Phyton (Austria)	Vol. 20	Fasc. 1—2	37—45	15. 2. 1980

Frictional Resistances to Water Transport in Water-Cultured Wheat Plants

By

Peter RUCKENBAUER and Hanno RICHTER *) **)

With 2 figures

Received January 30, 1979

Key words: water transport, frictional resistance, wheat, *Triticum*

Summary

Frictional resistances in the body of water-cultured wheat plants were investigated. A major potential drop under stress conditions was found in the transition zone between culm and leaf, whereas the contribution of the roots and gradients in the leaf were small. Ecophysiological implications of this result are discussed.

Zusammenfassung

Reibungswiderstände beim Wassertransport von Weizenpflanzen in Wasserkultur

Die Untersuchung galt den Reibungswiderständen im Körper von Weizenpflanzen, die in Wasserkultur gezogen waren. Unter Streßbedingungen fand sich ein starker Potentialabfall in der Übergangszone zwischen Halm und Blatt; die Beiträge der Wurzel und Gradienten im Blatt waren klein. Die ökophysiologische Bedeutung dieses Ergebnisses wird diskutiert.

Introduction

The water status at a given point in the plant body is the result of environmental and plant factors acting in the soil-plant-atmosphere

---

*) P. RUCKENBAUER, Institut für Pflanzenbau und Pflanzenzüchtung, H. RICHTER, Botanisches Institut, Universität für Bodenkultur, Gregor-Mendel-Str. 33, A-1180 Wien, Austria.

**) Dedicated to Prof. Dr. phil. Dr. forest. h. c. Josef KISSER on the occasion of his 80th birthday.

continuum. In a steady state situation, these continuum demands may be split into three components:

$\psi_t = \psi_s + \psi_g + \psi_f$ (1)

where ψ_t = total water potential, ψ_s = static substrate water potential, ψ_g = gravitational potential, and ψ_f = frictional potential.

In herbaceous plants at mesic sites, where ψ_s and ψ_g are close to zero, it is only the frictional potential losses which lower total water potential during the day. Even under less favorable substrate water relations, friction may account for vast differences between pre-dawn and noon potentials in crop plants (e. g. HSIAO *et al.* 1976).

A comparison of frictional potential losses during water transport in the bodies of different plants reveals a curious fact: overall resistances seem to be as high in small herbs as in towering trees (HELLKVIST *et al.*, 1974). This is a matter of considerable ecophysiological and evolutionary interest (RICHTER 1976), and it would be desirable to exactly localize these high resistances in the body of herbaceous plants. Earlier experiments (BEGG & TURNER 1970, MEIRI *et al.* 1975) indicate a high resistance between axes and leaves in dicotyledons. For monocotyledons, DENMEAD & MILLAR (1976) provide a detailed study of water transport in wheat plants. They separate flow resistances in the root from those in stems and leaves. However, there is no answer in their data to the question whether these resistances are distributed evenly or confined to certain sections of the stem-leaf pathway. Our paper tries to provide some information on this problem.

Material and Methods

Spring wheat (*Triticum aestivum* cv. Solo) and, for some additional experiments, Durum wheat (*T. durum* cv. Pandur) were rooted in small, perforated dishes filled with quartzite gravel. Ten of these dishes were put into a frame over a shallow tray filled with dilute nutrient solution of less than 0.2 bar osmotic potential (RUCKENBAUER 1969). The plants were kept in a partly climatized glasshouse up to the flowering stage (Solo) or to the beginning of the grainfilling period (Pandur) and received additional light from fluorescent tubes. Several hours before the experiments, the trays were transferred to a climatized chamber lighted with xenon lamps (Karl Weiß, Gießen, FRG). A stress climate of 31° C and 18 torrs vapor pressure deficit was employed. In some cases the roots of the wheat plants were cut off under distilled water and the shoots were exposed under the same climatic conditions. Transpiration of single leaves could be reduced by covering both surfaces with a thin layer of petroleum jelly.

Water potentials were determined on leaves and whole shoots with the pressure chamber technique (SCHOLANDER *et al.*, 1965, RITCHIE & HINCKLEY, 1975). For leaves, a special rubber compression gland with a narrow slit was used, so that the leaf blade could be tightly sealed into the lid of a chamber with a height of 20 cm. Culms with attached leaves were cut about 5 mm below the uppermost (sixth) or the fifth node and inserted into a very large chamber (50 cm height; cf. RICHTER *et al.*, 1972). The appearance of water at the cut surface was observed with a stereo microscope.

Transpiration and stomatal opening were not followed closely. A recent paper (MORGAN 1977) has shown that stomatal regulation in a number of wheat varieties became not apparent until total leaf water potential (ψ_t^{leaf}) reached about —18 bars, which would be at the lowermost limit of potential values in our experiments. — The significance of the differences in water potentials between treatments was evaluated with the t-test.

Results

Figures 1 and 2 summarize most of our results with *Triticum aestivum* cv. Solo. Figure 1 shows an appreciable difference between measurements on culms and leaves. Leaf water potentials are always more negative and, moreover, the difference between leaves no. 5 and 6 is statistically highly significant ($P < 0.001$), whereas the small difference between the corresponding nodes is not. The apical third of a leaf has a value only slightly more negative than that for the whole leaf blade. Removal of the roots by means of a cut through the stem base has a minor effect: potentials in such plants rise only slightly, and the difference is statistically not significant.

The experiments in figure 2 were aimed at suppressing the transpiration of individual leaves. A petroleum jelly cover increases the potentials of leaves dramatically ($P < 0.001$ in both cases). Values for untreated leaves on plants with petrolatum on either of the two uppermost leaves are only slightly less negative than on completely untreated controls (no significance for flag leaves, $P < 0.05$ for leaves no. 5). Removal of the ear and a jelly cover on both the sixth and the fifth leaves leads to a further reduction in the potentials.

Some supplementary experiments, mostly on the Durum variety Pandur, will be mentioned in the context of the discussion.

Discussion

The climate chosen for our experiments on Solo leads to values of about —13 bar in the fifth and about —16 bar in the sixth leaf. The pathway from the high-potential nutrient solution to the leaf must, therefore, contain resistances responsible for major frictional potential losses. Our results give some information on the localization and relative magnitude of these resistances.

Fig. 1 shows that a removal of the whole root system has only a very slight effect on total water potentials of the leaves. This is probably due to the special conditions under which our plants were grown: the shallow trays provide excellent aeration, and the dilute nutrient solution enhances root growth. A dense cluster of many short roots in parallel is formed, which apparently does not offer an appreciable total resistance against water flow. Root resistances would however certainly be significant under other conditions, as has been shown for soil-rooted wheat plants (GREACEN *et al.*, 1976), where the water is withdrawn from deep soil horizons and transported over a long distance in root xylem of limited cross-sectional area.

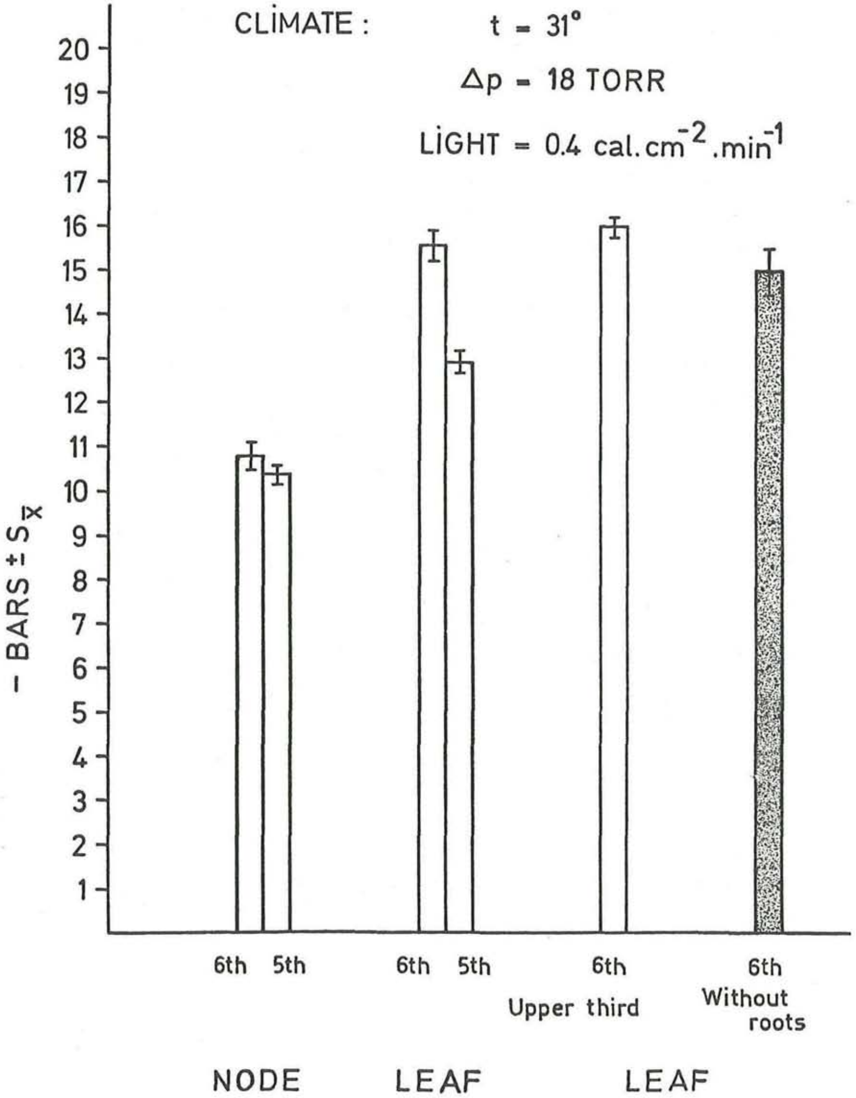

Fig. 1. Total water potentials in culms and adjacent leaves of Triticum aestivum cv. Solo in water culture

The next possible candidate for the location of a major resistance is the leaf blade; indeed there have been reports of a steep potential gradient in wheat leaves (Meiri *et al.*, 1975): the apical third of a blade was found to be at about —23 bars, when the entire length gave a value of —16 bars. Since these results were obtained from measurements on the same, repeatedly cut leaf, their significance remains somewhat doubtful. However, a comparison by Meiri *et al.* of whole leaves vs. apical halves freshly cut from other leaves showed again a pronounced difference, —15 vs. —20 bars. Although our values for entire flag leves in fig. 1 are very similar to those of Meiri *et al.*, we cannot report on such vast gradients. The difference between entire leaves and upper thirds is highly significant ($P < 0.01$), but small. Additional experiments with Triticum durum corroborated this result. There was no significant difference between basis and apical third (16.3 ± 0.51 vs. 16.0 ± 0.16 bar, $P > 0.05$) in a low-stress climate of 15.5° C and 5 torrs vapor pressure deficit. A higher evaporative demand (31° C, 15.5 torr vpd) gave differences with a significance at the 5% level, which were however still less than 2 bars (18.0 ± 0.35 for the entire length vs. 19.85 ± 0.60 bars for the apical third. It would thus seem that the leaf blade was not the site of the predominant potential drops in our experiments. A recent paper (Maxwell & Redmann 1978) reports on large gradients in *Agropyron* leaves; these gradients were present only in emerging leaves and did not occur between the base and the blade of fully emerged leaves. The discrepancies between our results and those of Meiri *et al.* on wheat leaves could be due to a similar phenomenon.

An estimate for the relative importance of stem resistances requires the measurement of stem water potentials at different points. Culm resistances may be determined by two methods. First, one may assume the value found in pressure chamber measurements of whole shoot systems to represent the correct potential for the cut xylem vessels. Pressure chamber readings for two points in the culm separated by a node and an internode of about 20 cm length are almost equal. However, a technical question arises from the fact that the potentials found in this way were always considerably less negative than those from the adjacent leaves: pressure chamber values from a system with internal potential gradients might be biased. Meiri *et al.* present evidence that water appears at the cut surface under an overpressure equivalent to the highest potentials in the system. However, there might be a tendency for an internal equilibration which could obscure small differences in stem water potentials, especially in objects with a different number of leaves attached to the culm.

Therefore, a second, independent approach was tried: transpirational water losses were restricted by means of a mechanical antitranspirant (cf. Begg & Turner 1970). Leaves were covered with a thin layer of petroleum jelly; a non-transpiring leaf should adjust its potential to that in the culm at the point of departure between leaf-trace bundles and stem bundles.

Our method cannot completely prevent transpiration: this may be seen from the potentials of plants covered with petrolatum all over the transpiring surface and still having negative leaf potentials of some bars (fig. 2). Experiments on a number of sclerophyllous evergreens showed some residual transpiration even after the most careful treatment with petrolatum (Karlic & Richter, 1979).

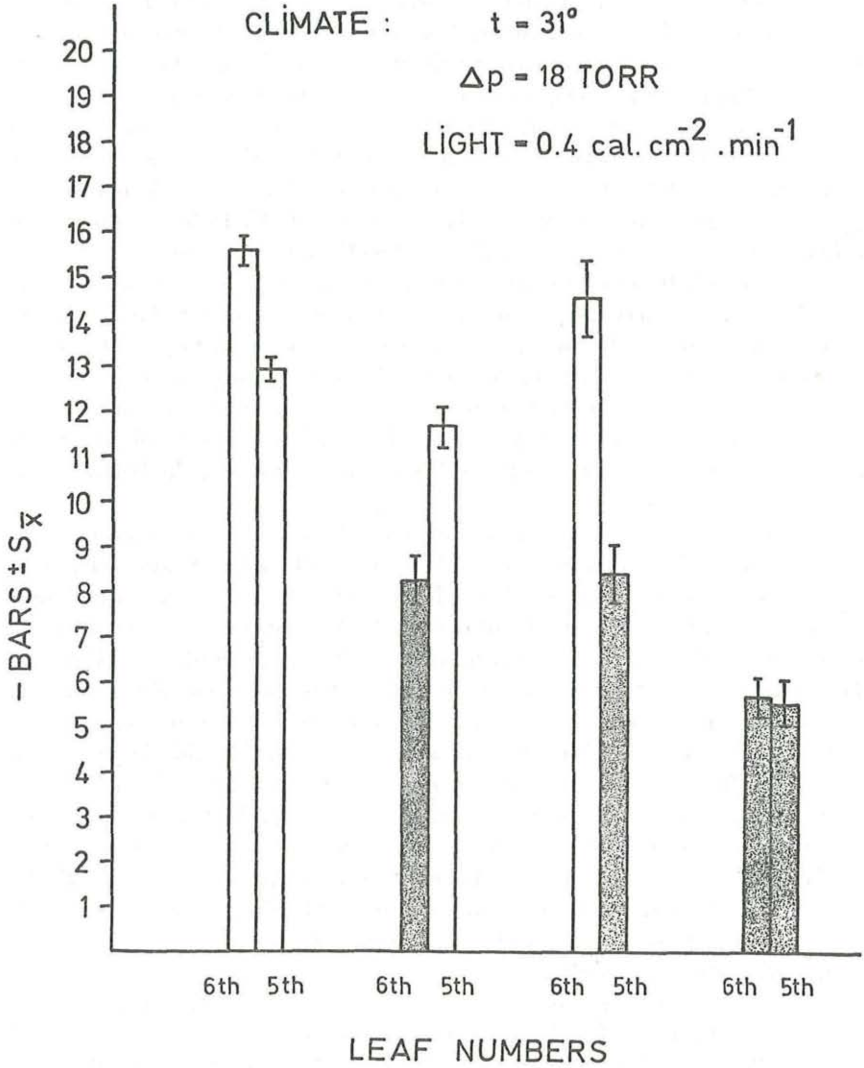

Fig. 2. Total water potential in freely transpiring (light columns) and petrolatum-covered leaves (dark columns) of *T. aestivum* cv. Solo in water culture

Yet, the antitranspirant effect is enough to raise the total water potential in treated leaves to a uniform level of about —8.5 bars, whereas their freely transpiring neighbors on the same plant are affected only slightly, if at all (fig. 2). Results with the petrolatum cover corroborate therefore those abtained from stem-node measurements: resistances between two adjacent nodes are small. There must however be a large resistance between the stem bundles and the leaf blade, which provides for nearly half the potential drop in the plant body. Further observations on durum wheat showed that this resistance must be situated below the base of the leaf sheath, which is at the potential of the leaf blade.

A recent paper by LARSON & ISEBRANDS (1978) indicates an anatomical basis for this striking phenomenon. The authors describe a zone of minimum vessel number and vessel cross-sectional area, the "constricted zone", in the nodal region of vascular traces serving the leaves of Populus deltoides Bartr. They show that such a zone may account for appreciable increases in xylem resistances between stem and leaf, which were repeatedly found in work with the pressure chamber (cf. RITCHIE & HINCKLEY 1975). TOMLINSON (1970) and ZIMMERMANN (1973) describe similar structures for the leaf trace of monocotyledons.

A large hydraulic resistance causing a steep potential drop between stem and leaf of a transpiring angiospermous plant is therefore not surprising in the light of anatomical data. However, this very resistance seems at first sight to be contrary to established principles and trends of evolution: friction in the xylem of angiosperms has been minimized by evolutionary progress, especially by the development of tracheae. Yet, a high-friction bottleneck for water transport exists in the short transition zone of the nodal region, where a few additional vessels or tracheids in parallel would suffice to remove the resistances almost completely. Thus, the maintenance, during the evolution of the conducting system, of a frictional potential gradient in transpiring herbs seems to be due to environmental pressure rather than to anatomical necessities.

RICHTER (1976) suggested an explanation for this fact: friction in the plant body might be necessary to conserve substrate water during periods of high evaporative demand. A potential drop coupled to the flow of large volumes of water could activate stomatal closing reactions by inducing turgor loss and hormonal reactions. Edaphic aridity on periodically dry sites, where water conservation plays a major role for the survival of plants, was apparently an important factor in angiosperm evolution (AXELROD 1972, STEBBINS 1974). One may therefore speculate that constricted zones providing major resistances first evolved in angiosperm trees and tree seedlings and afterwards further developed in the evolution of herbs. In fact, potential differences between leaves and twigs may be found in angiospermous trees, but not in conifers (RITCHIE & HINCKLEY 1975). Another benefit of potential drops occurring between culm and leaves could be the maintenance of balanced and favorable turgor relations for the meristems in the apex and the nodes of a wheat plant; such an effect has been suggested by MAXWELL & REDMANN (1978) for the high resistance found in emerging leaf blades, and their concept may be applicable also to the relation between developed leaves and stem meristems.

Acknowledgement

We thank the Fonds zur Förderung der Wissenschaftlichen Forschung, Wien, for support from project 1465.

References

AXELROD D. I. 1972. Edaphic aridity as a factor in angiosperm evolution. — Amer. Naturalist 106: 311—320.

BEGG J. E. & TURNER N. C. 1970. Water potential gradients in field tobacco. — Plant Physiol. 46: 343—346.

DENMEAD O. T. & MILLAR B. D. 1976. Water transport in wheat plants in the field. — Agron. J. 68; 297—303.

GREACEN E. L., PONSANA P. & BARLEY K. P. 1976. Resistance to water flow in the roots of cereals. In: LANGE O. L., KAPPEN L., SCHULZE E.-D. (Eds). Water and Plant Life — Problems and Modern Approaches, p. 85—100.— Berlin—Heidelberg—New York.

HELLKVIST J., RICHARDS G. P. & JARVIS P. G. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. — J. appl. Ecol. 11: 637—668.

HSIAO T. C., FERERES E., ACEVEDO E. & HENDERSON, D. W. 1976. Water stress and dynamics of growth and yield of crop plants. In: LANGE O. L., KAPPEN L., SCHULZE E.-D. (Eds), Water and Plant Life — Problems and Modern Approaches, p. 281—305. — Berlin—Heidelberg—New York.

KARLIC H. & RICHTER H. 1979. Storage of detached leaves and twigs without changes in their water potential. — New Phytol. 83: 379—384.

LARSON P. R. & ISEBRANDS J. G. 1978. Functional significance of the nodal constricted zone in Populus deltoides. — Can. J. Bot. 56: 801—804.

MAXWELL J. O. & REDMANN R. E. 1978. Water potential and component potentials in expanded and unexpanded leaves of two xeric grasses. — Physiol. Plant. 44: 383—387.

MEIRI A., PLAUT Z. & SHIMSHI A. 1975. The use of the pressure chamber technique for measurements of the water potential of transpiring plant organs. — Physiol. Plant. 35: 72—76.

MORGAN J. M. 1977. Changes in diffusive conductance and water potential of wheat plants before and after anthesis. — Aust. J. Plant Physiol. 4: 75—86.

RICHTER H. 1976. The water status in the plant — experimental evidence. In: LANGE O. L., KAPPEN L., SCHULZE E.-D. (Eds), Water and Plant Life — Problems and Modern Approaches, p. 42—58. — Berlin—Heidelberg—New York.

RICHTER H., HALBWACHS, G. & HOLZNER W. 1972. Saugspannungsmessungen in der Krone eines Mammutbaumes (*Sequoiadendron giganteum*). — Flora 161: 401—420.

RITCHIE G. A. & HINCKLEY T. M. 1975. The pressure chamber as an instrument for ecological research. — Adv. Ecol. Res. 9: 165—254.

RUCKENBAUER P. 1969. Die Beurteilung der Leistungsfähigkeit von Winterweizensorten nach bestimmten Organrelationen. — Ztschr. f. Acker- und Pflanzenbau 130: 273—290.

SCHOLANDER P. F., HAMMEL H. T., BRADSTREET E. D. & HEMMINGSEN E. A. 1965. Sap pressure in vascular plants. — Science 148: 339—346.

TOMLINSON P. B. 1970. Monocotyledons — towards an understanding of their morphology and anatomy. — Adv. Bot. Res. 3: 207—292.

ZIMMERMANN M. H. 1973. The monocotyledons: their evolution and comparative biology. IV: Transport problems in arborescent monocotyledons. — Quarterly Rev. Biol. 48: 314—321.

Zeitschrift/Journal: Phyton, Annales Rei Botanicae, Horn

Jahr/Year: 1980

Band/Volume: 20_1_2

Autor(en)/Author(s): Richter Hanno, Ruckenbauer Peter

Artikel/Article: Frictional Resistances to Water Transport in Water - Cultured Wheat Plants. 37-45