

## Water Uptake

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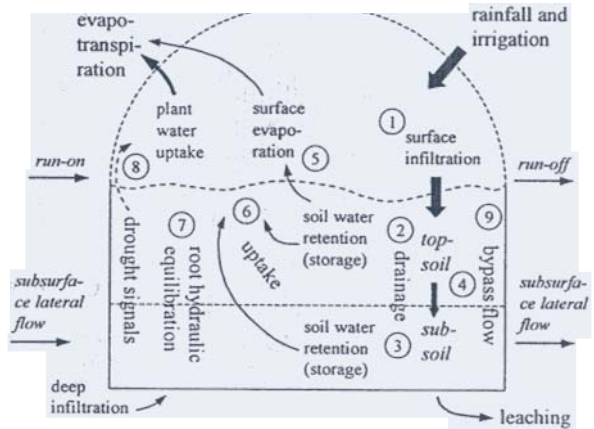
## 14.1 Introduction

Uptake of water by the root system is critical for plant functioning, as it balances aboveground water losses by transpiration and facilitates movement towards the roots of nutrients and other chemicals. The coupled processes in the soil-plant-atmosphere continuum are controlled at the plant, the cellular, or even molecular level (Kramer and Boyer 1995; Steudle and Peterson 1998). A basic understanding is needed of the process of root water uptake, combining soil physical and plant physiological perspectives in models of plant behaviour. This can be related to the water status in their environment to determine accurate plot-level soil water balances, evaluate plant adaptation to drought, and analyse below-ground competition in mixed vegetation systems.

At the most basic level, the soil-plant-atmosphere continuum concept (Huber 1924; Gradmann 1928; Van den Honert 1948) assumes steady-state flow and constant resistance. Obviously this is an oversimplification (Kramer and Boyer 1995), but it serves to remind us of the interrelationships between the soil, plant, and atmospheric factors that have to be taken into account when determining plant water status. Any analytical description, or model, of the soil water balance needs to consider many processes that act simultaneously across a number of different time and spatial scales. These processes include (Fig. 14.1):

1. Water entry into the soil by either rainfall or irrigation and its separation into either infiltration or surface run-off. This process of water entry into the

**Fig. 14.1.** Soil water balance for a unit of soil with vertical as well as lateral inputs and outputs

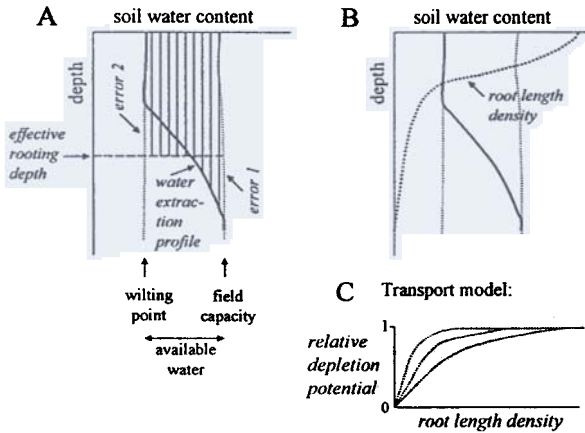


root zone operates on a seconds-to-minutes time scale throughout the depth of the root zone, say centimetres to many metres.

2. Infiltration through and drainage from the cascade of soil layers, and/or via bypass flow through macropores. This internal movement operates on a seconds-to-hours time scale across distances from millimetres to metres.
3. Evaporation from surface soil which operates on an hours-to-days time scale across the scale of centimeters.
4. Water uptake across the spatially distributed root system, which operates on a hour-to-days time scale up to a spatial scale of many (at least up to 50 in some trees) metres. Uptake normally occurs during daytime when the stomata are open, although capacitance recharge of the plant itself can result in nocturnal uptake.
5. Root uptake and discharge from and into soil (“hydraulic lift”) can occur through hydrostatic equilibration across the root systems on an hour-to-days time scale, but mostly at night when plant transpiration is negligible. The spatial scale is that of the entire root system.
6. Root uptake strategies in response to hormonal signals can occur locally on an hours-to-weeks time scale.

Better understanding of root uptake can thus be seen to demand knowledge of the roots themselves, as well as information about the coupled biophysical processes operating in the soil and the atmosphere.

When the water balance of a plant, or tree, is calculated over a whole growing season, total water uptake will often be constrained by the amount of water freely available in the soil. The traditional definition of “available” water on the basis of a water retention curve as the difference between “field capacity” and “wilting point” may be adequate for the topsoil, but in the deeper layers of the root zone, not all of this “available” water might actually be accessed by



**Fig. 14.2.** A Definition of “effective rooting depth” for water uptake and “available water” (McKeague et al. 1984) In this pragmatic definition error 1 cancels error 2, so that the total amount of water available for the plant per unit soil area can be estimated from the difference in volumetric soil water content between field capacity and wilting point, times the “effective rooting depth”; B and C provide alternative concepts to estimate total water uptake on the basis of the complete root system and relative water depletion efficiency as a function on root length density (de Willigen and van Noordwijk 1987)

plants either in quantity, or at the rate at which it is needed. As illustrated in Fig. 14.2, a simple way around this conundrum is via the definition of an “effective rooting depth”. This then makes up for the difficulties in defining “available” water because the “effective rooting depth” is defined in such a way that the overestimate of possible water uptake above the “effective” rooting depth equals the underestimate due to lack of complete water uptake below this depth. This definition (McKeague et al. 1984) couples and may appear to render useful both the concepts of “available water” and “effective rooting depth”, even though it is not very satisfactory from a rigorous scientific viewpoint. Thus the challenge is to quantify better the form of the entire root system, and to predict better the biophysical functioning of roots in their quest to take up water and chemicals. To achieve this link between form and function, we need better descriptions of the root system, and improved comprehension of the chain of resistances to water flow in the soil-root-shoot-leaf-atmosphere pathway.

Researchers of root system form and function, being aware of the importance of understanding the processes of water uptake, have developed a considerable number of techniques to improve the measurement and modelling of water uptake (Fig. 14.3). The objective of this chapter is to give a comprehensive and detailed description of the most effective of these techniques. We

**Table 14.1.** Spatial resolution of the methods used for assessing water uptake by roots

Measured variable	Resolution 1–100 $\mu\text{m}$	0.1–10 mm	0.01–1 m
Water content, $\theta$		Gamma densiometry	Gravimetry Neutron scattering NMR TDR FD
Soil water potential, $\Psi_s$		Microtensiometer Psychrometer	Tensiometer Resistance blocks
Root water potential, $\Psi_r$ , and resistance, $1/L_p$	Pressure probe	Psychrometer	Pressure chamber
Flow within roots, $J_v$			Sap flow techniques Split-rootbox

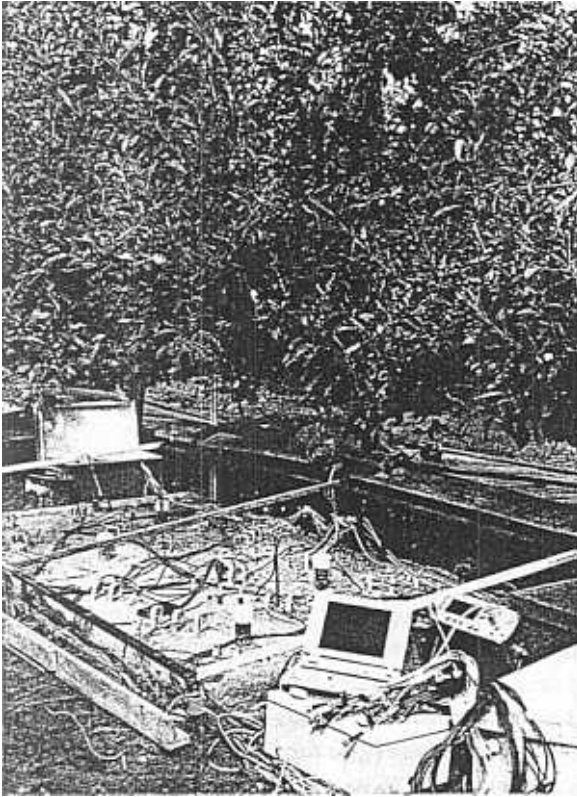
first discuss methods for measuring water uptake by roots that can be detected via changes in the soil's water content or water potential. We then describe methods for determination of water fluxes in plants, as well as methods to assess the sources of water absorbed by roots, and determination of the resistance to flow and uptake. We conclude with methods to quantify root-shoot communication via plant hormones. These methods all differ in their temporal and spatial resolution, and thus they are intended for use for different purposes (Table 14.1).

## 14.2 Evaluation of Water Uptake from Changes in Soil Water Status

A variety of methods can be used to determine changes in both soil water content and potential for identifying areas of the soil where roots are actively taking up water. Especially interesting are those suitable for continuously monitoring changes in soil water content with the required resolution in both space and time, and with minimum disturbance to soil conditions.

### 14.2.1 Methods for Determining Soil Water Content

*The Gravimetric Method.* The water content of soils can be determined from the moist and dry weights of soil samples. To obtain the moist weight, samples



**Fig. 14.3.** An apple tree whose root zone has been isolated by a  $3 \times 3$  m trench. This isolated tree can also be covered by a ground level rainout shelter. The tree is instrumented with heat-pulse sensors of sap flow measurement in both the trunk and diametrically opposite structural roots. The soil is instrumented with TDR probes, minirhizotron tubes, and tensiometers. (Courtesy of Peter Spring, HortResearch, New Zealand)

are weighed at the time of sampling, or later if they are kept in sealed containers in a cold environment. To determine the dry weight, the sample is dried to a constant weight in an oven at  $105^{\circ}\text{C}$ . The water content per unit soil dry weight or gravimetric wetness is the ratio of the weight loss by drying, to the weight of the dried sample. If bulk density of the soil is known or measured, volumetric soil water content can be calculated by multiplying the gravimetric reading by the bulk density.

The method does not require expensive instrumentation. However, it is destructive and time consuming. Errors can be made at every step – sampling, transporting, drying and weighing. Recommendations about the use of the technique can be found elsewhere (Hillel 1980; American Society of Agronomy

1986). Errors can be reduced by increasing the size and number of samples, but this requires more time and effort, and eventually disturbs the experimental plot.

*The Neutron Scattering Method.* This is one of the methods most widely used for determining soil water content. It requires the use of a neutron probe, an instrument with a source of fast neutrons and a detector of slow neutrons (Gardner and Kirkham 1952). When the probe is lowered into an access tube inserted into the soil, the fast neutrons that are emitted collide with various atomic nuclei in the surrounding medium. Through repeated collisions the neutrons are deflected and "scattered", and lose kinetic energy. Their speed decreases to the characteristic speed for particles at the ambient temperature. Those slow neutrons are said to be thermalised. The nuclei of hydrogen, being of similar size, are the most effective in thermalising the fast neutrons, and so the flux of slow neutrons scattered by the soil is proportional to the soil water content. The source of fast neutrons is obtained by mixing a radioactive emitter of alpha particles (radium or americium) with beryllium. The flux of slow neutrons is converted to a count rate by an electronic scaler.

The neutron scattering method is less time consuming and not as laborious as the gravimetric method. It is less destructive, and repeated measurements can be made at the same locations, directly surrounding the access tubes. The main disadvantages are the high cost of the neutron probe and the emission of neutron and gamma radiation. In addition, the method is not suitable close to the soil surface zone due to the escape of fast neutrons through the surface. The effective volume of measurement is a sphere which varies in size with soil water content. It ranges from a radius of less than 10 cm in a wet soil, to more than 25 cm in a dry soil (Stone et al. 1955; Holmes 1956). The neutron probe has to be calibrated, usually by making many measurements of soil moisture with the neutron and the gravimetric methods simultaneously. Once calibrated, it should work on different soil types, except in unusual soils, like very heavy clays or in soils with a high boron content. When changing soils, one or two readings can be obtained gravimetrically to see if points fall on the calibration line, to find out whether a new calibration is required. Different soil layers may require different calibration lines. A good example of the use of the neutron probe to infer root uptake is the work by Rambal (1984). He used the technique for 7 consecutive years to examine seasonal water extraction to 4.5 m in a *Quercus coccifera* evergreen scrub system. Different calibration curves were required for soils with different rock distributions.

*Gamma Densitometry.* The theory and practice of gamma densitometry were documented by van Bavel (1959) and Gardner (1986). Briefly, when a source of gamma radiation is placed in the soil close to a detector, the amount of

radiation passing through the soil decreases in proportion to soil water content, if bulk density is constant. Simultaneous measurements of bulk density and soil moisture changes can be made with dual-source gamma-ray scanners, in which both  $^{137}\text{Cs}$  and  $^{241}\text{Am}$  are used (Gardner 1965). Small changes in soil water content can be detected with spatial resolution and precision that is difficult to attain using other methods (Baker and van Bavel 1986, 1988). For example, the effective depth resolution of measurement is about 1 cm, much better than the neutron probe (Table 14.1). The access tubes for the source and detector probes must be strictly parallel, which make installation difficult in certain soils. The technique is likely to be used less in future, as non-nuclear methods improve.

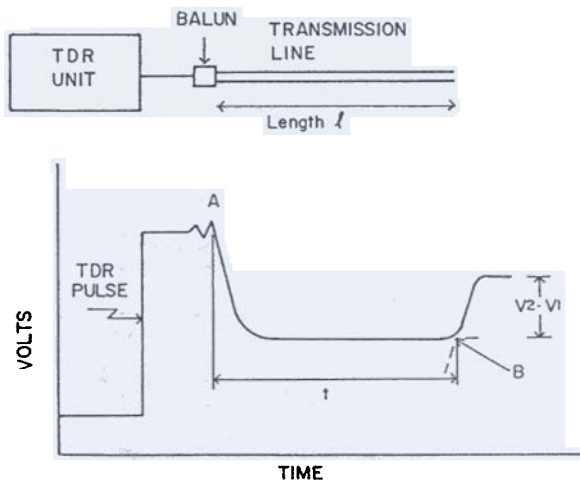
*Dielectric Methods.* Over the last decade a revolution has occurred in the technology of soil water measurement. The water content and electrolyte concentration of a soil can be accurately determined from the measurement of its dielectric properties. Two methods can be used, one with measurement in the frequency domain between 30-3000 MHz (Schmugge et al. 1980), and the other in the time domain at frequencies above a GHz (Topp and Davis 1985a). These methods, based on the measurement of the electrical capacitance of the soil, depend on the fact that water has a much higher dielectric constant than either air or the dry constituents of soil. The dielectric constant for free water is about 80, and for soil-bound water varies between about 4 and 80, while for dry soil it is about 5 and for air, 1.

#### 14.2.1.1 Time Domain Reflectometry (TDR)

For the time domain method, the most popular instrument uses time domain reflectometry (TDR). The principle of the technique is well explained by Topp and Davis (1985a). TDR determinations are based on the propagation of high frequency ( $\approx$ GHz) electromagnetic waves through the soil. The propagation constants for electromagnetic waves in the soil depend on the soil properties, especially its water content and electrical conductivity. In the TDR technique, a voltage pulse is propagated along a transmission line which terminates with a wave guide inserted in the soil. Wave guides are composed of two or three parallel metal rods. The signal is reflected from the end of the wave guide and returns to the TDR receiver. The propagation velocity and the amplitude of the reflected signal are then recorded. Because the propagation velocity depends on the dielectric constant of the medium, it is proportional to volumetric water content, becoming smaller as water content increases (Fig. 14.4). The determination of water content is essentially independent of soil texture, temperature and salt content. However, Herkelrath et al. (1991) found that calibrations run on soil cores did not compare well with published curves



**Fig. 14.4.** Essential components for measurement of soil water content by TDR (top) and idealised output trace. Electrical conductivity is calculated from the signal travel time ( $t$ ) between the beginning (A) and the end (B) of the soil transmission line, and from the reflected signal amplitude ( $v_2-v_1$ ). (From: Topp and Davis 1985b)



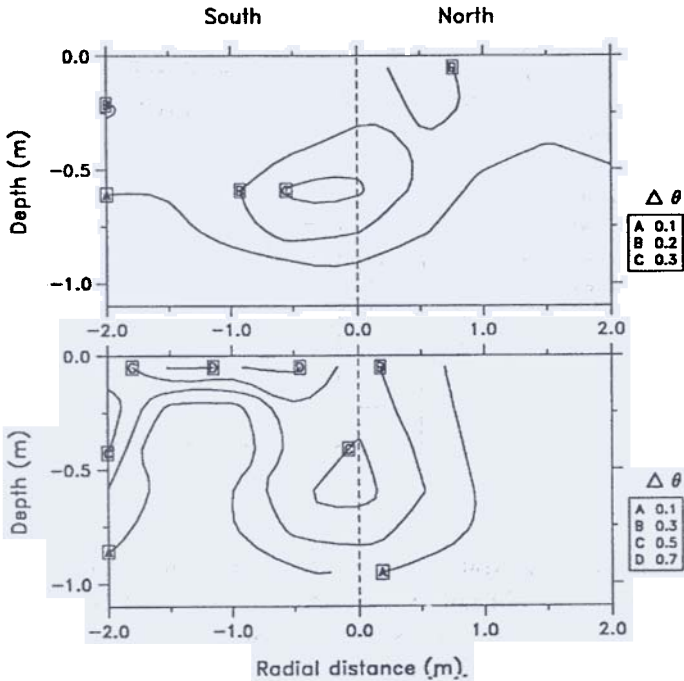
developed for mineral soils, probably because of high soil organic matter content. The authors did not explain why organic soils shift the calibration. Measurements in dry cracking soils may also be difficult, due to the poor contact between probes and soil.

The TDR technique has the same order of accuracy and reproducibility as nuclear methods, and usually does not require site-specific calibration (Wraith and Baker 1991). Several wave guides can be multiplexed and continuously monitored by an unattended TDR unit (Baker and Allmaras 1990; Heimovaara and Bouten 1990). This makes TDR a powerful technique for studying root water uptake. Wraith and Baker (1991) used an automated TDR system to study water uptake and reported high spatial and temporal resolution with high precision; standard deviations in water-content measurements were between 0.0008 and 0.001  $\text{m}^3 \text{m}^{-3}$ . Clothier and Green (1994) used 22 TDR probes around a kiwifruit vine to monitor the pattern of root water uptake (Fig. 14.5). The near surface preference of roots for wetted soil can be seen in the lower figure. They also used a bank of tensiometers and sap flow measurements in the stem of the tree, in an example of the combined use of several techniques to understand and quantify the spatial and temporal pattern of water uptake by roots.

Further developments of the TDR technique will continue to improve the precision and accuracy of measurement and reduce cost.

#### 14.2.1.2 Frequency Domain Method (FD)

The first dielectric soil water content sensors that worked with frequency domain (FD) were developed in the 1930s (Ferguson 1933; Smith-Rose 1933; Lück 1964). Modern instruments (Turski and Malicki 1974; Wobschall 1978;



**Fig. 14.5.** An example of the spatial resolution of measurements by TDR where the ordinate is soil depth and the abscissa is the radial distance from the kiwifruit vine. The *upper part* shows the average daily change in soil water content around a kiwifruit vine over a 4-week period; the *lower part* gives results for a 2-week period following irrigation of the south side (*left side*); the rate of water extraction  $\Delta\theta/\Delta t$  is given in  $\text{m}^3 \text{m}^{-3} \text{day}^{-1}$ . (From Clothier and Green 1994)

Hilhorst et al. 1992) use improvements that make the technique an accurate method of measuring soil water content, suitable for automatic measurements in situ (Hilhorst and Dirksen 1994; Dirksen and Hilhorst 1994). The FD method involves the measurement of capacitance and conductivity at a fixed frequency. Most commercially available FD sensors have an operating frequency between 10 and 150 MHz. A sinusoidal current is fed through an impedance formed by two electrodes with the soil as the dielectric. From the amplitude of the voltage developed across the electrodes and the phase angle between current and voltage, the dielectric properties of the soil can be calculated. Electrodes can be plates, rods or rings. The electronic equipment associated with the FD technique is less expensive than that of TDR, and they are easy to operate. Calibration, however, is soil specific and non linear (Bell et al. 1987). A description of different instruments using capacitance probes and a comparative study with the TDR method can be found in Paltineanu and Starr (1997) and Robinson et al. (1998).

Measurements of the dielectric properties of soil in the time domain and the frequency domain were compared by Hilhorst and Dirksen (1994). Despite the advantages attributed by the authors to the FD technique, TDR instruments have become more widely used.

### 14.2.2 Methods for Measuring Soil Water Potential

The measurement of water potential both in the soil and in roots is used for determining the state of water in both systems. It is the thermodynamic potential of water that provides the continuous and causal link in the transport chain from water in the soil, to the plant and to the atmosphere.

The main components of the total soil water potential are the matric potential, the osmotic potential and the gravitational potential (Kramer and Boyer 1995). The matric potential results from the capillary and adsorptive forces imposed on water by the soil matrix. The osmotic potential is due to the presence of solutes in the soil water. The gravitational potential of the soil water is determined by the elevation of a given point relative to a reference level, usually the soil surface or the water table. For measuring matric potential – the main component of the total water potential in the field – resistance blocks and tensiometers are used. Total soil water potential can be measured with thermocouple psychrometers. Hydraulic gradients can also be determined, with several tensiometers placed at different depths, so that Darcy's Law can be used to compute fluxes of water in the soil.

*Electrical Resistance Blocks.* Blocks of porous materials, such as gypsum, nylon or fiberglass, containing a pair of electrodes, can be used to measure matric potential (Bouyoucos and Mick 1940; Colman and Hendrix 1949). The underlying principle relies on the fact that the electrical resistance of many materials depends on water content. The resistance of a porous block in soil decreases as the quantity of soil water absorbed by the block increases. At equilibrium, the water content of the block is dependent on the matric potential of surrounding soil, which is therefore proportional to the resistance of the block. Porous blocks have to be calibrated per individual soils. Measurements are made by an ohmmeter connected to the electrodes of the resistance block.

Blocks made of gypsum behave better than blocks made of inert materials, since they are less sensitive to variations in the salinity of the soil solution. However, the solubility of gypsum makes the blocks eventually deteriorate in the soil. Gypsum blocks are more responsive in the dry range, whereas porous nylon blocks, because of their larger pore sizes, are more sensitive in the wet range of soil moisture variation (Hillel 1980). Porous blocks can be

considered a complementary tool to tensiometers, since they work better in soils drier than  $-0.05$  MPa. Reasonably accurate measurements can be obtained at matric potentials as low as  $-2.0$  to  $-3.0$  MPa. Goltz et al. (1981) described electronic improvements to make resistance blocks useful at water potentials as high as  $-0.03$  MPa. Although the porous blocks are not very accurate, they are frequently used to schedule irrigation, partly because they can be used for automatic recording of in situ changes in soil suction (Schlub and Maine 1979).

*Tensiometers and Microtensiometers.* A tensiometer consists of a water-filled container with porous cup, usually ceramic, which is inserted into the soil. The water container is connected to a manometer. The de-aired water within the cup equilibrates with the soil water through the pores of the ceramic walls. Soil water, usually under suction, draws water out of the tensiometer to achieve equilibrium, causing a drop in pressure inside the container which is indicated by the manometer. The manometer can be a water, or mercury-filled U tube, a vacuum gauge or an electrical transducer.

Tensiometers may be used at water potentials between 0 and  $-0.08$  MPa. Higher suction causes air entry through the cup. For dry areas, as near the soil surface, however, potentials can often go below  $-0.08$  MPa. The size of the ceramic cup will determine the sphere of influence within which the soil matric potential is measured. Several tensiometers are needed for characterising the distribution of moisture in the soil. Maintenance and measurement operations are not greatly time-consuming, and little training is required.

Vetterlein et al. (1993) described microtensiometers for measuring variations in soil matric potential in the vicinity of a living root system. They used ceramic capillaries with a length of 5 mm, a diameter of 1 mm and a wall thickness of 0.3 mm. The ceramic cells were melted into a glass tube, which was connected to a pressure transducer via a plexiglass body. Measurements were taken every 36 min throughout a 14-day period. The microtensiometers were operational at matric potentials between 0 and  $-0.08$  MPa, with a standard error  $<5\%$  below  $-0.008$  MPa. Temporal resolution was in the range of seconds.

*Soil Psychrometers.* Soil psychrometers are thermocouple psychrometers housed in a ceramic cup (Fig. 14.6), which is embedded in the soil. The thermocouple is used to measure the relative humidity inside the cup, which, at equilibrium, is equal to that of the soil atmosphere. This is accomplished by using the Peltier effect to condense water on the thermocouple junction within the ceramic cup. Relative humidity is then determined, in the psychrometric mode of operation, from the wet-bulb depression of the junction, or, in dew point mode, from its dew point temperature (see Sect. 14.6.1). Soil psychrome-

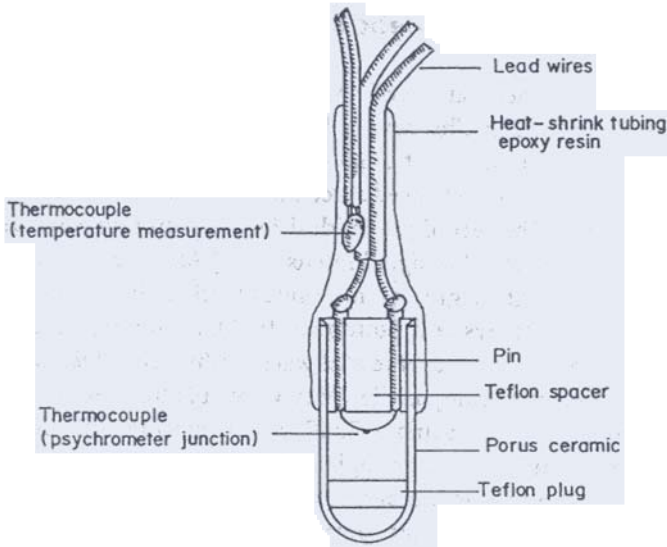


Fig. 14.6. Structure of a typical soil psychrometer. (From Pearcy et al. 1989)

ters can be used when the potential is below the tensiometer range, but they are not accurate above  $-0.2$  MPa.

Thermocouple psychrometers have been used to measure soil water potential by many authors. Savage et al. (1987) described the use, calibration, installation and maintenance of commercial soil psychrometers, both in disturbed and undisturbed soil. They listed precautions necessary for accurate measurement of soil water potential in the laboratory, glasshouse and lysimeters. Thus, direct sun on the aluminium covered lead wires of the soil psychrometers has to be avoided to achieve an acceptable value of zero offset. In addition, the screen cage cover cannot be in contact with soil, in order to reduce thermal gradients within the psychrometer to acceptable levels. Differences in temperature between soil and instrument, as well as within the psychrometer circuitry itself, can greatly affect the accuracy and precision of measured water potentials. Brown and Chambers (1987) discussed the magnitude of these errors and analysed the influence on results of temperature gradients between psychrometer and soil. Fonteyn et al. (1987) and Schlesinger et al. (1987) used soil psychrometers in the field. They found a good correlation between soil water potential and predawn plant xylem sap potential.

Soil psychrometers are easily installed, but should be placed parallel to the soil surface to minimise thermal gradients. They retain calibration characteristics for several years, but salt deposition in saline soils can seriously degrade their performance.

### 14.2.3 The Nuclear Magnetic Resonance (NMR) Technique

The principles and other features of proton nuclear magnetic resonance (NMR) imaging are described in Chapter 11. Here we show main applications to the study of water distribution and transport in plant root systems, a field in which the technique has been widely used since the 1980s (Bottomley et al. 1986, 1993; Brown et al. 1986). The technique is ideal for determining water distribution around and within roots. The signal intensity in NMR images is most sensitive to protons with a high degree of molecular-level mobility such as those of hydrogen in water (Rogers and Bottomley 1987). Bottomley et al. (1986) were able to analyse uptake and movement of water within *Vicia faba* plants growing in pots with different potting media. They were able to monitor the process of plant wilt and recovery by using a  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$  solution with  $\text{Cu}^{2+}$  as a tracer ( $\text{Cu}^{2+}$  is paramagnetic) and water application alone to a plant growing in a plot with dry soil. NMR imaging has been used by Omasa et al. (1985) for monitoring changes in root and soil water content. MacFall et al. (1990, 1991) used it for observing the development of a water depletion zone around suberized pine roots.

The major advantage of the technique is that it is non-destructive, as it employs non-ionising radiation that penetrates the soil media. This has no known effect on plants (Bottomley et al. 1986). The technique is sensitive to the presence of ferromagnetic particles occurring naturally in the soil, which can disturb the magnetic field and thereby distort the NMR information. Rogers and Bottomley (1987) investigated the range of potential applications of NMR imaging in root systems and assessed the impact of soil magnetic properties and water content on the results from the use of the technique. They found that the NMR technique was not useful in soils with ferromagnetic particle contents greater than about 4% by weight. The equipment is expensive and requires highly trained technicians. The technique cannot provide images of large root systems.

### 14.2.4 Applications to the Study of Water Movement Between Soil Layers via the Root System

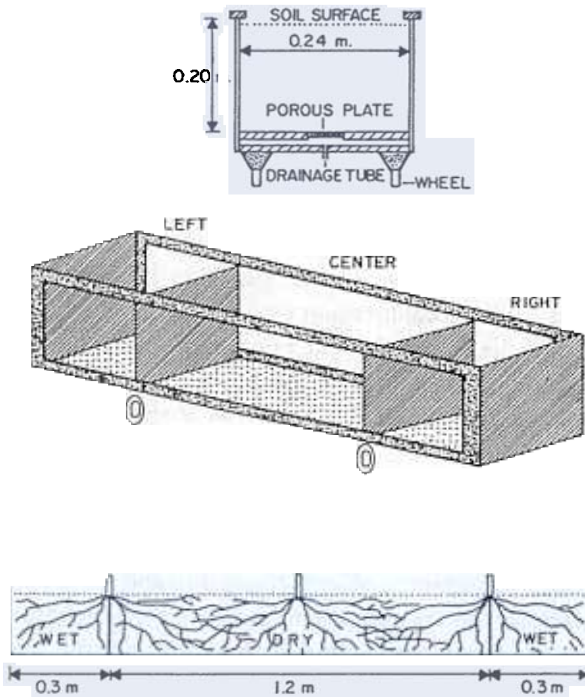
Water efflux from roots into surrounding soil can occur under certain conditions. Water will move out of roots that are permeable to water when the water potential of the soil falls below the water potential within the root. Hydraulic continuity via root systems can lead to transfers of water between soil layers, on the basis of water potential and resistance. If the subsoil is wet and the surface layers are dry, this process is called "hydraulic lift" (Baker and van Bavel 1986; Caldwell and Richards 1989; Xu and Bland 1993). The reverse process,

transfers from wet surface layers to dry subsoil is possible as well and has recently been observed in Machakos (Kenya; Smith et al. 2000). Although the total quantities involved in these water transfers may be relatively small, it can be important in the competition between shallow and deep rooted plants. Hydraulic lift can re-wet nutrient-rich dry topsoil layers and thus facilitate nutrient uptake. The reverse process, deep water storage by deep rooted plants after moderate rainfall which only infiltrates into the topsoil, can increase their overall resource capture vis-a-vis shallow rooted plants.

Water efflux from roots is a phenomenon that needs to be taken into account when considering survival and competition within a plant community. Thus, hydraulic lift can help the plant to withstand a period of drought. It can even benefit neighbouring plants with shallow root systems. On the other hand, rapid storage of water in subsoil around the deep roots of trees, beyond the wetting front, may give trees a competitive edge over rather shallow rooted plants.

*Measurement of Water Efflux and Hydraulic Lift.* Water efflux and hydraulic lift can be determined by detailed measurement of local changes in soil water conditions. Vetterlein and Marschner (1993) used microtensiometers to measure the transfer of water to upper soil layers from lower layers by hydraulic lift. The microtensiometer technique was sensitive enough to detect water release by roots in the top soil. Vetterlein and Marschner (1993) mentioned other attempts to measure hydraulic lift by using gamma densimetry or psychrometers (Mooney et al. 1980; Dirksen and Raats 1985; Baker and van Bavel 1988; Saab and Sharp 1989). Dawson (1993) used standard water relations methods and stable hydrogen isotope analysis to determine the magnitude and radial extent of hydraulic lift by sugar maple trees. He observed that ground water taken up by the trees was redeposited at night into the upper 35 cm of soil, benefiting neighbouring plants. Direct measurements of the direction and rate of water movement in roots based on heat-pulse methods will be discussed below.

*Split-Root Boxes.* Water movements within the root system can be also studied using *split-root* boxes. In these experiments, the root zones of plants are divided by barriers so that water can move from one side to another only through root systems which bridge the partitions. Different conditions can be imposed on each side. Split-root experiments were used by Zhang and Kirkham (1995a) to determine the effect on crop behaviour of having half of the root system under water and nutrient stress. The authors explain a way of splitting the root systems of grain sorghum and sunflower. Baker and van Bavel (1986) worked with *Cynodon* growing in a split-root box. After creating a large difference in soil water potential between the two sides of the root system, they observed noc-



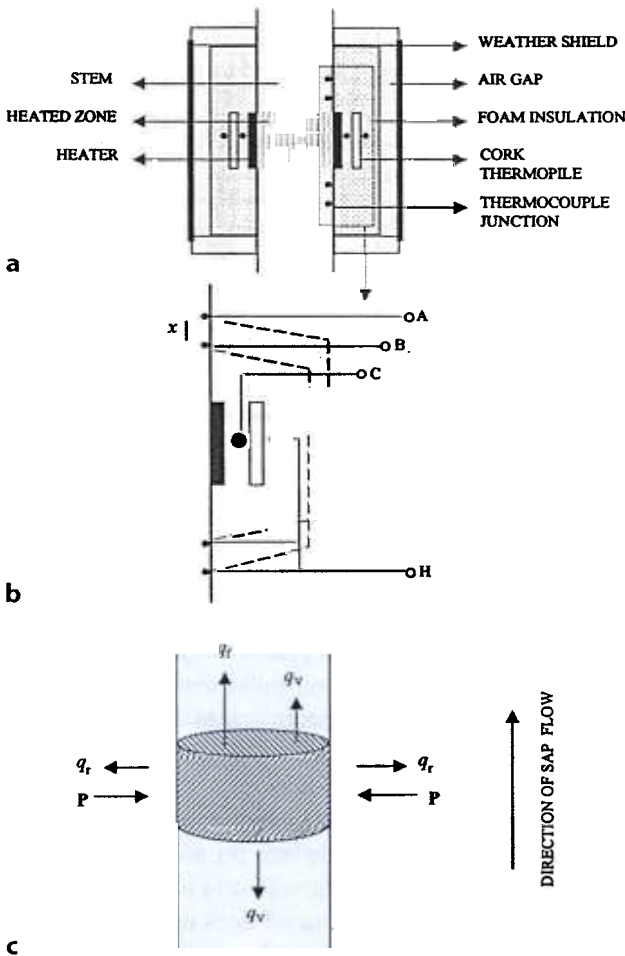
**Fig. 14.7.** A split-root box for quantifying hydraulic equilibration of soil via plant roots from wet to dry compartments. (From Baker and van Bavel 1986)

turnal transfer through the plant of significant amounts of water from one side to the other. This was detected by frequent measurements of volumetric water content in the box with a gamma probe. Overnight movements of water from wet to dry soil in a split-box (Fig. 14.7) were also observed by Baker and van Bavel (1988) when the potential gradient between dry and wetted compartments reached 1.0 MPa.

### 14.3 Evaluation of Water Uptake from Water Movement in Plants

Some 60 years ago Huber (1932) used heat as a qualitative tracer of sap flow in plants, by monitoring the downstream temperature rise following application of a short pulse of heat. He observed the rate of ascent of sap. Three thermal tracer techniques have been developed to quantify the volumetric rise of sap; the heat pulse method, the heat probe, and that of heat balance technique. These methods have been applied to a wide range of woody and herbaceous plants, both in the stem and in roots (van Bavel 1992; Swanson and Perttu 1994; Zhang





**Fig. 14.8.** Principles of heat balance and heat pulse technique for recording water flow through roots and stems. (From Smith and Allen 1996). **a** Vertical cross section through a stem heat balance gauge. The *dashed box* in **a** is expanded in **b** to show wiring details of thermocouples in the gauge; copper wires are shown as *solid lines* and constantan wires as *dotted lines*. For the determination of sap flow, the temperature differentials  $\Delta T_a$ ,  $\Delta T_b$  and  $\Delta T_c$  are obtained from measurements of the voltages across *AH*, *BH* and *CH*, respectively. **c** The heat balance of the length of stem heated by the gauge, where *P* is heat applied to the stem,  $q_v$  is the rate of vertical heat loss by conduction,  $q_r$  is radial heat loss by conduction and  $q_t$  is heat uptake by the sap stream. **d** Configuration of a single set of heat-pulse probes implanted radially into a stem of radius *R* at the cambium and *h* at the heartwood boundary. The upstream temperature sensor is installed at a distance  $X_u$  below the heater and the downstream sensor at a distance  $X_d$  above the heater. For calculating the heat-pulse velocity, the system measures the time delay for the temperatures at points  $X_u$  and  $X_d$  to become equal

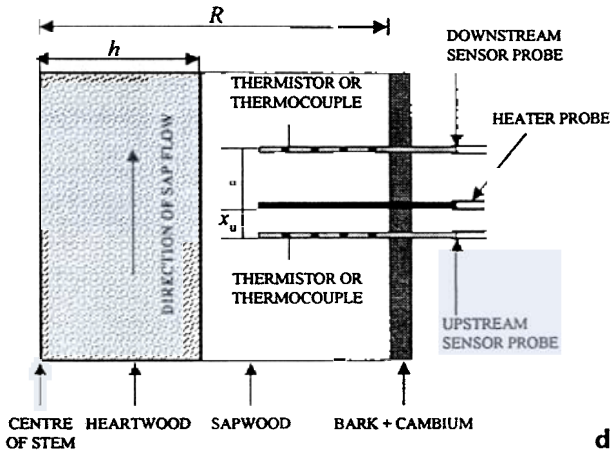


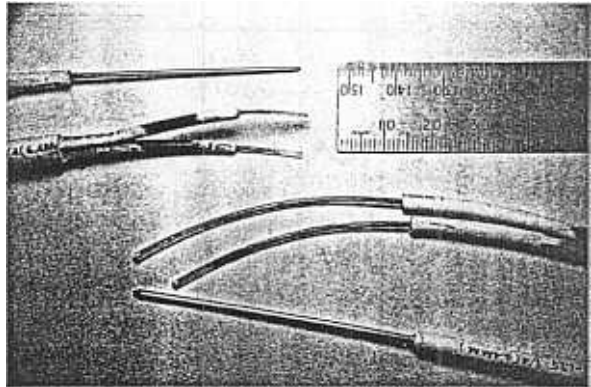
Fig. 14.8. (co

and Kirkham 1995b). Smith and Allen (1996) reviewed principles and applications of both the heat balance and heat pulse methods (Fig. 14.8). Scaling up from measurements of individual plants to that of a whole stand over a growing season requires special attention.

**Heat-Pulse.** In the heat pulse technique, which is best adapted to woody plants, a line-source heater is inserted radially into the stem, or root (Fig. 14.9). Every so often, say every 15–30 minutes, a short (1–2 s) pulse of heat is applied by the heater. Temperature sensors can be located both upstream and downstream of the heater, as in the case of the compensation method (Swanson and Whitfield 1981); or simply on the downstream side (Cohen et al. 1981). Solution of the heat flow equation (Marshall 1958), with appropriate wound factors (Green and Clothier 1988), allows the local velocity of sap flow to be inferred from the measured time-of-travel of the heat pulse. Sap flow rate is then obtained by integration of sap velocity over the cross-sectional area of the stem.

**Heat Probe.** In the probe technique of Granier (1985) the dissipation of heat from a heater probe is empirically related to sap flow rates. Two probes are inserted radially into the stem or root of a woody plant; one probe is both a heater and temperature sensor, whereas the other measures the reference temperature upstream of the heater. From the regularly measured rise in temperature whilst the heater is supplied with a constant current, an empirical relation provides the time-varying trace in the local sap velocity.

**Fig. 14.9.** Heat-pulse sensors for both measurement in the trunk using thermistors, and a miniaturised version for use in roots which uses thermocouples. Also shown is the stainless steel heater probe. (Courtesy of Dr. Brent Clothier, HortResearch, New Zealand)



**Heat Balance.** Unlike the two previous techniques, wherein a temperature change is related to a sap velocity, the heat-balance technique relies on measuring all-but-one of the components of the thermal balance of a stem or root section. The basic equation is:

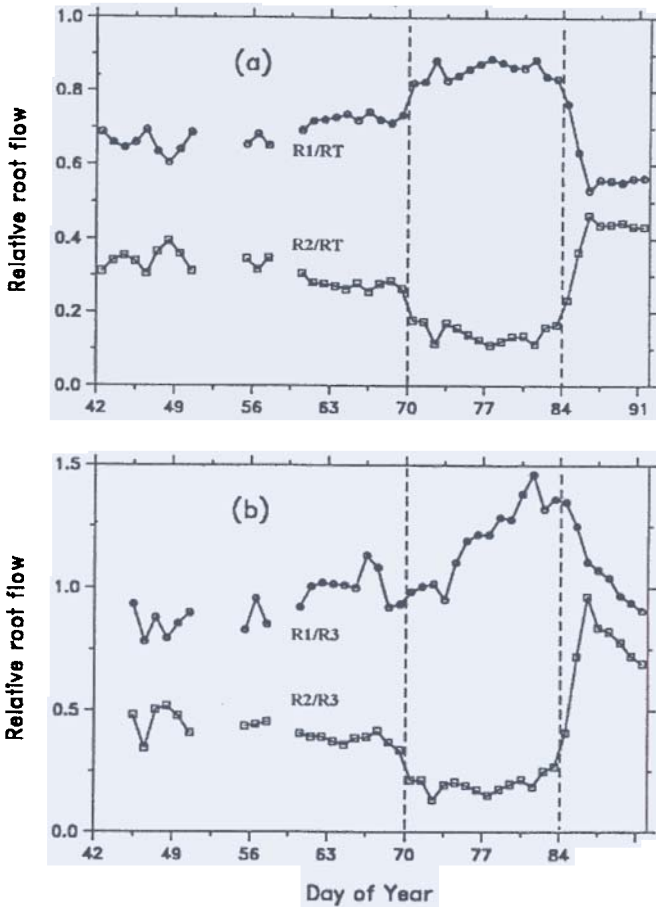
$$q_i = q_v + q_r + q_f \quad (14.1)$$

where  $q_i$  is the heat input to the stem,  $q_v$  is the vertical heat loss by conduction in the stem,  $q_r$  is the radial heat loss and  $q_f$  is the heat uptake by the moving sap stream, the only term of the equation which cannot be measured directly; it must be found by difference.

In closing the thermal balance, the amount of heat carried away by the ascending sap can be used to determine the volumetric efflux of sap from the stem, or root section. This technique is well adapted to herbaceous plants or fruit rachilla (Sakuratani 1981), as well as for larger trunks of woody species using a different configuration (Cermák et al. 1973).

Over the last 25 years, these three techniques have been extensively applied in the trunks and stems of a wide variety of plants. These data have provided many insights into the aerial mechanisms controlling the amount of water transpired by plants, and also into the mechanisms of plant hydraulic functioning. More recently these techniques have been applied in roots so that the subterranean functioning of plants has become observable in more detail.

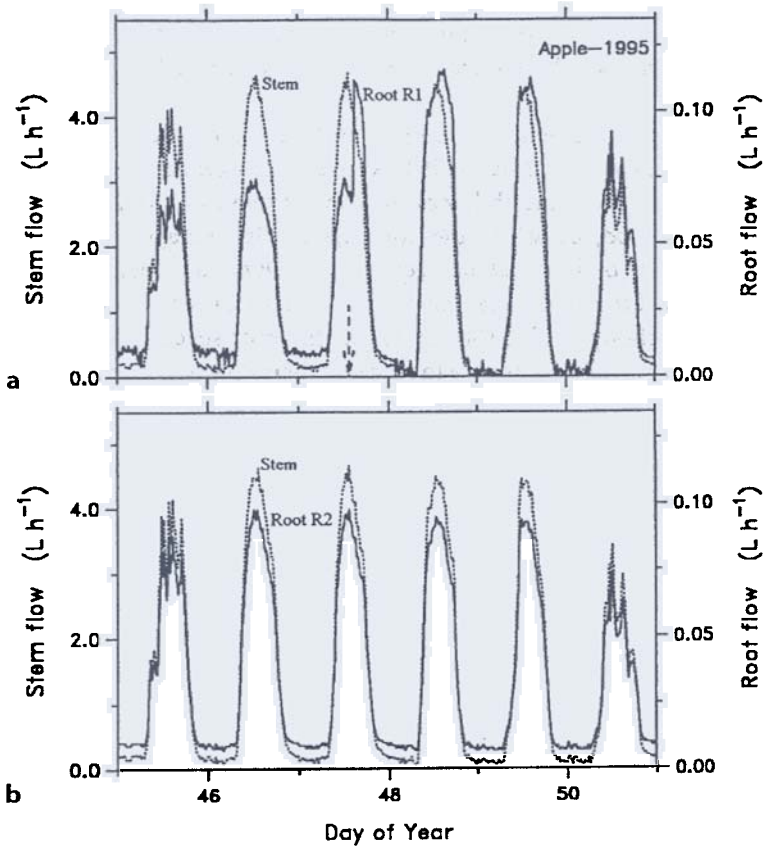
**Sap-Flow Measurements in Individual Roots.** Green and Clothier (1991) miniaturised their heat-pulse equipment so that they could observe sap flow in 25-mm-diameter roots of kiwifruit. Their results (Green and Clothier 1995) provided a clearer picture of how vine roots that have dried down the soil can respond preferentially to localised wetting (Fig. 14.10). In Fig. 14.10, The rise of sap flow in R1 3–4 days after wetting on DOY 84 was thought to have resulted



**Fig. 14.10.** Sap flow in kiwifruit roots measured with the heat-pulse technique: a relative sap flow in two roots, R1 and R2, relative to their total,  $R_T$ .  $R1/R_T$  is the top line, and  $R2/R_T$  the lower. In b the root flow is expressed as a ratio to that measured in a control vine R3. Here  $R1/R_3$  is the top line, and  $R2/R_3$  the lower. On day 70 the soil surrounding R1 only was wetted and on day 84 the entire root zone was wetted. (From Green and Clothier 1995)

from growth of new roots, as sap flow in R1 was higher, after rewetting, than prior to the dry down.

For apples, Green, Clothier, McLeod (1996) reported quite a different response to localised wetting (Fig. 14.11). The sap flow in R1 shows an immediate and sustained response to the localised wetting of DOY 47. The rapidity of the response, and the subsequently unchanging ratio to stem flow would be the response expected from Gardner's (1960) hydraulic model of water uptake.



**Fig. 14.11.** Response of sap flow in two apple roots to localised wetting around R1 at the time indicated by the *arrow* in the *top* diagram (from Green et al. 1996). **a** The *dotted line* is the sap flow measured in the trunk and the ordinate scale is on the *left*. The sap flow in root R1 is given as the *solid line* and the flow can be seen to rise immediately following the irrigation on Day 47. The ordinate for root flow is on the *right*. **b** Again stem sap flow is given as the *dotted line*, and here the sap flow in root R2 is given as the *solid line*

In the case of apples, the root form is one of high occupancy in the explored zone, and so it would appear that with such a root system form, apple uptake functioning does not rely on root growth. Kiwifruit root system form, in comparison, has low occupancy in the explored zone, so that uptake functioning relies in part on the growth of new roots, much as Nobel et al. (1990) found with desert succulents.

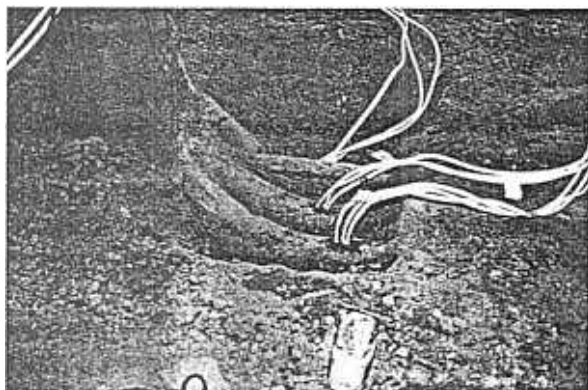
Using the heat-probe technique, Cabibel and Do (1991) observed the diurnal trace of sap flow in apple roots that were either drawing water from a

zone of localised wetting, or from drier soil. They found sap flow in the dry root tended to be out of phase with that in the trunk such that flow actually peaked at night, and they attributed this to be a result of nocturnal recharge of the tree's capacitance.

Using the heat-balance technique on the roots of the African tree *Croton melagocarpus*, Ong and Khan (1993) were able to examine, by branch pruning and root amputation, the ability of the root system to function when the soil's water is depleted, or when the root system is damaged. A commercially available brand of heat balance equipment (Dynamax Inc., Houston, Texas, USA) was used to monitor sap flow in 20–30 mm diameter roots of *Eucalyptus grandis* (Lightbody et al. 1994). By sequential root severance, they noted that other remaining roots were able to increase their flow to accommodate the flow required by the tree. Thus flow in individual roots and shoots of perennials can be quite decoupled, whereas this might not be the case in annuals.

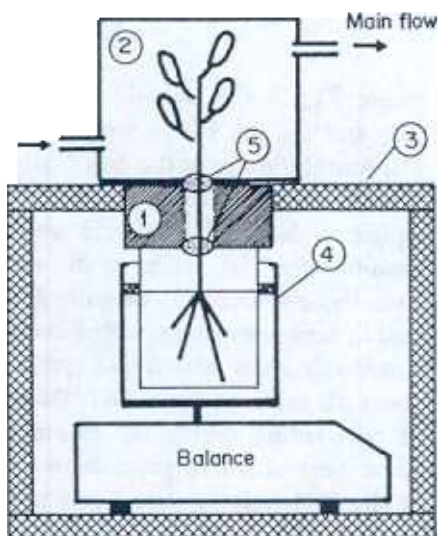
For the sclerophyllous olive, Moreno et al. (1996) used the heat pulse technique to observe the inability of near-surface roots to recover immediately from emboli caused by water stress, despite a thorough but single wetting of the soil around the once very-dry root.

By extension into roots of heat tracer techniques of sap flow monitoring, new observations are being made of the link between root form and functioning (Fig. 14.12). This includes details of root response to localised wetting, the nocturnal recharge of a plant's capacitance, the respective roles of near-surface roots and roots deeper in the profile, the impact of emboli, and the fraction of the plant's uptake functioning that can be carried out by just some fraction of the root system. Further use of heat-tracer techniques will be useful in providing modellers with data that have hitherto been unavailable. It is important to realise that water flow in any part of a stem or root can be in all directions, and deep roots may pump water out of subsoil during droughts, but may also leak water taken up after rainfall has rewetted the surface layers.



**Fig. 14.12.** A set of three instrumented apple tree roots. Each of the roots dips away from the trunk at a different angle, so that comparison between the measured flows can be used to indicate the depthwise uptake strategy by the root system. (Courtesy of Dr. Brent Clothier, HortResearch, New Zealand)

**Fig. 14.13.** Schematic design of water-budget meter: 1 control unit with attached inner and outer containers mounted on a balance; 2 gas exchange cuvette for determining  $\text{CO}_2$  exchange and transpiration; 3 steel cage connecting control unit with platform of the balance; 4 outer container on the pan of the balance with oil seal to prevent evaporation to ambient air; 5 air-tight seals fixing the plant to the control unit and gas exchange cuvette; wind and radiation shields not shown. (From Flach et al. 1995)



*The Water-Budget-Meter.* For detailed laboratory-scale experiments, Flach et al. (1995) used an improved potometric water-budget-meter (WBM; Fig. 14.13), based on a system described by Eller et al. (1993). Plants are mounted in a gas exchange cuvette where  $\text{CO}_2$  exchange and transpiration can be measured. The roots are bathed in water in a container on a balance which is used to determine water uptake. Water uptake is the weight change of the container. They reported an error of less than  $\pm 3\%$  for water uptake, if a time period of more than 1 day was considered. For shorter periods (6–24 h) the error was larger, but still less than  $\pm 6\%$ . This improved WBM is able to quantify water uptake of a whole plant during time periods of several weeks. It will be a useful instrument for detailed and controlled studies of the processes controlling root water uptake.

## 14.4 Measuring Stable Isotopes in Plants to Assess Water Uptake from Different Depths

The principles underlying the use of stable isotopes for understanding of water uptake processes are explained in Chapter 12. In this section we only mention illustrative applications of these techniques that can be used for assessing the sources of water absorbed by roots.

*Deuterium.* The isotopic composition of a sample is usually expressed in terms of delta units relative to some standard (Friedman and O'Neil 1978):

$$\delta X_{\text{std}} = (R_{\text{sam}}/R_{\text{std}} - 1)1000, \quad (14.2)$$

where  $\delta X_{\text{std}}$  is the isotopic ratio in delta units relative to the standard, and  $R_{\text{sam}}$  and  $R_{\text{std}}$  are the isotope abundance ratios of the sample and standard respectively. Water is the only hydrogen source for a plant under the natural conditions of rainfall. Water absorbed by roots can either come from precipitation during the growing season, or from stored soil water, or from the groundwater. The values of  $\delta D$ , the deuterium/hydrogen ratio of the water from those sources can be quite different. This difference arises from the fact that in temperate areas, with a continental climate,  $\delta D$  values of precipitation commonly show a seasonal cycle. High  $\delta D$  values occur in summer, with lower  $\delta D$  values in the winter (Dansgaard 1964; Gat 1980). Thus, the  $\delta D$  values of rain falling during the summer growing season are generally different from those of stored groundwater. Flanagan et al. (1992) used measurements of the D/H ratio in stem water to determine the relative uptake of summer precipitation by four co-occurring plant species in southern Utah. They found that it was possible to determine the uptake of summer precipitation by measuring the stable isotopic composition of stem water (Flanagan and Ehleringer 1991). Since no isotopic fractionation occurs during water uptake by plant roots (Dawson and Ehleringer 1991), the isotopic composition of water in roots and stems reflects that of water taken up by roots. White et al. (1985) carried out measurements of D/H ratios of tree sap to determine the source of water. They took sap samples from the trunk around noon, when sap flow rate was high. Wood samples were taken from the trunk using an increment borer and the sap drawn into capillary tubes. They demonstrated that the  $\delta D$  values of sap could be used to quantify the relative contributions of summertime rainfall and groundwater. Dawson and Pate (1996) were able to identify the sources of the water taken up by the lateral and tap roots belonging to several woody shrubs and trees. They did this by studying the seasonal changes in the  $\delta D$  of xylem water within different parts of the root system and lower shoots.

Dalton (1988) studied water extracted by the roots of tomato plants. He explained that water will be either  $\text{H}_2\text{O}$ , characterised by water when both hydrogen atoms are the isotope  $^1\text{H}_1$ , or  $\text{HDO}$  (D for deuterium) when one hydrogen atom is the isotope  $^2\text{H}_1$ . The vapour pressure of the lighter  $\text{H}_2\text{O}$  molecule is slightly greater than that of the  $\text{DHO}$  molecule. Therefore, vapour phase water in equilibrium with liquid phase water will have a slightly lower ratio  $\text{HDO}/\text{H}_2\text{O}$  than that of the liquid phase. If there is no vapour component to root water extraction, then the proportion of  $\text{HDO}$  in the residual soil water will remain constant. This experimental technique and isotopic ratio measurements were shown to be useful for determining the vapour component of water uptake by the plant roots.



*The  $^{18}\text{O}/^{16}\text{O}$  Ratio.* Measurements of  $^{18}\text{O}/^{16}\text{O}$  ratios in samples of water drawn from the xylem can also be used for determining whether the water absorbed by roots is coming from either surface or deep waters. Allison and Hughes (1983) analysed isotope ratios of  $^{18}\text{O}$  and D in soil profiles down to 15 m depth. This was carried out in areas of *Eucalyptus*, and *Eucalyptus* areas that had been converted to wheat. During the rainy season, the soil surface of the cropped land showed an increase of the isotopic ratio, as compared with the measurements taken during summer. This indicates a degree of infiltration of the precipitation that possesses a higher  $\delta\text{D}$  and  $\delta^{18}\text{O}$ . Such an increase was not observed in the soils with *Eucalyptus*, indicating negligible infiltration since most of the precipitation has been intercepted by the tree canopy.

The  $^{18}\text{O}/^{16}\text{O}$  composition of water at equilibrium is known. The  $^{18}\text{O}/^{16}\text{O}$  composition of water can be determined by equilibration with a small volume of  $\text{CO}_2$ , followed by repeated cryogenic distillation to free the  $\text{CO}_2$  which has reached isotopic equilibrium (Epstein and Mayeda 1953; Compston and Epstein 1958). For very small samples, the  $^{18}\text{O}/^{16}\text{O}$  composition can be found by a reaction with guanidine hydrochloride to produce  $\text{CO}_2$  (Dugan et al. 1985; Wong et al. 1987).

Smith et al. (1996, 1997) found a clear difference in the  $^{18}\text{O}/^{16}\text{O}$  isotopic ratio between late and early rainfall. In the early season rain, the rain results from the northward advance of the inter tropical convergence zone (ITCZ), and during the later part of the growing season in the Sahelian region of Africa, the rain is due to the southward return of the ITCZ. This isotopic discrimination can be used to distinguish between surface and deep water uptake by the roots of Sahelian trees.

## 14.5 Measuring the Ability of Roots to Take Up Water

Water uptake by roots can be assessed with the methods described so far. In this section, we refer to methods for studying the ability of roots to take up water, and the role of root-shoot signalling mechanisms which lead to stomatal closure and, ultimately, to water uptake.

### 14.5.1 Soil and Root Hydraulic Conductivity

The water status of a plant is largely determined by the balance of transpiration and water uptake from the soil. Water uptake depends on the soil water status, root distribution and activity in the soil, and the hydraulic properties along the pathway of water movement. The four main components of the soil-root-shoot pathway are: (1) the soil, (2) the root-soil interface, (3) entrance to

the xylem in the root, and (4) the axial pathway from root to shoot in the xylem (Huang and Nobel 1994). The conductance of this pathway is not independent of rate of flow or soil water content, and the relative importance of the four main components varies. Changes in the conductivity of the soil-root-shoot pathway can be due to:

1. Reduction in soil water conductivity as the soil dries out,
2. Changes in continuity of the soil-root pathway by air gaps and reduced root-soil contact,
3. Changes in osmotic potential outside of the root,
4. Changes in true permeability of the cell walls along the pathway,
5. Changes in osmotic potential inside the root,
6. Changes in the continuity of the axial pathway by embolism.

Different perspectives exist on the relative importance of these processes (Sands et al. 1982; Weatherley 1982; Passioura 1988; Rüdinger et al. 1994; Stirzaker and Passioura 1996), but there is now general agreement that past conclusions on the importance of (4) ignored a number of alternative explanations. When the soil's water content is high, water movement from the soil to the shoots depends mainly on the hydraulic conductivity of the root itself (3–5 and possibly 6; Blizzard and Boyer 1980; Passioura 1988). As the soil dries, the conductance of the soil-root interface (2) can become limiting for water movement, due to root shrinkage (Taylor and Willatt 1983; Fernández et al. 1992), but possibly also because of increases in the osmotic potential of the soil solution (3; Stirzaker and Passioura 1996). At lower soil water contents, the soil conductivity (1) becomes the primary limitation on water movement in the root-soil pathway. See Box 14.1 for the components related to the permeability of roots.

A range of techniques is available for determining  $L_p$ ,  $L_r$  and  $K_h$ , usually based on measuring the volume of water flowing through a root that is exposed to a known difference in water potential, by varying hydrostatic or osmotic pressure (Huang and Nobel 1994).  $L_p$  has been determined for individual roots by measuring  $J$ , induced by applying a partial vacuum to the distal end of an excised root (Nobel et al. 1990), but also by applying external pressure to the whole root system. Typical results for  $L_p$ ,  $L_r$  and  $K_h$ , as measured by different authors in different species are reviewed by Huang and Nobel (1994). They show how hydraulic conductivity changes with plant stage and environmental conditions. From all the techniques, the root pressure probe technique seems to be the most widely accepted method to determine  $L_p$ ,  $L_r$  and  $K_h$  (Sect. 14.5.1).

The relative importance of the axial and radial component of  $L_p$  varies with plant species and the developmental stage of the root (Huang and Nobel 1994). Rowse and Goodman (1981) studied water movement in broad bean roots. They analysed the relative effects of axial resistance, calculated from the xylem dimensions, and radial resistance calculated using a potometer developed to

**BOX 14.1. The Permeability of Roots**

Water from the surrounding soil moves radially into the root and axially along the xylem. Therefore, the permeability of roots to water depends on the root hydraulic conductivity,  $L_p$  ( $\text{m s}^{-1} \text{Pa}^{-1}$ ) which can be defined as (Moreschet and Huck 1991; Nobel 1991):

$$L_p = J_v / (\Psi_{\text{surface}} - \Psi_{\text{xylem}}), \quad (14.3)$$

where  $J_v$  ( $\text{m}^3 \text{m}^{-2} \text{s}^{-1}$ ) is the volumetric flux density of water into the root,  $\Psi_{\text{surface}}$  (Pa) is the water potential at the root surface, and  $\Psi_{\text{xylem}}$  is the water potential of the root xylem. Also,

$$L_p = Q_v / (\Delta P A), \quad (14.4)$$

where  $A$  ( $\text{m}^2$ ) is the root surface area,  $Q_v$  is the volumetric flow rate of water ( $\text{m}^3 \text{s}^{-1}$ ), and  $\Delta P$  (Pa) is the pressure drop along the root.  $L_p$  can be partitioned into two components: radial conductivity ( $L_r$ ) for water movement into the roots and up to the xylem, and axial conductance ( $K_h$ ) for water movement along the root xylem (Dryden and van Alfen 1983; Nobel et al. 1990). For a root segment of length  $L$  (m),  $K_h$  ( $\text{m}^4 \text{s}^{-1} \text{Pa}^{-1}$ ) can be expressed as:

$$K_h = (L Q_v) / \Delta P. \quad (14.5)$$

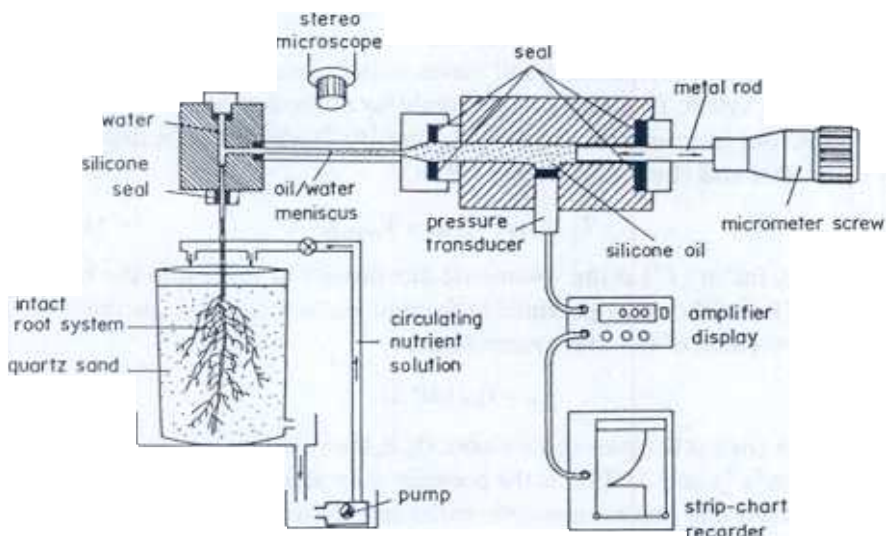
The radial conductivity  $L_r$  ( $\text{m s}^{-1} \text{Pa}^{-1}$ ) averaged over the root segment can be calculated by incorporating  $L_p$ ,  $K_h$ ,  $L$ , and the root radius  $R_0$  (m) into the model of Landsberg and Fowkes (1978):

$$L_r = (L_p \alpha L) / \tanh(\alpha L), \quad (14.6)$$

where  $\alpha$  ( $\text{m}^{-1}$ ) equals  $(2 \pi R_0 L_r / K_h)^{1/2}$ , which represents the inverse of the length along the root xylem between which the pressure drops to a half (Landsberg and Fowkes 1978; Frensch and Steudle 1989; Alm et al. 1992).

measure the rates of water uptake by small portions of an intact root system. They found that axial resistance was not likely to be important. This conclusion may apply to most dicotyledonous plants with secondary development of xylem transport capacity; in monocots without the capacity to adjust xylem dimensions, however, axial resistance may dominate  $L_p$  in well-branched root systems. The continuity of the axial pathway may be dramatically reduced in all plants, however, by embolism.

Sperry and Tyree (1990) observed that embolism caused by water stress reduced hydraulic conductivity in roots of *Picea rubens*. The appearance of air embolism in the xylem, as the soil dries, caused a marked reduction of  $K_h$ . The



**Fig. 14.14.** Device for measuring root pressure and root pressure relaxation on spruce roots; root pressure was monitored by a pressure transducer connected to an amplifier and display; movements of the oil water meniscus are recorded in a measuring capillary (stereo microscope); hydrostatic pressure relaxations are measured by moving the micrometer screw rapidly into and out of the pressure probe. (From Rüdinger et al. 1994)

extent of air embolism can be determined by the ratio of axial conductance measured on segments before, and after, pressurisation in solution to remove the emboli (Sperry et al. 1994; Magnani and Borghetti 1995). Xylem at the junctions between lateral roots and main roots, and between main roots and stems, differs from that elsewhere in the root system. Embolism occurs more easily at the junctions.

*The Pressure Probe Techniques.* The cell pressure probe technique has been adapted for use on excised roots (Stuedle and Jeschke 1983). The root pressure probe is described by Hallgren et al. (1994), Melchior and Stuedle (1994), and Stuedle (1994). Root pressure is measured using a small manometer tightly fixed to the cut end of excised roots (Fig. 14.14). Excised roots exude xylem sap because of the active accumulation of solutes in the xylem. When exudation is stopped by attaching a "root manometer", the system reaches a root pressure which can be recorded continuously. Half of the interior of the root pressure probe is filled with silicone oil and the other half with water, so a meniscus is formed. The position of the meniscus is monitored with the aid of a stereo-microscope. Volume changes can be induced in the measuring system, being responses of root pressure monitored. Measurements begin when a steady root

pressure is attained. Changes in pressure with time can be converted into water flows (Melchior and Steudle 1993). Hydraulic conductivity can be calculated from analysis of the pressure/flow relations (Peterson and Steudle 1993; Peterson et al. 1993). Rüdinger et al. (1994) used the root pressure probe to determine the hydraulic and osmotic properties of a spruce root.

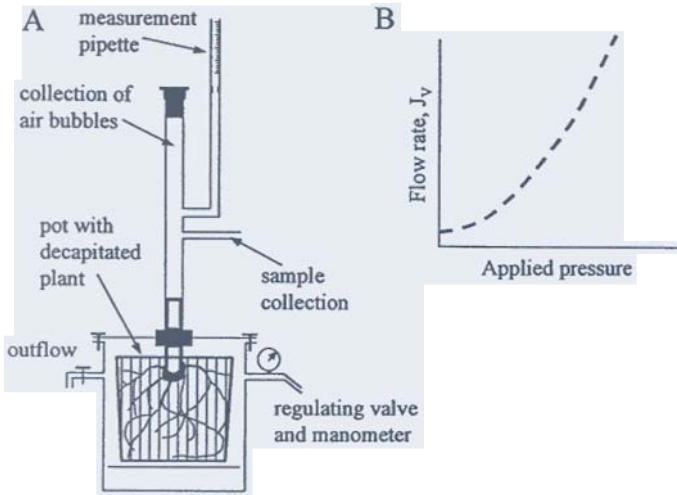
Root pressures can be measured on root tips, segments, or whole root systems. In a single root tip, measurements are usually possible for 1 to 2 days. In root systems, measurements have been performed for up to 10 days (Steudle 1994). Measurements on excised roots may not, however, be representative of those of intact plants.

Pressure in individual xylem vessels of intact plants can be directly measured by the *xylem pressure probe*, described in detail by Balling and Zimmermann (1990) and Zimmerman et al. (1994). Zhu et al. (1995) used this technique to measure hydraulic properties in roots of maize. This technique allowed, for the first time in intact plants, the direct measurement of diurnal and seasonal changes in xylem pressure, plus xylem flow and, in principle, the solute composition of the xylem sap at the single vessel level. The xylem pressure probe is filled with "denucleated" water and incorporates a pressure transducer. A microcapillary probe is advanced slowly through xylem tissue until the transducer registers a pressure below atmospheric. In order to verify that the probe is present in a vessel, the microcapillary is loaded within a dye solution prior to insertion, so that the penetrated vessel can be seen in cross-sections after the removal of the probe (Benkert et al. 1991). Model experiments have shown that the probe can accurately read pressure values down to at least about  $-1$  MPa (Balling et al. 1988; Zimmermann et al. 1994).

Zimmermann et al. (1995) stated that single measurements with the xylem pressure probe indicate that the xylem tension in the leaves of intact, transpiring plants is often much smaller than that predicted for transpiration-driven water ascent through continuous water columns. Studies with the xylem pressure probe, together with other evidence, indicates that different mechanisms need to be considered to explain water movement within plants.

### 14.15.2 Resistance to Flow

*Principle.* The relation between applied hydrostatic pressure and flow out of decapitated root systems is non-linear (Fig. 14.15). This non-linearity was initially interpreted as a change in the inherent conductance of roots with increasing flow rates. Fiscus (1975) and Dalton et al. (1975) showed that the non-linearity can be explained by the interaction of osmotic and hydrostatic pressures, at a constant hydraulic conductance of the roots. In fact, the osmotic



**Fig. 14.15.** A Pressure bomb design to measure the rate of water flow through excised root systems at different external hydrostatic pressures. B Typical result, showing non-linear relationship of flow rate and applied pressure. (From de Willigen and van Noordwijk 1987)

pressure component changes with changing flow rates, depending on the solute reflection coefficient  $\sigma$ , of the membrane. The models were initially based on a single membrane in a well-stirred solution, but can be extended to a membrane in an unstirred solution with salt accumulation in front of the membrane, counteracted by diffusion away from the root surface (Fiscus 1977; Passioura 1984; de Willigen and van Noordwijk 1987). Recently, Steudle and Peterson (1998) described the composite transport model, to explain how external factors may influence water passage across roots, and how plants optimize water uptake according to demands from the shoot.

**Methods.** Rieger (1995) measured the hydraulic conductivity of the roots of fruit trees using the technique of Rieger and Motisi (1990). The canopy of each plant was enclosed in a gas exchange chamber, with the root container and one basal side shoot left outside the chamber. The container was then placed in 1 cm distilled water to ensure that the soil water potential was virtually zero. Leaves on the basal shoot outside the chamber were wrapped in parafilm and foil, and allowed to equilibrate with the water potential of the stem base. At steady-state, the water potential gradient across the root system was assumed equal in magnitude, but opposite in sign, to the water potential of the wrapped leaf. Total water flow through the plant was measured by pumping chamber air through a desiccant column at a rate that maintained a constant dewpoint. A regression equation was developed for water potential gradient ( $y$ ) versus water

flow on a root length basis ( $x$ ) from the two points obtained for each plant, assuming linearity. The  $y$ -intercept of the regression gives the minimum gradient required for flow through the root system (Passioura and Munns 1984; Rieger and Motisi 1990), and the reciprocal of the slope gives  $L_p$ . With this technique,  $L_p$  measurements are time consuming.

Measurements of the flow rate through decapitated root systems can be made for single roots or whole root systems in permeable pots, by enclosing the roots in a pressure chamber with the stem attached to a pipette (Fig. 14.15). At low applied pressures (around 0.1 MPa) the osmotic component is not negligible and samples of the exudate can be collected for analysis. At high applied pressures (around 0.5 MPa) the osmotic component is negligible, but physical damage to the roots may occur. If root systems are used which were grown under incomplete aeration and have created cortical air spaces in response to this, a substantial volume of air may bubble out of the root, as the cut end of the stem includes the cortex. The air bubbles can disturb the measurement of flow rates, but their escape from the root can also cause physical damage to the root. A sequence of low and high pressures should be used, including zero-pressures to check for root leakiness under the pressure of the water column in the pipette.

The method can be applied with large potted plants, provided the dimensions of the pressure chamber are suitable. For roots in their natural habitat, however, a reversal of the direction of flow is needed. Tyree et al. (1994, 1995) developed a novel method of measuring hydraulic conductance of tree root systems using a high-pressure flow meter in the laboratory and field. They measured the amount of water flowing into root systems through a cut end on the proximal side (either close to the tree stem or at some distance away) at a range of pressures. By rapidly testing a range of pressures, total water flow during the measurements is small and therefore osmotic adjustments or changes in soil water content around the roots are probably negligible. By pressuring the roots internally, root-soil contact may be improved. At pressures above 0.1 MPa a linear response of flow  $J_v$  to applied pressure  $\Delta P$  can be obtained, from which  $L_p$  for the whole root system can be derived if total root surface area is known. The latter will need destructive measurement on the root after completing measurements, and/or the use of allometric equations relating tree root diameter to total root surface area. When the method is applied to dead roots very high flow rates can be obtained, so a check on the integrity of the root system is needed, especially for "outliers".

### 14.5.3 Root-Shoot Communication

Tardieu and Davies (1993) consider that the root-shoot signalling mechanism acting over the stomatal conductance of plants in drying soil is better explained

by considering the integrated effect of hydraulic and chemical signals, and not only chemical signals or water relations alone. They studied the ABA concentration in the xylem sap. ABA was synthesized by dehydrating the roots (Cornish and Zeevaart 1985). This synthesis can take place in different root tissues (Hartung and Davies 1991). Synthesis is roughly proportional to the root water potential. Therefore, the "root message" in drying soil should be linked to the water status of the root system. The authors mention different hypothesis for root messaging.

Ternesí et al. (1994) analysed root-shoot signalling in sunflower. They collected the sap of container-grown sunflower plants by cutting the shoot of the plant at 2.0 cm above the beginning of the root, and placing a latex tube on the top. Sap was collected in test tubes during 6 h and immediately frozen and stored at  $-20^{\circ}\text{C}$  until required. The ABA content in collected sap was measured by using an ABA-specific monoclonal antibody (Ephyscience EP120, Phytoscience, France) using the protocol suggested by the manufacturer. Results suggested the synthesis of a chemical signal in roots of plants under mechanical stress – a seven times higher ABA concentration in confined roots than in roots of control plants –, which can induce the inhibition of plant growth.

Jackson (1994) mentioned the difficulties of correct measurement of the amounts of hormones transported from root to shoot by the transpiration stream. The problem is that sap flow rates have a marked diluting influence on hormone concentration. If the sap taken for analysis flows at a slower rate than in the intact plants, which is usual, estimates of concentration present in the xylem sap of intact plants will be in error. Thus, variable sap flows mean that concentration alone is not a reliable guide to the amounts moving into the shoot. What is needed is a delivery rate per unit of time. Such a value is obtained easily by multiplying concentration with the sap flow rate. The most appropriate concentration measurements will be those made in sap flowing from the roots at rates as close as possible to the transpiration rate. Jackson (1994) mentioned that in pot-grown plants, the latter can be obtained gravimetrically over a few minutes immediately before the shoot is removed, or by using similar whole plants set aside for this purpose. One alternative approach has been to expel small amounts of sap from cut veins of leaves after pressurizing the roots of intact plants (Schurr et al. 1992). A second alternative method has been to sample the first few drops of sap issuing from the cut surface of the detopped root system (Zhang and Davies 1990), though the samples can be contaminated with ABA, sucrose, and other substances as a consequence of compression forces exerted on the stem when tubing is applied to collect the sap (Else et al. 1994).

Else et al. (1995) mentioned the difficulties in determining whether root signals are hydraulic or chemical. They observed that ABA, ethylene, and the



ethylene precursor ACC increased in shoots of flooded plants. Trejo et al. (1995) determined ABA concentration in leaves of *Phaseolus acutifolius*. Sampled leaves were frozen in liquid nitrogen and freeze-dried. Bulk leaf ABA concentration was determined using a radioimmunoassay. The monoclonal antibody AFR MAC 62 was used, which is specific for (+)-ABA. Samples were extracted using different ratios of extraction (leaf dry weight:solvent) depending on the concentration of the ABA fed (1:65–1:150), and further dilutions were made when found necessary.

## 14.6 Measurement of Plant Water Status

Measurements of the plant water status at a certain time could give us valuable information for estimating water uptake rates by the roots. Techniques for measuring stem diameter changes are also discussed in this section, as a more direct way to estimate water uptake.

### 14.6.1 Root Water Potential

Root water potential can be indirectly calculated (Jones 1983) from measurements of leaf water potential made using the pressure-chamber technique (Scholander et al. 1965). For more direct determination, thermocouple psychrometers, the sucker method or the root pressure probe can be used. However, these are all techniques that, by virtue of their delicate nature, are limited to use in the laboratory.

*The Psychrometer Technique.* Thermocouple psychrometers have been widely used for measuring root water potential. See Box 14.2 for details on the techniques. In situ psychrometers were developed in the 1970s for leaves (Boyer 1972; Campbell and Campbell 1974), stems (Michel 1977) and roots (Fiscus 1972). The last is easy to install on roots of various diameters, just by changing sleeves and bottom caps. By placing soil psychrometers close to root psychrometers, the potential gradient from the bulk soil to the root surface can be estimated.

Errors associated with the use of thermocouple psychrometers are caused by vapour pressure disequilibria; the resistance to vapour diffusion from the sample to the chamber atmosphere; thermal gradients and instability caused by fluctuations in environmental temperature; respiratory heat production from the sample; and by solar heating (Koide et al. 1989). Changes in sample water potential can also result from excision of the sample and growth during the equilibration period. This causes a reduction in water potential since the turgor

### BOX 14.2. Thermocouple Psychrometers

After placing a tissue sample in an enclosed psychrometer chamber held at a constant temperature, the water in the sample equilibrates with the chamber atmosphere. The value of the sample water potential can then be determined by measuring the equilibrium relative humidity ( $h$ ) of this atmosphere (Turner 1981):

$$\psi = \frac{RT \ln(h)}{V_w} \quad (14.7)$$

where  $R$  ( $\text{JK}^{-1} \text{mol}^{-1}$ ) is the universal gas constant,  $T$  is the temperature (K) and  $V_w$  ( $\text{m}^3 \text{mol}^{-1}$ ) is the partial molar volume of water. Since a water potential of  $-2.0$  MPa represents a wet bulb depression of about  $0.25^\circ\text{C}$ , facilities for accurate temperature control and measurement have to be available. Slow drifts in temperature can be tolerated, so long as the reference temperature is known at the time when the sample is measured. In practice, the sealed chambers are usually placed in an accurate water bath in a constant temperature room controlled  $1$  or  $2^\circ\text{C}$  below that of the water bath. There are two main techniques to measure  $h$  in the psychrometer chamber. In the first, the psychrometric mode, pure water is allowed to evaporate into the chamber atmosphere from the surface of a thermocouple junction. The resulting wet-bulb depression at the thermocouple junction is related to  $h$  by

$$h = \frac{e_w - a \gamma(T - T_w)}{e} \quad (14.8)$$

where  $a$  (Pa) is the atmospheric pressure,  $\gamma$  ( $\text{K}^{-1}$ ) is the psychrometric constant,  $T$  the dry-bulb temperature of the psychrometer,  $T_w$  is the wet-bulb temperature,  $e$  (Pa) is the saturation vapour pressure at  $T$ , and  $e_w$  (Pa) is the saturation vapour pressure at  $T_w$  (List 1968). A procedure based on the Peltier effect is commonly used for placement of the pure water on the thermocouple junction. A cooling current reduces the temperature of the junction below the dew point of the chamber atmosphere, so water is condensed on it (Spanner 1951).

With the second technique, called dewpoint hygrometry,  $h$  is determined by measuring inside the psychrometer chamber the dew-point temperature (Neumann and Thurtell 1972; Campbell et al. 1973). Dew-point hygrometers hold the thermocouple junction at the dewpoint temperature using a pulsed cooling current. An advantage of this technique is that the dew-point depression is larger than the wet-bulb depression; the thermocouple signal is therefore larger. In addition, the signal is stable, as there is no net movement of water at the dew point, so that vapour equilibrium in the chamber is not disturbed by measurement.

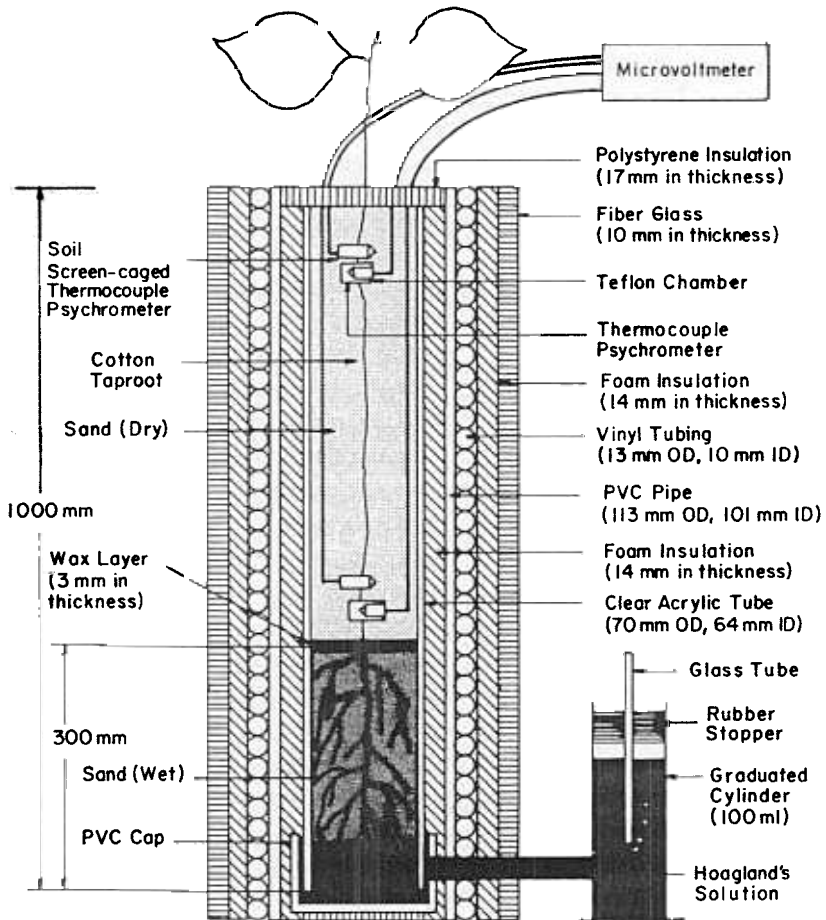
pressure will decline in the absence of a water supply. To minimise errors, psychrometers must be kept clean and the sample surface area per unit chamber volume should be maximised. Errors due to thermal gradients and instability can be reduced by assuring good contact between the sample and the chamber and by using chamber materials with a high thermal conductivity. Errors due to changes in water potential resulting from the excision and growth of the sample in the chamber can be reduced by working at low temperatures or with mature tissue.

Brown and Collins (1980) noted errors caused by temperature gradients after using different types of psychrometers to measure water potential, and they developed a new screen-caged psychrometer. Oosterhuis (1987) described a method to measure components of the root water potential in cotton plants grown in pots. He used screen-caged thermocouple psychrometers mounted in sample chambers. Water potential was determined after a 4-h equilibration time in a 25°C isothermal water bath. Osmotic potential was measured by freezing the sample-chamber in liquid nitrogen for 3 min, and then allowing it to thaw at room temperature for 30 min, before reequilibration in the water bath for 4 h. Pressure potential was obtained by subtraction.

Simonneau and Habib (1991) measured root water potential on small root samples from peach trees with psychrometers. For calibration, they used strips of filter paper soaked in standard sodium chloride solutions (Brown and Collins 1980); calibration curves were then obtained for temperatures between 20 and 35°C. Schildwacht (1988) avoided errors resulting from the nutrient solution adhering to roots by centrifuging the root sample in wire mesh on a plastic tube before transferring it to the psychrometer chamber. Bennet and Cortes (1985), among others, stated that the volume of sample has to be large enough to limit the effect of water adsorption by the chamber.

Yamauchi et al. (1995) used a modification of the method proposed by Fiscus (1972; Fig. 14.16) to measure xylem water potential in cotton taproots. They constructed teflon chambers so that screen-caged thermocouple psychrometers could be attached to the taproot at points 0.4 and 0.6 m apart. A screen-caged thermocouple psychrometer was buried near each root psychrometer to measure the soil water potential. Subsequent changes in root and soil water potential were measured. Temperature fluctuations were minimized by isolation of the system. Psychrometer readings were corrected for any observed temperature difference from the psychrometer calibration temperature at the time of the reading. Axial resistance was also measured by root psychrometers attached to roots growing in a device that ensured all the water flowed only through the taproot to which the psychrometer was attached.

*The Pressure-Chamber Technique (Sucker Shoots).* When leaves are not transpiring, the pressure chamber (Scholander et al. 1965) can be used to determine

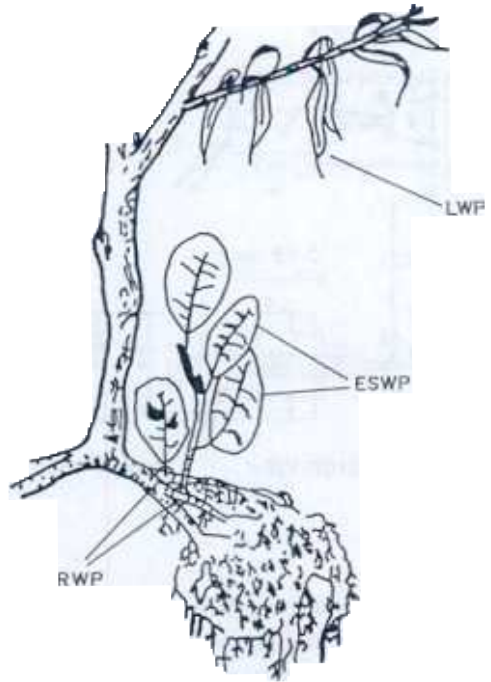


**Fig. 14.16.** Apparatus for measuring root axial resistance to water flow. (From Yamauchi et al. 1995)

root water potential. Simonneau and Habib (1991) developed the sucker shoot method. They used sucker shoots of young peach trees (Fig. 14.17) to estimate the water potential at the root-sucker branching point. They enclosed the sucker shoots in plastic bags and aluminium foil to prevent transpiration and measured the water potential of sucker shoots with a pressure chamber. As there is no flow in the suckers, the measured water potential should be equal to the water potential in the root xylem at the branching point.

Turner (1981, 1987) detailed the main precautions for measuring water potential with a pressure chamber. Thus, in rapidly transpiring leaves, measurements with the pressure chamber have to be taken as soon as possible after

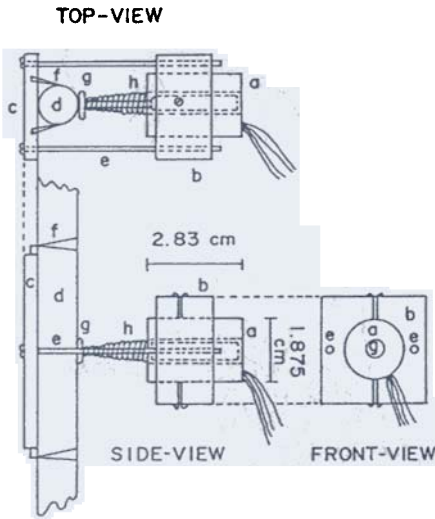
**Fig. 14.17.** Water potential in trees at different positions; *LWP* leaf water potential, *RWP* root water potential, *ESWP* enclosed sucker water potential. (From Simonneau and Habib 1991)



excision (not later than 10–30 s); the leaf petiole should not be recut; the length of the petiole left outside of the pressure vessel should be as short as possible; gas must not escape from the pressure vessel during the measurement process; pressurization in the vessel has to be slower than  $0.005 \text{ MPa s}^{-1}$ . The pressure chamber is robust and inexpensive. Time required for each measurement varies among species. The technique is, however, destructive and, in some species, the determination of the end point is complicated by resin exudation from ducts in the xylem or fluid exudation from the pith and cortex (Ritchie and Hinckley 1975).

### 14.6.2 Stem Diameter Changes

Water stress in a plant can lead to shrinking and swelling of the stem. Measurement of stem diameter variations and the analysis of the relation with the water status of the plant have been made in both herbaceous and woody plants (Molz and Klepper 1973, in cotton; So et al. 1979, in soybean; Brough et al. 1986, in apple trees; Castel 1994, in citrus trees). Molz and Kepler (1972) found that the relationship between stem diameter and leaf water potential had significant hysteresis, mainly due to the time lag in transmittance of water potential



**Fig. 14.18.** Design (top, side and front view) of linear variable difference transformer (LVDT) attached to a plant stem to record changes in stem diameter; *a* LVDT, *b* perspex holder, *c* perspex backing plate, *d* plant stem, *e* machine screw for adjusting mechanical zero, *f* rubber bands, *g* LVDT-core, *h* light metal spring. (From So et al. 1979)

changes from the xylem into the phloem and its surrounding cortical tissues. Using an analogy between a tensiometer-soil system, and a linear variable differential transformer (LVDT – other authors use the word ‘transducer’ instead of ‘transformer’) plant system, So et al. (1979) developed a dynamic method to correct for the time lag observed when using stem diameter fluctuations to predict changes in plant water potential. They used a LVDT system continuously to monitor changes in stem diameter. The holders were similar to that used by Klepper et al. (1971; Fig. 14.18). They reported small errors due to wind fluctuations. LVDT holders with a low expansion coefficient have also been described by Huguet (1985) and Li et al. (1989). The holder and sensor system can reach a precision of  $5\ \mu\text{m}$ . The system can be mounted on a stem or branch. Outputs can be electronically recorded and stored in a data logger.

Simonneau et al. (1993) used a LVDT system in roots of a 4-year-old peach tree growing in pots supplied with nutrient solution. The sensor and holder was of the type described by Huguet (1985). They observed that the diurnal evolution in diameter of the terminal shoot, main branch, trunk and main root followed a similar pattern, close to changes in climatic conditions.

## 14.7 Summary and Conclusions

The biophysical processes involved in the movement of water through soil to roots, hydraulic lift (and the reverse process), and root-shoot communication, provide many challenges for the researcher. A considerable variety of techniques have been developed for such studies, with different spatial and tempo-

ral resolution. Sophisticated technological methods for evaluation of water movement, and water distribution around and within roots, e.g. the NMR technique and the use of isotopes, are now at the disposal of researchers. Also, new electronic devices and innovative sensors are now capable of working in the soil, in the vicinity of roots, and are miniaturised and automated to provide the researcher with powerful tools for studying the biophysical functioning of the root system. Using such high-resolution tools, however, will not necessarily contribute to the understanding of water balances on ecologically relevant time scales, unless such study is accompanied by a better understanding of the range of internal regulation and feedback processes operating in the plant as a whole. The functionality of plant responses to temporary or local droughts depends on the chances it provides for long-term survival and reproduction, rather than in maximizing short-term productivity. The tools that the researcher chooses will thus continue to depend on the goals of the study, and the way detailed knowledge contributes to the overall objectives.

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