PHYSICAL MODEL FOR MOVEMENT OF WATER IN SPLIT-ROOT WHEAT PLANTS

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A b s t r a c t. Roots can be split between soil and nutrient solution to determine the effect of soil matric potential on water relations. When such experiments are done with wheat, water from the nutrient solution side moves to the soil side and keeps it wet. Wheat grown with roots split between soil and nutrient solution grows taller than wheat with roots split between soil and soil or between nutrient solution and nutrient solution. A physical model, based on Darcy's law and an Ohm's-law analogy, is used to explain the movement of water between the roots. The model shows that the direction of water flowing in each part of a split-root system depends upon the total head for the stem, crown, and each half of the root. In practice, a root split between soil and nutrient solution acts as a wick and draws solution from the solution side to the soil side of the system. At the crown, the flow of the solution splits, and part of the solution goes up to the shoot and part goes down to the roots in soil. Nutrients feed the roots and shoots. As long as the roots can wick over the nutrient solution into the soil, the plants thrive. Such a split-root system might be realized under furrow-dike irrigation in the field, where part of a root might be in soil and part in water with fertilizer. The model permits the estimation of a crown water potential, which determines the direction of water movement (down to root in soil and/or up to shoot). The crown water potential can be used to compare cultivars and treatments.

K e y w o r d s: Darcy's law, Ohm's-law analogue, split-roots, wheat

INTRODUCTION

Soil matric potential controls plant growth. Yet the effect of soil matric potential, by itself, on growth is difficult to determine. W.R. Gardner (personal communication, 1973) suggested that one way to isolate soil matric potential is to split roots between soil and nutrient solution, because the soil has a matric potential, whereas the nutrient solution has a matric potential of zero. In follow-up to Gardner's suggestion, three split-root experiments were done with winter wheat (*Triticum aestivum* L.) [2,3,5]. In this paper, the results of these experiments are interpreted using a physical model for flow of water in a split-root system [6]. Practical applications of roots split between soil and water for increased growth under field conditions are considered.

MATERIALS AND METHODS

In the experiments [2,3,5], roots of winter wheat were split between soil and soil (abbreviated soil: soil), between soil and nutrient solution (soil:nutrient solution), and between nutrient solution and nutrient solution (nutrient solution:nutrient solution). The nutrient solution was full strength Hoagland's with an osmotic potential of -0.08 MPa. Each split-root system consisted of two 1127 cm^3 (23x7x7 cm) milk cartons with three plants. The nutrient solutions were aerated.

Details of two experiments have been published [3,5]. In this paper, we describe the

split-root experiment in unpublished work by Erickson [2]. Methods were similar to those of Erickson and Kirkham [3] and Kirkham [5], except instead of using 'Osage' wheat (with no exceptional drought resistance or sensitivity), Erickson [2] used 'KanKing,' a drought-resistant wheat, and 'Ponca,' a drought-sensitive wheat. The wheat was planted on 18 July 1979, and roots were split on 24 August 1979, when 54 seedlings were transferred to 18 split-root containers, 3 per container. The experiment was a 2 x 3 factorial design with two cultivars, three split-root treatments, and three replications arranged in a completely random design. The measurement period was 5 September 1979 (13 d after splitting) to 31 October 1979 (69 d after splitting). Measurements of height were taken every 7 days throughout the experiment. One plant of the three in each container was chosen randomly and measured on each measurement day. Each measurement of height is reported as the mean of three values. At the end of the experiment, shoot weight, root weight, and root length were determined. Half way through the experiment (on 3 October, 40 d after roots were split), water was withheld from one side of the roots split between soil: soil and from the soil side of the roots split between soil:nutrient solution. The time during which water was withheld was called the beginning of the 'water stress' period. After water stress was imposed, the level of the nutrient solution was maintained at a constant height by adding nutrient solution back to the container. Both the soil and solution containers were kept covered with black plastic to minimize evaporation.

RESULTS

Both the drought-resistant (KanKing) and drought-sensitive (Ponca) wheat cultivars had a faster shoot growth rate when water was withheld from the soil side of roots split between soil: nutrient solution (Fig. 1, arrow indicates beginning of water stress period) than before water stress. For KanKing, the increase was 3.2 times faster (0.23 cm d^{-1} before water was withheld vs. 0.74 cm d^{-1} after water was

withheld), and for Ponca, the increase was 4.4 times faster (0.08 vs. 0.35 cm d^{-1}). Both KanKing and Ponca with roots split between soil:nutrient solution had the highest shoot weight, although the difference was not significant at the 0.05 level for Ponca (Table 1).

KanKing and Ponca plants with roots split between soil:soil also increased in growth rate after water was withheld from one side of the soil (Fig. 1). Growth rate of KanKing increased from 0.11 to 0.54 cm d^{-1}, and that of
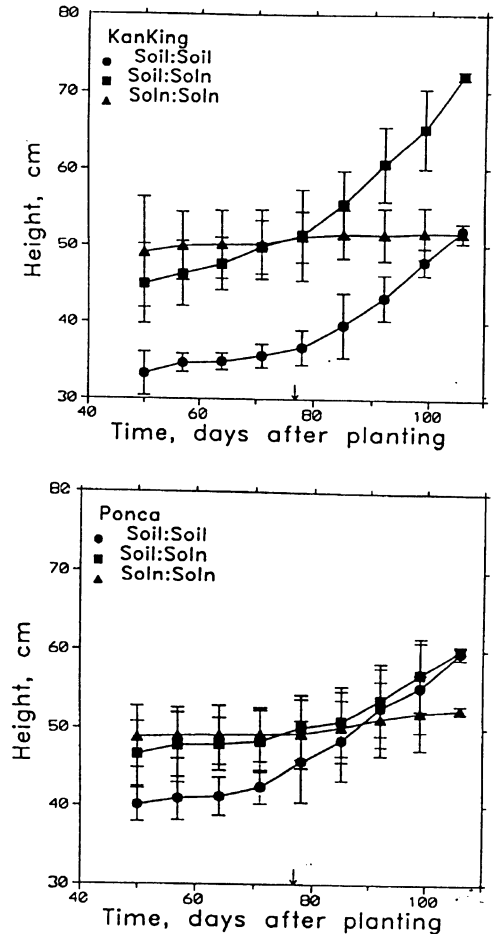

Fig. 1. Height of a drought-resistant cultivar (KanKing) and a drought-sensitive cultivar (Ponca) of winter wheat with roots split between soil and soil (circles), soil and nutrient solution (squares), or nutrient solution and nutrient solution (triangles). Vertical bars indicate ± standard deviation. The arrow indicates when water was withheld from half of the roots in soil: soil and from the soil side of roots in soil:nutrient solution. Data are from [2].

T a b l e 1. Shoot weight, root weight, and root length at harvest of a drought-resistant cultivar (KanKing) and a drought-sensitive cultivar (Ponca) of winter wheat with roots split between soil: soil, soil:nutrient solution, and nutrient solution: nutrient solution. Plants were 37 days old at the time of splitting, and 40 days after splitting, when the plants were 77 days old, water was withheld from the soil side of roots split between soil: nutrient solution and from one side of roots split between soil: soil. Plants were 106 days old at harvest. Note that in each treatment there are two values for roots (each half of the root system) and only one value for the shoot. Values are means. Means within treatments followed by the same letter do not differ at $\alpha = 0.05$. L.S.D. values are given at the bottom of the table. Data are from [2]

Cultivar	Soil:Soil		Soil:Soln		Soln:Soln	
	no water after Day 77	watered side	no water after Day 77	watered side	no water after Day 77	watered side
			Shoot weight (g)			
KanKing	4.27a*		11.33b		7.23c	
Ponca	3.46a		4.50a		2.26a	
			Root weight (g)			
KanKing	0.83a†	0.49a	5.03c	4.26c	1.36ab	1.79ab
Ponca	0.36a	0.42a	1.08a	0.55a	0.24a	0.30a
			Root length (cm)			
KanKing	1247d‡	928bc	3071h	2826g	1770e	1966f
Ponca	697ab	756ab	1284d	912bc	482a	572a

Explanation: * - L.S.D. = 2.40 g; † - L.S.D. = 0.93 g; ‡ - 246 cm.

Ponca increased from 0.11 to 0.50 cm d^{-1}. Height of plants with roots split between nutrient solution:nutrient solution was generally constant during the experimental period (Fig. 1).

For both KanKing and Ponca at harvest, the soil side had more roots than the solution side (3071 vs. 2826 cm for KanKing; 1284 cm vs. 912 cm for Ponca) (Table 1). The growth results for Ponca and KanKing [2] agree with those obtained for Osage wheat that was not stressed by wind [3]. Osage wheat grew taller when roots were split between soil:nutrient solution than when all roots were in soil or in solution. Roots proliferated on the soil side, when they were split between soil: nutrient solution.

When roots of Osage [3] and Ponca and KanKing [2] wheats were split between soil:nutrient solution, the soil remained wet, even though no water was added to the soil by watering. Water apparently was transported from the roots in nutrient solution into roots in soil. A simple model indicates how the transport of water might occur [5]. One can take two containers, connected by a wick, and fill one container with water and leave the other one empty. Water will drip into the dry container as long as the wick in the dry container is below the solution surface. If the wick is above water surface, however, water will not drip. When roots were split between soil:nutrient solution, solution probably was moving by capillarity from the solution side into the soil side. The part of the roots exposed to the air (a 1-2 cm section) looked dry, which suggested that water moved inside the roots. Such wicking action could occur under field conditions, as will be discussed later.

SPLIT-ROOT MODEL

We now address the following question: Why did shoot growth of Ponca and KanKing increase when roots were split between soil: nutrient solution and grown under water stress?

A physical model, based on Darcy's law and an Ohm's-law analogy, was developed [6] to show how water moves in a split-root system. (The model is generic and does not specify a plant.) Total heads (sum of head due to gravity and head due to pressure-other heads were negligible) and flows of water

were calculated or measured for each part of the system (left root, right root, crown, stem). The results showed that the direction and quantity of water flowing in each part of the plant depended upon the total head for the stem, crown, and each half of the root (the flow could be up or down), and that the gravity component of the total head was important in moving water down the plant when light intensity was low. The results also showed that the total head of the crown determined the direction of flow of water in the plant.

The schematic representation of the model is given in Kirkham [6; see Fig. 1 in that paper]. In the model, walls of the roots, the crown, and the stem are taken to be impervious, except that near the bottom of the roots, where they are active, water can enter (or leave) via equipotential surfaces. Even though the cylindrical model is three-dimensional (3-D), as are plants, we may treat it as a more convenient two-dimensional (2-D) equivalent system. In Fig. 1 of Kirkham [6], the third dimension of the split-root system extends perpendicularly to the paper. The 2-D form of the split-root system looks like an inverted tuning fork. It has parallel front and back faces. In the model, we have a symmetrical flow system with no potential gradients and, hence, no flow in a direction perpendicular to the front and back faces. Therefore, no z coordinate is needed to describe a 2-D (x, y coordinate) flow system. In such a system, only a unit distance perpendicular to the x,y flow plane needs to be considered, and this unit distance was 1 cm in the model [6].

When the system is made 2-D, an alternative type of crown and stem also may be considered, where the wide stem and equally wide crown are equal in width to the combined width of the roots and the space between them, as illustrated in Kirkham [6; Fig. 3]. That figure showed that, when roots are split between potentials (total head) of 0 and -100 (arbitrary units) and the stem is at a potential of -100 (arbitrary unit), water can move up from the root at 0 potential to the shoot (stem) or down to the root at -100 potential. A 'stagnation point' occurs

in the crown where flow is zero. At this point, water moves upward to the shoot at -100 potential or downward to the roots at -100 potential.

APPLICATION OF THE SPLIT-ROOT MODEL TO DATA

As stated before, when roots were split between soil:nutrient solution, the soil remained wet even though no water was added to it. Because the soil was saturated, Darcy's law applies and, hence, the physical model of Kirkham [6]. If we consider a 2-D system, we can take the results for KanKing and Ponca and estimate a crown water potential (total head), following calculations given by Kirkham [6]. However, we had only one split-root setup (a pair of milk cartons) in the real experiment. For the data to be applicable to the 2-D model, we would need many milk cartons forming a row with the tall sides, perpendicular to the direction of the row, removed, so that the potential in the z direction is uniform. That is, we could think of many split-root setups being placed one next to each other in a long row with no barrier in the direction perpendicular to the x, y plane.

Recognizing this limitation, we take data for KanKing and Ponca at harvest (Fig. 2), when KanKing was 72 cm tall and Ponca was 60 cm tall. We assume that 1 cm of the root is exposed where the root splits. The milk cartons were 23 cm deep, and we assume that roots were at the bottom of the milk carton. We assign points A, B, C, and D, as was done in the model [6] (A = base of left root; B = base of right root; C= crown; D = top of plant).

Applying Darcy's law, we use the following equation presented by Kirkham [6; Eq.(3)]:

$$KA(h_C - h_D)/CD = [KA(h_A - h_C)/AC] +$$

$$[KA(h_B - h_C)/BC] \quad (1)$$

where K - hydraulic conductivity (cm d^{-1}), h_A, h_B, h_C, h_D are total heads (cm) at points A, B, C, and D, CD, AC, and BC are lengths (cm) of the shoot, left root, and right root, respectively (Fig. 2), and A - cross-sectional area through which flow occurs (cm^2).
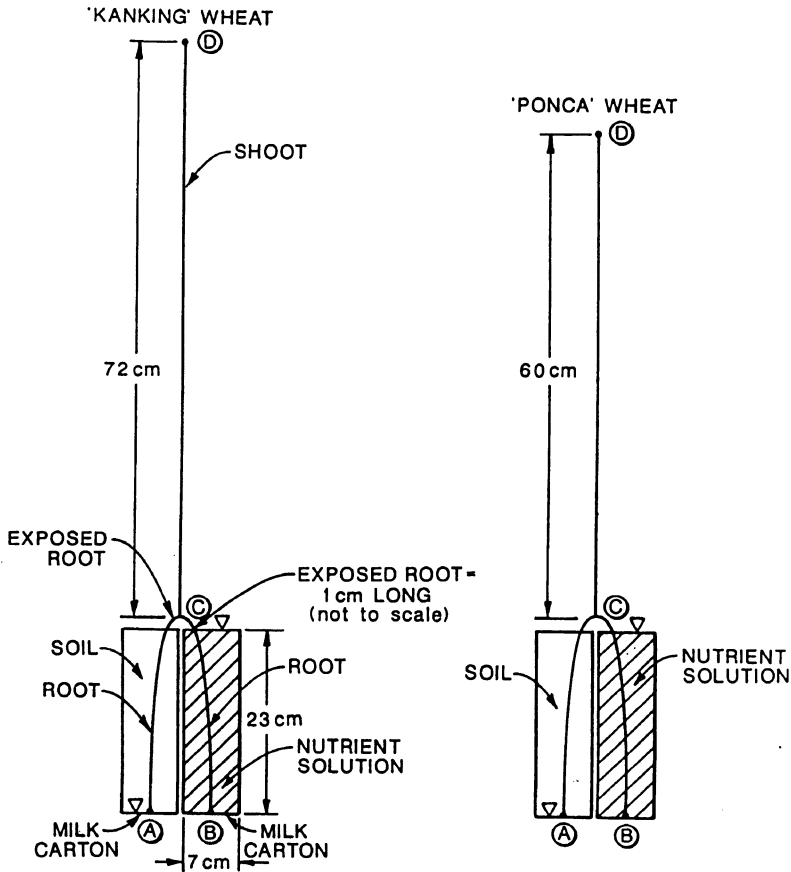
Fig. 2. Schematic representation of KanKing (left) and Ponca (right) wheat with roots split between soil:nutrient solution at harvest (106 days old). Total heads at A (bottom of left root), B (bottom of right root), and D (top of shoot) are known, and the head (potential) at the crown is calculated. The upside-down triangle at the base of the left carton (point A) is arbitrarily taken as the reference level (0 cm). The upside-down triangle at the top of the right carton shows the level of the nutrient solution, which was maintained at this height throughout the experiment.

In the split-root experiment with KanKing (Fig. 2, left), we have: $h_A = 0$ cm (by definition); $h_B = 23$ cm (depth of milk carton); $h_D = -(72 + 1 + 23$ cm$) = -96$ cm; $h_C = ?$ (what we want to determine).

Because KA is a common term in each part of Eq. (1), we cancel it and get for KanKing:

$$(h_C+96)/72 = [(0-h_C)/24] + [(23-h_C)/24]. \quad (2)$$

We solve Eq.(2) and get $h_C = -27/7 = -3.86$ cm. We can do the same calculations for Ponca (height at harvest = 60 cm) (Fig. 2, right) and get $h_C = -53/12 = -4.42$ cm.

The values are negative, which means that at least part of the water is going up to the shoot, as necessary. If a crown water potential is positive, then all the water is going to the root at the lower water potential.

The results suggest that a root system with roots split between soil and nutrient solution could be used to calculate such an estimated crown water potential, which might be useful to compare treatments and drought resistance of cultivars.

When roots of Ponca and KanKing were split between soil:soil and water stress was imposed, the growth rate was faster than before stress was imposed. But because we are not dealing with soil saturated with water on each side of the root zone, we cannot apply Darcy's law to calculate a crown water potential.

WATER USE OF SPLIT-ROOT PLANTS

The amount of water added to cartons was not recorded in the experiment with Ponca and KanKing [2], but it was in the experiments by Erickson and Kirkham [3; Table 1] and Kirkham [5; Table 2]. When plant roots were split between soil:nutrient solution, more water was added to the nutrient solution side than to either carton when roots were split between nutrient solution:nutrient solution. For example, in Erickson and Kirkham [3], before 'water stress' was imposed and roots of control plants (no wind) were split between soil:nutrient solution, 210 mL and 2310 mL were added to the soil side and nutrient-solution sides of the cartons, respectively, over a 14-d period. During this time, an equal amount of water was added to each carton when roots were split between soil:soil (an average of 476 mL per side) or between nutrient solution:nutrient solution (an average of 1267 mL per side). After water stress was imposed, no water was added to the soil side when roots were split between soil:nutrient solution, but 4368 mL were added to the nutrient solution side over a 21-d period. During this time, an average of 2320 mL was added to each side when roots were split between nutrient solution:nutrient solution.

EXPLANATION OF INCREASED GROWTH OF SPLIT-ROOT PLANTS

When roots were split between nutrient solution:nutrient solution, water potential on each side of the root zone was equal. Thus, water probably moved up to the shoot, and no water moved from one side of the root to the other side, because no potential gradient existed. When roots were split between soil:nutrient solution, a potential gradient existed, and part of the solution moved to the root in the soil and part moved to the shoot. When water stress was imposed (no water added to the soil side), the gradient became stronger and more water moved from the solution side to the soil side. At the same time, growth increased. Paradoxically, a 'water stress', even though the soil remained wet on the surface, resulted in increased growth. This was probably due to the fact that more roots were produced on the soil side of roots split between soil:nutrient solution (compared to roots grown only in solution or only in soil), and the increased root growth permitted increased shoot growth.

When all water moves up from the roots to the shoot (each side of root system only in nutrient solution or each side only in watered soil), roots on each side of the split-root system grow equally, and the shoot grows optimally for the conditions that Nature provides. But when nutrient solution can move from one part of a root system to another, plants grow even better. Apparently, we see here a situation where we can 'trick' Nature into more growth, as was done when the hormone kinetin was sprayed on plant leaves, which resulted in larger stomatal conductance than occurs under natural conditions [8]. The reason for the increased growth in the split-root system probably was not hormonal, because, even after 'water stress' was imposed, the roots were still in watered soil, and no stress hormones would have been produced. The reason was probably nutritional. The extra nutrients that the root system in soil got via wicking of the nutrient-laden solution probably permitted the extra growth.

In sum, the process appears to be the following when roots are split between soil and nutrient solution. A split root, acting as a wick, draws solution from the solution side to the soil side of the system. At the crown, the flow of the solution splits, and part of the solution goes up to the shoot and part goes down to the roots in soil. Nutrients feed the roots and shoots. As long as the roots can wick over the nutrient solution, the plants thrive. But environmental conditions can change this balance. When Osage wheat was grown in wind [3], roots split between soil:nutrient solution did not proliferate on the soil side. Shoots grown in wind had a lower water potential than shoots grown without wind, and this lower leaf water potential apparently caused more water to move upward to the shoot than downward to the roots in soil.

FIELD APPLICATION OF SPLIT-ROOTS

Because roots of a tree can extend widely and graft onto the roots of another tree, movement of water from wet soil (e.g., flooded soil) to unsaturated soil by roots probably occurs frequently under natural conditions [9]. Under field conditions, a split-root system, with part of the roots in saturated soil and part in unsaturated soil, might be realized at times under furrow (row) irrigation systems. The seeds could be planted on the side of the ridge, so that part of the roots would grow into the furrow and part would stay on the ridge. If the seeds were planted on south-facing slopes in the northern hemisphere, this would have the added advantage of a warm seed bed to hasten germination [1]. If a plant produced prop roots, like corn does, those roots in the irrigation furrow might transport water to roots in unsaturated soil.

In drip irrigation systems already in use, water probably is moving from the part of a root system near the drip source under saturated conditions to parts of the system under unsaturated conditions. In addition to gravity and capillarity moving water through the soil around a drip source, the movement of the water through the root also needs to be considered.

A relatively new irrigation system, based on research in Texas [12], is being developed in semi-arid regions of the USA to conserve water. It is called furrow-dike irrigation. Water is applied directly from a center pivot spinkler system to a furrow that has small dikes placed across it every 30 cm (foot) or so. The furrow dikes hold the water in place until it can soak into the soil [10]. The soil is saturated in the pools between the dikes in the rows, but unsaturated between the rows. We recognize that eventually soil in the root zone under a differentially irrigated surface soil may attain the same water potential, and a demarcation at some depth in the soil between saturated and unsaturated soil cannot be made, because the soil water will all be at the same water potential. See Philip [11] on this point, who discusses and mathematically analyzes infiltration under fractional wetting of the soil surface. If a plant could be positioned so that part of its root would grow in the pond of a furrow and part in the adjacent unsaturated soil, then the part of the root in the pond would be transferring water to the part of the root in unsaturated soil. In a diked system, if one wanted to apply the 2-D split-root model described above, the distance between dikes would need to be long enough for the model to be applicable.

The split-root system could have an added advantage under semi-arid conditions, because less water might be lost by evaporation from the furrow than if no root were there. Water in the furrow would be transferred to the root in the unsaturated soil, which might minimize water lost to the atmosphere.

If the irrigation water also contained fertilizers, the nutrients would be wicked to the roots in the unsaturated soil. Artificial foam wicks have been used by commercial greenhouse growers for two decades to supply water and nutrients to horticultural crops [7]. The technique is called 'capillary watering' or 'wick culture'. Under field conditions, roots themselves could act as the wicks transferring water and nutrients from saturated soil to roots in unsaturated soil. The deeper and bigger the root system is on the unsaturated side, then the larger the plant might be, and yields also might increase. This should be checked out in the field.

Gardner [4], in his oral presentation at the International Crop Science Congress in 1992, stated that advances in efficient use of water under irrigated conditions are going to come in small steps through 'micromanagement'. Growing plants so that part of the root system is in saturated soil and part in water or fertilizer solution will require micromanagement, but the possibility of increasing growth might be worth the trouble.

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