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WATER TRANSPORT at the SOIL-ROOT INTERFACE

INTRODUCTION

The movement of water from soil into roots is a subject of great complexity, since the interface between soil and absorbing root elements has properties that differ from those of the bulk soil, and are often difficult to characterize. For instance, roots tend to grow in special regions of the soil (i.e. biopores, cracks, areas of high nutrient content), and the water-transmission characteristics of such regions only recently have become the subject of research. Furthermore, the root system changes the physical and chemical conditions of the soil surrounding it by uptaking only selected ions, by exuding organic compounds and by affecting the microbial populations. It is also able to symbiotically bind to fungi and bacteria. This creates special characteristics - including those related to water uptake - of the rhizospheric soil.

Also, the root system is highly dynamic, and the features that affect water extraction change in space and time: roots grow; thus the absorbing front moves in the soil. Roots evolve, and the anatomical characteristics that vary with age affect the movement of water both radially (from the root surface to the xylem vessels) and axially (through the xylem, from the absorbing roots to the plant top).

The properties related to water uptake also change as a result of environmental conditions - like soil water content - and they do not depend on local characteristics only: the root acts in coordination with root soil environment (Brouwer, 1981), and single parts may act differently according to the conditions of the rest of the root system. For instance root growth has been reported to decrease in dry soil, below -0.8 MPa, and to stop at -1.9 MPa, even though there are variations between soil type and density (Ehlers et al., 1983). But growth can continue in dry soil if the rest of the root is in wet conditions (Portas and Taylor, 1976).

All of the above suggests why the field of root water uptake is an especially challenging one, and it has to be treated with appropriate methods according to the scale and type of the problems addressed.

SOIL-ROOT INTERFACE

Plant Roots

Regarding water uptake, the plant root is viewed as a system of absorbing elements - usually fairly young roots at the periphery, and conducting ones - the larger structures. Uptake occurs radially from the soil through several root layers into the xylem, and transport occurs axially through the xylem. The resistance that water encounters in its way from the soil to the aboveground plant organs is divided into a radial and an axial component. Both change with root age, along a root axis, as illustrated in Fig. 1.

When roots are young, water moves quite easily through the cell walls (apoplastic or extracellular pathway, Drew, 1979) to reach the xylem, but with age the walls become largely impermeable, especially in an annular region of cells located at the endodermis. This region, called the Casparian strip, becomes the location of one of the major resistances to radial water flow in roots, although depositions of suberin occur in other areas (e.g. epidermis. Recently a formation similar to the Casparian strip has been reported in the hypodermis by Peterson et al., 1982). Therefore water has to find different ways to move radially; these ways involve the passage through cell membranes (symplastic and transcellular pathways, through cell vacuoles or plasmodesmata - Steudle, 1989), much slower than the apoplastic transport. Also, cell membranes are semipermeable, and they can exclude ions. So, descriptions of water movement that involve the passage of water through cells (i.e. from the soil to the xylem) include an osmotic component that is not present in the movement of water through soil only. In older roots the transport is further limited by the deposition of suberin lamellae in the endodermis or hypodermis, and by the presence of cork cells in woody plants.

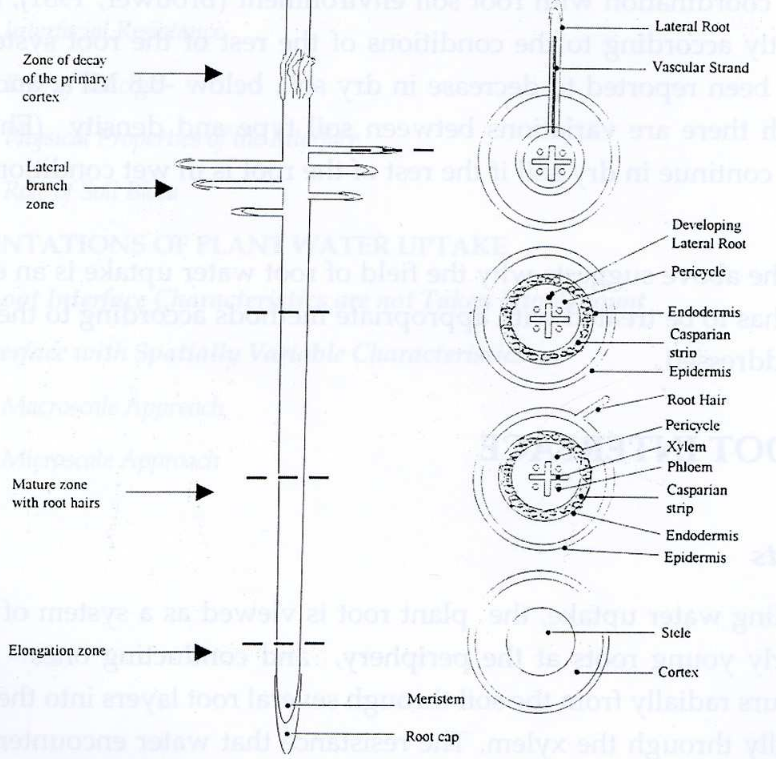

Fig. 1 - Longitudinal and transverse sections of the growing root of a plant.

Regarding axial transport, the xylem is initially a string of living cells, characterized by a high resistance to water movement, and with age it matures by loosing its cytoplasm and therefore allowing water to flow much more rapidly through it. So, the classical view is that roots take up water mainly in the region located at 1-10 cm from the tip, that corresponds to that where root hairs are present, because older regions are too suberized to allow substantial radial water flow, and in younger ones (the root tip) the axial flow is too slow, because the xylem is still immature.

The number and diameter of xylem elements determines the rate of axial transport. It is different with plant species and conditions of growth. In dicots, roots undergo secondary growth with decay of the primary cortex and the creation of new xylem vases, whereas the roots of monocotyledons do not have secondary growth, so the transport characteristics of the xylem are fixed at the time of primary root growth. These roots, though, may loose their cortex as a result of age, and this may decreases the radial resistance to water movement (Fig. 1), although the resistance located in the endodermis still remains a major obstacle to apoplastic water movement (Drew, 1979).

Due to the different branching geometry, large roots are connected to one-another and to the central tap root in dicots, whereas they are independent in monocots, in which they converge at the seed (seminal roots) or at the crown (nodal roots). Therefore, in formalisms that depict the root water transport as an electric analog, the former systems more closely resemble a series of resistances, whereas the latter are largely parallel (Klepper, 1990) (Fig. 2).

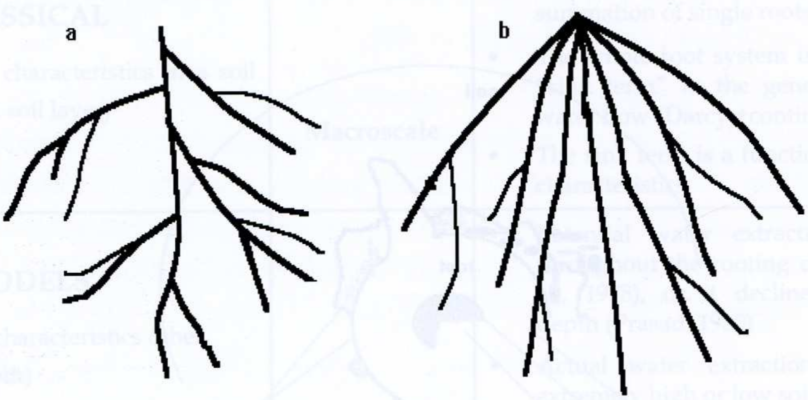

Fig. 2 - Root architecture of a) dicots and b) moncots.

Soil-Root Interface

The interface is certainly complex and several features play a role. Roots may grow in the bulk soil, pushing it laterally, and thus creating compression around them (Foster, 1994) especially after secondary thickening, or they follow pathways of least resistance like preexisting channels created by soil fauna or previous roots (Edwards and Lofty, 1978, Wang et al., 1986), or cracks (Amato, 1991). Often roots are found preferentially in regions of higher biological activity or nutrient content (van Noordwijk et al., 1993). All of these regions have properties that differ from those of the bulk soil, because of reorientation of soil particles, caused by the soil properties at those locations (e.g. friction of peds faces in cracking clays), or by biological activity of fauna (es. deposition of organic matter in pores, see in Foster, 1994) or microflora (e.g. Dorioz et al., 1993) or as an effect of the growth of roots (e.g. Jaillard and Callot, 1987).

Also, roots exudate polymeric substances, mainly carbohydrates, that harbor bacteria and fungi (Fig. 3). Such organisms may lose carbohydrates in the soil as well. These substances are relatively hydrophilic when fresh, but they undergo changes that make them hydrophobic and that stabilize soil aggregates against the action of water. The sheet of gels, root hairs, microbes and soil particles that remains attached to fresh roots even after washing, has been called rhizosheet (e.g. McCully and Canny, 1988), and its water uptake characteristics are only scarcely known. It has been described in the distal region of roots of grasses, although researchers often fail to notice it because it rarely develops in pot media and it is easily lost by mishandling in soil studies (McCully and Canny, 1988). Its presence is accompanied by other root features that affect the movement of water (see below). Furthermore, the interface includes mycorhizal myceliums that are intimately connected with the roots.

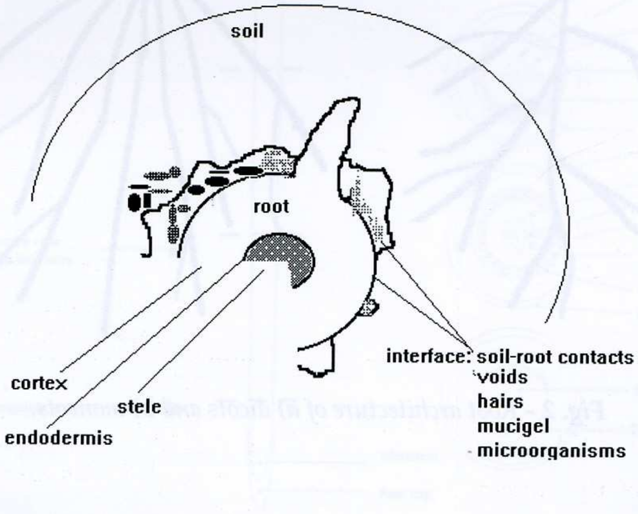

Fig. 3 - The soil-root interface with its biotic and abiotic components.

WATER TRANSPORT FROM SOIL TO ROOTS

The interface between soil and roots may be viewed at different levels of detail, depending on the purpose of research. The roots system may be considered as a system transferring water from the soil to the aboveground organs of the plant, through water uptake characteristics of root components.

In any case, root water uptake has been described classically by models based on the average characteristics of roots in a volume of soil (usually a soil layer). Such models were classified as microscale if they account for water flow in a single root with 'average' characteristics and then extend it to the whole root system, or macroscale if they describe the root system as a sink in its totality. Both types of models share the problems related to quantifying the 'average' or 'representative' root characteristics.

Theoretical considerations and difficulties in reproducing experimental data have stimulated, on one side, the development of models that do not take root features into account, and describe water uptake as a function of maximum rooting depth only. On the other side, different approaches model the root system as a spatially variable water sink, at least for some of its characteristics.

Classical and alternative approaches are summarized in Table 1 and described in the following paragraphs.

Table 1 *- Approaches to the description of root water uptake*

CLASSICAL (based on average characteristics in a soil volume, generally a soil layer)	**Microscale**	• Radial flow to a single root with "avg." characteristics • Extension to the whole system as a summation of single roots
	Macroscale	• The whole root system is described by a "sink term" in the general equation of water flow (Darcy +continuity) • The sink term is a function of root & soil characteristics
MODELS (not based on root characteristics other than maximum depth)		• Potential water extraction is constant throughout the rooting depth (Feddes et al., 1978), or it declines linearly with depth (Prasad, 1980) • Actual water extraction is limited at extremely high or low soil water potential
SPATIAL DESCRIPTION (based on spatial pattern of the physical distribution of roots)	**Microscale**	• Flow to single roots conditioned by their position relative to other roots (Petrie and Hall, 1992; Lafoile et al., 1991). The contribution of each root is not equal
	Macroscale	• Flow to root clusters based on the geometry of rooting (Passioura, 1985)

CLASSICAL APPROACHES

Microscopic Approach

Each root is considered as an infinitely long cylinder, of uniform radius and water uptake characteristics (Philip,1957; Gardner, 1960; Cowan 1965). Water flow towards such a root is therefore described as radial (Fig. 4), and expressed as a function of water potential gradients and hydraulic conductivity of the soil:

$$\frac{\delta\theta}{\delta t} = \frac{\delta}{r\delta r}\left(r \cdot k_s \frac{\delta\psi}{\delta r}\right) \qquad (1)$$

where θ = volumetric soil water content

t = time

r = radial distance across which water moves

k_s = soil hydraulic conductivity

ψ = soil matric water potential[1]

Various assumptions on the type of flow and boundary conditions have yielded different analytical solutions of this non-linear equation, for the calculation of water flow between the bulk soil and the root surface, or between the bulk soil and the root xylem. In the latter case, both resistances in the soil and across the root had to be considered, and k_s was replaced by k_{sys} : the composite hydraulic conductivity of the soil-root system (Taylor and Klepper, 1975), and the osmotic component of soil water potential was included because the symplastic ways were included in the model.

The extension of the model to the whole root system is based on the simplifying hypothesis that each root draws water exclusively from a given soil region. The complete root system is then viewed as a summation of single roots, since no overlapping between extraction zones is considered, nor is there any other interaction between roots. The watershed of each root is calculated as a cylinder whose radius is half the average distance between roots (Gardner, 1960; Tinker, 1976) (Fig. 4).

Criticisms have been made of this approach (Molz, 1981; Passioura, 1988; Klepper and Taylor, 1978), mainly of its application to the whole root system, for theoretical and practical reasons. Problems in application include difficulties in defining the boundary conditions, and in measuring the parameters involved, inaccuracies in determining the whole root

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[1] in most cases, the formalism ψ = matric potential is used because flow to a single root is considered to occur over a short distance where gravity is negligible.

length of a plant at each time, and more important the problems in establishing the relative contribution of each part of the total root length to active water uptake. Of course, the attempt to address these questions has stimulated a large body of research on processes related to water uptake, and especially on establishing which of the soil and root resistances to water flow were most important in determining the water uptake rates in different situations (Gardner, 1964; Molz, 1971; Taylor and Klepper, 1975; Passioura, 1988; Newman, 1969 a and b; Boyer, 1971; Miller et al., 1971; Barrs and Klepper, 1968; Begg and Turner, 1970; Reicosky and Ritchie, 1976; So et al., 1976; Samui and Kar,1981).

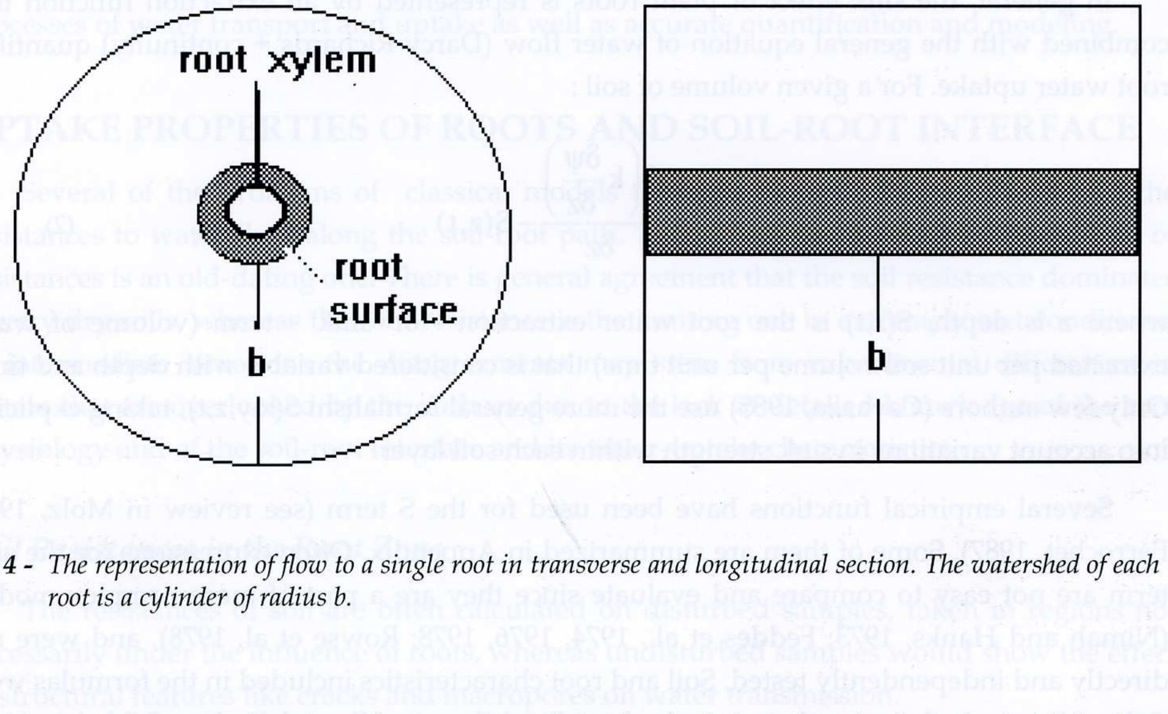

Fig. 4 - The representation of flow to a single root in transverse and longitudinal section. The watershed of each root is a cylinder of radius b.

From a theoretical point of view, ignoring physical (overlapping) and physiological interactions between single roots is a cause of error. The model has, in many cases, proved inadequate to describe accurately the water uptake of root systems (Brenner et al, 1986; Faiz and Weatherley, 1977; Faiz and Weatherley, 1978; Miller, 1985; Herkelrath et al, 1977 a and b; Zur et al, 1982), although the behavior of single roots has been shown to be modeled fairly accurately in some cases (Hainsworth and Aylmore, 1986; Passioura, 1980; Taylor and Klepper, 1975).

Macroscopic Approach

The root is characterized as a water sink in its totality. Many types of models can be listed under this category. Early works (e.g., Wadleigh, 1946) proposed an integrated soil water value to represent the entire root water status. Based on thermodynamics, Wadleigh's view was that the root system adjusts water absorption so that the soil water potential is constant throughout the root zone.

Subsequent models used the concept of root as a diffused sink but the sink strength is not regarded as necessarily uniform throughout the rooted volume (Whisler et al., 1968; Molz and Remson, 1970,1971; Nimah and Hanks, 1973; Hillel et al, 1976). Therefore different parts of the root were recognized to experience different water status. In particular, some models recognize non-uniformity in the vertical dimension for soil and rooting patterns that affect water extraction.

In general, the sink effect of plant roots is represented by an extraction function that combined with the general equation of water flow (Darcy-Richards + continuity) quantifies root water uptake. For a given volume of soil :

$$\frac{\delta\theta}{\delta t} = \frac{\delta\left(k\frac{\delta\psi}{\delta z}\right)}{\delta z} - S(z,t) \qquad (2)$$

where z is depth, S(z,t) is the root water extraction - or 'sink' - term (volume of water extracted per unit soil volume per unit time) that is considered variable with depth and time. Only few authors (Cavazza, 1985) use the more general formalism S(x,y,z,t), taking explicitly into account variations in sink strength within each soil layer.

Several empirical functions have been used for the S term (see review in Molz, 1981; Perrochet, 1987). Some of them are summarized in Appendix. Often expressions for the sink term are not easy to compare and evaluate since they are a part of more complex models (Nimah and Hanks, 1973; Feddes et al., 1974, 1976, 1978; Rowse et al, 1978), and were not directly and independently tested. Soil and root characteristics included in the formulas were rather chosen as the ones that gave the best fit of the overall model when field data were used for calibration (Molz, 1981).

Early formulations of the sink term are rather simple and include soil hydraulic properties alone, ignoring root resistance to water flow, and have therefore been criticized from a conceptual (Molz, 1981; Reicosky and Ritchie, 1976) and practical (Klepper and Taylor, 1978) point of view. Others regard root-soil hydraulics with more detail (Molz, 1981; Klepper and Taylor, 1978). In an attempt to overcome some of these limitations, more recent macroscale models include a more mechanistic treatment of soil and plant behavior, showing more attention to water uptake processes (Nimah and Hanks, 1973; Rose et al, 1976; van Bavel and Ahmed, 1976; Hillel et al., 1976; Taylor and Klepper, 1975). Several of them include root density per unit volume. Those models are sometimes regarded as 'hybrid' models and have some problems of microscale approaches encountered in describing and quantifying water withdrawal mechanisms. Among those problems are the quantification of root structures which are active in uptake, the determination of the relative importance of soil and root resistance to water flow, the variation of soil-root interface resistance with soil water content (Herkelrath et al., 1977 a and b), and the question whether the root resistance to water outflow is higher than that to water inflow.

Advantages, theoretical problems, practical disadvantages and inability to accurately describe experimental data and predict plant water use have been reviewed (Molz, 1981; Klepper and Taylor, 1978; Passioura, 1988) for the various approaches. Some of the problems, common to the most models, need to be addressed for a better understanding of the processes of water transport and uptake as well as accurate quantification and modeling.

UPTAKE PROPERTIES OF ROOTS AND SOIL-ROOT INTERFACE

Several of the problems of classical models relate to the actual determination of the resistances to water flow along the soil-root path. The debate on the relative magnitude of resistances is an old-dating one. There is general agreement that the soil resistance dominates in very dry soils, whereas the root resistance is the limiting one in extremely wet conditions. In intermediate situations the disagreements may stem from experimental differences in factors that are overlooked by the authors due to the lack of detailed knowledge of the root physiology and of the soil-root interface and its water-uptake characteristics.

Soil Resistances in the Root Zone

The resistances of soil are often calculated on disturbed samples, taken in regions not necessarily under the influence of roots, whereas undisturbed samples would show the effect of structural features like cracks and macropores on water transmission.

Exudates and microbial biomass constitute a peculiarity of rhizospheric soil. These materials are polymers, mainly polysaccharides that are likely to affect the hydraulics of the soil. They have been shown to be highly hydrophilic when excreted, but after a wetting-drying cycle they create stable aggregate with soil particles, that are not affected by further wetting. This changes the pore-size distribution of the soil, and therefore its water movement characteristics. Passioura (1988) has pointed out that rhizosperic compounds may act as surfactants. In this case they would change the water content - water potential relations of the soil, by changing the angle of water menisci in the soil pores. In particular they would reduce the water potential (suction) at a given water content.

Root Resistances

Axial

Theoretically, it could be estimated by Poiseuille's law, which states that flow is a function of the fourth power of the radius; but the radius of xylem elements changes along the root, and common are irregularities like discontinuities, and obstruction by gums, micelia, etc.

In some plants the axial resistance appears to be irrelevant, since total root resistance doesn't change with root length. In others it seems important, amounting 10^{-2}-10^{-3} cm·day·bar·cm^{-3} of water (Klepper and Taylor, 1978). Passioura (1980) points out that the root system of monocotyledons consists of a few seminal roots, and adventitious roots develop only if there is enough soil water. Since there is no secondary growth in dry soil, water transport is severely limited by axial resistance due to the small number of total xylem vases in the plant. This may be an advantage since a slow consumption of water helps saving a substantial amount of the soil water for the post-anthesis period, which is the most important for yield. A similar effect of water deficit on the reduction of subsequent water uptake through the reduction of axial conductivity is exerted through the reduction of the diameter of xylem vases in dry soil (Cruz et al, 1992).

Radial

The assessment of which part of the root is to be considered active in radial uptake of water was one of the first, and still is one of the main problems of determining the average characteristics of an absorbing root system, due to the difficulties of the measurements involved.

Early works and a number of more recent ones (Drew, 1979; Boyer, 1985) identify 1 to 10 cm of the root behind the tip as the active region (see above) but the involvement of root regions in uptake is quite controversial and depends on various other conditions:

- It varies with species (Newman, 1976; Drew, 1979; Sanderson, 1983; more recently Perumalla and Peterson, 1986 show differences among herbaceous species). Steudle and co-workers, in a series of experiments conducted with a pressure probe technique, show that in some species (maize) apoplastic movement seems more important than in others (barley, bean), which have a larger proportion of cell - to -cell pathways (see in Zhu and Steudle, 1991).
- It is affected by growth conditions (Brar et al., 1990), and in particular stress. For instance water deficit induces suberification and lignification and the deposition of Casparian strips closer to the root apex (Cruz et al. 1992; Perumalla and Peterson, 1986).

- It varies with roots hierarchical position. Waisel and Eshel (1991) report that main axes grow faster and the non-suberized region behind the root tip is longer than in laterals; main roots therefore take up water and nutrients less selectively than laterals.
- The uptake region expands to older root regions as the rate of transpiration increases (Kilic, 1973; Newman, 1976; Drew, 1979). Experiments show that in case of fast flow, the basal regions may have an even higher permeability than apical ones (see in Newman, 1976).
- Kramer (1983), and Muromtsev (1969) argue that in woody species there is cork deposition at the periderm, and the external tissues are shed; therefore the resistance varies, and can be lower since lentils and cracks in the cork are easy pathways for water penetration. Drew (1979) reports a high permeability of these layers. According to Kramer the amount of water extracted by old roots may be higher than that of young roots even in case of lower permeability because of the higher surface involved in uptake.
- McCully and Canny (1988) have shown that in maize roots, the region characterized by the presence of root hairs and rhizosheet may extend to the distal 30 cm from the tip. They show that in this region some of the xylem vases (the late metaxylem) are still full of cytoplasm, this severely limiting the transport of water. They therefore suggest that the role of this region in water uptake has been overestimated, and that a major role is likely to be played by the older segments, bare of both root hairs and mucigel. They argue that in spite of the presence of many seemingly impermeable structures, these areas have been shown to exude carbohydrates in the same amount as those with root hairs. They also show an important role of laterals in conveying water to these regions across the suberized layers.
- Recent work shows that the flow rate of water through the root is different according to the type of water potential gradient applied. It is slower under osmotic than under hydrostatic gradients (Steudle, 1989; Shone and Clarkson, 1989; Zhu and Steudle, 1991). Steudle (1989) suggests that the reason is the difference in pathways: under hydrostatic forces water would move primarily in the apoplast, while osmotic gradients would imply in larger proportion of cell-to cell movement.
- By using a double pressure probe technique Zhu and Steudle measure simultaneously the water flow and the hydraulic characteristics of roots and single cells, thus measuring the hydraulic conductivity of each layer of cells in the root. They found that the contribution of apoplastic movement decreased from the root surface inwards, due to an increase in permeability of the cell membranes. .

- The recent discovery of a Casparian strip at the root hypodermis (Peterson et al., 1982) has arisen questions whether this tissue is the location of a major source of root resistance in addition to the endodermis. This formation appears at a different time and is affected by stress differently than the Casparian strip at the endodermis, this changing the extent of the most actively absorbing roots in the plant.

Factors other than plant anatomical features play a role. An example is temperature that may vary considerably with soil depth, and that may affect root activity rate to a large extent (Allmaras et al., 1975). Small anaerobic soil areas, likely present in structured soils, will also change local root permeability (Everard and Drew, 1987).

Is Root Resistance Constant or Variable with Flow?

Experimental evidence is controversial. In a series of experiments and theoretical analysis Passioura and co-workers (i.e. Passioura, 1984) argue that part of the differences between authors may be due to the different growth medium of plants. At high flow rates they find a constant resistance in soil, and a variable one in nutrient solution. At low rates there is variability also in soil. Furthermore, the authors find a circadian variation of resistance

Does Root Resistance Vary According to the Direction of Flow?

Many authors hypothesize that roots act as rectifiers, allowing the inwards flow of water but trying to make the outwards flow (reverse flow) more difficult in order to avoid water losses in case the soil is drier than the root. This would prevent the root from extracting water from regions of wet soil and releasing it in dry soil, generally at the surface (hydraulic lift). Experimental results are few and controversial: at the whole root level Nobel and Sanderson (1984) showed a major reduction in the permeability of roots of desert succulents upon drying. Both these authors and Dirksen and Raats, 1985 found no flow of water from wet to dry soil, while others did, both vertically and horizontally (i.e. Baker and van Bavel, 1986 and 1988; Glenn and Welker, 1993). At the tissue level Shone and Clakson (1989) measured a different rate of water flow in the root hypodermis according to the direction: the outflow was slower than the inflow.

Hypotheses about the mechanisms involved include:

- the loss of contact between root and soil in dry environments (see discussion below).
- the fact that in dry soils the suberization of roots occurs earlier (Nobel e Sanderson, 1984). This mechanism is rarely reversible, and would explain why re irrigation causes only partial recovery of water uptake in the short term. It takes at least 48 hours to

recover normal rates of water extraction at the whole plant level, and this is compatible with times required for the growth of new roots.

- Tanner (personal communication in Passioura, 1988) speculates that the outflow of water would cause an accumulation of solutes inside the root, and they would act osmotically impeding any further flow of outgoing water.

Speculations about the advantages and disadvantages of allowing reverse flow are listed hereafter.

Among the disadvantages, water would be lost to dry soils, especially at the soil surface where it would be evaporated. On the other hand, if the dry soil is not at the surface, it may be beneficial to transfer water there during the night, so it would be available for the following day's uptake and transpiration at a faster rate than if it came from deep soil only (see discussion in Passioura, 1988).

The advantages would be manifold:

- for water management: Baker and van Bavel (1988) suggest the possibility that cotton plants redistribute water in systems where irrigation is applied in alternated rows (Fig. 5).

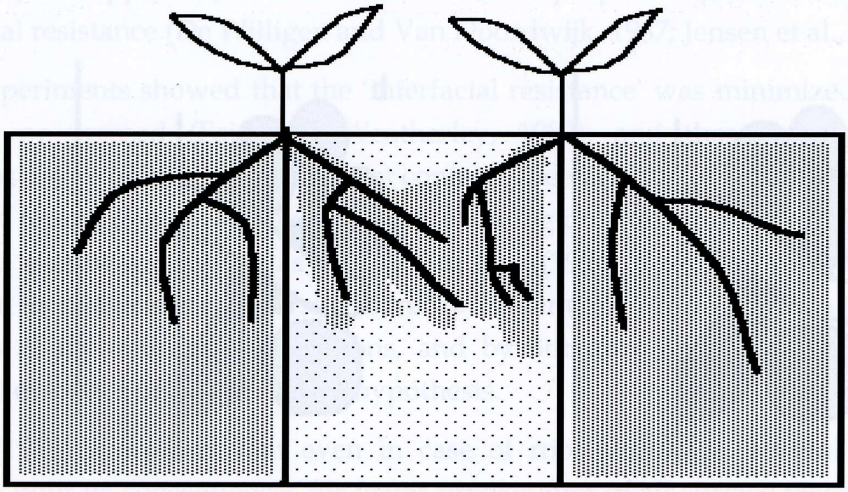

Fig. 5 - Water transport from irrigated to dry soil in a split-root experiment (Baker and van Bavel, 1988). The intensity of soil shading is proportional to soil water potential.

This kind of lateral transport is conceivable for dicots, in which the different parts of the root are hydraulically connected through the tap-root (Fig. 2), but much less for monocots, in which the axes are relatively independent until they converge in the crown, where connections are possible due to the occurrence of anasthomoses (Klepper, 1990). Results suggest that the lateral transport in cotton exists, although it does not guarantee a uniform water distribution. Glenn and Welker (1993) document the same type of transport in peach and claim its function in reducing competition between trees and grass cover in orchards.

- for the improvement of fertilizer uptake in otherwise dry soil patches (Passioura, 1988).
- for the fast recovery of water uptake in case of light rains or irrigations after a period of drought.

A separate case is that of nocturnal water efflux from roots of grasses in the rhizosheet region, detected by cryo-scanning electron microscopy (McCully, 1995). This phenomenon seems to be due not to the passive effect of a lower soil water potential, but to root pressure, as suggested by the shape of the menisci of water (Fig. 6). The role of this water exudation would be that of allowing the expansion of the rhizosheet gels even in dry soils, so that the gels can reach soil particles. The subsequent drying under diurnal transpiration transforms the gel into an adhesive that binds the soil to the root surface enhancing contact. This binding is stable and unaffected by subsequent wetting.

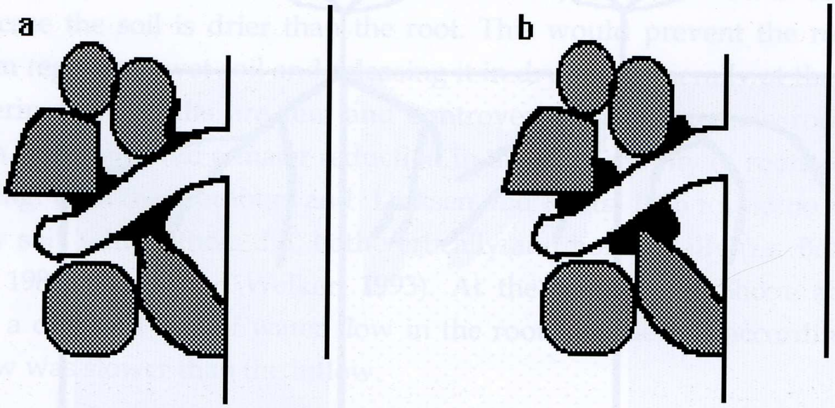

Fig. 6 - Shape of the water menisci at the soil-root interface a) if water is drawn from the soil; b) if water is forced out of the root under pressure. Redrawn from McCully (1995).

Resistance at Soil-Root Interface

Interfacial Resistance

Many researchers have speculated or presented evidence for resistance to water flow at the interface between soil and root. These works considered that the total resistance in the soil-plant atmosphere system could not be explained by simple summation of resistance within the soil and that within the plant. The debate was opened by comments of Taylor and Klepper (1975) and data by Faiz and Weatherley (1977) and Herkelrath et al. (1977a), who reported a big drop in water potential between soil and root or a very slow water extraction, in soil still having a considerable water diffusivity. Their data could not be explained in terms of the classical water extraction models unless the following assumptions were made:

- A very small proportion of roots (1% for Herkelrath et al., 1977a) was involved in water uptake; or
- There was a major resistance at the interface between soil and root. It was further assumed that this resistance was dependent on incomplete root-soil contact, in turn a function of soil water content. In case of a gap between soil and root, water in unsaturated soil could only move as vapor, in one order of magnitude slower than liquid water (Passioura, 1988). Herkelrath et al. (1977b) have proposed modifications of water uptake models to incorporate such resistance, with a term dependent on soil water content (see Appendix). Other authors have proposed models incorporating an interfacial resistance (De Willigen and Van Noordwijk, 1987; Jensen et al., 1993).

Later experiments showed that the 'interfacial resistance' was minimized when the soil was shaken or pressed (Faiz and Weatherley, 1982), and these manipulations were interpreted as a way of improving soil-root contact. The variation of contact between soil and root has been reported in several experiments, showing diurnal variations (Huck et al., 1970), or reductions due to soil drying as reported in Nye (1994). This root contraction has been questioned in its relevance for field situations by Tinker (1976) and Passioura (1982 and 1988) on the basis of theoretical considerations, and by Stirzaker and Passioura (1996) by the experimental evidence of an alternative hypothesis.

Tinker (1976) speculates that even in case of root shrinkage, several factors would contribute to limit its consequences for water uptake: first of all surface tension would keep the viscous flow of water even in the absence of complete contact, and then root hairs and exudates would bridge the gap. Nye (1994) replies that at low water contents exudates and root hairs and gels would not likely be hydrated enough to perform these functions. The lack of data on the actual hydraulic properties of the perirhizal region do not allow us to draw conclusions on this issue, but the recent findings of McCully (1995) on the mechanisms of soil binding in the rhizosheet of grasses even in dry soils (see above) seem to support Tinker's view.

Passioura (1982 and 1988) argues that roots would shrink in drying soil only if the location of the main resistance within the root lied at the root surface, as in a root growing in a large preexisting pore, in which the contact of soil and root is poor from the beginning. But in a root growing in intimate contact with the soil the location of the main resistance is thought to be at the endodermis (Casparian strip); in this situation water potential in the cortex would be coupled with that of the soil and quite uncoupled with that of the xylem, this preventing shrinkage due to the quite fast diurnal plant water potential fluctuations. As to the soil potential fluctuations, the author argues that they are slow enough to be compensated for by the root osmotic adjustment, or at least new growth, except in pot experiments, or in sandy soils[2]. In fact, besides the above experiments and subsequent ones (i.e. Zur et al., 1982) needing to invoke an additional source of resistance, there are in the literature other cases in which all of the resistance to water movement can be explained in terms of classical models by simply considering the soil and the plant resistances (Reicosky and Ritchie, 1976, Passioura, 1980).

Passioura (1988) also pointed out that experimental evidence of root shrinkage comes from large pores, and that other research fails to show shrinkage (Taylor and Willat, 1983).

In a recent work Stirzaker and Passioura (1996) find experimental evidence to support the hypothesis of a buildup of solutes at the root surface or in the apoplast. This accumulation outside the root xylem would create a large osmotic pressure in the direction opposite to flow, thus explaining the interfacial resistance. Although such a buildup would seem likely only in situations in which the roots exclude a large part of the solutes, like in saline soils or in the presence of toxic ions, the authors show an accumulation effect in a situation of relatively common osmotic potential, but not in case of soil flushed with water. The proposed explanation is that roots do not take up solutes uniformly, so exclusion of osmotically active substances may occur locally at sites that take up water but not salts.

Role of Mucigel

Chenu (1993) showed that the associations of clays and polysaccharides of the types produced by soil biota have a high water retention, an increased stability, and a reduced rate of water uptake and loss.

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[2] sandy soils, being much more uniform in particle size than other soils, show a sharp drop in hydraulic conductivity as the soil dries, since the diameter of water-filled pores is more discontinuous. See Cavazza, 1985.

The rhizosheet of grasses was shown to have higher water retention than the surrounding soil. These authors simulate the effect of rhizosheet on water uptake by considering it water retention properties only, and conclude that it enhances uptake. They speculate that the presence of root hairs would increase this effect. The authors don't take into account the considerations of McCully and Canny (1988) that discount the importance of the rhizosheet region in water uptake due to the root anatomical features associated with it (see above).

Physical Properties of the Interface

Another issue is that of roots growing in pre-existing pores. For those roots the contact with soil might be incomplete all along, thus suffering from partial desiccation, for the part growing in air. Other issues for these roots are the compaction of soil, that reduces penetration of laterals through the pore wall. Pore walls are often coated with materials transported from upper layers (Sullivan, 1987), or with earthworm or previous root-originated organic matter. These substances are likely to play a role in limiting the movement of water and ions from the bulk soil to the roots.

Similar situations cause the roots to grow on surface of peds (Amato,1991) due to the surface properties of clay structural units like coatings (see Soileau et al., 1964) or compaction due to friction during shrinking-swelling processes.

Roots creating their own pores in clay materials show the formation of concentric fissures around them, even in the absence of shrinking-swelling phenomena (Dorioz et al., 1993). Wetting and drying cycles then promote the formations of tangential and other fissures that originate from the discontinuities in the mineral fabric created by the root presence. These fissure are often filled with polysaccharides or root hairs that provide some root-soil continuity. In silty and sandy soils, the main effect is that of compaction around growing roots.

Role of Soil Biota

Mycorhizal effect in enhancing the root ability to take up water is controversial and depends on a series of genetic and environmental factors (Ruiz-Lozano and Azcon, 1995) that further complicate the issue. Indirect effects include those of pathogens which may reduce root permeability (see in Amato and Govi, 1996), or symbionts that improve the general status of roots.

In this situation, in which many issues are still open, the root models described above must include at least some semi empirical assumptions. The problem is that those empiricism are situation specific and need calibration, which takes away some of the strengths of mechanistic modeling, first of all transferability.

NEW REPRESENTATIONS OF PLANT WATER UPTAKE

Soil-Root Interface Characteristics are not Taken into Account

Due to all of the uncertainties involved, relatively recent expressions of the sink term have been devised, that take no root characteristics into account other than rooting depth (Feddes et al., 1978). Water uptake in each soil layer is modeled as a function of a maximum sink strength equal for all rooted layers, and soil water potential. Root length is not taken into account: the other determinant of water uptake are difficult to quantify, and may be so important that an inverse relation between root density and water extraction in a soil region is found (e.g.,. Gregory et al., 1978). These factors are not only linked to the above mentioned problems, but also to root spatial distribution (see following sections) or to the coordinated behavior of root systems (Klepper, 1990).

The hypothesis of these models is that the ability to extract water is the same throughout the whole volume of soil where roots are present (Feddes et al., 1978) (Fig. 7 b). The effective amount of water extracted depends therefore on soil water potential only, and it is limited both in dry and in extremely wet soil. In this formulation the sink term S is a function of:

- soil hydraulic potential h
- a maximum sink $S\max = T\max / z_r$

where $T\max$ = maximum transpiration

z_r = root depth

S is reduced at high soil moisture (anaerobiosis) and at low soil moisture, decreasing linearly after a threshold of h, until it reaches the wilting point (Fig. 7a).

The underlying hypothesis is that roots compensate their properties in order to maintain water uptake at the levels allowed by soil conditions.

In general, though, if the upper soil layers are kept at a high water content the root extracts water mainly from these layers. Even neglecting the higher root density and the more favorable temperature, this happens because of the mechanisms of water movement: it occurs because of the gradients in water potential between root xylem and soil. Uptake in the upper layers causes higher values of xylem potential, so that a lower gradient is available for water extraction in the deeper layers (Klepper, 1990). Therefore, even for models that don't take root distribution into account, some authors propose an uptake function that decreases with depth, and given the difficulties in determining the effective root characteristics they chose a simple linear variation (Prasad, 1980):

$$Smax = a - b\ (z)$$

with a and b to be determined experimentally (Fig. 7c)

This calls into question the role of deep roots in water extraction: they have been often described as more capable of extracting water per unit length compared to surface roots, because younger and characterized by a larger surface area in moist soil (Taylor e Klepper, 1975). According to some authors they can meet the whole crop requirement in case of water shortage in the upper layers (Ritchie, 1981), if total soil water content is above a certain limit, generally expressed as percent of available water. Others report that uptake is sufficient only if the variations in water potential in the upper layers are limited (Proffitt et al., 1985), hence the superiority of methods of frequent irrigation. In order to address the question from a more general point of view, there should be more information available on two questions: the role of axial conductivity to transport, that makes water transport from deep layers more difficult, and the importance of signals sent to the plant top by surface roots located in dry soil (Klepper, 1990).

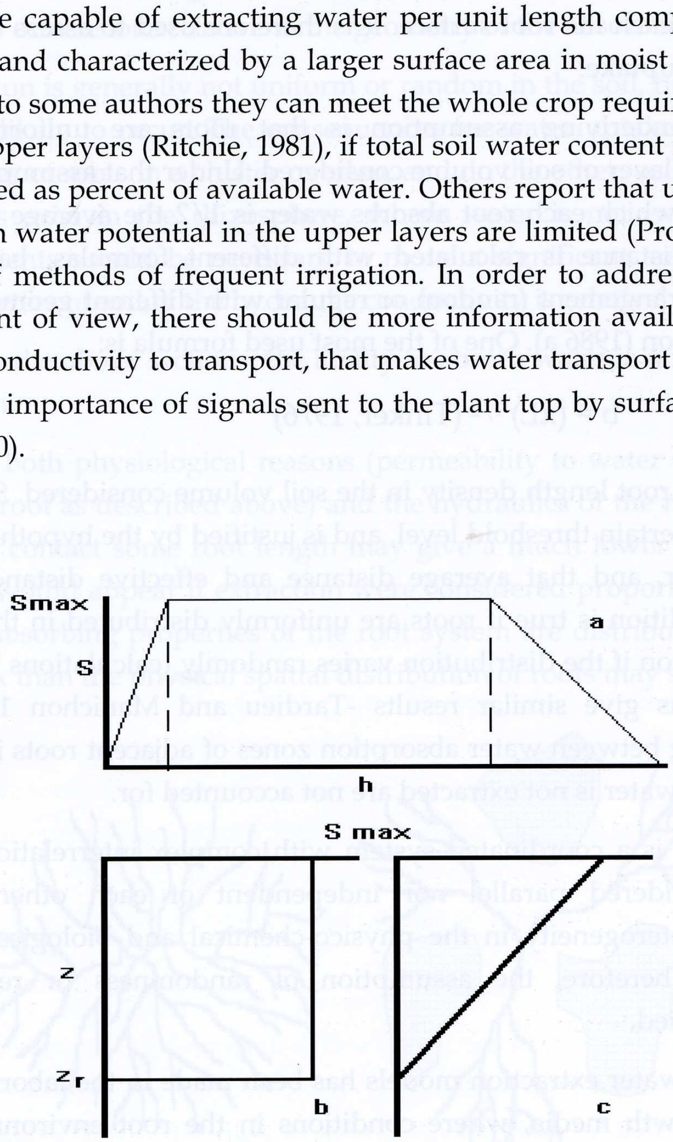

Fig. 7 - Root water uptake in models that don't take the soil-root interface characteristics into account: a) maximum sink (Smax) as a function of soil hydraulic potential (h); b) root ability to extract water as a function of soil depth according to Feddes et al. (1978); c) root ability to extract water as a function of depth according to Prasad (1988).z = depth; z_r = depth of the root system.

An Interface With Spatially Variable Characteristics

The issues addressed by studies about the spatial distribution of roots change the estimation of water status at the soil-root interface: most water uptake models calculate extraction based on root density per unit volume of soil. Such density is either measured or estimated in the volume considered, and generally varies with soil depth. Root density is used in both microscale and macroscale models to calculate the maximum distance water has to travel in the soil to reach the root surface. It is therefore used to assess the importance of soil resistance to water uptake.

The explicit or underlying assumption is that roots are uniformly or regularly distributed in each soil layer or soil volume considered. Under that assumption the radius of the soil cylinder from which each root absorbs water is 1/2 the average distance between roots (Fig. 4). Such distance is calculated with different formulas, based on different assumptions of root arrangement (random or regular with different geometry) as reviewed by Tardieu and Manichon (1986 a). One of the most used formula is:

$$b = (\pi L)^{-1/2} \text{ (Tinker, 1976)} \qquad (3)$$

where L is the average root length density in the soil volume considered. Such an approach is valid if L is above a certain threshold level, and is justified by the hypothesis that roots are parallel to one another, and that average distance and effective distance between roots coincide. This last condition is true if roots are uniformly distributed in the soil, and it is a reasonable approximation if the distribution varies randomly (calculations based on random or regular distributions give similar results -Tardieu and Manichon 1986 a-). In such conditions, overlapping between water absorption zones of adjacent roots is not considered, and regions where soil water is not extracted are not accounted for.

In reality, the root is a coordinated system with complex interrelations so that single roots cannot be considered parallel nor independent of each other. Also, the soil environment shows heterogeneity in the physico-chemical and biological properties that affect root density. Therefore, the assumption of randomness or regularity in root distribution is not justified.

Testing of several water extraction models has been made in the laboratory, in artificial or often disturbed growth media, where conditions in the root environment were likely much more uniform than what generally happens in the field. However, a well defined relation between root length density and water uptake is not always found in water uptake studies. In field situations even greater differences between calculated and measured uptake are found. Root spatial variability in the horizontal (xy or areal according to Hamblin, 1985) dimension can account for a part of the discrepancies found between measurements and calculations.

Several authors (i.e., Tardieu and Manichon, 1986 b) in fact argue that the assumption of root uniformity leads to computation of distances between roots smaller than they actually are if root clustering exists. They show how, in case of structurally heterogeneous soil, the real distance between some adjacent roots is remarkably larger than the average distance (Tardieu and Manichon, 1986 b, Tardieu, 1988), (Fig. 8).

The problem of characterizing roots as a spatially variable water sink is complicated by the presence of two dimensions relative to the geometry of the absorbing system:

a) roots distribution is generally not uniform or random in the soil, but different degrees of clustering are likely to occur. The consequences for water uptake are that on one side, extraction zones of roots in a cluster overlap, and on the other, soil regions relatively far from the roots exist in the rhizosphere, where water is not extracted because large potential gradients would be necessary to move a significant amount of water across several centimeters of soil, if the hydraulic conductivity is relatively small.

b) as discussed in the above sections, the ability to absorb water is not uniform throughout the root system.

This is due to both physiological reasons (permeability to water varies with respect to position along the root as described above) and the hydraulics of the root-soil interface (due to lack of soil-root contact some root length may give a much lower contribution to water uptake than what would appear if extraction were considered proportional to root density). The result is that absorbing properties of the root system are distributed in space in a way even more complex than the physical spatial distribution of roots may suggest.

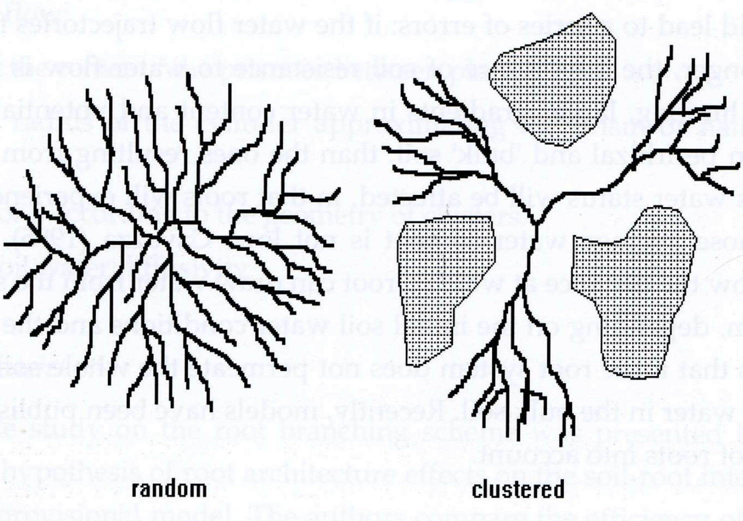

Fig. 8 - Different distributions of roots. In clustered distributions the distance between soil and the nearest absorbing root may be so large that unextracted water (shaded areas) is left in the soil.

The composite spatial arrangement of the uptake properties of the root system, resulting from physical and physiological spatial variation, is what is relevant. Some of the existing models in the literature propose water extraction functions for the root sink term that are based on an 'effective ' root density, rather than on a physical one (Gardner, 1964; Molz and Remson, 1970,1971; Molz, 1971; Feddes et al., 1976; Herkelrath et al, 1977 a and b; Passioura, 1980 and 1983). The concept was introduced for the purpose of accounting for the differences in permeability of different root parts (i.e. Passioura, 1983), or for the regions of poor soil-root contact (i.e. Herkelrath et al, 1977 b) and not for root spatial arrangement. The application of this concept encounters great difficulty in the actual determination of the degree of 'effectiveness' of roots. Nonetheless, it is conceptually interesting in that it is a way of expressing root density in functional rather than physical units, attempting to model water absorption in a slightly more mechanistic way than just relating it to total root length.

Also, even if physical and physiological root spatial variations are conceptually separated, any testing of hypothesis on the effect of one of them on water extraction patterns will have to deal with the other.

In addition to the variability in space of the root absorbing characteristics, a temporal dimension is to be considered: roots grow and their absorbing surface moves in the soil. Phenological factors may imply that the roots found in deep soil have important time constraints for the extraction of the water present at the bottom of the root zone. Furthermore, water absorption often occurs in non-stationary conditions. Some of the dimensions of complexity introduced by these factors have been treated by Kilic (1973).

Where roots are far from homogeneous distribution, overlooking of root spatial arrangement would lead to a series of errors: if the water flow trajectories from the bulk soil to the roots are longer, the importance of soil resistance to water flow is probably greater, and if it becomes limiting, larger gradients in water content and potential will exist in the root zone, between perirhizal and 'bulk' soil, than the ones resulting from average distance calculations. Roots water status will be affected, in that roots will experience water shortage even in a soil whose average water content is not low. Cavazza (1985), using data from Gardner, shows how the distance at which a root can draw water from the soil is of the order of a few mm or cm, depending on the initial soil water conditions and the velocity of water uptake. He argues that if the root system does not permeate the whole soil, it may not have access to all of the water in the bulk soil. Recently, models have been published, that take the spatial variability of roots into account.

Macroscale Approach

Passioura (1985) suggests that if roots are clustered, i.e. constrained in wormholes (Fig. 8) , each cluster should be considered like a single root, having access to a cylinder of soil of radius:

$$B = (\pi L^*)^{-1/2} \tag{4}$$

where L* is the length of occupied pore per unit soil volume, and replaces the root length density of the single root model (equation 3). This way, water extraction is no longer a function of the actual root density. Rather, it becomes dependent on the geometry of soil pores accessible by the roots, and of the actual presence of roots in such pores. The values for B would be considerably higher than those of b (equation 3) based on average root length density. The author calculates a time constant that describes the rate of water uptake when flow through the soil is entirely limiting. Such a constant is proportional to b^2 if equation 3 is used, and to B^2 if equation 4 applies. Therefore, in case of clustered roots, the time constant may become quite large, and possibly limiting the access of the roots to soil water in a time useful for crop survival or stress relief. A more general treatment of a clustered root distribution (for roots growing along planes or soil prisms) is formalized as the clumped root model :

$$Q = \frac{2n}{B^2}\int_{\theta_B}^{\theta_o} D(\theta)\,d\theta \qquad \text{(Passioura, 1985)} \tag{5}$$

where: Q is the flow;

θ_o is θ at the center of the prism or between planes;

B is the radius of the cylinder approximating the prism or half distance between planes;

n is 1, 2 or 3 according to the geometry of clusters.

$D(\theta)$ is soil water diffusivity

Microscale Approach

A small scale study on the root branching scheme was presented by Petrie and Hall (1992) to test the hypothesis of root architecture effects on the soil-root interface water status, rather than as a provisional model. The authors compare the efficiency of two root systems: *Pennisetum americanum*, characterized by a high root density and clumped, against *Vigna unguiculata*, with a lower root density and distributed more uniformly. The different distributions regard branching pattern: few axes with a high density of laterals inserted 'fishbone' - style in the *graminea,* and dicotomic ramification in the legume (Fig. 9,1a and b). In spite of a higher root density the *graminea* develops pre-dawn leaf potentials (taken as representative of root potentials) which are more negative than those found in the legume, but the water extracted amounts to about the same. A bidimensional model (finite elements) simulates water extraction by an elemental unit representing the branching scheme of each species. The root of Pennisetum is less efficient: uptake occurs only at the root tips, and therefore it develops higher gradients between root and soil (Fig. 9). Inefficiency is due to the combined effect of aggregation and high density: reducing root density in the simulation, uptake extends to part of the root length. The root of Vigna extracts along the whole length of branches, and it therefore is more efficient, and lower gradients are required in order to extract the same amount of water.

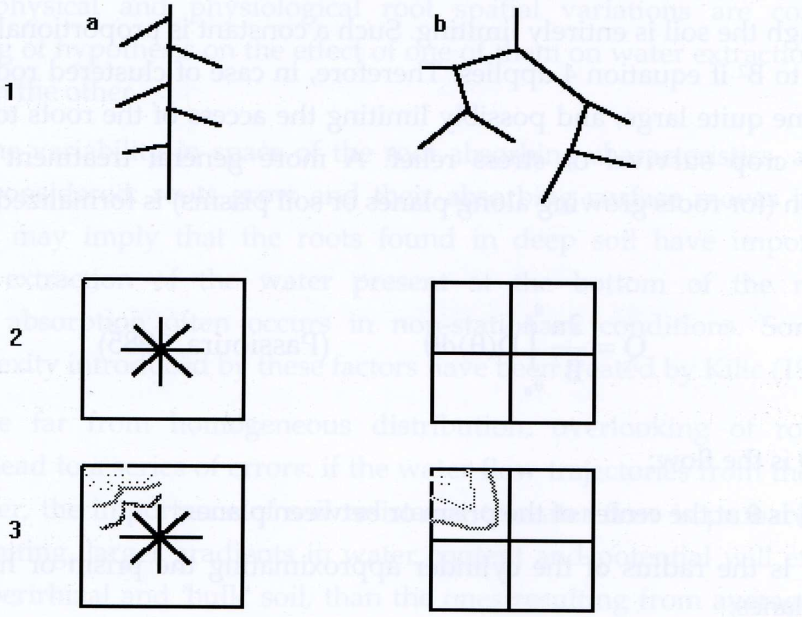

Fig. 9 - Schematic representation of roots of a) Pennisetum americanum; *b)* Vigna unguiculata. *1) longitudinal representation of root architecture; 2) projection on the horizontal plane; 3) projection with isopotential lines.*

At the field scale, Lafolie et al. (1991) propose a model (finite elements for spatial discretization and finite differences for the time discretization) based on actual root position (from a root map) in order to calculate root water potential. Under a series of hypotheses about the driving forces of water movement, the authors simulate water uptake per unit root in case of non-uniform root distribution due to a lower root density in compacted inter-rows. Results show that water uptake per unit root length is not constant: it is lower where roots are more dense, since their uptake regions overlap.

REFERENCES

Amato M. (1991). "Spatial distribution and water uptake of roots in structured soils". Ph.D. thesis. Michigan State University. *East Lansing*. pp xiii - 204.

Amato, M, and Govi, G. (1996). L'apparato radicale delle piante coltivate in relazione alla gestione idrica delle colture. in press on: *Irrigazione e Drenaggio.*

Allmaras R.R., W.W. Nelson and W.B. Voorhees (1975). Soybean and corn rooting in southwestern Minnesota:II. Root distribution and related water inflow. *Soil Sci.Soc.Amer.Proc.* 39:771-777.

Baker, J.M., and van Bavel, C.H.M. (1986). Resistance of plant roots to water loss. *Agron. J.* 78: 641-44.

Baker, J.M:, e van Bavel, C.H.M. (1988). Water transfer through cotton plants connecting soil in regions of differing water potential. *Agron. J.* 80(6):993-997.

Barrs,H.D., and Klepper, B. (1968). Cyclic variations in plant properties under constant environmental conditions. *Physiol. Plant.* 21:711-730.

Begg, J.E., and Turner N.C., (1970). Water potential gradients in field tobacco. *Plant Physiol.* 46:343-346.

Boyer J.S. (1971). Resistances to water transport in soybean,bean,and sunflower. *Crop Sci.*, 11:403-407.

Boyer, J.S. (1985). Water transport. Ann.Rev.Plant Physiol. 36:473-516. Brar, G.S., McMichael, B.L., and Taylor, H.M. 1990. Hydraulic conductivity of cotton roots as influenced by plant age and rooting medium. *Agron. J.*, 82:264-266.

Brar, G.S., McMichael, B.L., and Taylor, H.M. (1990). Hydraulic conductivity of cotton roots as influenced by plant age and rooting medium. *Agron. J.* 82:264-266.

Brenner, P.M., Preston, G.K., Fazekas de St.Groth, C., (1986). A field comparison of sunflower (Helianthus annuus) and sorghum (Sorghum bicolor) in a long drying cycle.I.Water extraction. *Aust. J. Agric.Res.* 37:483-93.

Brouwer, R. (1981). Co-ordination of growth phenomena within a root system of intact maize plants. In: Brouwer et al. (eds.) : Structure and function of plant roots. Martinus Nihoff. pp 269-276.

Cavazza, L. (1985). Fisica del terreno agrario. U.T.E.T. (Torino) pp xvi-425.

Chenu, C. (1993). Clay- or sand-polysaccharide associations as models for the inerface between micro-organisms and soil: water related properties and microstructure. *Geoderma* 56: 143-156.

Cowan, I.R. (1965). Transport of water in the soil-plant-atmosphere system. *J.Appl.Ecol.* 2:221-239.

Cruz, R.T., Jordan, W.R., and Drew, M.C. (1992). Structural changes and associate reduction of hydraulic conductance in roots of Sorghum bicolor L. following exposure to water deficit. *Plant Physiol.* 99:203-212.

De Willigen, P. , and Van Noordwijk, M. (1987). Roots, plant production, and nutrient use efficiency. Doctoral thesis, Wageningen Agric. University. 282 pp.

Dirksen, C., and Raats, P.A.C. (1985). Water uptake and release by alfalfa roots. *Agron. J.* 77: 621-26.

Dorioz, J.M:, Robert, M., and Chenu, C. (1993). The role of roots, fungi, and bacteria on clay particle organization. An experimental approach. *Geoderma*, 56:179-194.

Drew, M.C., (1979). Properties of roots which influence rates of absorption. in Harley, J.C., and Scott Russell, R. (eds) The soil-root interface. Acad. Press (London) :21-38.

Edwards, C.A., and Lofty, J.R. (1978). The influence of arthropods and earthworms upon root growth of direct drilled cereals. *J. Appl. Ecol.* 15: 789-795.

Ehlers, W., Kopke, U., Hesse, F., Boehm, W. (1983). Penetration resistance and root growth in tilled and untilled loess soil. *Soil Till. Res.* 3:261-75.

Everard J.D. and M.C. Drew (1987). Mechanisms of inhibition of water movement in anaerobically treated roots of Zea mays L. *J. Exp. Bot.* 38: 1154-1165.

Faiz, S.M.A., and Weatherley, P.E. (1977). The location of the resistance to water movement in the soil supplying the roots of transpiring plants. *New Phytol.* 78:337-47.

Faiz, S.M.A., and Weatherley, P.E., (1978). Further investigations into the location and magnitude of the hydraulic resistances in the soil-plant system. *New Phytol.* 81:19-28.

Faiz, S.M.A., and Weatherley, P.E. (1982). Root contraction in transpiring plants. *New Phytol..* 92:333-43.

Feddes, R.A., Bresler E., and Neuman S.P. (1974). Field test of a modified numerical model for water uptake by root systems. *Water Resour.Res.*, 10:1199-1206.

Feddes, R.A., Kowalik P.J., Malinka K.K., and Zaradny H. (1976). Simulation of field water uptake by plants using a soil water dependent root extraction function *J.Hydrol.* 31:13-26.

Feddes, R.A., Kowalik P.J., Zaradny H. (1978). Simulation of field water use and crop yield Centre for agricultural publishing and documentation, Wageningen, the Netherlands, 1978.

Foster, R.C. (1994). The ultramicromorphology of soil biota in situ in natural soils: a review. in: Rngrose-Voase, A.J., and Humphreys, G.S. (eds): Soil micromorphology: studies in management and genesis. Developments in soil science n. 22. Elsevier. pp 381- 393.

Gardner,W.R. (1960). Dynamic aspects of water availability to plants. *Soil Sci.*, 89:63-73.

Gardner,W.R., (1964). Relation of root distribution to water uptake and availability. *Agron.J.* 56:41-45.

Glenn, D.M., e Welker, W.V. (1993). Water transfer diminishes root competition between peach and tall fescue. *J. Am. Soc. Hortic. Sci.* 118 (5): 570-574.

Gregory, P.J., McGowan, M., Biscoe, P.V. (1979). Water relations of winter wheat. 2. Soil water relations. *J. Agric. Sci.* 91:103-116.

Hainsworth, J.M. and Aylmore L.A.G. (1986). Water extraction by single plant roots. *Soil Sci.Soc.Am.J.* 50:841-48.

Hamblin, A.P. (1985). The influence of soil structure on water movement, crop root growth, and water uptake. *Adv. Agron.* 95-157.

Herkelrath W.N., E.E. Miller and Gardner,W.R., (1977 a). Water uptake by plants:I.The divided root experiment. *Soil Sci. Soc. Am. J.* 41 1033-1038.

Herkelrath W.N., E.E. Miller and Gardner,W.R. (1977 b). Water uptake by plants: II. The root contact model. *Soil Sci. Soc. Am. J.* 41 1039-1043.

Hillel D., Talpaz H., and van Keulen H., (1976). A macroscopic scale model of water uptake by a nonuniform root system and of water and salt movement in the soil profile. *Soil Sci.* 121(4):242-255.

Huck, M.G., Klepper,B., Taylor,H.M. (1970). Diurnal variations in root diameter. *Plant Physiol.* 45:529-30.

Jaillard, B., and Callot, G. (1987). Action des racines sur la segregation mineralogique des constituants du sol. in: Fedoroff, N. et al. (eds.) Micromorphologie des sols. *Association Francaise pour l'etude du sol*. pp 371-375.

Jensen, C.R., Svendsen, H., Andersen, M.N., and Loesch, R. (1993). Use of the root contact concept, an empirical leaf conductance model and pressure - volume curves in simulating crop water relations. *Plant and Soil* 149: 1-26.

Kilic, N.K. (1973). The analysis and simulation of water transfer through the soil-root domain. Ph. D. Thesis, Michigan State University, East Lansing (MI).

Klepper, B. (1990). Root growth and water uptake. In: ASA-CSSA-SSSA Agroonomy monograph n. 30: Irigation of agricultural crops. pp. 281-322.

Klepper, B., and Taylor, H.M. (1978). Limitations to current models describing water uptake by plant root systems. in Harley and Scott Russell (eds.) The soil root interface. Academic Press, London, pp. 51-65.

Kramer,P.J. (1983). Water relations of plants. Academic Press Orlando pp.489.

Lafolie, F., Bruckler, L., and Tardieu, F. (1991). Modeling root water potential and soil-root water transport: I. Model presentation. *Soil Sci. Soc. Am. J.* 55:1203-1212.

McCully, M.E. (1995). Water efflux from the surface of field-grown grass roots. Observations by cryo-scanning electron microscopy. *Physiol. Plant.* 94:

McCully, M.E., and Canny, M.J. (1988). Pathways and processes of water and nutrient movement in roots. *Plant Soil*, 111: 159-170.

Miller, A.A., Gardner, W.R. and Goltz,S.M. (1971). Internal water status and water transport in seed onion plants. *Agron. J.* 63:779-784.

Miller D.M. (1985). Studies of root function in Zea mays. III. Xylem sap composition at maximum root pressure provides evidence of active transport into the xylem and a measurement of the reflection coefficient of the root. *Plant physiol.* 77:162-67.

Molz, F.J., (1971). Interaction of water uptake and root distribution. *Agron.J.* 63:608-610.

Molz, F.J., (1981). Models of water transport in the soil-plant system: a review. *Water Resources Res.* 17 (5):1245-1260.

Molz, F.J., and Remson I., (1970). Extraction-term models of soil moisture use by transpiring plants. *Water Resources Res.* 6 (5):1346-1356.

Molz, F.J., and Remson I., (1971). Application of an extraction-term model to the study of moisture flow to plant roots. *Agron. J.* 63(1).

Muromtsev, I.A. (1969). Active parts of root systems of fruit plants. *Kolos*, 193 pp.

Newman, E.I., (1969 a). Resistance to water flow in soil and plant. I. Soil resistance in relation to amounts of root: theoretical estimates. *J. Appl. Ecol.*, 6:1-12.

Newman, E.I., (1969 b). Resistance to water flow in soil and plant. II. A review of experimental evidence on the rhizosphere resistance. *J. Appl. Ecol.*, 6:261-272.

Newman, E.I. (1976). Water movement through root systems. *Phil. Trans. R. Soc. Lond.* B. 273: 463-478.

Nimah, A. and Hanks, R.J. (1973). Model for estimating soil, water, plant and atmospheric interrelations :I. Description and sensitivity. *Soil Sci. Soc. Am. Proc.* 37:522-527.

Nye, P.H. (1994). The effect of root shrinkage on soil water inflow. *Phil. Trans. R. Soc. Lond.* B. 345: 395-402.

Nobel, P.S., and Sanderson, J. (1984). Rectifier - like activities of roots of two desert succulents. *J. Exp. Bot.* 35: 727-737

Passioura J.B. (1980). The transport of water from soil to shoot in wheat seedlings. *J. Exp. Bot.* 31: 333-345.

Passioura, J.B. (1982). Water in the soil-plant-atmosphere continuum. in: Lange, O.L. et al. (eds.). *Encyclopedia of plant physiology*. New series, vol. 12 B. Springer – Verlag pp. 5-33.

Passioura, J. B. (1983). Roots and drought resistance. *Agricultural Water Management* 7:265-80.

Passioura, J.B. (1984). Hydraulic resistance of plants. I. Constant or variable? *Aust. J. Plant. Physiol.* 11: 333-345.

Passioura, J.B. (1985). Roots and water economy of wheat. in Day, W. and Atkin, R.K. (eds) Wheat growth and modeling. *Plenum.* 185-198.

Passioura, J.B. (1988). Water transport in and to roots. *Ann. Rev. Plant Physiol.* 39:245-65.

Perrochet,P. (1987). Water uptake by plant roots-a simulation model, I. Conceptual model. *J. Hydrol.*, 95 55-61.

Perumalla, C.J., and Peterson, C.A. (1986). Deposition of Casparian bands and suberin lamellae in the exodemis and endodermis of young corn and onion roots. *Can. J. Bot.* 64: 1873- 1878

Peterson, C.A:, Emanuel, M.E:, and Wilson, C. (1982). Identification of a Casparian band in the hypodermis of onion and corn roots. *Can. J. Bot.* 60:1529-1535.

Petrie, C.L., and Hall, A. E. (1992). Water relations in cowpea and pearl millet under soil water deficits. II. Water use and root distribution. *Aust. J. Plant. Physiol.* 19(6): 591-600.

Philip,J. R. (1957). The physical principles of soil water movement during the irrigation cycle. *3 rd Congr. Intern. Comm. on Irrig. and Drain.*, Quest. 8,pp 8.125-8.154.

Portas, C.A.M., e Taylor, H.M. (1976). Growth and survival of young plant roots in dry soil. Soil Sci. 121:170-175.

Prasad, R. (1988). A linear root water uptake model. *J. Hydrol.* 99: 297-306.

Proffitt, A.P.B., Berliner, P.R., Oosterhuis, D.M. (1985). A comparative study of root distribution and water extraction efficiency by wheat grown under high- and low-frequency irrigation. *Agron. J.* 77 2(5): 655-662.

Reicosky D.C., Ritchie J.Y. (1976). Relative importance of soil resistance and plant resistance in root water absorption. *Soil Sci. Soc. Am.J.* 40:293-297.

Ritchie, J.T. (1981). Soil water availability. *Plant Soil* 58: 327-338.

Rose, C.W., Byrne, G.F., and Hansen,G.K. (1976). Water transport from soil through plant to atmosphere: a lumped parameter model. *Ag. Meteor.* 16:171-184.

Rowse H.R., Stone D.A., Gerwitz A. (1978). Simulation of the water distribution in soil.2.The model for cropped soil and its comparison with experiment. *Pant Soil* 49:534-550.

Ruiz-Lozano, J.M. and Azcon, R. (1995). Hyphal contribution to water uptake in mycorrhizal plants as affected by the fungal species and water status. *Physiol. Plant.* 85:472-478

Samui, R.P., and Kar,S. (1981). Soil and plant resistance effects on transpirational and water responses by groundnut to soil water potential. *Aust. J. Soil Res.* 19:51-60.

Sanderson,J., (1983). Water uptake by different regions of the barley root. Pathways of radial flow in relation to the development of the endodermis. *J.Exp.Bot.* 34:240-53.

Santini, A., Pitacco, A. et al. (1990). Modellizzazione del trasporto dell'acqua nel sistema suolo-pianta-atmosfera. *Riv. di Agron.* 24: 273-290.

Shone, M.G.T:, and Clarkson, D.T. (1989). Rectification of radial water flow in the hypodermis of nodal roots of Zea mays. in: Loughman et al. (eds). Structural and functional aspects of transport in roots. Kluwer. pp. 157-163.

So, H.B., Aylmore,L.A.G., and Quirk,J.P. (1976 a). The resistance of intact maize roots to water flow. *Soil Sci. Soc. Am.J.*,40:222-225.

Steudle, E. (1989). Water transport in roots. in: Loughman et al. (eds.). Structural and functional aspects of transport in roots. Kluwer. pp. 139-145.

Stirzaker, R. J., and Passioura, J.B. (1996). The water relations of the root-soil interface. *Plant, Cell and Env.* 19: 201-208.

Soileau, J.M., Jackson, W.A., and McCracken, R.J. (1964). Cutans (clay films) and potassium availability to plants. *J. Soil Sci.* 15: 117-123.

Sullivan, L.A. (1987). Structural pore pedofeatures: influence on some soil processes. in: Fedoroff, N. et al. (eds.) Micromorphologie des sols. Association Francaise pour l'etude du sol. pp 613-622.

Taylor, H.M., (1983). Managing root systems for efficient water use: an overview. In Taylor H.M., Jordan, W.R., Sinclair, T.R.(eds.) Limitations to efficient water use in crop production. *Madison Am.Soc.Agron*:124-37.

Taylor, H.M., and Klepper,B. (1975). Water uptake by cotton root systems: an examination of the single root model. *Soil Sci.* 120 1:57-67.

Taylor, H.M:, and Willatt, S.T. (1983). Shrinkage of soybean roots. *Agron. J.* 75: 818-820.

Tardieu, F. (1988). Analysis of the spatial variability of maize root density. II. Distance between roots. *Plant and Soil* 107, 267-272.

Tardieu, F., and Manichon,H., (1986 a) Caracterisation en tant que capteur d'eau de l'enracinement du mais en parcelle cultivee. I.-Discussion des criteres d'etude. *Agronomie* 6,4:345-354.

Tardieu, F., and Manichon,H. (1986 b) Caracterisation en tant que capteur d'eau de l'enracinement du mais en parcelle cultivee. II. Une methode d'etude de la repartition verticale et horizontale des racines. *Agronomie* 6(5):415-425.

Tinker,P.B. (1976). Transport of water to plant roots in soil. *Philos. Trans. R. Soc. London* Ser.B. 273:445-61.

van Bavel, C.H.M. and Ahmed,J. (1976). Dynamic simulation of water depletion in the root zone. *Ecol. Modelling*, 2:189-202.

van Noordwijk, M., de Ruiter, P.C., Zwart, K.B., Bloem, J., Moore, J.C., van Faassen, H.G., and Burgers, S.L.G.E. (1993). Synlocation of biological activity, roots, cracks, and recent organic inputs in a sugar beet field. *Geoderma* 56:265-276.

Wadleigh, C.H. (1946). The integrated soil moisture stress upon a root system in a large container of saline soil. *Soil Sci*. 6:225-238.

Waisel, Y., and Eshel, A. (1991). Multiform behavior of various constituents of one root system. in: Waisel et al (eds.) Plant roots: the hidden half. Marcel Dekker, pp 39-52.

Wang, J., Hesketh, J.D., Wooley, J.T. (1986). Preexisting channels and soybean rooting patterns. *Soil Sci.* 141:432-7.

Whisler, F.D., Klute,A., and Millington R.J. (1968). Analysis of steady state evapotranspiration from a soil column. *Soil Sci.Soc.Am.Proc.* 32:167-174.

Zhu, G.L., and Steudle, E. (1991). Water transport across maize roots. *Plant Physiol*. 95: 05-315.

Zur, B., Jones, J.W., Boote, K.J., and Hammond L.C. (1982). Total resistance to water low in field soybeans. II. Limiting soil moisture. *Agron.J.* 74:99-105.

APPENDIX

Some Approaches to the Calculation of the Sink Term

Initial formulations included soil resistances to water movement only:

$$S=f[(\Phi s - \Phi r), L, Ks]$$

Φs = soil water potential

Φr = root water potential

L = root length density

Ks = soil water conductivity

Subsequently, based on experimental evidence on the importance of root resistance to water flow (i.e. Klepper and Taylor, 1978), it was included (i.e. Hillel at al., 1976):

$$S = \frac{\Phi_s - \Phi_{plant}}{rs - rr}$$

$\Phi plant$ = water potential at the stem base;

rr = axial + radial root resistance;

rs = soil resistance = 1/(BKL),

with B an empirical coefficient (function of L and root characteristics), K the soil water conductivity, and L the root length density;

Herkelrath et al (1977), Taylor e Klepper (1975), e Faiz e Weatherley (1978) found that an important source of resistance to water movement is at the soil-root interface, and hypothesised that it was dependent on soil water content due to loss of soil-root contact (root contraction). A term based on the ratio of actual and maximum soil water content was therefore included to reduce the sink strength (Herkelrath et al., 1977):

$$S = \frac{\theta}{\theta_{sat}} \rho L(\Phi_s - \Phi_r)$$

therefore:

$$rr = \frac{\theta_{sat} \cdot A}{\theta \cdot L}$$

θ = soil water content

θsat = saturated soil water content

ρ = root membrane permeability per unit length

rr = root resistance + interfacial resistance

A = empirical coefficient, representing the effect of potential, temperature, and root age. It may include a rectifier effect of the root, and in this case there are different values for inflow and outflow.

Santini et al. (1990) pooled some of the above:

$$S = \frac{\psi - z - \psi\pi - \psi c}{rs + rr}$$

ψ = soil matric potential

z = soil depth

$\psi\pi$ = osmotic potential

ψc = water potential at the plant stem base

rs = 1/BKL

rr = $\theta sat/\theta * A/L$