

Xylem pathways in rose plants in relation to basal shoot development

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SUMMARY

Application of dyes to roots or shoots is an easy way to visualize xylem pathways in plants. It was shown that upward transport was sectorial straight. A main root appeared to contribute to the transport to several basal shoots. Application of dyes to shoots showed that each basal shoot is supplied by only a part of the root xylem. It is supposed that at the moment of appearance of a new basal shoot, the root xylem becomes enveloped by a new xylem cylinder, resulting in a limited area of root xylem serving the former developed shoot. The large variation in shoot diameter in a rose crop is discussed in relation to xylem systems.

Key-words: dyes, root–shoot connection, *Rosa hybrida*, water transport, xylem pathways.

INTRODUCTION

In a rose crop, considerable variation in number and diameter of shoots occurs, resulting in variation in shoot yield. Little attention has been paid to water pathways in rose plants, apart from some work on cut rose flowers (Mayak *et al.* 1974; Dixon *et al.* 1988; Darlington & Dixon 1991). In several trees the pattern of water transport has been studied in relation to insect and disease control (Vité & Rudinsky 1959; Kozłowski & Winget 1963).

Vité & Rudinsky (1959) described five types of water-conducting systems in sapwood of conifers: (1) spiral ascent, turning right; (2) spiral ascent, turning left; (3) interlocked ascent; (4) sectorial, winding ascent; (5) sectorial, straight ascent. Kozłowski & Winget (1963) found no clear and consistent differences in patterns of water ascent between gymnosperms and angiosperms.

The xylem transport pathway and as a result the pathway of water movement in plants can simply be followed by using water coloured by dyes (Zimmermann 1978; Fisher & Ewers 1992). The movement of the dyes should not be hampered by the pathway construction and the concentration of dye should be sufficient so that any reactions which may take place along the pathway have no significant effect on the transport. Acid fuchsin has often been used for this purpose (Vité & Rudinsky 1959;

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Kozłowski & Winget 1963; Altus & Canny 1985), but also alcian blue, eosin and fast green (Altus & Canny 1985), toluidine blue-O (Shigo 1985), safranin and crystal violet (Fisher & Ewers 1992) appeared useful.

In the present study xylem pathways in rose plants were visualized to show: (1) the type of the water conducting system; (2) which shoots are connected to one root; and (3) which roots are connected to one shoot. This information may contribute to the explanation of the large variation in shoot diameters within plants and between plants in a rose crop.

MATERIALS AND METHODS

In a commercial rose crop, plants are propagated vegetatively by cutting or grafting a piece of stem bearing one leaf and an axillary bud. When propagated, the axillary bud grows into the so-called primary shoot. Later at the base of this shoot, basal buds sprout, which become strong growing shoots. These so-called basal shoots form the main frame of the plant. The part of the stem between the basal shoots and the roots, which was the piece of stem used for propagation, will be referred to as basal stem.

For our experiments we used more than 60 plants of *Rosa hybrida* cv. Sweet Promise and *Rosa hybrida* cv. Madelon, grown in a heated glasshouse for 1.5 years, having a primary shoot and one or two basal shoots. Plants were propagated by cutting or by stenting, i.e. grafting a piece of stem bearing a leaf and an axillary bud onto an internode as described by van de Pol & Breukelaar (1982). To show both the type of the water conducting system according to the classification of Vité & Rudinsky (1959) and which shoots were connected to one particular root, one main root (diameter at least 1 mm) was immersed in a dye solution in a vial. The remaining roots were kept in water or soil. As soon as the dye became visible in the veins of the leaves (after several hours), the experiment was terminated and the bark of the stem was removed to study the pathway of the dye.

To determine which main roots were connected to one shoot, the two or three shoots were cut transversely and vials, each containing a different coloured dye solution, were placed upside down on top of them (van de Pol & Marcelis 1988). Soil between the roots was removed as far as possible to promote evaporation. To distinguish effects of gravity, plants were held either upright or upside down. In some trials the roots were wrapped in aluminium foil in order to prevent them from drying out. As soon as the roots coloured, the experiment was terminated. The main roots were cut transversely and the basal stem was split longitudinally to show the pathway of the dyes.

Aqueous solutions of 1% acid fuchsin (Merck AG-Darmstadt no. 42685, colour red), 1% light green yellow (Merck AG-Darmstadt no. 1315, colour green) and 0.5% trypan blue (Merck Darmstadt no. 23850, colour blue) were used.

RESULTS

Dyes applied to both roots and shoots coloured only the xylem. Positioning of the plant (upright or upside down) did not affect the distribution of the dye. However, when roots were wrapped in aluminium foil, dye applied to the shoot did not move further than the root collar. Dye applied to a main root showed a sectorial, straight upward transport, even through the grafting area (Fig. 1a). Also, in transverse sections of the basal stem, the dye was found in a sector of the xylem. No deviations from a straight path were observed. A main root appeared to contribute to the transport to several basal shoots.

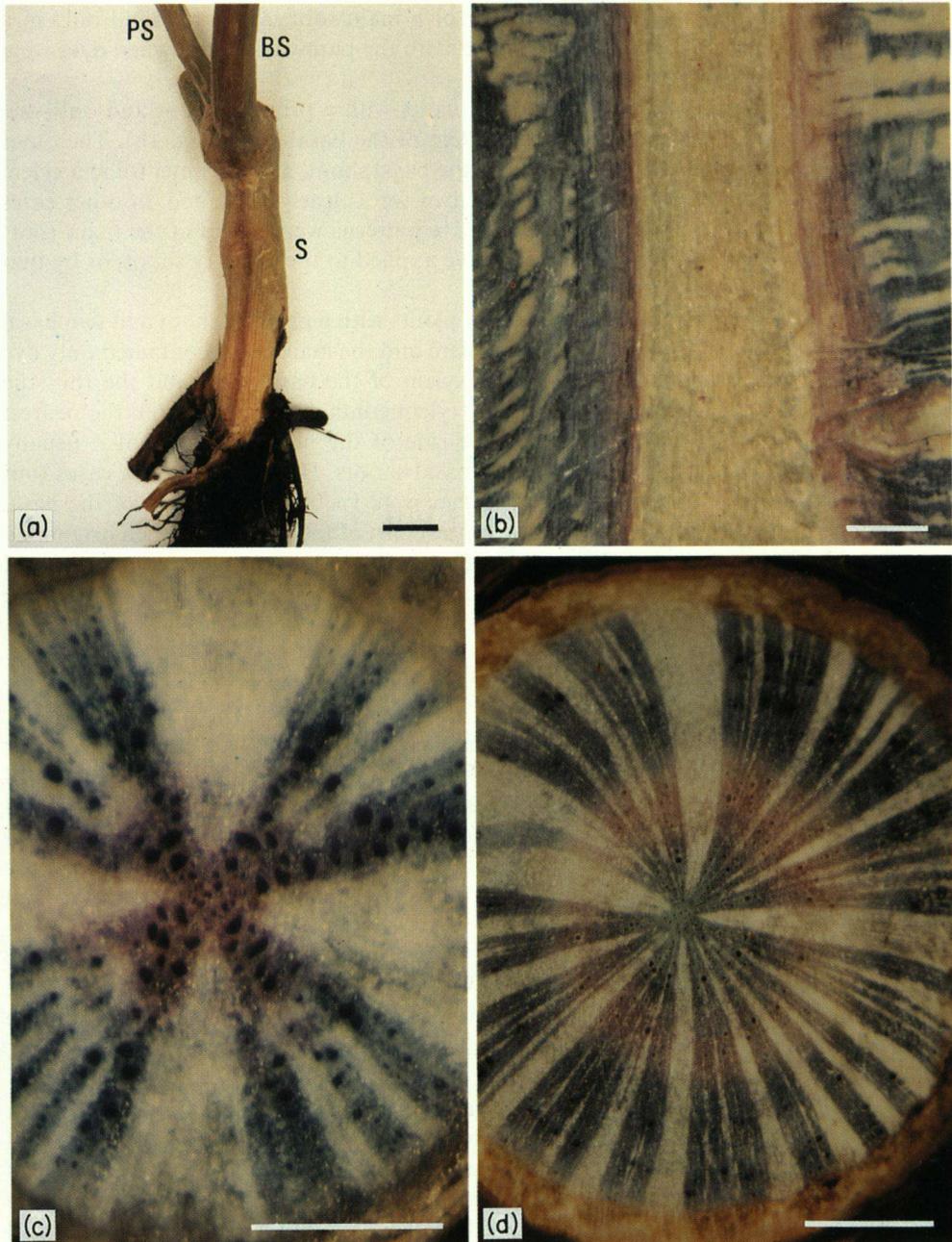


Fig. 1. (a) Sectorial dye pattern in the basal stem when red dye (acid fuchsin) was applied to a root. A slight bend in the path of the dye occurs at the grafting area, half-way up the basal stem. The bark was removed when the experiment was finished. PS: primary shoot; BS: basal shoot; S: basal stem, i.e. piece of stem used for propagation. Bar=1 cm. (b) Dye pattern in a radial longitudinal section of the basal stem, and (c) in a transverse section of a main root. The plant had a primary shoot and one basal shoot. Red dye (acid fuchsin) was applied apically to the primary shoot and blue dye (trypan blue) to the basal shoot. The pith and a part of the xylem of the basal stem were not involved in dye transport. Large vessels in the root appear as dark dots. (b) Bar=1 mm; (c) bar=0.5 mm. (d) Dye pattern in a transverse section of a main root of a plant having a primary shoot and two basal shoots. Green dye (light green yellow) was applied apically to the primary shoot, red dye (acid fuchsin) to the first basal shoot and blue dye (trypan blue) to the second basal shoot. Bar=1 mm.

However, when dye was applied to a sector of a main root, dye was found only in a sector of the xylem of a shoot, corresponding with the pathways found when dyes were applied to shoots (data not shown).

When dye was applied to both shoots of plants with a primary shoot and only one basal shoot, both dyes were found in the xylem of the basal stem (Fig. 1b). The outer (younger) xylem contained dye coming from the basal shoot, and the inner (older) xylem dye from the primary shoot. Sometimes the dyes were clearly separated, in other cases there was also a transitional region. Similar dye patterns were found in the main roots (Fig. 1c). Smaller roots were stained by the dye applied to the primary shoot, or by that applied to the basal shoot, or by both.

When dye was applied to all three shoots of plants with a primary shoot and two basal shoots, the inner (oldest) xylem of the basal stem and the main roots contained only dye applied to the primary shoot. In the outer xylem of the basal stem and the root the situation varied. In the basal stem the outer xylem contained the dye from the nearest basal shoot, i.e. from the shoot at the same side of the plant. In the root it usually contained only dye coming from one of the basal shoots. However, in a few cases (out of 20) three different coloured concentric zones were visible in the xylem of the basal stem and the root (Fig. 1d). The dye in the central part of the root xylem then originated from the oldest shoot (which is the primary shoot). The outer, youngest, zone contained the dye applied to the youngest shoot (which is the second basal shoot). The dye in the middle zone came from the first basal shoot.

DISCUSSION

By feeding a dye solution to a main root it has been shown that the type of water conducting system in rose is sectorial, straight ascent, according to the classification of Vité & Rudinsky (1959). A main root was found to contribute to the transport to several shoots. A shoot was found to be connected to a part of each main root. Comparison of the pathways visualized when dye was applied to (a part of) a main root and those visualized when dye was applied to shoots, support the assumption that upward and downward pathways are similar.

Kozłowski & Winget (1963) found that in trees a straight vertical pathway for water transport is not so common. Rudinsky & Vité (1959) noted that the most complete distribution of water in the plant was achieved by spiral ascent and the least effective distribution by vertical ascent. Dye was transported with little tangential spreading, which was also found in *Cayratia* by Fisher & Ewers (1992).

It is assumed that the discovered pathways represent xylem connections between shoot and root and show the preferred water pathways, which is in accordance with Fisher & Ewers (1992) who mentioned that dye flow indicates the fastest and most efficient pathway for water movement, although it is not the only one possible in the intact plant. Canny (1990), however, argued that due to diffusion the movement and distribution of dye through a plant does not always correctly reveal the pattern of water flow. In these experiments the movement of the dye stopped when roots were wrapped in aluminium foil, indicating that the movement was not due to diffusion but due to water flow driven by evaporation from the roots. As position of the plant did not affect the distribution of the dye, movement of the dye was not achieved by gravity. It was shown that the pith and the cortex tissues are not the preferred pathways for water transport through the stem, which is in accordance with Darlington & Dixon (1991).

In roses the first basal shoot emerges from a basal axillary bud of the primary shoot, while the second basal shoot emerges either from a basal axillary bud of the primary shoot or from a basal axillary bud of the first basal shoot (Marcelis-van Acker 1993). Application of dyes to shoots indicates that obviously each (basal) shoot is supplied with water through a distinct zone of the basal stem xylem and root xylem. This fits in with work done by Sachs (1970) who found that buds growing on an intact shoot were connected to the roots by vascular strands which ran parallel to the vascular system of the stem. Neeff (1914) showed that large tree branches also have a relatively independent vascular system. Eames & MacDaniels (1925) stated that in the region where tissues of the main stem and a branch meet, their conducting tissues remain more or less distinct. This means that the vasculature of the branch is not directly connected with that of the stem above the branch.

The dye patterns found in rose plants suggest that the area of xylem in the basal stem and root, which supplies the primary shoot, becomes fixed soon after the appearance of the first basal shoot (a lateral shoot of the primary shoot). The basal shoot is expected to induce new formation of vascular tissue downwards, since growth of lateral shoots resulted in an increase in diameter of its parent shoot (Marcelis-van Acker, unpublished data). Zimmermann & Brown (1971) also reported for trees that growing shoots have a definite influence on the amount of radial growth in the stem beneath. The formation of this so-called branch collar (Shigo 1985) starts at the side of the growing basal shoot and subsequently envelops the entire basal stem xylem. Also, the root xylem becomes enveloped by new vascular tissue.

The dye pattern found in plants with two basal shoots was not always the same. Observation of many plants led to the following hypothesis. Where a basal shoot is the result of the outgrowth of an axillary bud of the latest developed shoot, basal stem and root are composed of separated xylem cylinders, each cylinder connected to one shoot. Where two basal buds on opposite sides of the primary shoot sprout simultaneously, branch tissue differentiations start from each side and will meet half-way around the stem. If these two basal buds do not sprout exactly simultaneously, a more complicated pattern will occur. Where successive sprouting of basal buds of any shoot is interrupted by a long time interval, xylem of basal stem and root will be composed of separated concentric zones, each zone connected to one shoot.

Growth of the primary shoot and the first basal shoot is assumed to become limited due to a restricted xylem system. The xylem system becomes restricted because it will be enveloped by xylem serving a younger shoot. Shigo (1985) reported for trees that a branch is structurally attached to the trunk by a series of trunk and branch collars. Every growing season a branch collar is formed, which is enveloped by a trunk collar. However, this was not observed in roses. Moreover Kool *et al.* (1991) found for rose that the diameter increase of the first basal shoot was restricted when a new basal shoot emerged, while the growth of this new basal shoot was not influenced by the older basal shoot. These observations support the hypothesis that the xylem system serving a single shoot becomes fixed and will be limited after some time.

The variation in xylem capacity of basal stem and root probably influences the growth of future shoots. The addition of new xylem induced by a shoot depends on the time elapsed until a new shoot is formed. When a new shoot is formed the xylem supplying the former shoot will become fixed. As xylem ages it becomes less functional in conduction (Milburn 1979), so its capacity will decrease. The effects of fixing and ageing

combined with differences in the length of the time interval in basal shoot formation will result in a variability of xylem capacity for individual shoots. This capacity may partly be expressed in the shoot diameter.

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