# 13

# Measuring Water Availability and Uptake in Ecosystem Studies

Robert B. Jackson, Laurel J. Anderson, and William T. Pockman

## Introduction

Terrestrial productivity depends strongly on the availability of water in the environment (Lieth 1972). Measuring the availability and movement of water among soil, plants, and the atmosphere requires methods from ecosystem studies, plant physiology, soil science, and biogeochemistry (Casper and Jackson 1997). Techniques for estimating the water status of soils have been reviewed recently (Rundel and Jarrell 1989; Boyer 1995) and those for measuring plant water status at cellular and whole-plant levels are thoroughly described in physiological ecology and plant physiology texts (e.g., Koide et al. 1989; Kramer and Boyer 1995). Rather than reviewing all methods for estimating plant and soil water, we emphasize techniques that are increasing in importance or changing rapidly for ecosystem studies. We include methods for determining the water content of soil, the availability of that water for plant uptake, and the transport of water through the plant (Fig. 13.1). Since many of these methods are also used in physiological ecology, our chapter is designed to bridge the gap between the scales of physiological and ecosystem ecology, as a foundation for other contributions in this book.

We begin by defining terms that describe water in the environment, including a brief discussion of water potential, the currency that allows the water status of soil, plants, and the atmosphere to be compared and the direction of flow to be predicted (Slatyer and Taylor 1960). We describe various techniques for measuring soil water in the field, emphasizing such recent innovations as time domain reflectometry and remotely sensed data. We also discuss methods for estimating the vegetative component of ecosystem water fluxes, including sap flow measurement and whole root/shoot hydraulic conductivity. Such techniques for estimating whole-plant water use are important for interpreting canopy and ecosystem water fluxes in eddy covariance and other net ecosystem approaches (see Chapter 11). We summarize the advantages and disadvantages of various techniques and recommend some future directions for research.

## Theory and Currencies for Measuring Water in the Environment

To understand differences among methods it is helpful first to describe common ways of estimating water availability. The three most common terms for expressing soil water attributes are mass water content, volumetric water content, and soil water potential. Soil water content calculated on a mass basis, $\theta_m$, is defined as

$$\theta_m = \frac{\text{soil water mass}}{\text{soil dry mass}} = \frac{(\text{wet soil mass} - \text{oven-dry soil mass})}{\text{oven-dry soil mass}} \tag{13.1}$$

$\theta_m$ is a proportion; the mass water percentage ($P_m$) is calculated by multiplying $\theta_m$ by 100%. The volumetric water content, $\theta_v$, is defined as

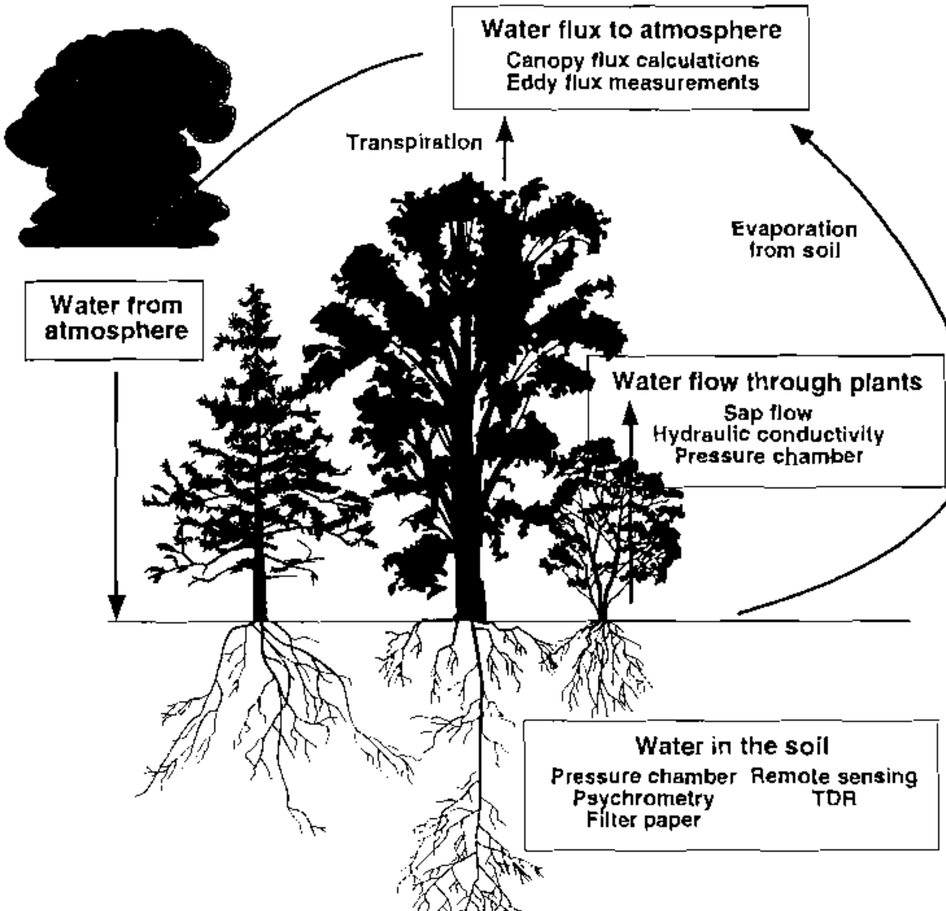


FIGURE 13.1. A simplified water cycle and some of the approaches used to measure water availability and movement in ecosystem studies.

$$\theta_v = \frac{\text{water volume}}{\text{bulk soil volume}} = \frac{\text{soil water mass}/\rho_w}{\text{bulk soil volume}} \qquad (13.2)$$

where $\rho_w$ is the density of water. $\theta_v$ is also a proportion and can be converted to the volmnetric water percentage ($P_v$) by multiplying by 100%. Further details can be found in Hanks and Ashcroft (1986) and Donahue et al. (1983).

Although $\theta_m$ and $\theta_v$ are important for understanding soil water properties, there is no consistent way to link either to the state of water in the atmosphere or in plants. To create a common currency for water in the environment, Slatyer and Taylor (1960) introduced water potential, $\psi$, based on the chemical potential of water:

$$\psi = \frac{(\mu_w - \mu_w^0)}{\bar{V}w} \qquad (13.3)$$

where $\mu_w$ is the chemical potential of water in the system under study, $\mu_w^0$ is the chemical potential of pure, free water at a reference height and temperature aud at atmospheric pressure (the reference state), and $\bar{V}_w$ is the partial molal volume of water (volume per mole of water) (Slatyer 1967). The upper term in the equation reflects the disequilibrium between the state of water in the experimental system and in its defined reference state. or, in thermodynamic terms, a measure of the work that may



be obtained from this dise
tial is most commonly ex
sure such as megapascals
$N m^{-2} = 1 (kg m s^{-2})$ m
tential of most systems is
low) because the referenc
= 0. When comparing t
such as the soil and an ad
from the system with a les
a more negative $\psi$.

Total water potential, $\psi$
into several components:

$$\psi_w = \psi_g + \psi_o$$

where $g$, $o$, $m$, and $p$ refer
motic, matric, and pressur
potential. The gravitational
work required to lift water
$= \rho_w gh$, where $g$ is the acc
and $h$ is the vertical change
$\psi_g$ changes approximately
difference in height, so rela
are required for $\psi_g$ to beco
motic component, $\psi_o$, is c
Hoff relation for dilute idea
where $T$ is absolute tempera
gas constant (8.314 $m^3$ Pa m
osmolality of the solution.
$\psi_m$ is a function of the su
among soil particles: $\psi_m$ =
is the surface tension of the
angle between liquid and so
the soil pore (Hanks and As
ree and Karamanos, 1980; S
sure, $\psi_p$, is generally taken a
the system is at atmospheric
$\psi_p$ is typically negative in th
in the symplast due to turgor
More detailed descriptions
the accompanying thermody
in Slatyer (1967), Nobel (1
Boyer (1995).

Conversions between $\psi$, $\theta$
based on correlations with s
tion of sand [0.05 to 2 mm],
and clay [<0.002 mm] part
soil). The amount of availab
ference between field capac
wilting percentage) is smal
greatest for a loam, and inte

be obtained from this disequilibrium. Water potential is most commonly expressed in units of pressure such as megapascals (MPa, and 1 Pa = 1 N m$^{-2}$ = 1 (kg m s$^{-2}$) m$^{-2}$). The total water potential of most systems is usually negative (see below) because the reference state is defined as $\psi = 0$. When comparing two experimental states, such as the soil and an adjacent root, water flows from the system with a less negative $\psi$ to that with a more negative $\psi$.

Total water potential, $\psi_w$, can be broken down into several components:

$$\psi_w = \psi_g + \psi_o + \psi_m + \psi_p \qquad (13.4)$$

where *g*, *o*, *m*, and *p* refer to the gravitational, osmotic, matric, and pressure components of water potential. The gravitational component reflects the work required to lift water and is described by $\psi_g = \rho_w gh$, where *g* is the acceleration due to gravity and *h* is the vertical change in height. The value of $\psi_g$ changes approximately 0.01 MPa per meter of difference in height, so relatively large values of *h* are required for $\psi_g$ to become significant. The osmotic component, $\psi_o$, is described by the Van't Hoff relation for dilute ideal solutions: $\psi_o = cRT$, where *T* is absolute temperature, *R* is the universal gas constant (8.314 m$^3$ Pa mol$^{-1}$ K$^{-1}$), and *c* is the osmolality of the solution. The matric component, $\psi_m$ is a function of the surface tension of water among soil particles: $\psi_m = (-2\gamma\cos\vartheta)/r$, where $\gamma$ is the surface tension of the liquid, $\vartheta$ is the contact angle between liquid and soil, and *r* is the radius of the soil pore (Hanks and Ashcroft 1986 but see Tyree and Karamanos, 1980; Sperry, 1997). The pressure, $\psi_p$, is generally taken as zero in the soil where the system is at atmospheric pressure. In the plant, $\psi_p$ is typically negative in the apoplast and positive in the symplast due to turgor generated by osmosis. More detailed descriptions of water potential and the accompanying thermodynamics are presented in Slatyer (1967), Nobel (1991), and Kramer and Boyer (1995).

Conversions between $\psi$, $\theta_m$, and $\theta_v$ are generally based on correlations with soil texture (the proportion of sand [0.05 to 2 mm], silt [0.002 to 0.05 mm] and clay [<0.002 mm] particles that make up the soil). The amount of available soil water (the difference between field capacity and the permanent wilting percentage) is smallest for a sandy soil, greatest for a loam, and intermediate for a clay soil (Fig. 13.2, bottom). Moisture tension release curves showing the relationship between $\psi$ and $\theta_m$ or $\theta_v$ are generated by measuring $\psi$ directly with thermocouple psychrometry (see below) and then destructively harvesting the soil to measure $\theta_m$ or $\theta_v$ (see Fig. 13.2, top).

## Methods for Estimating Plant and Soil Moisture

We describe four approaches for measuring water status in the environment. The first is a brief discussion of gravimetric techniques, included because most other methods are calibrated against gravimetric $\theta_m$ and $\theta_v$. The second approach is methods for measuring $\psi$ directly in the environment, including the plant pressure chamber, thermocouple psychrometry, and the filter-paper method. The third is time domain reflectometry, an increasingly important technique described in some detail. The fourth and final approach is microwave radiometry for remotely sensing soil moisture, a technique with considerable promise for ecosystem and landscape studies.

### Gravimetric Measurements of $\theta_m$ and $\theta_v$

The mass water content of soils ($\theta_m$) is determined simply and accurately using gravimetric techniques. Field samples are collected in soil cores sealed in plastic bags or in metal tins sealed with electrical tape. The wet samples are best weighed with a balance in the field, but transporting them to the laboratory in a cooler for weighing is also common. After drying the soil to constant weight at 105°C, the wet soil mass and oven-dry soil mass are used to calculate $\theta_m$ in Equation 13.1. The volumetric water content of soils ($\theta_v$) is similarly obtained by collecting soil samples of known volume and assuming a density of 1 g cm$^{-3}$ for water. Both $\theta_m$ and $\theta_v$ are easily converted if the soil's bulk density is known.

The advantages of the gravimetric method are its simplicity and low cost, requiring only a drying oven and a balance. This technique is used to calibrate other soil moisture instruments and can be applied under a range of soil depths and moisture conditions; it is one of the only techniques accurate

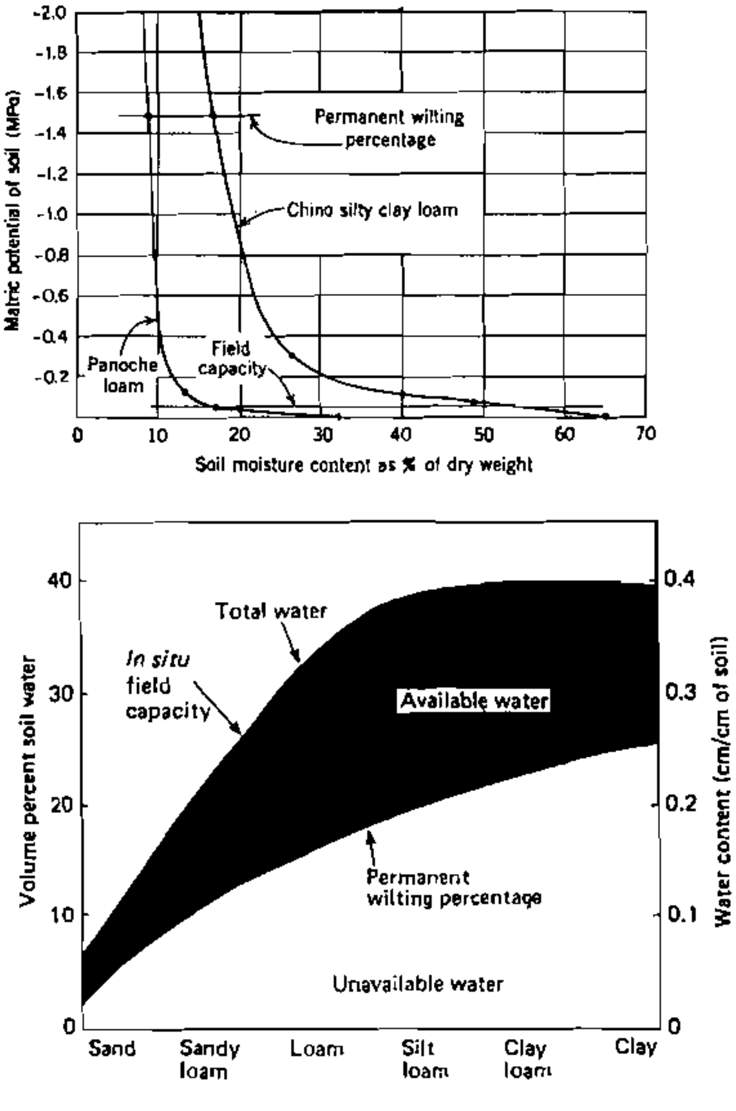


FIGURE 13.2. Top, Soil matric potential (MPa) for two sandy loam and clay loam soils as a function of soil water content. Bottom, Available and unavailable soil water across a range of soil textures (volume %, left axis; cm $H_2O$ $cm^{-1}$ soil, right axis). (From Kramer and Boyer [1995]. Used by permission of Academic Press.)

in very wet and very dry soils. Its major limitation is the requirement for destructive sampling. Other complications arise for stony soils, where $\theta_m$ and $\theta_v$ can be underestimated by including the mass and trivial water-holding capacity of stones. Stones >2 mm in diameter should be sieved from all samples and removed from calculations of $\theta_m$ and $\theta_v$ (Gardner 1986; Rowell 1994), though the volume of stones must be taken into account when ecosystem estimates of total water content are calculated. Sampling an accurate soil volume for $\theta_v$ can also be difficult in stony soils. Rowell (1994) discusses practical approaches for soil sampling and bulk density calculations in stony soils. Gardner (1986) gives a detailed treatment of the gravimetric method.

## Techniques for Direct Measurement of $\psi$

There are at least two advantages to measuring water potential directly in the soil–plant–atmosphere continuum. First, water status anywhere along the continuum may be directly compared. Second, soil water can be expressed in terms of the energy needed by a plant to remove a unit of water from the soil. The two most commonly used techniques



to measure $\psi$ in ecosystem s
ple psychrometry and the pl
both methods are widely us
viewed elsewhere (e.g., Rur
Boyer 1995). We provide an
proach and direct the reac
sources. We also outline a fil
is a low-cost alternative for
some conditions.

### *Thermocouple Psychromet*

Water potential (expressed in
be described based on the re
of water in the experimental s
that of free, pure water at an e
and pressure:

$$\psi = \frac{RT}{\bar{V}_w} \ln$$

where $R$ is the universal gas c
temperature in °K, $\bar{V}_w$ is the
of water, and $e$ and $e_0$ are th
water in the experimental sys
pure state, respectively. The a
vapor pressure of water in eq
situ volume of soil or quanti
vides a convenient method to
mocouple psychrometry.

Thermocouple psychrometr
beck effect: If a circuit consis
if the two metal junctions are
tures, then a current flows arc
direction dependent on the m
junction temperatures. A mic
used to measure the voltage in
sequently, the temperature dif
two junctions. The thermocou
measure relative humidity typi
chromel and constantan wires
(Brown 1970). The reference j
a series of gold or copper post
are connected. Ceramic or scree
the measurement junction to co
with $\psi$ in the surrounding soil

The most common method f
soil $\psi$ is Peltier thermocouple p
plying a current to the circuit
junction in equilibrium with t
cooled below the dew point of
causing droplets of water to fo

to measure $\psi$ in ecosystem studies are thermocouple psychrometry and the plant pressure chamber; both methods are widely used and have been reviewed elsewhere (e.g., Rundel and Jarrell 1989; Boyer 1995). We provide an overview of each approach and direct the reader to more detailed sources. We also outline a filter paper method that is a low-cost alternative for measuring soil $\psi$ in some conditions.

### *Thermocouple Psychrometry*

Water potential (expressed in units of pressure) may be described based on the relative vapor pressure of water in the experimental system compared with that of free, pure water at an equivalent temperature and pressure:

$$\psi = \frac{RT}{\bar{V}_w} \ln\left(\frac{e}{e_0}\right) \tag{13.5}$$

where $R$ is the universal gas constant, $T$ is absolute temperature in °K, $\bar{V}_w$ is the partial molal volume of water, and $e$ and $e_0$ are the vapor pressures of water in the experimental system and in the free, pure state, respectively. The ability to measure the vapor pressure of water in equilibrium with an in situ volume of soil or quantity of leaf tissue provides a convenient method to estimate $\psi$ in thermocouple psychrometry.

Thermocouple psychrometry is based on the Seebeck effect: If a circuit consists of two metals and if the two metal junctions are at different temperatures, then a current flows around the circuit in a direction dependent on the metals chosen and the junction temperatures. A microvoltmeter may be used to measure the voltage in the circuit and, consequently, the temperature difference between the two junctions. The thermocouple junction used to measure relative humidity typically consists of fine chromel and constantan wires <25 μm in diameter (Brown 1970). The reference junction is typically a series of gold or copper posts to which the wires are connected. Ceramic or screen-cage covers allow the measurement junction to come into equilibrium with $\psi$ in the surrounding soil solution.

The most common method for measuring in situ soil $\psi$ is Peltier thermocouple psychrometry. By applying a current to the circuit, the measurement junction in equilibrium with the soil solution is cooled below the dew point of the surrounding air, causing droplets of water to form on the junction. When the Peltier current is turned off, the water on the junction begins to evaporate at a rate dependent on $e$ in Equation 13.5. Isopiestic psychrometry ("iso" = equal, "piestic" = pressure) is a second type of psychrometry used to measure leaf $\psi$ and ex situ soil $\psi$ (Boyer and Knipling 1965). Drops of a series of solutions of known $\psi$, created using the Van't Hoff relationship discussed earlier, are placed on looped thermocouple wire and allowed to come to equilibrium with a leaf or soil sample. The solution that provides the same output as a dry thermocouple, neither warming nor cooling the junction, yields the sample $\psi$. Although no calibration is required and the technique is very accurate ($\pm 0.01$ MPa) (Boyer 1995), it is also time consuming and can not be automated or used for in situ soil analysis.

Thermocouple psychrometry is a powerful, accurate technique for estimating $\psi$ in a small soil volume, but it has a number of difficulties. Except for the isopiestic technique, each psychrometer must be calibrated individually, making the method laborious and expensive. Contaminants, particularly salts, present on the measurement junction can alter the rate of evaporation and lead to inaccurate estimates of $e$ (Rundel and Jarrell 1989). Because of problems with thermal gradients (Wiebe et al. 1977), in situ thermocouple psychrometers are usually positioned horizontally (making sure that the wire leading to them cannot act as a conduit for flowing water) and are generally only used below 30-cm soil depth. Thermocouple psychrometers are also not especially accurate in very wet soils. Boyer (1995) provides a much more detailed description of the theory of thermocouple psychrometry and its use in measuring $\psi$ in plant tissue; Rundel and Jarrell (1989) provide an overview of thermocouple psychrometry for soil measurements. Commercial manufacturers include JRD Merrill Specialty Equipment (Logan, UT), Wescor, Inc. (Logan, UT), and Isopiestics Co. (Lewes, DE).

### *Plant Pressure Chamber*

A second technique for measuring $\psi$ in the environment is the plant pressure chamber. First used in the 1800s (Dixon 1914), the modern version dates to Scholander et al. (1965). A stem, branch, or leaf is cut from a plant and placed upside-down in an air-tight chamber with the point of excision protruding outside the chamber through a rubber stopper. Pressurized gas (usually $N_2$) is gradually applied to the chamber until the pressure is sufficient to force water back to the cut surface. The pressure at which this occurs is an estimate of $\psi$ for the tissue being measured. Assuming a rehydrating plant comes to equilibrium with the soil overnight, predawn measurements of $\psi$ also provide an indication of the wettest soil $\psi$ in which the plant's roots are actively taking up water. Midday measurements of $\psi$ provide an indication of the water stress a plant experiences (Jackson et al. 1994).

The plant pressure chamber provides a simple, inexpensive method for estimating plant $\psi$ and soil $\psi$ within the active rooting zone of the plant. Measurements should be obtained within minutes after cutting the plant and the tissue should be placed in a sealed plastic bag to minimize evaporation until measurement. The point of excision should not be re-cut at any time during the procedure and it should protrude minimally outside the chamber. In some cases, it may be important to standardize the age/position of selected leaves where large phenological or physiological gradients occur. Some disadvantages of the pressure chamber are that it is labor intensive and difficult to automate. Because compressed gas is used, safety glasses should be worn and the plant sample should be viewed from the side rather than from above. For a more comprehensive treatment of the theory and assumptions behind the pressure chamber see Koide et al. (1989) and Boyer (1995).

### *Filter Paper Method*

The filter paper method is a simple, low-cost alternative for determining soil $\psi$. The technique was developed by hydrologists and soil scientists, and its use has been largely restricted to these fields (Gardner 1937; Fawcett and Collis-George 1967; Hamblin 1981; Greacen et al. 1989). The method uses a known relationship between $\psi_m$ and the gravimetric water content of a homogeneous porous material such as filter paper to estimate soil $\psi$ (Gardner 1937). Filter paper disks are placed in contact with field soil, extracted core samples, or loose soil samples and left undisturbed until equilibrium is established between the paper and soil. The filter paper disk is either sandwiched between two intact core sections bound together or placed within loose soil samples lightly tamped down to establish soil–paper contact. While field equilibration must occur under prevailing conditions, laboratory samples are placed in a sealed container in an isothermal environment and left for periods between 1 hour (saturated soils) to 6 days (dry soils) to establish equilibrium between soil and paper.

After equilibration, the filter paper is removed, weighed immediately, and the gravimetric water content calculated using the oven-dry weight. Soil water potential is determined either from published calibrations for the selected filter paper or from local calibrations. While local calibration is required at high soil water potentials (soil $\psi > -0.1$ MPa), reliable measurements are possible using published data for the drier conditions often observed in the field (e.g., Whatman's No. 42 paper, Greacen et al. 1986; Greacen et al. 1989). The major sources of error are poor contact between paper and soil, temperature gradients/fluctuations during equilibration, and insufficient time for equilibration (e.g., Campbell and Gee 1986). When these errors are avoided, the approach may offer a low-cost alternative for estimating soil $\Psi$ over a wide range of conditions.

## Time Domain Reflectometry

Time domain reflectometry (TDR) measures soil $\theta_v$ and is based on the relationship between the apparent dielectric constant ($K_a$) of a soil and the soil's free water content (Davis and Chudobiak 1975). The unitless dielectric constant, also known as relative permittivity, is the ratio of electric field strength in a vacuum to that in a polarized substance (the dielectric)—the more polarized the dielectric, the greater the reduction in field strength (Parker 1983). As the dielectric constant for water (80) is much greater than that for air (1) or dry soil (3 to 7), the dielectric value for field soil is determined primarily by soil moisture (Cassel et al. 1994). Dalton and van Genuchten (1986) discuss the physical and mathematical principles of dielectric constants in detail.

Time domain reflectometry estimates $K_a$ by measuring the time needed for an electromagnetic pulse emitted by a TDR instrument to travel along a probe in soil and reflect back to the soil surface from the probe end (Fig. 13.3). $K_a$ is related to the propagation velocity ($V$) of an electromagnetic wave:



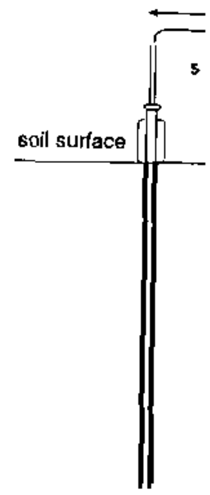


FIGURE 13.3. The basic compo
panel shows an example of a w
of attenuation. Waveforms can
conditions.

$V = c/(K$

where $c$ is the speed of lig
pressed as $V = 2l/t$ where
the pulse, and $l$ is the probe
related to the length and trav

$K_a = (ct/$

Once $K_a$ is estimated, $\theta_v$ ave
length is calculated from a ca
et al. 1994). Early research su
acteristics other than water
density, mineral and organic
ture, did not influence $K_a$ sig
1980, 1982). Consequently,
be converted to $\theta_v$ using a
(Topp et al. 1980):

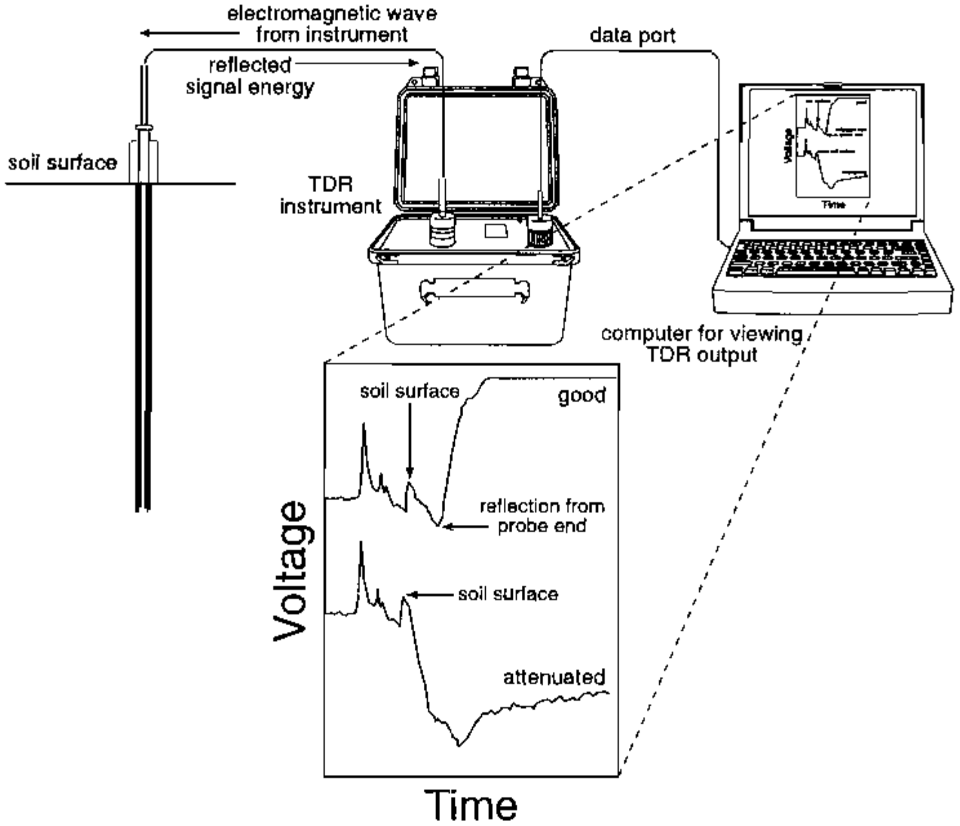


FIGURE 13.3. The basic components of a TDR system (not to scale) and two typical waveform outputs. The graph panel shows an example of a waveform associated with a good measurement of soil moisture and one with problems of attenuation. Waveforms can have different shapes than those shown here depending on the instrument and soil conditions.

$$V = c/(K_a)^{1/2} \quad (13.6)$$

where $c$ is the speed of light. $V$ can also be expressed as $V = 2l/t$ where $t$ is the travel time for the pulse, and $l$ is the probe length. $K_a$ is therefore related to the length and travel time:

$$K_a = (ct/2l)^2 \quad (13.7)$$

Once $K_a$ is estimated, $\theta_v$ averaged over the probe length is calculated from a calibration curve (Cassel et al. 1994). Early research suggested that soil characteristics other than water content, such as bulk density, mineral and organic content, and temperature, did not influence $K_a$ significantly (Topp et al. 1980, 1982). Consequently, $K_a$ for all soils could be converted to $\theta_v$ using a universal calibration (Topp et al. 1980):

$$\theta_v = -5.3 \times 10^{-2} + (2.92 \times 10^{-2} * K_a) - (5.5 \times 10^{-4} * K_a^2) + (4.3 \times 10^{-6} * K_a^3) \quad (13.8)$$

Further work revealed that this relationship, while robust for many soils, is not sufficiently accurate for all types, particularly finely textured or highly organic soils (Topp et al. 1980, Roth et al. 1992). Some workers have found that variation in bulk density, the fraction of bound water, and temperature affect TDR (Dasberg and Hopmans 1992; Dirksen and Dasberg 1993; Pepin et al. 1995). Other "universal" equations, including linear relationships between $K_a$ and $\theta_v$ (e.g., Herkelrath et al. 1991, Whalley 1993), and dielectric mixing models that calculate $\theta_v$ using the volume fractions and dielectric constants of soil, air, and water (e.g., Roth et al. 1990, Dirksen and Dasberg 1993) have been proposed. Relationships for specific soil types such as organics, minerals, and peats have also been suggested (e.g., Roth et al. 1992). Depending on the goals and soils in each study, these published curves may be appropriate (Zegelin et al. 1992). However, local calibration curves significantly improve estimates of soil moisture (e.g., Dasberg and Hopmans 1992; Gray and Spies 1995). Despite claims of TDR manufacturers whose instruments output $\theta_v$ using universal curves, a calibration for each soil should be generated by the user. Calibrations are done using packed soil columns or field soil cores.

Raw TDR output is a wave trace showing voltage changes in the electromagnetic wave as it reflects back to the instrument (see Fig. 13.3). These voltage changes correspond to variations in impedance, defined as the total opposition to current flow in an electrical circuit (Parker 1983). Mismatches in impedance between different materials along the TDR circuit path cause part of the signal energy to reflect back. Strong reflections occur at the soil surface and probe end, showing as peaks on the wave trace (Fellner-Feldegg 1969, Cassel et al. 1994). The distance from the soil surface peak to the final upward inflection represents the travel time of the electromagnetic wave $t$, used to calculate $K_a$. Early TDR required manual measurement of this distance on the wave trace (e.g., Topp et al. 1982), but many instruments now do this automatically using computer algorithms that search for characteristic changes in slope (e.g., Baker and Allmaras 1990).

Wave traces can vary substantially from the shape in Figure 13.3, making identification of the soil surface or probe end difficult. In highly conductive media, such as clays or saline soils, the electromagnetic pulse dissipates such that the final reflection is weak, called "signal attenuation" (see Fig. 13.3). While there are instrument and probe modifications that can address this problem, TDR is limited in very wet, conductive soils (Zegelin et al. 1992).

A wide variety of TDR probes (or wave guides) can be purchased or built. The most basic design includes a connection to conduct current from the coaxial cable into a set of stainless steel rods in the soil and a mechanism for holding the rods parallel. Probes generally range from 10 cm to 2 m in length and may be inserted into the soil at any angle (Topp and Davis 1985). They can be installed permanently or moved from site to site. Hook et al. (1992) created probes with diodes in the handles that switch from open to short circuits during a measurement. A shorted diode produces a strong reflection, but allows signal energy to pass into the soil when open. This identifies the soil surface without reducing signal strength. These workers also used diodes to divide long probes into segments, allowing measurements of moisture at different depths from one probe. For simple probe designs see Topp et al. (1984), Zegelin et al. (1989), and Heimovaara (1993).

Advantages of TDR include minimal soil disturbance and rapid, reliable measurements. Some probes can be built relatively cheaply. While TDR measures only the soil adjacent to the probe rods (Baker and Lascano 1989), $\theta_v$ is averaged over the probe length, providing an integrated measurement. Multidiode probes allow simultaneous sampling of moisture in different soil layers, which could give important insights into patterns of water flow and storage in ecosystems. Multiple probes can be connected to a data logger to allow simultaneous, regular readings at many sites (Baker and Allmaras 1990, Herkelrath et al. 1991).

Limitations of TDR include probe installation problems in stony or shallow soils. Signal attenuation in conductive soils may limit the probe lengths that can be used. Air pockets may form next to probes in soils that crack as they dry, causing measurement errors (Hokett et al. 1992). Sharply layered soils or large changes in the water profile with depth can create unexpected reflections in the wave trace, complicating interpretation (Nadler et al. 1991). Due to the variability of waveforms that can be generated in the field, TDR requires training and practice to use with confidence. Companies that sell TDR instrumentation include Environmental Sensors, Inc. (San Diego, CA), Soil Moisture Equipment Corporation (Goleta, CA), and Tektronix, Inc. (Redmond, OR). Detailed reviews of TDR are given in Zegelin et al. (1992) and Cassel et al. (1994).

## Remotely Sensed Data Using Microwave Radiometers

Remotely sensed data for estimating soil moisture have been used for several decades (e.g., Schmugge et al. 1974). Existing methods can be separated into two broad categories, passive and active techniques. Passive techniques measure the natural microwave radiation emitted by the ground surface (plants and the soil), while active techniques generate a pulse of microwave radiation and measure the backscatter to the sensor. The wavelengths most commonly used to minimize interference from the atmosphere are those greater than 5 cm (or a frequency of <6 GHz, where $\nu = c/\lambda$ and $\nu$ is frequency, $\lambda$ is wavelength, and $c$ is the speed of light). Data are generally taken with truck-mounted equipment or from airplanes, but satellite measurements are becoming increasingly common (e.g., Owe et al. 1988).

Soil brightness temperature ($T_B$) as measured by a radiometer is related to soil temperature ($T_{soil}$) by the following relationship for a bare surface and isothermal soil (the Rayleigh-Jeans approximation to Planck's law):

$$T_B = (1 - r)T_{soil} = \varepsilon T_{soil} \qquad (13.9)$$

where $r$ is reflectivity, $\varepsilon$ is emmisivity, and $r = 1 - \varepsilon$. The emissivity is dependent on surface roughness and the dielectric constant of the soil (Engman and Chauhan 1995). The ability to assess soil moisture remotely is therefore based on the same dielectric effect used by time domain reflectometers—an increase in the soil dielectric constant $K$ from <5 in dry soils to >25 in wet soils. Emissivity varies as a nonlinear function of $K$ from approximately 0.95 in dry soils to 0.6 in wet soils, for a decrease in soil brightness temperature of more than 100°K (Schmugge 1990). Such large changes in $T_B$ are easily measurable with microwave radiometers.

Several factors must be taken into account for interpreting remotely sensed soil moisture values. Surface roughness tends to increase emissivity and decrease reflectivity because of the increased surface area. The following equation was developed by Choudury et al. (1979) to incorporate roughness into the estimate of emissivity:

$$\varepsilon = R_0(1 - e^{-h}) \qquad (13.10)$$

where $h$ is an empirical roughness parameter and $R_0$ is the smooth surface reflectivity (<0.1 for dry soils and up to 0.4 for wet). A rough surface (e.g., root mean square height variations of 5 cm) can result in a $T_B$ that differs by 50°K compared with the same soil with a smooth surface (Choudury et al. 1979). A second complication arises from vegetation semitransparent to microwave radiation (Jackson and O'Neill 1987). With sufficient leaf area, the brightness temperature reflects the vegetation rather than the soil temperature. Corrections based on the water content of the vegetation are possible but complicated (Schmugge 1990). Additional factors for consideration are soil texture and the angle of measurement (if different from perpendicular).

The use of remotely sensed data is certain to increase. Overall, remote sensing of the moisture in the top 5 cm of the soil has great potential in deserts, crop systems, and some grasslands, and a number of field campaigns have shown good correlations between field and remotely sensed data across broad spatial scales (e.g., Lin et al. 1994). However, there are three primary disadvantages for microwave approaches in ecosystem research. The first is that current technologies are difficult to use in systems with high leaf area indices, such as forests, because the vegetation attenuates the microwave signal from the soil (Engman and Chauhan 1995). A dense thatch or dead vegetation layer causes similar problems (Schmugge et al. 1988). The second disadvantage is that microwave approaches are unlikely to provide information on soil layers deeper than 10 cm in the near future. The final disadvantage is that the approach is expensive, requiring airplane flights, truck-or tower-mounted equipment, or satellite imagery. Despite these problems, no existing technique has such potential for landscape and regional integration of soil moisture availability. Combining its use with ground-based methods and modeling provides a powerful approach for the coming century.

## Estimating the Vegetative Component of Ecosystem Water Fluxes

The above methods are used to determine soil water potential, water content, and the availability of water to plants. Measuring the amount of water transferred to the atmosphere by plants is also important for many ecosystem studies (e.g., Jackson et al. 1998). Methods for determining total canopy or ecosystem water fluxes are described in Chapters

11 and 12. In all but the simplest systems, these methods can obscure the contributions of different vegetative constituents to total water fluxes. To understand the contributions of individual species and to predict ehanges in ecosystem water fluxes associated with vegetation ehange, ecosystem-level measurements must be combined with measurements of individuals from the dominant species or functional types.

Numerous studies have addressed leaf-level gas exchange and plant water use, but sealing sueh measurements to provide reliable estimates of stand or eeosystem fluxes is difficult (Jarvis 1993; Ansley et al. 1994; Verhoef 1997). In this section, we address two approaches with considerable promise for ecosystem studies: sap flow methods and measurements of whole plant hydraulic conductance. Sap flow methods are used for measuring water fluxes through stems of a variety of species. When combined with canopy or eddy correlation measurements, these methods help partition the contribution of species and plant functional groups to ecosystem water fluxes. They ean also be coupled with stable isotope measurements (see Chapter 12) to estimate the volume of water transpired from different soil sourees. The second useful approach is measuring the hydraulic conductance of entire root and shoot systems. As context for ecosystem studies, hydraulic measurements provide a mechanistie perspective on the contribution of different species and functional types.

## Sap Flow Measurements

Sap flow techniques estimate the axial flow rate of water through root or stem xylem by applying heat and measuring the temperature of surrounding tissues. The methods used can be divided into three general groups: heat pulse, heat balance, and thermal dissipation techniques. Taken together, these methods permit measurement of sap flow through the roots and stems of herbs, grasses, crops, shrubs, and trees spanning a wide range of basal diameters (Lott et al. 1996; Baker and van Bavel 1987; Allen and Grime 1995; Kostner et al. 1992; Barrett et al. 1995). Several recent reviews cover various aspeets of these methods (Pearcy et al. 1989; Swanson 1994; Edwards et al. 1996; Smith and Allen 1996).

### *Heat Pulse Method*

The heat pulse method measures sap velocity through the xylem of woody stems. Two temperature probes are inserted in a stem above and below a heating element that is also inserted in the xylem of a woody stem. The lower temperature probe is positioned closer to the heater than the upper probe. Following the application of a 1- to 2-sec heat pulse, the temperature of both probes is measured continuously to determine the time ($t_e$) required for the two probes to reaeh the same temperature. The heat pulse velocity ($v_h$) is calculated as:

$$v_h = \frac{X_l - X_u}{2t_e} \qquad (13.11)$$

where $X_l$ and $X_u$ are the distances between the heater and the lower and upper temperature sensors, respectively. Measured values of $v_h$ are converted to sap velocity by accounting for sensor materials, wound effects, installation geometry, and the loss of heat to the stem during the measurement (e.g., Marshall 1958; Swanson and Whitfield 1981). Measuring the sap flow of entire stems often requires probes inserted to different depths and at different points around the stem to account for stem variation in sap flow. Integration of the resulting sap flow profile yields whole-plant water use (Green and Clothier 1988).

### *Heat Balance Methods*

As the name suggests, heat balance methods apply heat ($P$) to the plant and measure the contribution of sap flow to the distribution of that heat. The amount applied is calculated from the heater resistance and the voltage. For the stem heat balance method, generally used with stems <120 mm in diameter, a beater is wrapped around the circumference of the stem and surrounded by insulation. Thermocouples are positioned to measure the radial and vertical temperature differences used to solve the heat balance (Sakuratani 1981; Baker and van Bavel 1987). For larger-diameter stems, a trunk sector beat balance method applies heat internally to a stem sector using embedded eleetrodes and thermocouples to measure vertical and lateral temperature differences (Cermak et al. 1984). The heat balance for both approacbes is given by:



$$P = q_v + q$$

where $q_v$, $q_r$, $q_l$, and $q_f$ are
lateral heat loss by condu
ferred by convection in the
The lateral heat loss term
the trunk sector heat bala
heat balance method applie
stem circumference. In bo
lated by subtracting $q_v$, $q_r$
is then calculated using $q_f$
water.

To determine $q_r$ accurate
proaches require measure
no flow for estimating the
insulation around the heate
1987).

### *Thermal Dissipation*

The thermal dissipation m
tion of two probes in a wo
rectly above the other (Gr
upper probe contains a the
a heater powered by cons
lower probe contains only
temperature difference bet
function of the sap flow ra
the maximum difference occ
no flow ($\Delta T_0$) and the diffe
flow carries more heat a
(heated) probe. Addition of
helps remove the confound
occurring vertical and latera
in the stem (Goulden and F
to an empirical calibration
(Granier 1985), volumetric
given by:

$$u_v = 0.000119\left(\frac{\Delta T_0}{}\right.$$

Although this calibration ma
species (Granier et al. 1990
tion may be required (Smith

### *Advantages and Disadvan*

The primary advantage of
they provide continuous mea
in individuals over a wide ra
functional types. It is thus po

$$P = q_v + q_r + q_l + q_f \quad (13.12)$$

where $q_v$, $q_r$, $q_l$, and $q_f$ are the vertical, radial, and lateral heat loss by conduction and the heat transferred by convection in the xylem sap, respectively. The lateral heat loss term $q_l$ is only applicable in the trunk sector heat balance method since stem heat balance method applies heat evenly around the stem circumference. In both methods, $q_f$ is calculated by subtracting $q_v$, $q_r$, and $q_l$ from $P$. Sap flow is then calculated using $q_f$ and the specific heat of water.

To determine $q_r$ accurately, both heat balance approaches require measurements during periods of no flow for estimating the thermal conductance of insulation around the heater (Baker and van Bavel 1987).

### *Thermal Dissipation*

The thermal dissipation method uses the installation of two probes in a woody stem, one probe directly above the other (Granier 1985, 1987). The upper probe contains a thermocouple junction and a heater powered by constant current, while the lower probe contains only a thermocouple. The temperature difference between probes ($\Delta T$) is a function of the sap flow rate past the installation; the maximum difference occurs under conditions of no flow ($\Delta T_0$) and the difference decreases as sap flow carries more heat away from the upper (heated) probe. Addition of a thermocouple array helps remove the confounding effects of naturally occurring vertical and lateral temperature gradients in the stem (Goulden and Field 1994). According to an empirical calibration for three tree species (Granier 1985), volumetric sap flux density ($u_v$) is given by:

$$u_v = 0.000119\left(\frac{\Delta T_0 - \Delta T}{\Delta T}\right)^{1.231} \quad (13.13)$$

Although this calibration may apply to other woody species (Granier et al. 1990), independent calibration may be required (Smith and Allen 1996).

### *Advantages and Disadvantages*

The primary advantage of these methods is that they provide continuous measurements of sap flow in individuals over a wide range of plant sizes and functional types. It is thus possible to partition total plant water fluxes into the contributions of different species, at least in relatively simple systems. Simultaneous measurements at ecosystem and whole-plant scales can be combined in this way to address questions about the role of different species, life forms, or functional groups for ecosystem functioning (e.g., Ham et al. 1990; Kostner et al. 1992).

Sap flow methods are not without difficulties. Calibration is one important problem. The stem heat balance, trunk sector heat balance, and thermal dissipation methods depend on reliable measurements under no-flow conditions. If these conditions cannot be met, the accuracy of the methods is questionable (Smith and Allen 1996). A recently developed heat balance gauge may avoid this requirement through the incorporation of two heating elements (Peressotti and Ham 1996). In some installations, field values obtained using these methods can be checked by comparison with measurements of hydraulic conductance through the portion of the measured tissue containing the sap flow installation (e.g., Goulden and Field 1994).

Several other potential problems should also be considered. Heterogeneity in flow may confound whole-plant scaling when measuring flow in only a portion of the stem (Edwards et al. 1996). The accuracy of sap flow measurements may be compromised by tissue damage caused by prolonged heating effects (Smith and Allen 1996), toxic effects of silicone compounds used to improve thermal contact between heater and stem (Wiltshire et al. 1995), or wound responses and physical damage where portions of the apparatus are installed (Barrett et al. 1995). Finally, an error due to heat storage in the stem has been detected in some applications (Grime et al. 1995).

## Whole Root/Shoot Hydraulic Conductance

Measurement of whole-plant hydraulic conductance is useful for mechanistic studies of ecosystem water fluxes and in determining the relative importance of individual plant species to total plant transpiration. Hydraulic conductance is defined as the mass flow rate for a given pressure difference (e.g., kg sec$^{-1}$ MPa$^{-1}$) and may increase with the production of new xylem or decrease with cavitation caused by freezing or water stress. Seasonal and interspecific changes in hydraulic conductance can have important consequences for plant gas exchange, which may be extended to understanding changes in ecosystem water fluxes.

Whole plant hydraulic conductance can be calculated using the pressure chamber and stem flow methods already described (Cohen et al. 1983; Tyree et al. 1994). The pressure difference across the plant can be taken as the difference between soil $\psi$ estimated by predawn leaf water potential ($\psi_l$) and midday $\psi_l$. The pressure difference can be further divided into above- and belowground components by adding measurements of midday stem xylem pressure near the root crown. Pressure chamber measurements of a leaf or small branch attached to the main stem at ground level, and wrapped in advance with aluminum foil to eliminate flow, are used to measure stem xylem pressure. The hydraulic conductance of the whole plant, stem, or root system can be calculated by dividing the transpiration rate measured with sap flow methods by the appropriate pressure difference. These calculations assume the contribution of capacitance to the transpiration stream is negligible and that predawn $\psi_l$ accurately reflects the $\psi_s$ where water uptake occurs (Tyree et al. 1994).

Direct measurements of hydraulic conductance are also made by applying a pressure difference across the roots or shoots and measuring the flow through the system (Sperry and Pockman 1993; Kolb et al. 1996). Roots of potted plants can be measured by enclosing the soil and root system in a gas-tight container and measuring flow when the chamber pressure is increased (Saliendra and Meinzer 1992) or decreased by applying partial vacuum (Kolb et al. 1996). Until recently, field measurements have been more difficult because of the difficulty of generating a pressure difference without disturbing the root–soil interaction. The high pressure flowmeter (HPFM) (Tyree et al. 1993) permits the simultaneous application of pressure and measurement of flow into the cut stem or detopped root system. As originally developed, the HPFM method required the application of constant pressure over a period of hours until steady state flow was observed. During this extended measurement of roots, the accumulation of solutes caused by reverse flow through the roots changed the measured hydraulic conductance (Tyree et al. 1994). To minimize the effects of solute accumulation, a modified method measures flow as the applied pressure is increased at a constant rate (3 to 7 kPa sec$^{-1}$, Tyree et al. 1995). Using this approach, the hydraulic conductance of the measured tissue is calculated as the slope of the relationship between flow rate and applied pressure, and evidence suggests that this technique provides improved measurement of hydraulic conductance (Tsuda and Tyree 1997).

The development of the HPFM provides one method for measuring stem and root hydraulic conductances. Besides application to whole-plant physiology (Tyree et al. 1995), the availability of a technique for measurement of water transport through entire, intact root systems may prove useful in future ecosystem studies. In particular, measurements of whole-root systems and shallow and deep roots of the same plants may improve our understanding of how the characteristics of plant water transport influence ecosystem water fluxes.

## Summary

Ecosystem studies are becoming increasingly important for monitoring and solving today's problems, such as those associated with global environmental change. This chapter is meant to be integrated with Chapters 11 and 12 for designing a well-conceived study of ecosystem water fluxes. Our chapter describes the necessary background and accompanying field measurements that may be taken for interpreting canopy fluxes and eddy covariance data. Promising methods include time domain reflectometry, remotely sensed data, and stem flow measurements. By combining such measurements with those discussed in the other chapters of this section, net ecosystem water fluxes across the landscape can be determined meaningfully and interpreted mechanistically.

*Acknowledgments* This research was supported by grants from the National Science Foundation (DEB 97-333333), NIGEC DOE, and the Andrew W. Mellon Foundation, and a USDA postdoctoral fellowship (#98-35100-6079) to W.T.P. M. Shawn Brumbaugh, J.R. Ehleringer, W.A. Hoffmann, and E.G. Jobbágy provided helpful suggestions on the manuscript.



## References

Allen, S.J.; Grime, V.L. Mea
from savannah shrubs usin
For. Meteorol. 75:23–41; 1
Ansley, R.J.; Dugas, W.A.; H
Stem flow and porometer m
tion from honey mesquite
Exp. Bot. 45:847–856; 199
Baker, J.M.; Allmaras, R.R. S
multiplexing soil moistur
domain reflectometry. Soil
1990.
Baker, J.M.; Lascano, R.J. The
domain reflectometry. Soil
Baker, J.M.; van Bavel, C.H.
flow of water in the stems o
Cell Environ. 10:777–782;
Barrett, D.J.; Hatton, T.J.; Ash
tion of the heat pulse veloci
ment of sap flow in rainfore
cies of south-eastern Austr
18:463–469; 1995.
Boyer, J.S. *Measuring the Wa*
*Soils*. San Diego, CA: Acad
Boyer, J.S.; Knipling, E.B. Iso
suring leaf water potentials
chrometer. Proc. Nat. Acad.
1965.
Brown, R.W. *Measurement of P*
*mocouple Psychrometers: C*
*tions*. United States Dep
(USDA), Forest Service I
Washington, D.C.: U.S. Gov
1970.
Campbell, G.; Gee, G. Water
methods. In: Klute, A., ed. *M*
*Part 1. Physical and Minera*
omy Monograph 9. Madison
of Agronomy and Soil Scie
1986:619–633.
Casper, B.B.; Jackson, R.B. E
ground. Annu. Rev. Ecol. Sy
Cassel, D.K.; Kachanoski, R.G
considerations for using a TD
nol. 7:113–126; 1994.
Cermak, J.; Jenik, J.; Kucera, J
flow in a crack willow tree S
diurnal changes of environm
151; 1984.
Choudury, B.J.; Schmugge, T.
R.W. Effect of surface roug
emission from soils. J. Geop
1979.

## References


Allen, S.J.; Grime, V.L. Measurements of transpiration from savannah shrubs using sap flow gauges. Agric. For. Meteorol. 75:23–41; 1995.

Ansley, R.J.; Dugas, W.A.; Heuer, M.L.; Trevino, B.A. Stem flow and porometer measurements of transpiration from honey mesquite (*Prosopis glandulosa*). J. Exp. Bot. 45:847–856; 1994.

Baker, J.M.; Allmaras, R.R. System for automating and multiplexing soil moisture measurement by time-domain reflectometry. Soil Sci. Soc. Am. J. 54:1–6; 1990.

Baker, J.M.; Lascano, R.J. The spatial sensitivity of time-domain reflectometry. Soil Sci. 147:378–384; 1989.

Baker, J.M.; van Bavel, C.H.M. Measurement of mass flow of water in the stems of herbaeeous plants. Plant Cell Environ. 10:777–782; 1987.

Barrett, D.J.; Hatton, T.J.; Ash, J.E.; Ball, M.C. Evaluation of the heat pulse velocity technique for measurement of sap flow in rainforest and eucalypt forest species of south-eastern Australia. Plant Cell Environ. 18:463–469; 1995.

Boyer, J.S. *Measuring the Water Status of Plants and Soils*. San Diego, CA: Academic; 1995.

Boyer, J.S.; Knipling, E.B. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. Proc. Nat. Acad. Sci. USA 54:1044–1051; 1965.

Brown, R.W. *Measurement of Water Potential with Thermocouple Psychrometers: Construction and Applications*. United States Department of Agriculture (USDA), Forest Service Research Paper INT-80. Washington, D.C.: U.S. Government Printing Office; 1970.

Campbell, G.; Gee, G. Water potential: Miscellaneous methods. In: Klute, A., ed. *Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods*. Agronomy Monograph 9. Madison, WI: American Society of Agronomy and Soil Science Society of America; 1986:619–633.

Casper, B.B.; Jackson, R.B. Plant competition underground. Annu. Rev. Ecol. Syst. 28:545–570; 1997.

Cassel, D.K.; Kachanoski, R.G.; Topp, G.C. Practical considerations for using a TDR cable tester. Soil Technol. 7:113–126; 1994.

Cermak, J.; Jenik, J.; Kucera, J.; Zidek, V. Xylem water flow in a crack willow tree *Salix fragilis* in relation to diurnal changes of environment. Oecologia 64:145–151; 1984.

Choudury, B.J.; Sehmugge, T.J.; Chang, A.; Newton, R.W. Effect of surface roughness on the microwave emission from soils. J. Geophys. Res. 84:5699–5706; 1979.

Cohen, Y.; Fuchs, M.; Cohen, S. Resistance to water uptake in a mature citrus tree. J. Exp. Bot. 34:451–460; 1983.

Dalton, F.N.; van Genuchten, M.T. The time-domain reflectometry method for measuring soil water content and salinity. Geoderma 38:237–250; 1986.

Dasberg, S.; Hopmans, J.W. Time domain reflectometry calibration for uniformly and nonuniformly wetted sandy and clayey loam soils. Soil Sci. Soc. Am. J. 56:1341–1345; 1992.

Davis, J.L.; Chudobiak, W.J. In-situ meter for measuring relative permittivity of soils. Geol. Surv. Can. Ottawa. Paper 75-1A:75–79; 1975.

Dirksen, C.; Dasberg, S. Improved calibration of time domain reflectometry soil water content measurements. Soil Sci. Soc. Am. J. 57:660–667; 1993.

Dixon, H.H. *Transpiration and the Ascent of Sap in Plants*. London: Macmillan; 1914.

Donahue, R.L.; Miller, R.W.; Shickluna, J.C. *Soils: An Introduction to Soils and Plant Growth*. Englewood Cliffs, NJ: Prentiee-Hall; 1983.

Edwards, W.R.N.; Becker, P.; Cermak, J. A unified nomenclature for sap flow measurements. Tree Physiol. 17:65–67; 1996.

Engman, E.T.; Chauhan, N. Status of microwave soil moisture measurements with remote sensing. Remote Sens. Environ. 51:189–198; 1995.

Fawcett, R.; Collis-George, N. A filter paper method for determining the moisture characteristic of soil. Aust. J. Exp. Agric. Anim. Husb. 7:162–167; 1967.

Fellner-Feldegg, J. The measurement of dielectrics in the time domain. J. Phys. Chem. 73:616–623; 1969.

Gardner, R. A method of measuring capillary tension of soil moisture over a wide moisture range. Soil Sci. 43:277–283; 1937.

Gardner, W.H. Water content. In: Klute, A., ed. *Methods of Soil Analysis. Part 1. Physical and Mineralogical Methods*. Madison, WI: American Society of Agronomy and Soil Science Society of America; 1986:493–544.

Granier, A. A new method of sap flow measurement in tree stems. Annales des Sciences Forestieres 42:193–200; 1985.

Granier, A. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. Tree Physiol. 3:309–320; 1987.

Granier, A.; Bobay, V.; Gash, J.; Gelpe, J.; Saugier, B.; Shuttleworth, W. Vapour flux density and transpiration rate comparisons in a stand of maritime pine (*Pinus pinaster* Ait.) in Les Landes forest. Agric. For. Meteorol. 51:309–319; 1990.

Goulden, M.L.; Field, C.B. Three methods for monitoring the gas exchange of individual tree canopies: Ventilated-chamber, sap-flow and Penman-Monteith measurements on evergreen oaks. Func. Ecol. 8:125–135; 1994.

Gray, A.N.; Spies, T.A. Water content measurement in forest soils and decayed wood using time domain reflectometry. Can. J. For. Res. 25:376–385; 1995.

Greacen, E.; Walker, G.; Cook, P. Evaluation of the filter paper method for measuring soil water suction. *International Conference on the Measurement of Soil and Plant Water Status.* Logan, UT: Utah State Univ.; 1986:137–143.

Greacen, E.; Walker, G.; Cook, P. *Procedure for the Filter Paper Method of Measuring Soil Water Suction.* Divisional Report 108. Canberra, Australia: CSIRO Division of Soils; 1989.

Green, S.; Clothier, B. Water use of kiwifruit vines and apple trees by the heat-pulse technique. J. Exp. Bot. 39:115–123; 1988.

Grime, V.L.; Morison, J.I.L.; Simmonds, L.P. Including the heat storage term in sap flow measurements with the stem heat balance method. Agric. For. Meteorol. 74:1–25; 1995.

Ham, J.M.; Heilman, J.L.; Lascano, R.J. Determination of soil water evaporation and transpiration from energy balance and stem flow measurements. Agric. For. Meteorol. 52:287–302; 1990.

Hamblin, A. Filter paper method for routine measurement of field water potential. J. Hydrol. 53:355–360; 1981.

Hanks, R.J.; Ashcroft, G.L. *Applied Soil Physics.* Berlin: Springer-Verlag; 1986.

Heimovaara, T.J. Design of triple-wire time domain reflectometry probes in practice and theory. Soil Sci. Soc. Am. J. 57:1410–1417; 1993.

Herkelrath, W.N.; Hamburg, S.P.; Murphy, F. Automatic, real-time monitoring of soil moisture in a remote field area with time domain reflectometry. Water Resourc. Res. 27:857–864; 1991.

Hokett, S.L.; Chapman, J.B.; Cloud, S.D. Time domain reflectometry response to lateral soil water content heterogeneities. Soil Sci. Soc. Am. J. 56:313–316; 1992.

Hook, W.R.; Livingston, N.J.; Sun, Z.J.; Hook, P.B. Remote diode shorting improves measurement of soil water by time domain reflectometry. Soil Sci. Soc. Am. J. 56:1384–1391; 1992.

Jackson, R.B.; Paruelo, J.M.; Sala, O.E.; Mooney, H.A. Ecosystem water fluxes for two grasslands in elevated $CO_2$: A modeling analysis. Oecologia 113:537–546; 1998.

Jackson, R.B.; Sala, O.E.; Field, C.B.; Mooney, H.A. $CO_2$ alters water use, carbon gain, and yield for the dominant species in a natural grassland. Oecologia 98:257–262; 1994.

Jackson, T.J.; O'Neill, P. Temporal observations of surface soil moisture using a passive microwave sensor. Remote Sens. Environ. 21:281–296; 1987.

Jarvis, P. Prospects for bottom-up models. In: Ehleringer, J.; Field, C., eds. *Scaling Physiological Processes: Leaf to Globe.* San Diego: Academic; 1993:115–126.

Koide, R.T.; Robichaux, R.H.; Morse, S.R.; Smith, C.M. Plant water status, hydraulic resistance and capacitance. In: Pearcy, R.W.; Ehleringer, J.; Mooney H.A.; Rundel, P.W., eds. *Plant Physiological Ecology: Field Methods and Instrumentation.* London: Chapman and Hall; 1989:161–183.

Kolb, K.J.; Sperry, J.S.; Lamont, B.B. A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. J. Exp. Bot. 47:1805–1810; 1996.

Kostner, B.; Schulze, E.-D.; Kelliher, F.; Hollinger, D.; Byers, J.; Hunt, J.; McSeveny, T.; Meserth, R.; Weir, P. Transpiration and canopy conductance in a pristine broad-leaved forest of Nothofagus: An analysis of xylem sap flow and eddy correlation measurements. Oecologia 91:350–359; 1992.

Kramer, P.J.; Boyer, J.S. Water relations of plants and soils. San Diego: Academic; 1995.

Lieth H. Modelling the primary productivity of the world. Nature Resourc. 8:5–10; 1972.

Lin, D.-S.; Wood, E.F.; Troch, P.A.; Mancini, M.; Jackson, T.J. Comparisons of remotely sensed and model-simulated soil moisture over a heterogeneous watershed. Remote Sens. Environ. 48:159–171; 1994.

Lott, J.E.; Khan, A.A.H.; Ong, C.K.; Black, C.R. Sap flow measurements of lateral tree roots in agroforestry systems. Tree Physiol. 16:995–1001; 1996.

Marshall, D. Measurement of sap flow in conifers by heat pulse transport. Plant Physiol. 33:385–396; 1958.

Nadler, A.; Dasberg, S.; Lapid, I. Time domain reflectometry measurements of water content and electrical conductivity in layered soil columns. Soil Sci. Soc. Am. J. 55:938–943; 1991.

Nobel, P.S. Physiochemical and environmental plant physiology. San Diego: Academic; 1991.

Owe, M.; Chang, A.; Golns, R.E. Estimating surface soil moisture from satellite microwave measurements and a satellite derived vegetation index. Remote Sens. Environ. 24:331–345; 1988.

Parker, S.P., ed. *McGraw-Hill Encyclopedia of Physics.* New York: McGraw-Hill; 1983.

Pearcy, R.; Schulze, E.-D.; Zimmermann, R. Measurement of transpiration and leaf conductance. In: Pearcy, R.; Ehleringer, J.; Mooney, H.; Rundel, P., eds. *Plant Physiological Ecology: Field Methods and Instrumentation.* New York: Chapman and Hall; 1989:137–160.

Pepin, S.; Livingston, N.J.; Hook, W.R. Temperature-dependent measurement errors in time domain reflectometry determinations of soil water. Soil Sci. Soc. Am. J. 59:38–43; 1995.



Peressotti, A.; Ham, J.M. A
suring sap flow with
method. Agron. J. 88:149

Roth, C.H.; Malicki, M.A.;
ation of the relationship
stant and volumetric wat
calibrating soil moisture
Soil Sci. 43:1–13; 1992.

Roth, K.; Schulin, R.; Fluhle
tion of time domain refle
measurement using a con
Water Resourc. Res. 26:2

Rowell, D.L. *Soil Science:*
New York: Longman; 199

Rundel, P.W.; Jarrell, W.M.
Pearcy, R.W.; Ehleringer,
P.W., eds. *Plant Physiolog*
*and Instrumentation.* Lo
1989:29–56.

Sakuratani, T. A heat balance
flow in the stem of an int
teorology 37:9–17; 1981.

Saliendra, N.Z.; Meinzer, F.C
and drought-induced differ
ductance of contrasting s
Bot. 43:1209–1217; 1992.

Schmugge, T. Measurements
temperature. In Hobbs, R.
*mote Sensing of Biospher*
Springer-Verlag; 1990:31–

Schmugge, T.; Gloersen, P.;
mote sensing of soil mois
ometers. J. Geophys. Res.

Schmugge, T.; Wang, J.R.;
push broom microwave r
Konza Prairie in 1985. IE
Sens. 26:590–596; 1988.

Scholander P.F.; Hammel, H.
mingsen, E.A. Sap pressure
148:339–346; 1965.

Slatyer, R.O. *Plant-Water Re*
demic; 1967.

Slatyer, R.O.; Taylor, S.A.
soil-water relations. Nature

Smith, D.M.; Allen, S.J. Me
plant stems. J. Exp. Bot. 4

Sperry, J. Why you water
47:256–258; 1997.

Sperry, J.S.; Pockman, W.T.
by hydraulic conductance a
*tula occidentalis.* Plant C
1993.

Peressotti, A.; Ham, J.M. A dual-heater gauge for measuring sap flow with an improved heat-balance method. Agron. J. 88:149–155; 1996.

Roth, C.H.; Malicki, M.A.; Plagge, R. Empirical evaluation of the relationship between soil dielectric constant and volumetric water content as the basis for calibrating soil moisture measurements by TDR. J. Soil Sci. 43:1–13; 1992.

Roth, K.; Schulin, R.; Fluhler, H.; Attinger, W. Calibration of time domain reflectometry for water content measurement using a composite dielectric approach. Water Resourc. Res. 26:2267–2273; 1990.

Rowell, D.L. *Soil Science: Methods and Applications.* New York: Longman; 1994.

Rundel, P.W.; Jarrell, W.M. Water in the environment. In Pearcy, R.W.; Ehleringer, J.; Mooney H.A.; Rundel, P.W., eds. *Plant Physiological Ecology: Field Methods and Instrumentation.* London: Chapman and Hall; 1989:29–56.

Sakuratani, T. A heat balance method for measuring sap flow in the stem of an intact plant. Agricultural Meteorology 37:9–17; 1981.

Saliendra, N.Z.; Meinzer, F.C. Genotypic developmental and drought-induced differences in root hydraulic conductance of contrasting sugarcane cultivars. J. Exp. Bot. 43:1209–1217; 1992.

Schmugge, T. Measurements of surface soil moisture and temperature. In Hobbs, R.J.; Mooney, H.A., eds. *Remote Sensing of Biosphere Functioning.* New York: Springer-Verlag; 1990:31–63.

Schmugge, T.; Gloersen, P.; Wilheit, T.; Geiger, F. Remote sensing of soil moisture with microwave radiometers. J. Geophys. Res. 79:317–323; 1974.

Schmugge, T.; Wang, J.R.; Asrar, A. Results from the push broom microwave radiometer flights over the Konza Prairie in 1985. IEEE Trans. Geosci. Remote Sens. 26:590–596; 1988.

Scholander P.F.; Hammel, H.T.; Bradstreet, E.D.; Hemmingsen, E.A. Sap pressure in vascular plants. Science 148:339–346; 1965.

Slatyer, R.O. *Plant-Water Relationships.* London: Academic; 1967.

Slatyer, R.O.; Taylor, S.A. Terminology in plant- and soil-water relations. Nature 187:922–924; 1960.

Smith, D.M.; Allen, S.J. Measurement of sap flow in plant stems. J. Exp. Bot. 47:1833–1844; 1996.

Sperry, J. Why you water the garden. BioScience 47:256–258; 1997.

Sperry, J.S.; Pockman, W.T. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis.* Plant Cell Environ. 16:279–287; 1993.

Swanson, R.H. Significant historical developments in thermal methods for measuring sap flow in trees. Agric. For. Meteorol. 72:113–132; 1994.

Swanson, R.; Whitfield, D. A numerical analysis of heat pulse velocity: Theory and practice. J. Exp. Bot. 32:221–239; 1981.

Topp, G.C.; Davis, J.L. Measurement of soil water content using time-domain reflectometry (TDR): A field evaluation. Soil Sci. Soc. Am. J. 49:19–24; 1985.

Topp, G.C.; Davis, J.L.; Annan, A.P. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. Water Resourc. Res. 16:574–582; 1980.

Topp, G.C.; Davis, J.L.; Annan, A.P. Electromagnetic determination of soil water content using TDR: I. Applications to wetting fronts and steep gradients. Soil Sci. Soc. Am. J. 46:672–678; 1982.

Topp, G.C.; Davis, J.L.; Bailey, W.G.; Zebchuk, W.D. The measurement of soil water content using a portable TDR hand probe. Can. J. Soil Sci. 64:313–321; 1984.

Tsuda, M.; Tyree, M. Whole-plant hydraulic resistance and vulnerability segmentation in *Acer saccharinum.* Tree Physiol. 17:351–357; 1997.

Tyree, M.T.; Karamanos, A.J. Water stress as an ecological factor. In: Grace, J.; Ford, E.; Jarvis, P., eds. *Plants and Their Atmospheric Environment.* Oxford: Blackwell; 1980:237–261.

Tyree, M.T.; Patino, S.; Bennink, J.; Alexander, J. Dynamic measurements of root hydraulic conductance using a high-pressure flowmeter in the laboratory and field. J. Exp. Bot. 46:83–94; 1995.

Tyree, M.T.; Sinclair, B.; Lu, P.; Granier, A. Whole shoot hydraulic resistance in *Quercus* species measured with a new high-pressure flowmeter. Ann. Sci. For. 50:417–423; 1993.

Tyree, M.T.; Yang, S.; Cruiziat, P.; Sinclair, B. Novel methods of measuring hydraulic conductivity of tree root systems and interpretation using AMAIZED. Plant Physiol. 104:189–199; 1994.

Verhoef, A. The effect of temperature differences between porometer head and leaf surface on stomatal conductance measurements. Plant Cell Environ. 20:641–646; 1997.

Whalley, W.R. Considerations on the use of time-domain reflectometry (TDR) for measuring soil water content. J. Soil Sci. 44:1–9; 1993.

Wiebe H.H.; Brown, R.W.; Barker, J. Temperature gradient effects on in situ hygrometer measurements of water potential. Agron. J. 69:933–939; 1977.

Wiltshire, J.J.J.; Wright, C.J.; Colls, J.J.; Unsworth, M.H. Effects of heat balance stem-flow gauges and associated silicone compound on ash trees. Agric. For. Meteorol. 73:135–142; 1995.

Zegelin, S.J.; White, I.: Jenkins, D.R. Improved field probes for soil water content and electrical conductivity measurement using time domain reflectometry. Water Resourc. Res. 25:2367–2376; 1989.

Zegelin, S.J.; White, I.; Russell, G.F. A critique of the time domain reflectometry technique for determining field soil-water content. In: Topp, G.C.; Reynolds, W.D.; Green, R.E., eds. *Advances in Measurement of Soil Physical Properties: Bringing Theory into Practice*. Madison, WI: Soil Science Society of America; 1992:187–208.

# 14

# Nutrient Tr

John M. Stark

## Introduction

A question often asked in
What controls rates of rele
nutrients? Nutrient elemen
unavailable to available for
riety of transformation proce
Schlesinger 1991); however,
cycling patterns that are co
(Fig. 14.1). For example, mo
exist in both organic and mi
the processes of mineralizati
ganic to mineral forms) and
sion of mineral to organic f
these nutrients. Other nutrie
compounds and, thus, dissol
processes represent importan
and immobilization of plant-a
procedures used to measure
ferent nutrients vary conside
used to measure these transfo
erally quite similar.

In this section, I discuss a
that can be used to measure n
rates. Rather than describing
procedures, I emphasize the
advantages, and disadvantag
proaches. For descriptions o
the reader should consult on
methodology texts (e.g., W
Knowles and Blackburn 1993
In the following discussion,
vided into two groups: non-
isotope methods. Methods fo
(N) cycling processes will oft