system

After a local supply of minerals, Noble (1976) observed only a localised response in growth along the sand sedge rhizome. Kers (personal communication) found similar situations in the field. In the "Otterloose Zand" (The Netherlands) he found sand sedge plants growing vigorously in a restricted area, 1.2 m above the isolated remains of a B horizon. The particular section of the plant system growing above the remains of this B horizon did not seem to export the beneficial factor from that place to plant parts growing in less favourable circumstances within one metre.

A possible explanation of the observations of NOBLE (1976) and Kers (personal communication), based on the translocation phenomena presented above is schematically shown in *fig. 5*. The apical part of a rhizome growing in poor circumstances will show a water and mineral distribution pattern in which the xylem sap flows from the rhizome tip to the base of the rhizome (*fig. 5a*). When the tip grows through an area in which more water and/or minerals are available, the minerals absorbed by the roots growing in this area, will also be distributed in

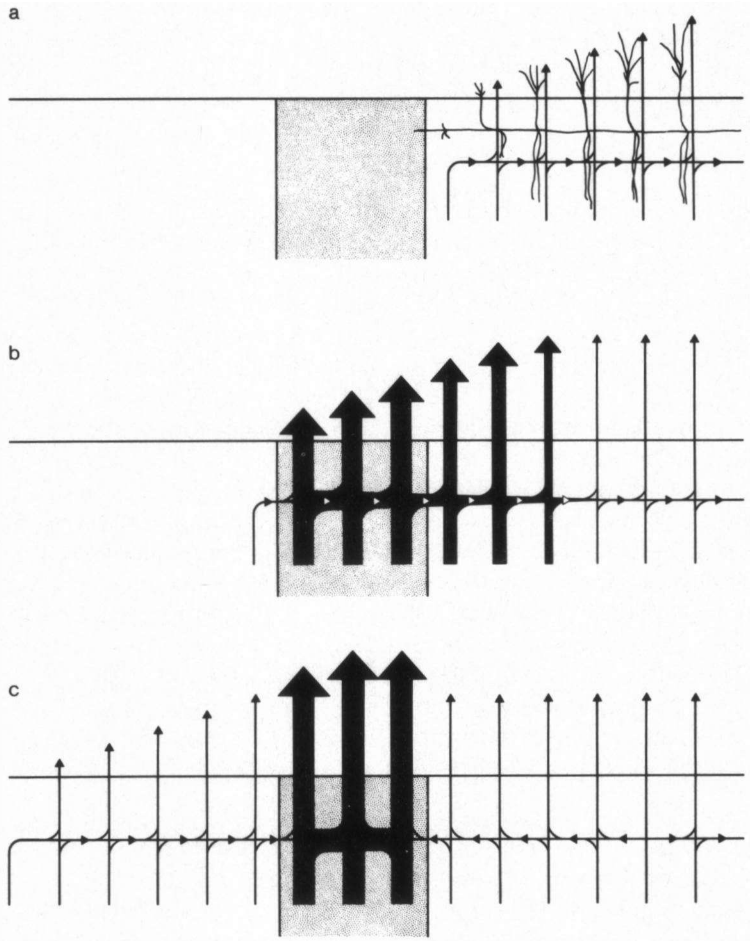

Fig. 5. The changes in water and mineral distribution in a plant system of a sand sedge, when growing through an area with a high nutrient status. The arrows indicate the direction of flow in the xylem; the length of the arrow indicates the water demand of a shoot, the width of the arrow indicates the nutrient status of the xylem translocation stream. The stippled soil part is the nutrient rich area. For further explanation see text.

the adjacent part of the plant system (*fig. 5b*). The main part of the water and minerals absorbed by the well fed roots will be translocated to their own shoots (*figs. 4a* and *4b*). The rest will be distributed over nearby, basally situated shoots. Their high nutrient status will cause an increased growth rate of the well fed shoots. They will become larger and have a larger leaf area than the more basally situated older shoots. The larger leaf area of the well fed shoots will increase their water demand and lower the ψ_{shoot} as compared with that of the shoots growing in the less favourable situation. Simultaneously the growth of the roots in the well fed section will fall behind in comparison to "their" shoots (NOBLE 1976). This is an additional cause in lowering ψ_{shoot} in the well fed situation. Once the ψ_{shoot} is lower than that in the older shoots on the rhizome, the flow of the xylem translocation stream through the older part of the rhizome will be reversed and will be directed apically to the well fed plant part (*fig. 5c*).

Thus if a rhizome passes through an area rich in water and/or minerals, this will induce a water translocation stream through the xylem of the rhizome directed to the well fed part of the rhizome system. The beneficial influences of the source of water and/or minerals encountered by the plant system will thus remain restricted to the plant part situated directly above the source.

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