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The hydraulic safety zone at the base of barley roots

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Abstract. A hydraulic constriction of the vessels occurs at the base of the primary roots of barley (*Hordeum vulgare* L.). The constriction and consequent hydraulic protection result from an extreme shortening of the vessel elements, leading to the accumulation of perforation plates with simple, broad-rimmed perforations which are smaller than those in normal-length vessel elements. It is compensated for by a local increase in the number of tracheary elements and an increase in their diameter. A similar trend of development was observed both at the base of other seminal roots and at the base of stem-borne adventitious roots. The rate at which compensation for the hydraulic constriction occurs could be of crucial importance for the axial resistance of water transport.

Key words: *Hordeum* (hydraulic safety zone, root) – Hydraulic safety zone (root) – Root base – Vascular pattern.

Introduction

Extensive literature has accumulated on the vascular connection of the transition region between the root on the one hand and the cotyledons and epicotyl on the other, as well as on the relationship between the vascular systems of the stem and lateral stem appendages. Less attention has been paid to the vascular construction of plants from the point of view of the conductive function. Research in recent years represents a true renaissance of such studies. Investigations on the xylem have been based on older reports and devoted to the overground system of trees (Tyree et al. 1983; Zimmermann 1978, 1983; Ewers and Zimmermann 1984a, b). On the basis of the properties of the vascular elements of the xylem, determination of the conductance of a given organ, or a particular segment of that organ, usually follow the Hagen-Poiseuille equation on the paraboloid flow through capillaries. Other conditions being equal, the critical values in these calculations are the number of vascular elements and their inner radius. The relative conductance is a function of the sum of the fourth power of the inside radius of individual water-conducting elements. Structural features by which the conducting elements differ from ideal capillaries lead to an increased resistance to flow and to a decreased conducting capacity of the xylem.

The results of various analyses have shown that the main stem is hydraulically favoured over the lateral stem appendages: leaves, vegetative branches and branches of inflorescences. In addition to this so-called hydraulic hierarchy, the nodal regions are sites of marked hydraulic constriction leading to hydraulic segmentation of the plant body (Zimmermann 1978, 1983). According to Zimmermann, hydraulic segmentation represents an important mechanism which protects the plant from widespread embolism and hence from a severe failure of its conductive ability following damage or loss of some organ. Sperry (1984) detected air embolisms in the xylem of the palm *Rhapis excelsa*, a species which had been the subject of detailed investigations by Zimmermann and Tomlinson (1965) and Zimmermann and Sperry (1983), and thus offered experimental support for Zimmermann's constriction hypothesis.

The present investigations on the basal region of barley roots were based on data obtained in studies of the hydraulic architecture of overground systems. In the region under consideration it can be presumed that there exists an anatomic adaptation which secures hydraulic protection and at the same time makes possible an efficient axial transport of solutions from the roots to overground parts and vice versa.

The selection of the experimental subject was ultimately based upon the results of studies on the resumption of growth and differentiation processes in barley seminal-root primordia during germination (Luxová 1986). Cells in the basal region of these seminal-root primordia had already undergone the programmed number of cell cycles during embryogenesis and their size did not increase essentially on germination. The vascular elements in this region, therefore, remained extremely short with broad rims around the perforations, a fact which could be indicative of hydraulic constriction.

Material and methods

The histological studies were carried out on spring barley (*Hordeum vulgare* L. cv. Karat). The basal parts of seminal-root primordia in mature embryos, the same region in differentiated seminal roots and, in pilot tests, the basal parts of adventitious stem-borne roots were examined. Embryo tissues were fixed in Navashin's solution and mature tissues in formalin-acetic acid-alcohol solution (FAA). After passage through tertiary butyl alcohol the samples were embedded in paraffin and serial cross and longitudinal sections 7 and 10 μm thick were stained with tannin and ferric chloride. For maceration, Schulze's method (concentrated nitric acid and potassium chlorate) was used. (All microtechnique procedures as described in Sass 1951).

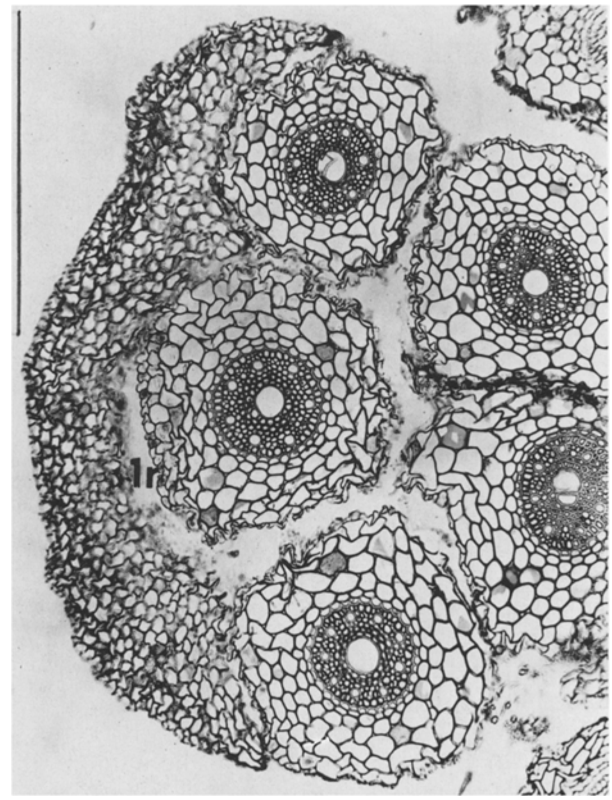

Fig. 1. Cross section of the group of barley seminal roots growing from the caryopsis. Central cylinder of the primary root (*1r*) is shown in detail in **Fig. 3A.** ×85. The scale bar = 500 μm throughout except for **Fig. 3A, B**

Results

In embryos of the barley cultivar used, from five to six root primordia are formed. In mature seminal roots, the solitary vessel of the central metaxylem is hydraulically the most important (Fig. 1). In view of its diameter its relative conductance under other constant terms is higher than the relative conductance of all the other vessels of the narrow peripheral metaxylem taken together. (Due to their small size the protoxylem elements may be omitted from these considerations). In the mature primary root shown, e.g., the inside diameter of the central metaxylem vessel was 30 μm and the diameters of the seven peripheral vessels varied from 9 to 10.5 μm. If taken to be an ideal capillary the wide central vessel could thus transport 93% of the water compared with only 7% for all of the peripheral vessels.

Even in the embryo, vessel elements of the prospective central vessel are markedly larger than the other cells. In the proximal part of the primary root primordium adjacent to the scutellar node, there are 12–15 squat, barrel-shaped vessel elements arranged in an axial column (Fig. 2A). Distally, the column continues as cylindrical isodiametric vessel elements of gradually decreasing length. In contrast to other non-meristematic vessel elements formed in the embryo, the barrel-shaped vessel elements do not elongate during germination. Their differentiation proceeds immediately and their characteristic shape also remains preserved after maturation (Fig. 2B). The development of extremely short vessel elements leads in the mature vessel to the formation of a zone characterized by an accumulation of horizontal end walls with simple perforations. Moreover, compared with the perforations in those parts of the root which grow subsequently, the diameter of the holes is reduced and the rims around the perforations are broad. With such short ($\bar{x} \pm s_{\bar{x}} = 19.99 \pm 0.72$ μm, $n = 30$) barrel-shaped vessel elements, perforations reduced to hardly a fifth of the vessel transection (the inside diameter of the vessel elements is 46.39 ± 0.78 μm, the diameter of the perforations is 21.60 ± 0.30 μm) and the broad rims, the most basal region of the central vessel represents a site of marked hydraulic constriction. The distal continuation of the vessel consists of about 50 non-meristematic vessel elements, which are also

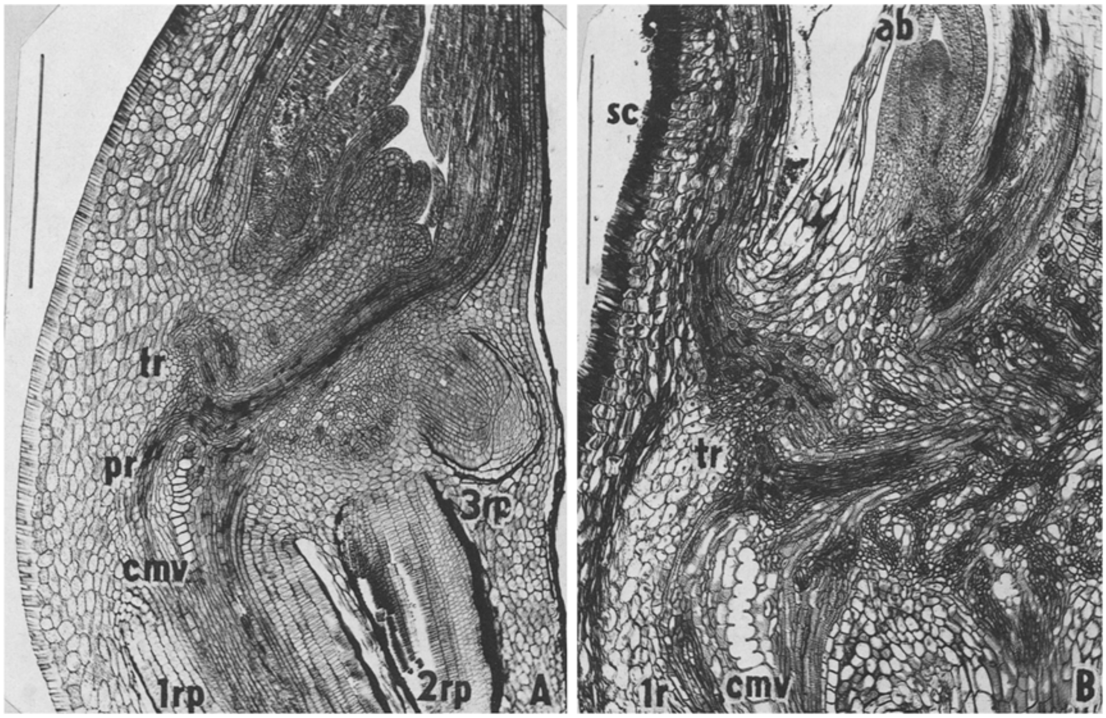

Fig. 2. A Median longitudinal section through the mature barley embryo showing the basal part of the primary root primordium (*1rp*) with the transition region (*tr*) and other seminal root primordia (*2rp, 3rp*). *cmv*, prospective central metaxylem vessel; *pr*, procambium. **B** Section through a similar, but fully differentiated region. *1r*, Basal part of the primary root; *tr*, transition region; *cmv*, central metaxylem vessel; *ab*, axillary bud; *sc*, scutellum. ×60

formed in the embryo and which lengthen upon germination. The most proximal of these elements show a successive increase in length, but in the more distal elements the lengths fluctuate rhythmically. This rhythmical fluctuation of length is also characteristic of new post-embryonic vessel elements (Luxová 1986).

A shortening of vessel elements in the basal region of the primary root and a reduction in diameter of their perforations also occur in the narrow peripheral metaxylem.

These phenomena lead to hydraulic constriction and thus to hydraulic protection. However, the constriction thus formed is compensated for by a local increase in the number and diameter of the vascular elements. Already in the embryo (Fig. 2A) the procambium in the basal region of the primary root primordium below the insertion of the scutellum is widened in the shape of a flask; in the central region of the primordium, distal to the basal zone, it is narrower. The vascular pattern in this narrower region, whose mature stage is illustrated in Fig. 3A, corresponds to the known pattern found in barley roots (Heimsch 1951; Hagemann 1957; Luxová 1975). By contrast, in the basal region of the root primordium, characterized by structural features leading to hydraulic constriction, longitudinal cell division, determining the character of the pattern, is enhanced. As the consequence of an increased number of cells and also in the mature root of their greater diameter, the central cylinder becomes broader (Fig. 3B, 4A, B). The number of radially alternating xylem and phloem poles is the same as in the central region of the root primordium, but the wide vessel of the central metaxylem is not isolated by vascular parenchyma from the peripheral xylem strands. Adjacent to the central vessel, radial groups of vessels are formed; they become connected to the peripheral xylem strands. This leads to a marked increase in the number of tracheary elements. The xylem appears in cross sections as a seven- to eight-armed star, the number of arms being determined by the number of xylem poles. Phloem strands also appear in cross sections to occupy a bigger area and consist of more cells than in the more distally situated root region. The uniseriate pericycle opposite the xylem is interrupted as a result of the differentiation of protoxylem. Opposite the phloem, the pericycle layer is double, two cell layers separate the sieve tubes of the protophloem from the endodermis. Most of the hydraulic safety zone of the

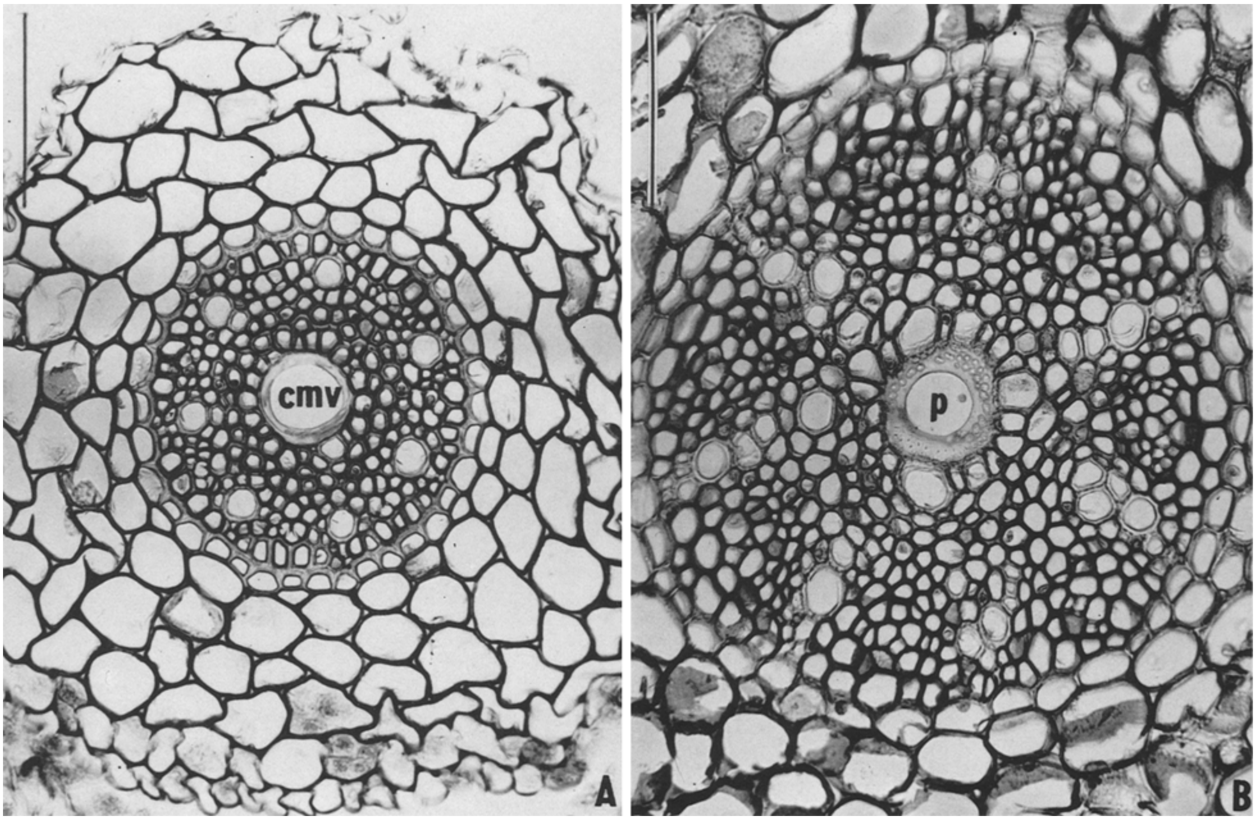

Fig. 3A, B. Cross section of a barley primary root showing its central cylinder at two levels. **A** Central cylinder at the level corresponding to the central region of the primary root primordium with seven xylem and phloem strands. *cmv*, Central metaxylem vessel. **B** Complexity of the vascular pattern in the basal hydraulic safety zone, i.e. more proximal than in **A**; xylem and phloem strands are more complex. *p*, Reduced perforation of the central metaxylem vessel. ×255. The scale bar = 100 μm

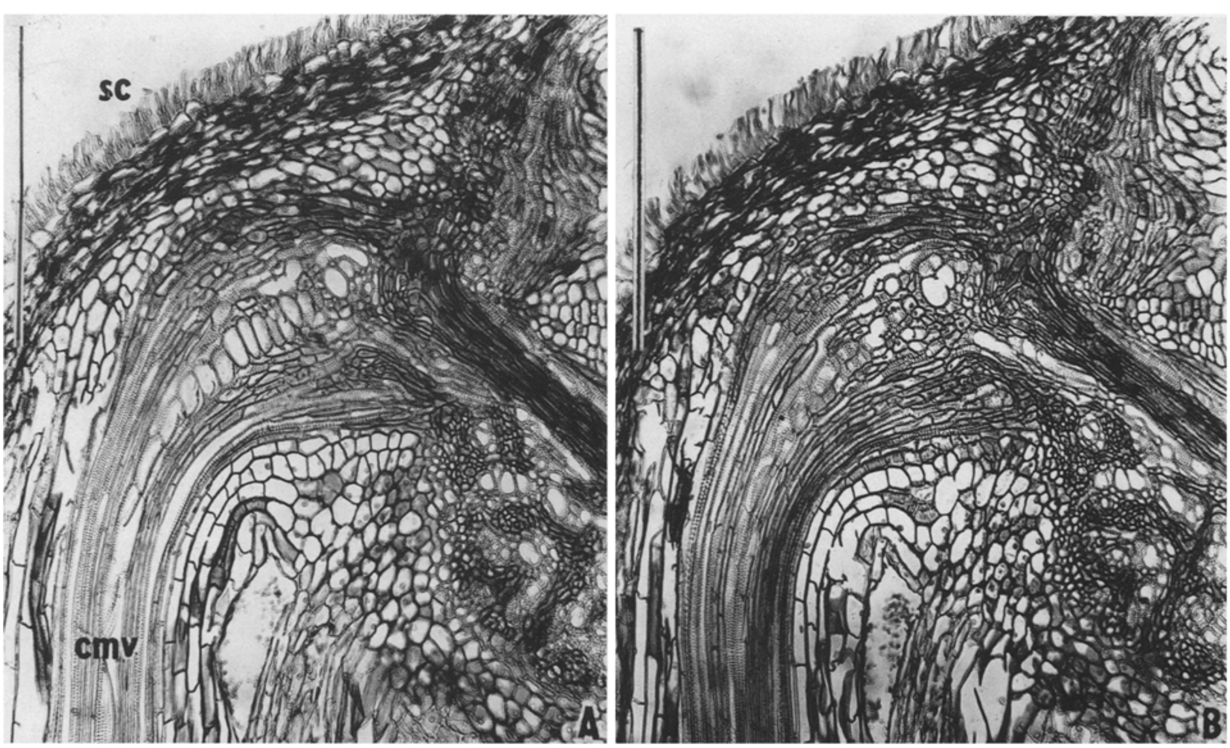

Fig. 4A, B. Longitudinal sections through the hydraulic safety zone at the base of a barley primary root at two levels. *cmv*, Central metaxylem vessel, *sc*, scutellum. ×85

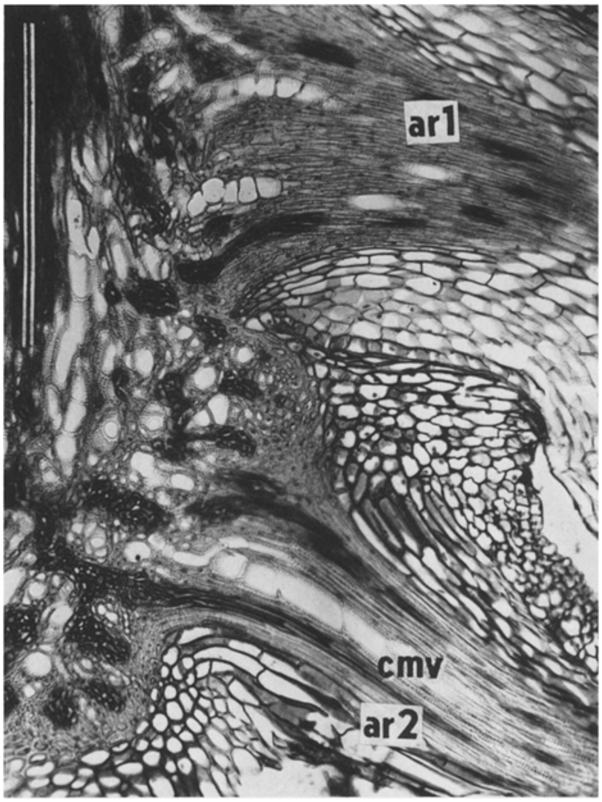

Fig. 5. Longitudinal section through the hydraulic safety zone at the base of two stem-borne adventitious roots (*ar1, ar2*). *cmv*, Central metaxylem vessel. ×85

primary root is connected to the scutellum so that in this root region there is no direct contact with the external environment. Basal xylem elements of the primary root are connected to the scutellar nodal xylem, the xylem elements of which are very small but very numerous. Short tracheids and vessel ends are of frequent occurrence here.

The basal regions of other seminal roots and stem-borne adventitious roots (Fig. 5) show in principle the same structure.

Discussion

The vascular pattern of the basal zone differs from the general pattern of the vascular system in barley roots both qualitatively and quantitatively. At the root base a hydraulic safety zone is formed. Of the structural features leading to hydraulic constriction and thus to hydraulic protection, the smaller diameter of the broad-rimmed perforations and the accumulation of perforation plates, resulting from a shortening of vessel elements, play an important role.

Analyses of nodal regions of overground systems have shown several constriction features appearing either individually or in combination: reduction in vessel number (Larson and Isebrands 1978; Zimmermann 1983); reduction in vessel length (Zimmermann 1978; Salleo et al. 1984); reduction in the diameter of vessel elements (Larson and Isebrands 1978; Zimmermann 1978); and interrupted continuity of the xylem (Zee and O'Brien 1970; Barlow et al. 1980; Zimmermann and Sperry 1983). In barley, there are very small, but numerous tracheary elements in the scutellar node, which is connected to the base of the primary seminal root. Short tracheids and vessel ends are also present here, an indication of a reduction in vessel length.

At the base of barley roots, structures leading to hydraulic constriction are combined with structures leading to enhanced conductivity. The diameter of the vessel elements is greater than in the more distally situated root regions. As distinct from the general pattern of barley seminal roots, the xylem at the base does not form, on the stele periphery, individual strands separated by nonconductive tissue from a single central vessel. More numerous and wider vessels and their compact arrangement are indicative of a more efficient water transport. In the central cylinder, water does not need to pass a barrier such as that formed in distal regions by living matter in the non-vascular tissue between the peripheral and central metaxylem. The barrel shape of the basal elements of the central vessel indicates the possibility of water storage. A qualitative and quantitative evaluation of the phloem in this region has yet to be undertaken. The observed doubling of the pericycle layer opposite the phloem has been reported to represent a rare type of pericycle development (Voronin 1945).

The results obtained by structural analysis of the barley root base allow the assumption that the finding of differences in the structure of the hydraulic safety zone in cereals and grasses could be of practical importance from the point of view of drought resistance and yield (grain production versus green-matter production). The compensation of constriction properties of the hydraulic safety zone could represent a limiting factor in the selection of plants for a high or low root axial resistance.

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