Roots of *Pisum sativum* L. Exhibit Hydrotropism in Response to a Water Potential Gradient in Vermiculite

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In the present study, root hydrotropism in an agravitropic mutant of *Pisum sativum* L. grown in vermiculite with a steep water potential gradient was examined. When wet and dry vermiculite were placed side by side, water diffused from the wet (−0.04 MPa) to the dry (−1.2 MPa) and a steep water potential gradient became apparent in the dry vermiculite close to the boundary between the two. The extent and location of the gradient remained stable between the fourth and sixth day after filling a box with vermiculite, and the steepest gradient (approx. 0.02 MPa mm⁻¹) was found in the initially dry vermiculite between 60 and 80 mm from the boundary. When seedlings with 25–35 mm long roots were planted in the initially dry vermiculite near where the gradient had been established, each of the main roots elongated toward the wet vermiculite, i.e. toward the high water potential. Control roots elongated without curvature in both the wet and the dry vermiculite, in which no water potential gradient was detectable. These results show that pea roots respond to the water potential gradient around them and elongate towards the higher water potential. Therefore, positive hydrotropism occurs in vermiculite just as it does in air. Hydrotropism in soil may be significant when a steep water potential gradient is apparent, such as when drip irrigation is applied.

Key words: Hydrotropism, pea, *Pisum sativum* L., root elongation, vermiculite.

INTRODUCTION

Root hydrotropism, as well as gravitropism, plays an important role in the direction in which roots elongate. This phenomenon has been observed when roots grown in air with a humidity gradient around them bend towards the higher humidity (Jaffe et al., 1985; Takahashi and Suge, 1991). Moreover, when agar blocks with different water potentials were applied to a root tip, the root elongated toward the blocks with the higher water potentials (Takano et al., 1995). Pea roots exhibited hydrotropism when the water potential gradient around them ranged from 0.4–0.5 % relative humidity (RH) mm⁻¹ in air (equivalent to 0.6–0.7 MPa mm⁻¹ at 25 °C) or when the difference in water potential between agar blocks applied to the 1-mm-thick root tip was more than 0.5 MPa mm⁻¹ (Takano et al., 1995; Hirasawa et al., 1997). Gradients of less than 0.2 % RH mm⁻¹ in air (equivalent to 0.3 MPa mm⁻¹ at 25 °C) and of less than 0.3 MPa mm⁻¹ in terms of the difference in water potential between agar blocks, do not induce hydrotropism (Takahashi and Scott, 1993; Takano et al., 1995). In contrast, in soil, much smaller water potential gradients of 7 × 10⁻⁴ MPa mm⁻¹ and 8 × 10⁻³ MPa mm⁻¹ have been recorded between a dry surface soil and wet deeper soil (Klepper et al., 1973; Kondo et al., 2000). A ten-fold steeper gradient has been found at the penetration front of water in irrigated soil (Gardner et al., 1970). The size of the water potential gradient in air, when root hydrotropism has been observed, is much larger than in soil. However, the water potential gradient in soil varies considerably, depending on ambient conditions. Therefore, it is unclear whether hydrotropism occurs in soil as it does in air. Since the cited experiments were performed in air over the course of just a few hours, it is possible that a root might respond to far smaller gradients if such a gradient were applied for a longer time. Moreover, since root gravitropism is stimulated by decreases in the water potential around roots (Oyanagi et al., 1992; Nakamoto, 1993), it is possible that a root might change its direction of elongation in soil in response to the water status of its environment.

In this study, an experimental system with a stable and steep water potential gradient was established in vermiculite, and the responses of roots of an agravitropic mutant of *Pisum sativum* L. to this gradient were investigated.

MATERIALS AND METHODS

Plant material

Seeds of the agravitropic *ageotropum* mutant of pea (*Pisum sativum* L.) were germinated on wet filter paper in a moisture-saturated Petri dish at 25 °C in the dark. Two-day-old seedlings with straight main roots 25–35 mm in length were used in all the experiments.
Wet and dry vermiculite were placed side by side to establish a steep water potential gradient in the dry vermiculite. Two glass plates (500 x 500 mm) with a rubber rod (25 mm thick) as a base and sides between them were used to make a container. One-third of the container was filled with wet vermiculite (light shading) and the rest with dry vermiculite (dark shading). The top of the container was sealed with polyvinyl film to prevent evaporation. The experimental system was set up by placing the container on a rubber rod (25 mm thick) and sides between them. The plate was then replaced. The tube was, therefore, located close to one of the glass walls and at a depth of more than 30 mm from the top of the container. The root axis was parallel to the boundary between the WV and the DV. The tube was a 40-mm portion of a Pasteur pipette (IK-PAS-9P; Asahi Technoglass Co., Chiba, Japan) close to the point where it becomes narrower (Fig. 1A). The root tip was placed about 15 mm from the narrower aperture so that the root was forced to elongate without bending for a while after transplanting. The root tip entered the vermiculite 1 d after transplanting. The root’s length and curvature were measured 2 d after transplanting. All experiments were performed in a room in which the air temperature was maintained at 25 °C.

RESULTS

In seedlings transplanted to the DV 60 mm from the boundary between the WV and the DV, where there was a steep water potential gradient, 74 % of their roots bent toward the WV, i.e. towards the higher water potential (Fig. 2). In seedlings transplanted to the DV 80 mm from the boundary, where a gradient was also present, 64 % of their roots bent toward the WV. In seedlings transplanted to the WV, where there was no water potential gradient, half their roots elongated without bending. The rest did bend, but the number of roots bending toward the DV was equal to the number bending in the opposite direction. In seedlings transplanted to the DV more than 100 mm from the boundary, where there was no gradient, 60 % of their roots elongated without bending (Fig. 2).

Mean curvatures at 60 and 80 mm from the boundary, where there was a steep water potential gradient around the seedlings, were greater than those within the DV and the WV at sites where no gradient was detected (Table 1). Elongation rates tended to decrease as the distance from the WV increased, i.e. as the water potential of the vermiculite decreased.
A water potential gradient of more than 0-02 MPa mm⁻¹ can easily be established at the penetration front of irrigation water, even several days after irrigation (Gardner et al., 1970). Root hydrotropism might contribute to limiting root growth into irrigated soil and would be important for the efficient use of irrigation water in such a system.

Interactions between tropisms, such as thigmotropism and gravitropism (Massa and Gilroy, 2003) and phototropism and gravitropism (Correll and Kiss, 2002), have been established. Hydrotropism is affected also by gravitropism (Takahashi and Scott, 1991, 1993; Oyanagi et al., 1995). Roots show a greater response to gravitropism than to hydrotropism when the intensity of gravistimulation is high. The direction of lateral root elongation is less sensitive to gravity (Ransom and Moore, 1983). Therefore, hydrotropism may be more significant for lateral roots than for main roots. The mechanism responsible for lateral root hydrotropism is not yet understood even though root systems consist mainly of lateral roots. Further studies of the actual development of root systems in irrigated soil are necessary to plan for the efficient use of water in the irrigation of crop plants.

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LITERATURE CITED


