

Plants, Isotopes and Water Use: A Catchment-Scale Perspective

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6.1 Introduction

6.1.1 *Plants and catchment-level processes*

Beginning with one of the very first well-documented catchment experiments in 1909 at Wagon Wheel Gap, Colorado, in the United States, hydrologists began to acknowledge that plants influence the *patterns* of water movement at the catchment scale (see Bates and Henry, 1928). Since that time, water resource and forest management practices have been closely coupled, based on the premise that forests do influence water yield and quality at the catchment scale (Bosch and Hewlett, 1982). Closer scrutiny of over 100 catchment studies (Bosch and Hewlett, 1982) that acknowledge the importance of trees and forests in hydrologic processes reveals, however, that little or no consideration is given to the regulatory role, through changes in *rates* of transpiration, that plants can play in water movement. In fact, commonly evaporation, a physical process, and transpiration, a biophysical process, are lumped into a single variable in estimating water balance -- evapotranspiration (E_t), as discussed in Chapter 1. This view is a gross oversimplification of the processes of evaporation and transpiration, and is very likely to be a primary reason for why the vapor-phase water-flux component of the hydrologic cycle is poorly understood and parameterized in many hydrologic models (Rind et al., 1992).

It is estimated that sixty-five percent of all rainfall that occurs over the land surface is effectively removed from those surfaces by the recycling force of evaporative processes (Chahine, 1992). It has also been estimated that plants cover approximately 70% of this surface (Whittaker, 1975) and are a primary route by which 80% of the water in surface and sub-surface soils re-enters the hydrologic cycle over land (Chahine, 1992; Gleick, 1993; Dawson, 1993a; Newson, 1994). However, just as streams do not behave as single geological conduits for water flux over the land because of various internal characteristics and processes (Likens, 1985), neither are plants passive meteorological conduits for water flux off of the land. Plants possess small pores on their leaf surfaces - stomata - that can finely regulate the quantities and rates of water loss. As such, when considering both the *patterns* and *rates* of water flux from a given piece of land, a catchment, or from a riparian zone, the regulatory influence of plants must not be ignored. With the notable exception of research with forested *Eucalyptus* catchments in Australia, India, and South Africa (reviewed in Calder et al., 1992a), rarely are plants considered explicitly in hydrologic research at the catchment level (Newson, 1994). The data which are commonly presented are biased towards a perspective which views plants as simply intercepting or evaporating water from their surfaces with no consideration for how well they can regulate water flux.

This chapter expands upon this perspective and considers, in some detail, the role of plants and vegetated surfaces in water movement patterns and their abilities to influence these patterns and rates of water movement at the catchment level. The analysis of stable isotopes of hydrogen and oxygen in plant- and source-waters has, in recent years, substantially improved our ability to better understand the soil-plant and plant-atmosphere interface so that we might better understand catchment level processes. We suspect that a major reason for why plants have not been considered more explicitly in catchment hydrology is because of (a) a lack of an easily applied method at the catchment scale, and (b) poor communication among hydrologists and forest tree biologists interested in hydrologic processes at the catchment level. Isotope tracer studies, especially with naturally occurring stable isotopes, provides a powerful method as well as a common arena for drawing these two groups of scientists together.

Our discussion begins with the plants themselves and builds toward a landscape- or catchment-scale perspective (after Burt, 1992) but does not reduce the plants growing in and on these catchments to simple evaporative surfaces or passive conduits for water movement. Rather, we view plants as "regulators" of water flux in the hydrosphere. To accomplish this, we first present existing information on plants, water, and stable isotope analyses and then expand upon this data base to provide a catchment-level perspective (for recent reviews focused on the botanical perspective see Ehleringer and Dawson, 1992 and Dawson, 1993b). We first discuss water transport processes as influenced by plants, how plants use and modify soil and ground water, and how they regulate water movement at the individual and stand levels. We present a number of examples of how stable isotope analyses of plant- and source-waters are providing new insights into the patterns of water movement, uptake and use for a diversity of ecosystems. We end by presenting a number of examples where we believe the isotope approach to studying plant-modified water movement may provide important insights into catchment-level processes on both a short-term and long-term basis.

6.1.2 Working premise concerning plants, isotopes and water use

The basis of what we present derives from the fundamental observation that there is no fractionation of either oxygen (^{16}O , ^{18}O) or hydrogen (H, D) isotopes in water during the uptake process by plant roots (Figure 6.1; Wershaw et al., 1966; Allison et al., 1984; White et al., 1985; Dawson and Ehleringer, 1991; Thorburn et al., 1993; but see Lin and Sternberg, 1993 for an unusual exception). Variation in the stable isotopic composition of water in catchment sources (soils, streams, and ground water) are largely produced by two phenomena: (1) evaporative isotopic enrichment from the surface layers (Allison et al., 1983; Allison and Hughes, 1983; Barnes and Allison, 1983, 1988), and (2) seasonal and storm-related changes in the isotope composition of precipitation inputs (Chapter 3; Friedman et al., 1964; Gat, 1980; Yurtsever and Gat, 1980; Ferronsky and Polyakov, 1982; Ingraham and Taylor, 1991). A third process, thermal and chemical modification along gradients that develop between the bulk soil and aquifers (Chapter 2; Fontes, 1980; Gat, 1982; Barnes and Allison, 1989), can also effect the composition of deep aquifers or in geothermal areas (Hoefs, 1997).

When water is transported between the roots and the shoots within a plant, its isotopic composition (the D/H or $^{18}\text{O}/^{16}\text{O}$ of xylem-sap) remains unaltered until it reaches tissues or organs such as leaves (Dongmann et al., 1974; Flanagan and Ehleringer, 1991; Flanagan et al., 1991) or young, unsuberized stems (Dawson and Ehleringer, 1993; Thorburn and Mensforth,

1993), that are losing water to the external atmosphere. Evaporative processes cause significant enrichment of the heavier isotopes (D or ^{18}O) within the xylem-sap. The magnitude of isotopic enrichment is a function of the leaf transpiration rate (E_p), the humidity gradient between the site of water loss and the atmosphere as well as the δD or $\delta^{18}\text{O}$ (see below) of the atmospheric water (Dongmann et al., 1974; Zundel et al., 1978; Leaney et al., 1985; Farquhar et al., 1993; Flanagan et al., 1991, 1994). In order to understand and document patterns of water use, uptake and transport by plants, it is essential to collect and analyze the xylem-sap before it is exposed to evaporative enrichment. If this is done, the analysis of this sap and of the source water δD and/or $\delta^{18}\text{O}$ can provide a powerful tool for tracing the spatial and temporal patterns of water uptake and use and the effect of these patterns on hydrologic processes.

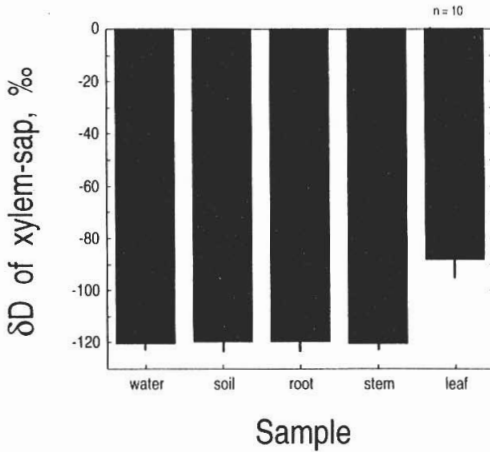


Figure 6.1. The stable hydrogen isotopic composition (δD) of water in the soil, the roots, and the suberized stems of *Acer negundo* (summer time; Utah, USA). The data show that there is no isotopic fractionation during water uptake (data taken from Dawson and Ehleringer, 1991, 1993b).

6.2 Water Uptake and Water Transport in Plants

6.2.1 Background

In order to understand the role of plants in catchment-level hydrologic processes, one must be able to accurately quantify the components of the catchment balance (Chapter 1). Some inaccuracies may result when parameters are estimated by difference. Accurate measures of each water balance parameter (Equation 6.1) permits us to achieve "closure" for forested catchment studies (see Kaufmann and Kelliher, 1991; Kaufmann and Landsberg, 1991). A catchment provides a convenient unit of study for advancing towards closure because inputs and outflows for an area where the boundaries are known can be directly measured (see for example chapters in Swank and Crossley, 1988). However, our task does not stop here. In addition to outflows, we must know the magnitude of water losses from the catchment via evaporation and plant transpiration. Spittlehouse and Black (1981) present a simple hydrologic mass balance model for a catchment:

$$\theta_{i-1} - \theta_i + (P - E_t - D - R) \Delta t / z = 0 \quad (6.1)$$

where the quantity $(\theta_{i-1} - \theta_i)$ is the change in the volumetric water content (θ ; m^3/m^3 ; see Topp and Davis, 1985) in the rooting zone over the time period Δt and $i-1$ and i are the beginning and end, respectively, of this time period. P , E_t , D , and R are the rates of precipitation, evapotranspiration, drainage (percolation) into the soil volume, and runoff during Δt (mm/time) respectively. Δ is equal to $i - (i-1)$ and z is the depth of the rooting zone. Rearranging Equation 6.1 as:

$$z(\theta_{i-1} - \theta_i) = ([E_t + D + R] - P)\Delta t \quad (6.2)$$

we can more easily relate the change in the volumetric water content of the zone in which a plant extracts its water ($z(\theta_{i-1} - \theta_i)$) to outputs ($[E_t + D + R]$) and inputs (P) to the catchment over time (Δt). P and R can be accurately measured if a catchment is appropriately gauged (see Swank and Crossley, 1988). D is more difficult to determine so it is often assumed to be zero for catchments underlain by bedrock (for example see Likens et al., 1970). Because assuming D is zero can be an important source of error in catchment water balance studies (Tanner, 1968; Calder, 1992b), some estimate of D must be obtained to gather sound water balance information for a catchment. Another important source of error comes with determining evapotranspiration (E_t), which must be broken into its component parts, evaporation (E_w) and plant transpiration (E_p) where:

$$E_w = g_a(e_s - e_a) \quad (6.3)$$

where g_a is the bulk aerodynamic conductance from any surface to a known reference height, e_s is the saturation vapor pressure at the surface -- including the soil surface (e_{ss}), leaf surfaces of understory plants (e_{sp}), and canopy tree leaf surfaces (e_{st}). All three of these parameters must be determined at their unique surface temperature. The all-inclusive term, e_s , includes water which is intercepted by a plant canopy and then re-evaporated back to the atmosphere. The actual vapor pressure in the atmosphere normalized to the conditions at the evaporating surface is e_a . Following Whitehead and Hinckley (1991), transpiration (E_p) from a dry canopy can be expressed as:

$$E_p = \Omega E_{eq} + (1 - \Omega)E_{imp} \quad (6.4)$$

where the coupling factor, Ω (Equation 6.9 below), determines the relative importance of the terms E_{eq} and E_{imp} where E_{eq} is the equilibrium rate of transpiration, expressed as:

$$E_{eq} = \varepsilon A / [(\varepsilon + 1)\lambda] \quad (6.5)$$

where A is the energy available as a driving force for transpiration, ε is the change in latent heat content relative to the change in sensible heat content of saturated air (equal to s/γ , where s is the slope of the relation between saturation vapor pressure and temperature, and γ is the psychrometric constant) with l being the latent heat of vaporization. The imposed rate of transpiration, E_{imp} , is:

$$E_{\text{imp}} = g_c D_m / P \quad (6.6)$$

where g_c is canopy conductance to water vapor, D_m is the saturation vapor pressure difference between the atmosphere measured at a known height in the mixed layer well above the surface of the canopy and the surfaces of the leaves where water is leaving, and P is atmospheric pressure. For simplicity, the term g_c incorporates both conductance of water vapor from inside of leaves into the boundary layer around a leaf (g_i) as well as the conductance from the boundary layer into the external atmosphere (g_{bl}). In practice, these two processes are usually separated and either measured or estimated independently. For catchment level studies this may be impractical; however, we combine them here. The air saturation deficit measured above plant canopy height, but still within the plant's canopy boundary layer, D , is related to D_m by the relation:

$$D = \Omega D_{\text{eq}} + (1 - \Omega) D_m \quad (6.7)$$

where D_{eq} , the equilibrium air saturation deficit, is expressed as:

$$D_{\text{eq}} = \gamma \epsilon A / [(\epsilon + 1) C_p g_c] \quad (6.8)$$

and the coupling factor, Ω , is expressed as:

$$\Omega = (\epsilon + 1) / (\epsilon + 1 + [g_a / g_c]) \quad (6.9)$$

where C_p is the volumetric (specific) heat capacity of air at a constant and known pressure and temperature. Often, tall, aerodynamically rough forest canopies commonly cause values of Ω to be small (0.1 - 0.3) because g_a is greater than g_c and E_p is largely driven by D_m (Whitehead and Hinckley, 1991; Meinzer, 1993). This is not always true, however, and the degree of coupling between the bulk atmosphere and a plant canopy will be significantly influenced by the species (Jarvis and McNaughton, 1986), the prevailing climatic conditions (e.g. wind velocity), and stand characteristics within the catchment (e.g. tree size and density; Dawson, 1996). Modification of the transpiration equation (6.4) for a partially dry canopy can be found in Whitehead and Hinckley (1991). Further details of Equations 6.3 - 6.9, the assumptions behind using them, and how they are obtained can be found in Jones (1992), Monteith and Unsworth (1990) and references therein.

6.2.2 Measurements of water uptake and transport by plants

It should be apparent from the very brief discussion presented above that vegetated lands cannot be treated as freely evaporating surfaces. Plants do exert a significant degree of control over the patterns and rates of evaporative water loss. In order to relate the leaf-level measurements to entire plant canopies and eventually to catchment studies, it is important that we understand how plants modify the patterns and rates of water movement at that scale. Tools and techniques for measuring or estimating water vapor flux through individual plants include

lysimeters (Rutter, 1968; Newson, 1994) or sap flow gauges (Swanson and Whitfield, 1981; Baker and van Bavel, 1987; Jones et al., 1988; Hinckley et al., 1994; Dawson, 1996). Techniques for entire forest stands include Bowen ratio-energy balance and eddy correlation (McNaughton and Jarvis, 1983; Kaufmann and Kelliher, 1991; Hollinger et al., 1994; Herbst, 1995; Dawson, 1996). Early studies using isotopes employed radioactive tracers to obtain estimates of E_p and E_t (Kline et al., 1970; Luvall and Murphy, 1982; Waring and Roberts, 1979; Waring et al., 1980) and these types of studies continue today, in both plantations (summarized in Calder et al., 1992a, b) and in natural stands (Bishop and Dambrine, 1995). While these studies are informative, radioactive tracer methods are impractical, especially in natural catchments because they not only "pollute" the basin for subsequent investigators but are prohibited in many areas because the catchment may be used for other purposes (e.g. public water supply).

In recent years, the use of stable isotopes of hydrogen and oxygen in water have provided not only a new and easily applied, non-radioactive method, but many new insights into how plants modify soil water and/or take up water from different regions in the soil or times of the year (reviewed in Ehleringer and Dawson, 1992; Dawson, 1993b). It has now been well documented (Walker and Richardson, 1991) that marked isotopic gradients exist in both δD and $\delta^{18}O$ within the soil profile (see Chapter 1 for a full explanation of isotopic fractionation in water). The upper soil layers are commonly enriched in the heavier isotopes in water (D and ^{18}O) due to evaporative fractionation which is the preferential loss of the lighter isotopes in the vapor phase as water evaporates from the upper soil surface (Figure 6.2).

The isotopic composition of water changes markedly with depth, often converging upon a relatively stable value at depths below an isotopically unstable zone (UZ) present in some soils (see Figure 6.2). This stable value most often reflects "stored" soil water or ground water. The isotopically unstable zone observed in some (but not all) soils is sometimes a result of old water that has remained in this zone from past rainfall or percolation events. However, more commonly it is caused by phase changes, such as condensation events when water vapor in the soil airspace/matrix reaches its dew-point as the soil becomes cooler with depth (Mazor, 1991). Chapters 5 and 7 provide detailed discussions of water in soils and ground water.

When plants are growing in the soils, further modification of soil-water isotopic composition can result from patterns of water uptake and water loss from plants rooted at different depths. In the simplest case, we might expect the magnitude of change in the isotopic composition of soil water to be different between a tilled and fully planted crop field, or between a forested and deforested catchment. The presence of plants, which can take water up from many different layers in the soil, should modify not only the soil volumetric water content, but also the isotopic soil water profile. It is well known that plants have a marked influence on the water yield of a catchment (Likens et al., 1970; McMinn and Hewlett, 1975; Bosch and Hewlett, 1982; Swank and Crossley, 1988) as well as on the transpiration rate (Figure 6.3; Lemon, 1966, Kramer and Boyer, 1995). Furthermore, on sites where plants are deeply rooted and take up deep soil water or ground water, the water within the profile will be depleted more quickly, resulting in a different soil moisture profile than on soils lacking plant cover (Figure 6.4).

Recent studies with crop plants (Croak et al., 1987, Baker and van Bavel, 1986), shrubs (Richards and Caldwell, 1987; J. Richards. pers. comm.), a desert treelet (Mooney et al., 1980a) and canopy trees (Dawson, 1993c, 1996; unpublished data) have all shown that water can be transferred within plant root systems from wet to dry regions of the soil and then released. This

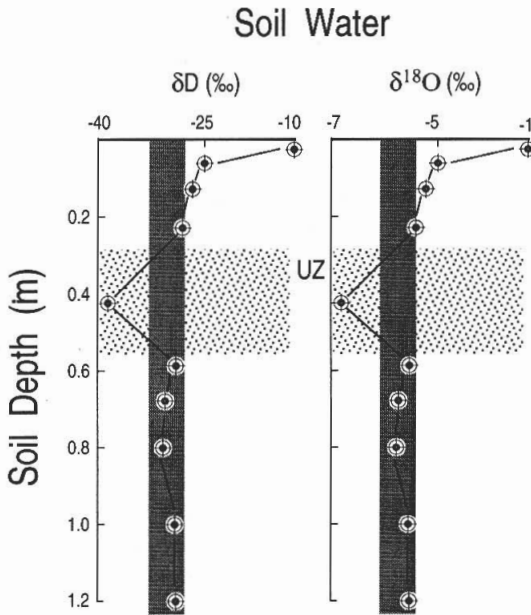


Figure 6.2. The δD and $\delta^{18}O$ of soil water as a function of depth in the Australian soil profile (modified from Walker and Richardson, 1991). Note a marked isotopic depletion zone depicted as a lightly stippled area at approximately 40 cm deep (UZ; unstable zone - see text for explanation). Such a zone can cause problems in studies of water uptake by plants if it is assumed that only surface soil water, which is enriched in the heavier isotopes, and deeper source water (ground water), which is depleted in the heavier isotopes, are the only two sources. Vertical shaded areas depict the range of isotopic values for the deep source water.

process (hydraulic lift) not only changes the volumetric water content of the soil, but also the isotopic profile. For example, Dawson (1993c) has recently demonstrated that large sugar maple trees (*Acer saccharum*) redistribute ground water into the upper soil layers by the process of hydraulic lift. Using δD , he demonstrated that the isotopic composition of soil water near large trees was indistinguishable from ground water and very different than the δD of the bulk soil sampled away from the trees (Figure 6.5). Additional studies using sap flow and energy balance methods showed that this additional "pool" of water created by hydraulic lift could be as much as 100 L every night (Emerman and Dawson, 1996). This process enhanced total water discharge from the forest by 2-fold (Dawson, 1996), and demonstrates how the presence of plants can have a marked effect on not only soil moisture and thus the hydrologic balance but on the isotopic composition of that moisture (Dawson, 1993c).

If we hope to use isotopic tracers in catchment-level studies, it will then be essential that we understand how the plants that grow in these catchments are influencing the isotopic composition of water in the soil profile, as well as the rates of water use from different water sources in the catchment. Below, we present a number of case studies which demonstrate the use of stable isotopes in plant water uptake and water source research (see Section 6.4). Our goal is to show how this kind of information can be used at the catchment scale. However, before the case studies we will briefly discuss water movement within plants.

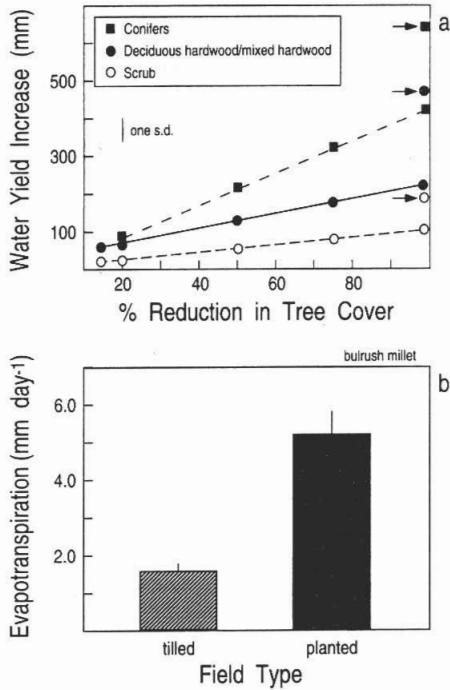


Figure 6.3. (a) Water yield as a function of percent reduction in tree cover for catchments of different forest types (USA). Lines are drawn through averages. Symbols with arrows at right show the extremes for each 'forest' type (redrawn from Bosch and Hewlett, 1982). (b) Evapotranspiration for tilled and planted plots (redrawn from data from in Lemon, 1966) in the northeastern (upstate New York) United States.

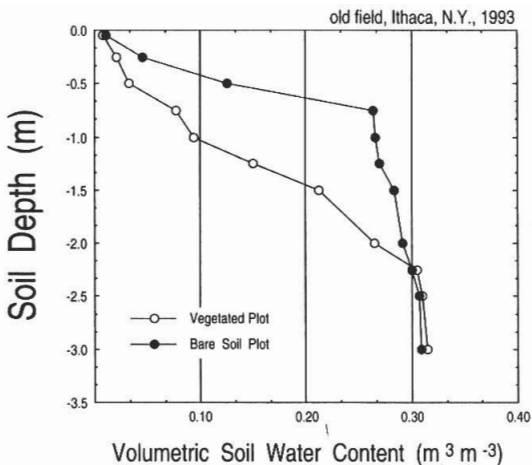


Figure 6.4. Volumetric soil moisture content (θ) as a function of depth for paired, 20 m², plots with and without plants growing on them. The vegetated plots support plant taxa composed primarily of grasses, perennial clonal herbs, and a few small trees and shrubs rooted to a maximum depth of 2.25 m. (θ) was determined by time domain reflectometry (TDR) for a clay-loam soil (Dawson, unpublished data).

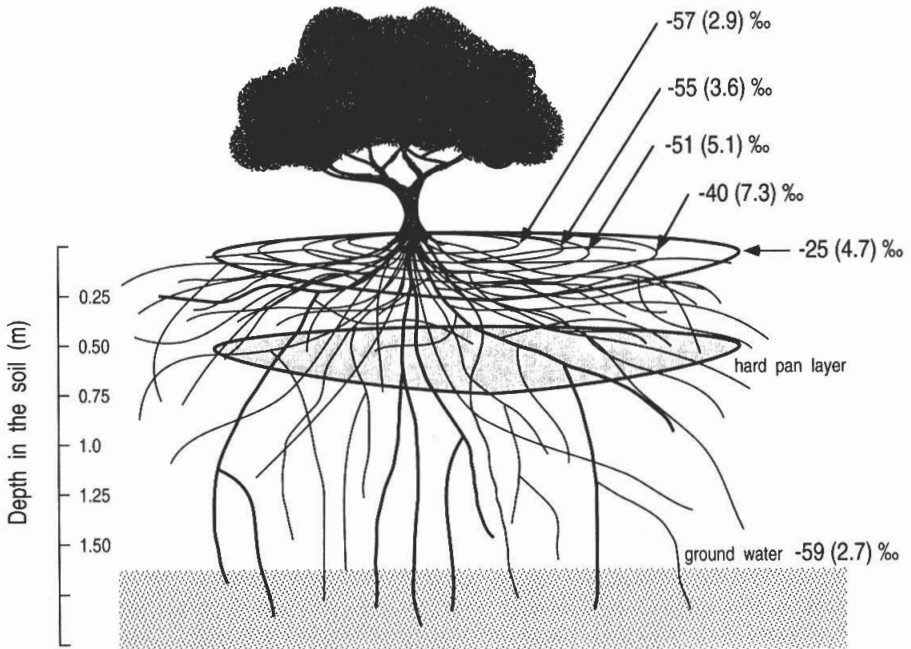


Figure 6.5. The δD of soil water (\pm s.d.) within the principle rooting depth of plants as a function of distance away from sugar maple trees (*Acer saccharum*) conducting hydraulic lift (HL) near Ithaca, New York, USA (HL is water transport from ground water through the root system to above the impermeable hard pan layer and loss to soil water below the trees - modified from Dawson, 1993c).

6.3 Stomatal Regulation of Water Movement in the Soil-Plant-Atmosphere Continuum

6.3.1 Water movement and the regulatory role of plants: the leaf-level

Water loss from plant leaves or canopies is governed by minute pores on their surface - stomata. The aperture of these stomata, and thus the rates of water loss, are markedly changed by a variety of environmental factors which include the plant and soil water status and atmospheric humidity (Ziegler et al., 1987), two factors which also influence the catchment water balance (Equations 6.1 and 6.2). Exposure of plant leaves to dry air (low humidity or high evaporative demand for water) can cause a direct change in leaf and canopy transpiration rates or an indirect change which is mediated through changes in the plant and soil water status (Figure 6.6; see Gollan et al., 1985, Schultze et al., 1987 for reviews). Leaf stomata also respond to changes in soil water potential and the soil-to-plant water potential gradient (Kramer and Boyer, 1995; Kozlowski, 1964-1983). As soils dry and the water potential gradient steepens, it becomes more difficult for a plant to extract enough soil water to meet its transpirational demands as well as its needs for growth and other metabolic functions. A consequence of a steeper water potential gradient between the soil and leaves is stomatal closure and a reduction in leaf and canopy transpiration (Figure 6.7).

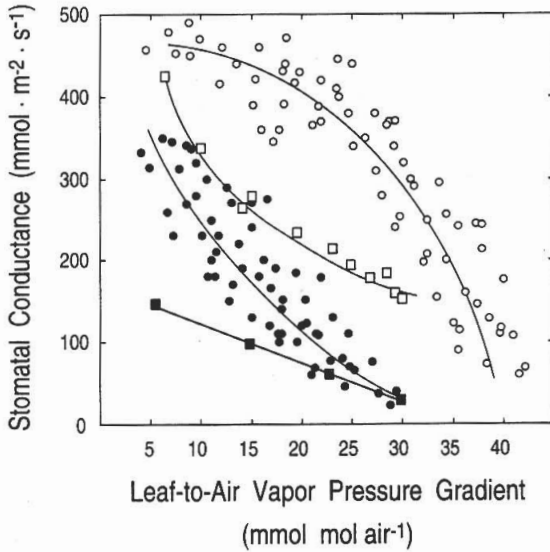


Figure 6.6. Stomatal conductance for water vapor (g_s) as a function of the leaf-to-air vapor pressure gradient for *Acer negundo* female (open circles) and male (closed circles) trees, *Sesamum indicum* (open squares), and *Corylus avellana* (closed squares). As the evaporative gradient from the leaf to the air increases (and relative humidity decreases) water loss rates decline because leaf stomata close (from Schultze and Hall, 1982; Schultze, 1986; Dawson and Ehleringer, 1993).

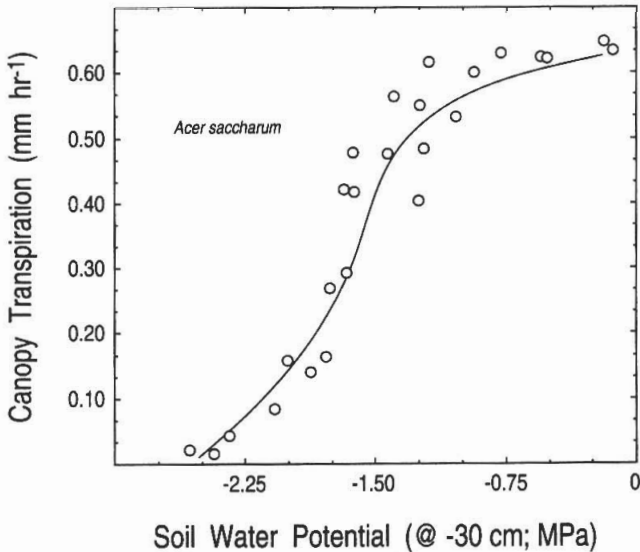


Figure 6.7. Mid-summer canopy transpiration based on sap flow from sugar maple (*Acer saccharum*, $n = 5$) trees as a function of soil water potential (closed symbols) near Ithaca, New York, USA. Soil water potential by psychrometry (modified after Dawson, 1993c and 1996).

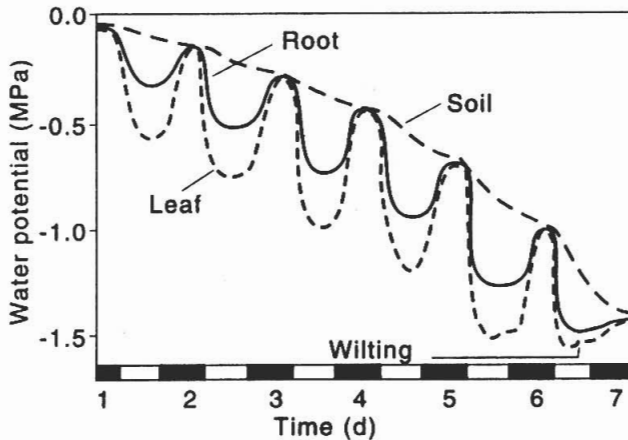


Figure 6.8. Schematic diagram of the changes in leaf, root, and soil water potential during the course of the day-night (shaded blocks) period and over a seven day drought. The greatest daily fluctuations occur in the plant leaves which are exposed to high evaporative demand from the environment at the same time soil water becomes progressively more limited. The gradual decline in maximum daily water potential is caused by plants using up stored soil water to the point at day 7 where permanent wilting occurs (after Slatyer, 1967 - taken from Larcher, 1995).

Soil and plant-water content (or water potential) also changes during the course of a day, or a growing season (Figure 6.8), or with changes in physiographic features such as slope exposure, soil type, and degree of vegetation cover (Figure 6.9). These changes will in turn influence the rates and patterns of water loss from individual plants as well as from plant stands.

6.3.2 Water movement and the regulatory role of plants: the stand-level

Water deficit or stress measured at the leaf level, induced by either low atmospheric humidity or soil moisture content, is manifest as a reduction in total canopy transpiration (E_p ; Equation 6.4) and thus a lowered total evapotranspiration (E_t) at the entire stand (or catchment) level. For example, using a simulation model, Lynn and Carlson (1990) show that plant water stress has an important influence on transpiration on remotely sensed plant canopies. The model is built around the correlation that when plant temperature (determined radiometrically) rises and leaf water potential declines, stomatal resistance to water loss increases. In their model, plants with a low critical leaf water potential (i.e. low tolerance to water stress-induced stomatal closure), have lower overall transpirational water loss due to a combination of soil, plant and atmospheric influences (e.g. soil water content, critical leaf water potential, vapor pressure gradient from the leaf to the air; Carlson, 1991). They conclude that the transpiration component of stand level water balance is a function of *both* soil water content and plant physiology. Therefore, understanding stand- (or catchment-) level water balance cannot occur if evaporation and transpiration are lumped into a single water balance term. Instead, separate attention must be given to the regulatory role of plants in land surface water flux and the interaction between water availability, water stress, and plant transpiration. Recent modeling work by Running and Hunt (1993) makes an important step towards making these types of linkages and has enhanced our understanding of forest water (and carbon) balance.

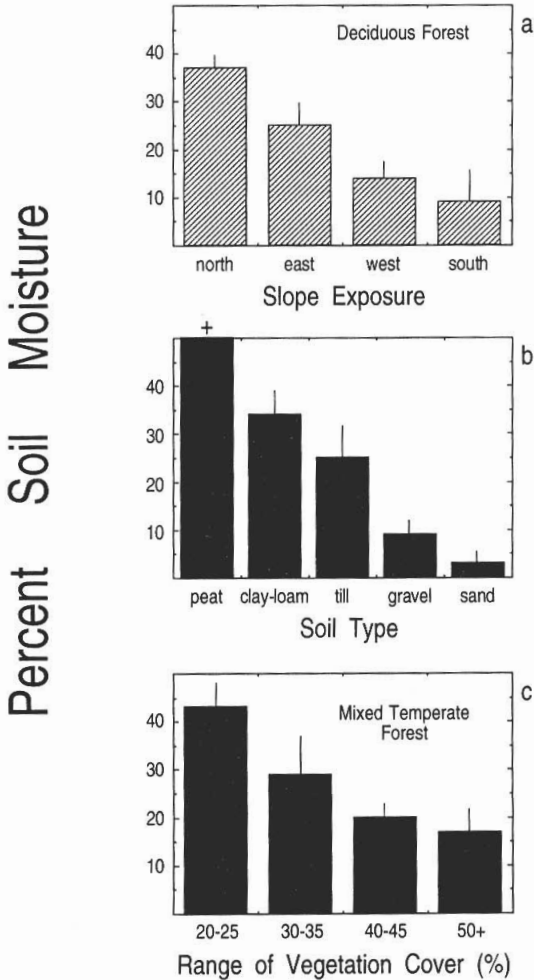


Figure 6.9. Percent soil moisture content as a function of (a) slope exposure, (b) soil type, and (c) percent vegetation cover (from data in Kramer and Boyer, 1995).

The amount of water consumed by a plant stand is a function of the area (and/or mass) of transpiring leaves. On a continental scale, as chronic water stress develops and water availability declines, it is manifest at the plant level as a significant decline in the amount of leaf area displayed per unit of land surface area -- the so-called, leaf area index (LAI; m^2/m^2). Data extracted from various sources (in Larcher, 1995) on the relationship between LAI and the average growing season soil water potential (the botanical index of plant water stress; more negative water potential values indicate greater water stress and/or lower water availability) shows that LAI increases as water availability increases (Figure 6.10). The slope of this relationship is shallow and linear when average soil water potential is relatively low (-1.25 to -3.20 MPa), indicating very small changes in LAI over a broad range of soil water potentials (and corresponding plant water stress). Interestingly, at higher soil water potentials (considered

mild plant water stress; -1.0 to -0.4 MPa), LAI increases exponentially with less water stress (high water potentials; Figure 6.10). This implies that in regions of higher average soil moisture content (higher water potentials), E_p would be predicted to increase exponentially with increased water availability (or progressively less plant water stress). This relationship would be predicted to have a marked influence on stand- or catchment-level water balance. For example, several recent studies, for a variety of vegetation types, using both empirical data and models, show that rates of E_p and/or E_t are reduced with declining soil water content (or water potential) and that the magnitude of the change is very often related to the LAI (notable examples are: Dolman et al., 1991; Hunt et al., 1991; McNaughton and Jarvis, 1991; and Kelliher et al., 1993).

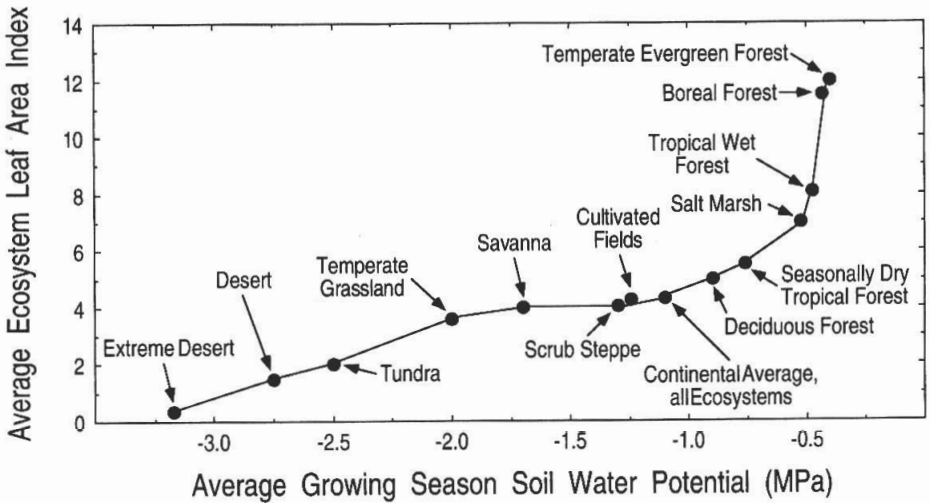


Figure 6.10. Average ecosystem leaf area index (LAI; m^2 leaves m^{-2} ground) as a function of the average seasonal soil water potential for major ecosystems of the world (drawn from data in Larcher, 1995).

6.4 Water Sources and Water Use by Plants: Case Studies Using Stable Isotopes

Understanding the patterns of water uptake by plants requires that the methods we employ provide a dynamic, rather than a static, picture of below ground water movement. The traditional methods used to study root systems (excavation, rhizatron, or even minirhizatron methods; Böhm, 1979; Caldwell and Virginia, 1988) have been largely inadequate for such purposes. The application of stable isotope analyses of water at natural abundance levels in the environment and in the plant are now providing new insights on the dynamics of root functioning including the utilization of water by plants across a broad range of taxa, inhabiting a variety of natural communities (see Dawson, 1993b; Ehleringer and Dawson, 1992). Although few of these studies have explicitly addressed how the patterns of water uptake, measured on individual plants may influence the dynamics of water movement at the catchment level, we believe that several of the examples we show here can be naturally and easily extended to this level.

Plants may utilize many potential water sources depending first upon the plant and secondly upon the spatial and temporal properties of the soils and climate in a particular region. Water sources include precipitation, soil water, ground water, runoff, fog and even salt water (see Dawson, 1993b). In order to know which one of these potential sources a plant may be using, it is necessary to collect these waters and determine their stable isotopic composition (δD and $\delta^{18}O$). These values are then compared with those of the water extracted from the xylem (water transport) tissues of plants growing in the same environment. This information also provides an indirect method for determining the rooting depth of a plant when clear differences in source water δD and $\delta^{18}O$ can be identified, such as between shallow-rooted plants which use soil water and deeply rooted plants which use groundwater. Detailed descriptions on water collection methods are given by Dawson (1993b,c), Dawson and Ehleringer (1993), Thorburn et al. (1993), Thorburn and Mensforth (1993), and Lajtha and Marshall (1994). The following case studies demonstrate the power of utilizing stable isotope analyses in plant and environmental waters as an avenue for improving our understanding of water uptake patterns in plants.

6.4.1 Riparian forest communities

An important component of most catchments are the forests that grow in variable source areas (Chapter 1) adjacent to streams. These riparian forests are important because they sit at the interface between the terrestrial and aquatic portions of the catchment and thus influence the surface and subsurface fluxes of water and other substances linked to water (e.g. nutrients and dissolved organic carbon). It is often assumed that the plants (trees in particular) that inhabit these streamside communities utilize the surface stream waters. However, in an investigation in the Intermountain west of the United States, Dawson and Ehleringer (1991) demonstrated that it was only the smaller trees which used the stream water, while mature trees growing in very close proximity to the stream used little or none of this water source (Figure 6.11). An analysis of the δD in source waters and the water extracted from the xylem sap of young and mature riparian trees revealed that the larger, mature trees, were using ground water, regardless of how close they were growing to the surface water source (Dawson and Ehleringer, 1991). In reviewing the long term stream flow data for this area, it became clear that although this stream was characterized as a "perennial" water course, for some years streamflow and thus tree water supply was extremely low during the long, dry summers of this semi-arid region. Hence, mature trees which use ground water are using the most reliable water source from a long-term perspective. By investing in deeper roots, plants inhabiting these riparian forest communities ensure that during drought periods they will have ample water to meet their requirements for growth and reproduction.

At least three other studies from riparian communities in both the United States and Australia have confirmed the findings of Dawson and Ehleringer (1991), that stream side trees do not necessarily use surface stream water. For example, Thorburn and Walker (1993) and Mensforth et al. (1994) have studied the water use patterns of *Eucalyptus camaldulensis* inhabiting the semi-arid flood plains along the River Murray in south eastern Australia and found that these riparian trees use ground water and not the surface stream water, especially if they were growing at distances greater than 15 m from the stream. Trees growing closer to the stream used stream water in the summer season and soil water in the winter. However, even the streamside trees, with roots growing directly in the water were only using, on average, 50% of this water source (Thorburn and Walker, 1993). These finding were similar to those reported

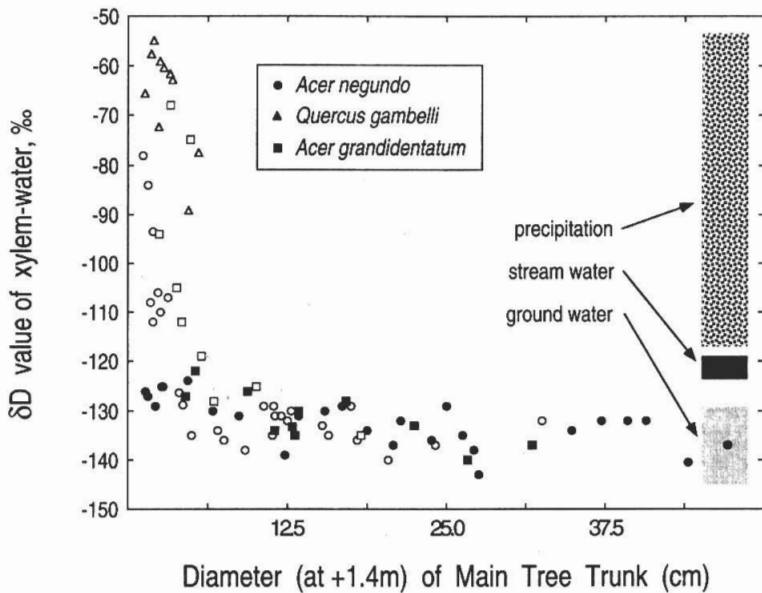


Figure 6.11. The hydrogen isotope ratio of water extracted from the xylem of three dominant tree species as a function of their size and distribution; trees growing nearest the stream are shown with open symbols and away from the stream with closed symbols. The bars along the right-hand side of the figure show the long term range of isotopic values for all of the water sources; local precipitation, stream water, and ground water (modified from Dawson and Ehleringer, 1991).

by Smith et al. (1991), who also demonstrated that riparian trees switch water sources, using water in the surface layers early in the growing season and then switching to the deeper ground water during drought periods. Another study conducted along the Colorado River in the western United States (Busch et al., 1992) has also demonstrated that the dominant riparian trees all used ground water rather than the river water (see examples reviewed in Figures 6.20 and 6.21 below). In summary, all of the studies conducted on riparian trees demonstrate that they can be very opportunistic in their water use patterns, either in time or in space. Although these also demonstrate some of the difficulty in predicting how riparian trees may behave with respect to water uptake and use, they do point out that these taxa can and do exploit several different water sources. Knowledge of this sort should make a difference in understanding how riparian trees influence catchment water balance.

6.4.2 Arid and semi-arid plant communities

Woodlands, shrub lands, savannas and deserts cover approximately 44% of the Earth's land surface (Whittaker, 1975). The plants that characterize these arid and semi-arid communities are often exposed to strong bimodal rainfall patterns (see Chapter 13 for examples). In summer, precipitation is derived from warmer climatic regions, and the isotopic composition reflects this (precipitation is more enriched in the heavy isotopes D and ^{18}O ; see Dawson 1993b). These summer rains are often very brief and thus do not penetrate very deeply into the soil layers

(Ehleringer et al., 1991). In contrast, water in the deep soil layers or in aquifers is derived primarily from winter recharge storms. These storms arrive from cooler regions that have precipitation that is significantly more depleted in the heavy isotopes D and ^{18}O (more negative) and often saturate the soil.

These bimodal rainfall patterns with different isotopic composition provide an ideal opportunity to study water uptake patterns by the diverse plant growth forms that characterize these communities. For example, Ehleringer et al. (1991) investigated differential utilization of summer rains by an array of plants living in the desert along the Utah-Arizona border in the United States. They showed that nearly half of the annual precipitation in this region is derived from summer rain. The annual plants and a shallow-rooted desert succulent relied on these summer rains, where the more deeply rooted perennial plants used a mixture of summer and winter rains or ground water (Figure 6.12). In an adjacent Pinyon-Juniper woodland, Flanagan and Ehleringer (1991) also observed that the dominant trees and shrubs used either only ground water (e.g. Utah juniper [*Juniperus osteosperma*] and rabbitbush [*Chrysothamnus nauseosus*]) or some proportion of summer precipitation and ground water (e.g. pinyon pine [*Pinus edulis*] and big sage [*Artemisia tridentata*]). Flanagan et al. (1992) extended this work and showed that pinyon pine and big sage which derived a large proportion of their water from summer precipitation also had lower predawn water potentials (greater water stress; Figure 6.13). This observation was also made by Valentini et al. (1992) for the evergreen shrubs and trees growing in the Mediterranean 'macchia' in northern-central Italy and Dawson (unpublished data) for temperate deciduous forests inhabiting central New York State in the United States (Figure 6.13). These studies showed that the species which utilize ground water also transpire more water for a given amount of carbon fixed in photosynthesis (poor water-use efficiency; see Farquhar et al., 1989). Working on Utah juniper along a gradient of summer precipitation, Gregg (1991) demonstrated that trees utilized a greater and greater proportion of deep ground water as summer precipitation became more unreliable (shown in Ehleringer and Dawson, 1992).

All of these studies demonstrate, that regardless of whether a plant inhabits arid, semi-arid, or mesic regions, there can be a strong relationship between water source and water use patterns. In cases where plants have access to deeper water sources they may not experience significant seasonal water stress and, in the end, may transpire more than plants which utilize shallow soil water (Figure 6.13). This was recently demonstrated by Dawson (1996) when he compared the water use patterns and water sources utilized by small, shallow-rooted and large, deeply-rooted sugar maple [*Acer saccharum*] trees (see below). Understanding the primary source of water for species inhabiting any region where water can become limiting should provide important insights for estimating and modeling regional-scale water balance.

6.4.3 Temperate forest communities

The very first studies which used stable isotopes in water from the xylem sap of plants were done in temperate forest communities. Temperate regions have also been the focus of some of the most extensive catchment hydrology studies (Likens et al., 1977; Bosch and Hewlett, 1982; Swank and Crossley, 1988). Oddly, no single study has merged the study of water uptake and water use by trees using stable isotopes with a hydrologic analysis of water movement at the catchment scale.

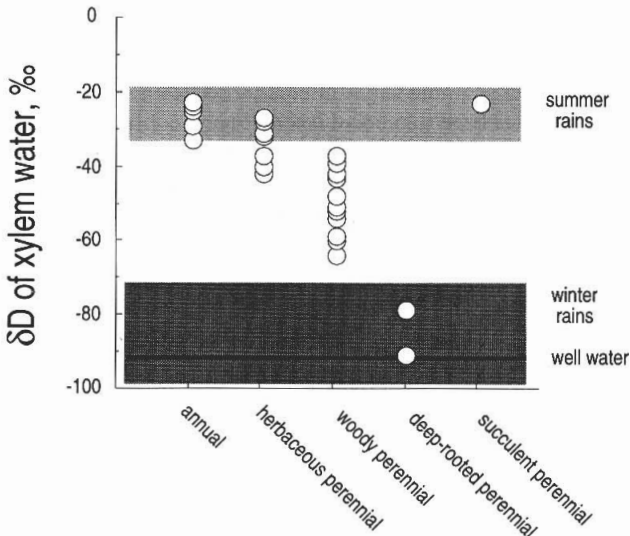


Figure 6.12. The hydrogen isotope ratio (δD) of water extracted from the xylem of several different desert plants species, grouped by life form, growing near the Utah-Arizona border, USA. The gray areas represent the range of δD values obtained for summer and winter rains which fell at the site. The solid line is the δD of well water (ground water) at this site. Based on a figure and data in Ehleringer et al. (1991).

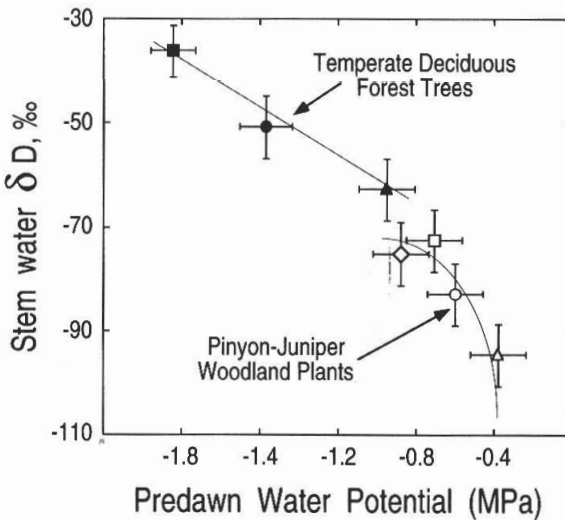


Figure 6.13. The hydrogen isotope ratio (δD) of water extracted from the xylem of a variety different trees and shrubs as a function of their predawn water potential. Open symbols are for plants growing in the semi-arid pinyon-juniper woodland in southern Utah, USA. Closed symbols are for plants growing in the temperate deciduous forests of central New York, USA. Plants noted with triangular symbols use ground water ($\delta D = -95$ and -64 ‰ for Utah and New York, respectively). Plants noted with square or diamond symbols use mostly rain water ($\delta D = -67$ and -34 ‰ for Utah and New York, respectively). Plants noted with circular symbols use some mixture of the two water sources (after data in Flanagan et al., 1992 and Dawson et al., in prep). See text for species names.

White et al. (1985) were among the first to analyze of stable isotopic variation in source waters and xylem sap extracted from tree cores. They showed that the eastern white pine, *Pinus strobus*, which inhabits a good portion of the northeastern United States, responds very quickly to summer precipitation events. Immediately after rain had fallen, trees growing in both wet and dry sites would take up water from upper soil layers (Figure 6.14). As the soils dried out, these same trees would show a shift towards using ground water or a mixture of rain water and deeper soil water (closed symbols in Figure 6.14). Interestingly, when rain water was not available, dry site trees could be shown to draw upon their heartwood water reserves, a pattern also seen in both red maple [*Acer rubrum*] and sugar maple [*A. saccharum*] inhabiting many of the same forest communities as white pine (Figure 6.15; White et al., 1985; Dawson, unpublished data). The ability of these trees to draw on both sapwood water which carries water from recent rain fall events and heartwood water which stores water from past water uptake events should be an important mechanism for buffering them against water stress and permitting them to meet their transpirational demands when soil water is limited.

Sugar maple has an additional mechanism for meeting its transpirational demands - the ability to take up water at night from deeper soil layers, transport it through its root system, and then release it into the upper soil layers where it is used the following day by both the tree itself as well as shallow-rooted neighbors growing in close proximity to these trees (Dawson, 1993c, 1996). This process is termed "hydraulic lift" (after Richards and Caldwell, 1987) and has been shown to occur now in both shrubs and trees. Utilizing stable isotope analysis of water, and standard water relations measurements, Dawson (1993c) was able to show that ground water that moved by the process of hydraulic lift into the upper soil layers by maple trees was used to some extent by all neighboring plants and that plants which were using this water source demonstrated less water stress (higher, or less negative leaf water potentials) and greater rates of stomatal conductance from their leaves (Figure 6.16). These data indicate that during drought periods water can not only move from deeper soil layers but that it can also be lost back to the atmosphere by both the trees and the adjoining plant community.

At the catchment scale this information has a number of potentially important implications. First, it means that more water moves through the soil-plant(s)-atmospheric continuum than would be expected (shown in Dawson, 1996). Secondly, a hydraulically lifted water source could have a strong influence on the distribution and abundance of *all* plant species and in turn of the amount of water movement within a catchment or forest stand. Third, estimates of E_p (from sap flow methods) and E , (from Bowen ratio data) are 1.5 to 3-fold higher for large trees "mining" deep water sources, allowing them to maintain a more favorable water status and thus greater rates of transpiration over the course of a day and the growing season (Dawson, 1996).

A common feature of the two studies cited above was the application of a mixing model as a way to determine the proportion of each water source with a unique stable isotopic signature used by a plant or plants within a particular ecological/hydrological setting. White et al. (1985, also see White, 1988) applied a model that estimated both the proportion of different water sources used by white pine trees at a particular point in time (e.g. after rain fall) as well as the proportions of surface soil water and ground water used by trees at different sites over the course of a growing season. Dawson (1993c) developed a simple two end-member mixing model to calculate the proportion of the end-members found in any xylem sap sample. The model was applied to the δD data gathered from environmental and plant-water sources. The isotopic composition of the two end-members used in the model were soil-water (SW), derived

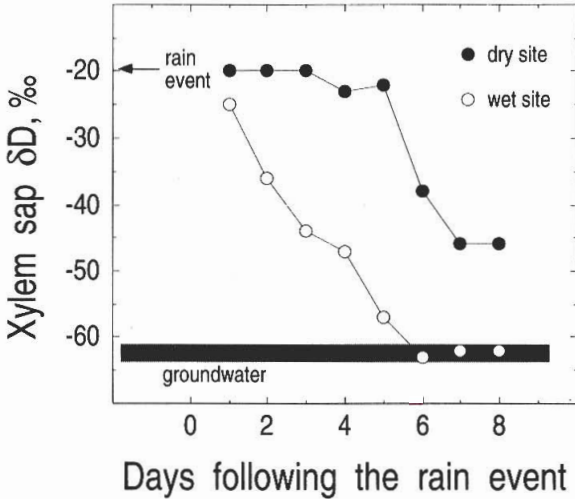


Figure 6.14. Changes in the hydrogen isotope ratio (δD) of water extracted from the sapwood of eastern white pine, *Pinus strobus*, growing in New York State, USA, following a summer rainfall event. Note that trees growing at the dry site did not have access to ground water while trees growing at the wet site did. Heartwood δD values from trees growing at the dry site were -47‰ (redrawn from data in White et al., 1985 shown in Ehleringer and Dawson, 1992).

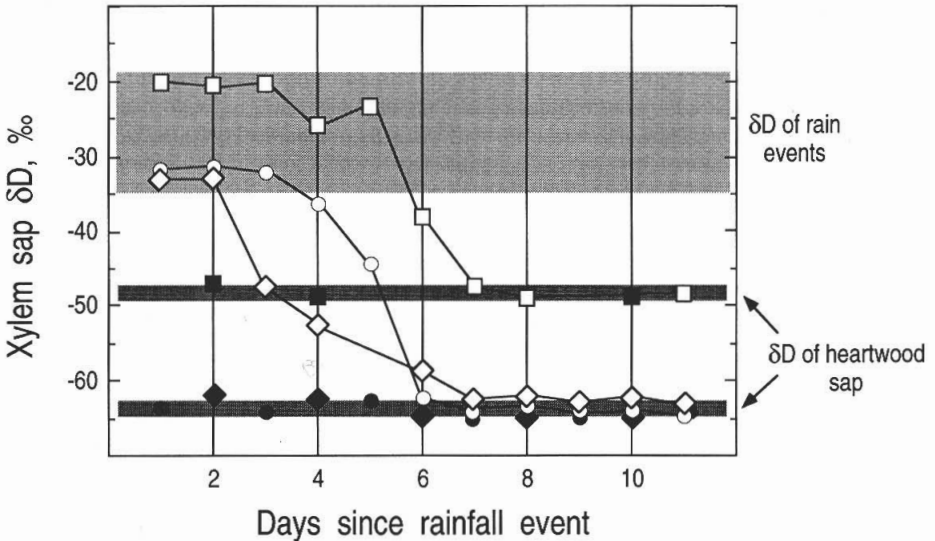


Figure 6.15. The changes in the hydrogen isotope ratio (δD) of water extracted from the sapwood (open symbols) and heartwood (closed symbols) of eastern white pine, *Pinus strobus* (squares), red maple, *Acer rubrum* (circles), and sugar maple, *A. saccharum* (diamonds), following a summer rainfall event. The trees were growing near Ithaca, New York, USA. Stippled areas show of range of δD values for rains (upper) and the lower two the δD of heartwood sap (data from White et al., 1985 and Dawson et al., in preparation).

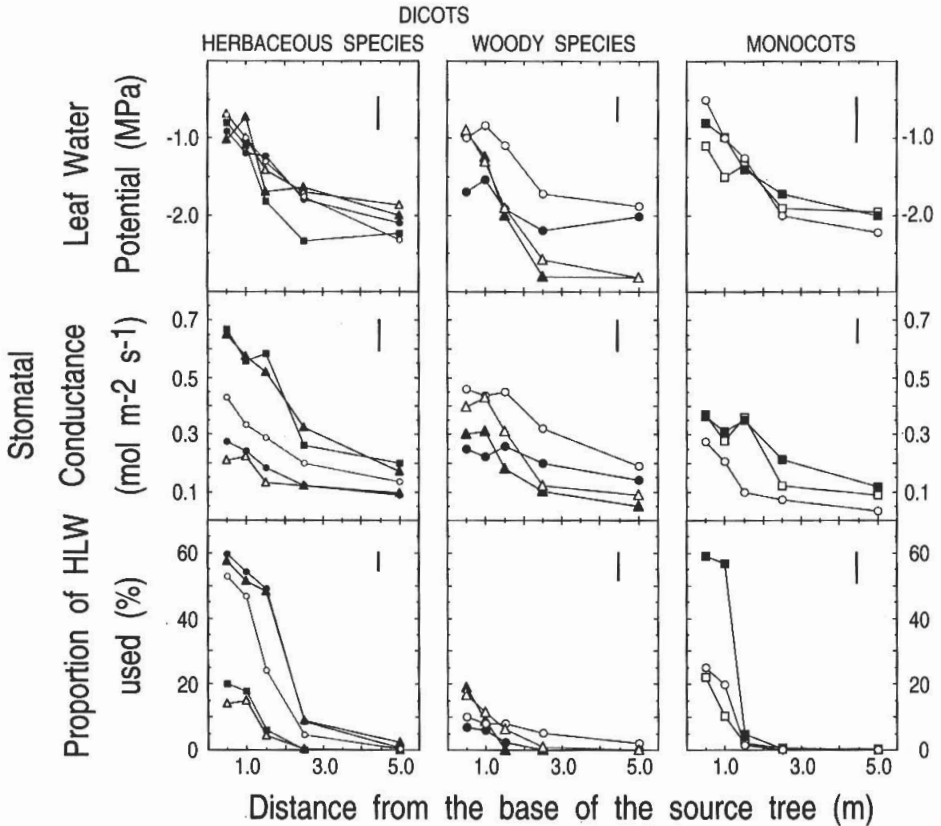


Figure 6.16. Midday leaf water potential (upper panel), maximal rates stomatal conductance to water vapor (middle panel), and the proportion of hydraulically-lifted water (*HLW*; lower panel) used by co-occurring plant taxa with mature *Acer saccharum* trees as a function of distance (m) from the tree base. The proportion of *HLW* used by these species was determined with a mixing model (Equations 6.10 - 6.12). Values are means ($n = 5$ per species at each distance). Bars in the upper right hand corner of each panel represent the standard deviation of the values which appear in that panel. For the purposes of being able to see the individual responses, plant taxa were grouped into dicot and monocot categories, and herbaceous and woody classes within the dicots. Symbols are as follows: dicots; herbaceous species, *Asarum canadense* (open triangle), *Fragaria virginiana* (closed triangle), *Thalictrum dioicum* (open circle), *Podophyllum peltatum* (closed circle), and *Solidago flexicaulis* (closed square). For dicots; woody species (central set of panels), *Vaccinium vacillans* (open triangle), *Lindera benzoin* (closed triangle), *Fagus grandifolia* (open circle), *Tilia heterophylla* (closed circle). For monocots; *Holcus lanatus* (open square), *Smilacina racemosa* (closed squares), and *Trillium grandiflorum* (open circle). Based on data taken from Dawson (1993c) and modified after Dawson, 1995. The study was conducted near Ithaca, New York, USA.

from the spring precipitation, and hydraulically-lifted water (*HLW*), derived from ground water and transported into the upper soil layers by sugar maple trees. The proportion of *HLW* in the xylem-water of a plant utilizing it is the ratio of difference along the mixing line between xylem-water (*XW*) and soil-water to the difference between *HLW* and *SW*. The difference (β) between *XW* and *SW* (β_{SW-XW}) is:

$$\beta_{SW-XW} = (\delta D_{SW} - \delta D_{XW}) \quad (6.10)$$

where δD_{SW} is the δD of the soil-water collected in a zone not influenced by hydraulic lift but at the principle rooting depth of that species, and δD_{XW} is the δD of the xylem-water extracted from each species. Further, the difference between *HLW* and *SW* (β_{SW-HLW}) can be given as:

$$\beta_{SW-HLW} = (\delta D_{SW} - \delta D_{HLW}) \quad (6.11)$$

where δD_{HLW} is the δD of hydraulically lifted water (from ground water) used during the growth period of interest. The proportion of *HLW* (P_{HLW}) in the xylem-water can then be given as:

$$P_{HLW} = \beta_{SW-XW} / \beta_{SW-HLW} \quad (6.12)$$

Dawson (1993c) points out that δD_{SW} will vary in the final calculation of P_{HLW} depending upon the unique rooting depth of each species such that plants with shallow roots will have a δD_{SW} that is less negative due to evaporative enrichment within the upper soil layers.

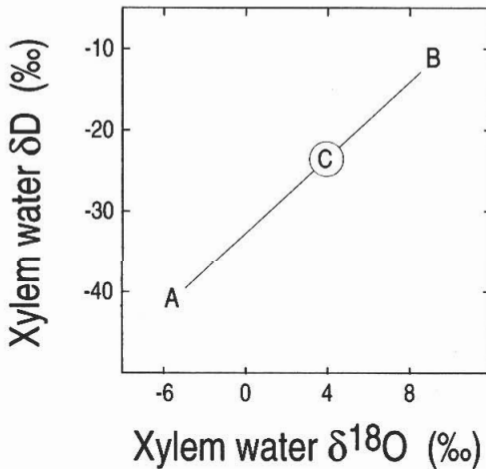


Figure 6.17. A hypothetical relationship between the stable hydrogen (δD) and stable oxygen ($\delta^{18}O$) isotopic composition of different water sources. The line connecting the points "A" and "B" is the "mixing" line. Assuming a linear relationship between A and B, this line can be used to determine the proportion of these two water sources ("end members") within the xylem sap of trees with a isotopic composition of "C" (modified from Thorburn et al., 1993).

Thorburn and Walker (1993) use a similar type of model that used both δD and $\delta^{18}O$ in the environment and the plant's xylem sap to determine the proportion of different waters that were transpired by *Eucalyptus camaldulensis* inhabiting riparian habitats exposed to soil water, ground water, or stream water (Figure 6.17). This model provided these researchers with an extremely powerful tool for demonstrating that trees of *E.camaldulensis* growing in creek-side habitats use between 0 and 45% of the creek water, and yet also used between 0 and 60% of the ground water depending upon the time of the year they sampled. Furthermore, inland trees

seemed to always use more ground water (40 - 63 %) than creek-side trees (Thorburn and Walker, 1993). All of these mixing models provide powerful ways to extend the isotope information obtained from source and plant samples towards a catchment perspective. That is, understanding not only which water sources plants are using, but the relative proportions of each provides a way to more accurately determine the water balance for plants inhabiting different community types and catchment with different physiographic characteristics (see below). The method employed by Thorburn and Walker (1993) is perhaps the most powerful since using both δD and $\delta^{18}O$ increases the precision of water budget estimates.

6.4.4 Coastal plant communities

Coastal plant communities are some of the most productive communities in the world and part of this productivity is due to the fact that water and perhaps nutrients move very rapidly through them (E_p can be as high as 1600 mm/yr of water or between 160 - 190 % of the rainfall that passes through these communities on an annual basis; Larcher, 1995). Much of the water in these communities is saline, however, and can have a marked influence on the vegetation type and thus patterns and rates of E_p . A series of studies conducted by Sternberg and coworkers (Sternberg and Swart, 1987; Sternberg et al., 1991; Ish-Shalom et al., 1992; Lin and Sternberg, 1993) have shown that along marked salinity gradients, plants demonstrate a clear partitioning of the different water sources (Figure 6.18). For example, marked transitions can be observed in the dominant plant community which grows along hydrogen isotope/salinity gradients of coastal Florida within the United States (Sternberg and Swart, 1987; Sternberg et al., 1991). At the high salinity end of the gradient which supports mangrove vegetation, the δD of source and plant waters shows direct uptake of sea water. Sea water is more enriched in the heavier isotopes D and ^{18}O . It has been shown that plant species which can take up sea water while also excluding the sea salts actually can isotopically fractionate the δD (but not $\delta^{18}O$) in water during the uptake process (an exception of the rule that no fractionation occurs during water uptake by plants; see Lin and Sternberg, 1993). Moreover, the red mangrove (*Rhizophora mangle*) grew many of its roots in an area where it had access to a water source that was less saline (near the surface; Lin and Sternberg, 1994). At the fresh water end of the gradient where the isotopic composition becomes more negative relative to sea water, hardwood hammock vegetation predominates (Figure 6.18). The use of either fresh water or sea water (and in a few cases a mixture of the two sources) coupled with different physiological tolerances among the array of coastal plant taxa leads to a diverse vegetation mosaic which are recycling all water sources through these coastal ecosystems.

Many coastal regions of the world are inundated by fog which is depleted in the heavier isotopes relative to the water source from which it was formed (Aravena et al., 1989; Ingraham and Matthews, 1988, 1990; see Chapter 3). Mooney et al. (1980b) and Rundel et al. (1991) have suggested that fog is likely an important source of water for plants, especially in coastal desert regions that receive very little or no precipitation input on annual basis (the Atacama or "fog-loma" coastal deserts of Peru and northern Chile; Aravena et al., 1989; Armesto and Vidiella, 1993). Hydrological studies within many coastal regions have shown that 25 - 75 % of all the moisture input comes from fog (Oberlander, 1956; Ornduff, 1974; Dawson, 1993b; Byers, 1953). For the Redwood (*Sequoia sempervirens*) inhabiting the coastal regions of northern California and southern Oregon in the United States, it has been estimated that between 25 - 45 % (an in some years more) of the soil moisture is fog-derived (250 mm/year;

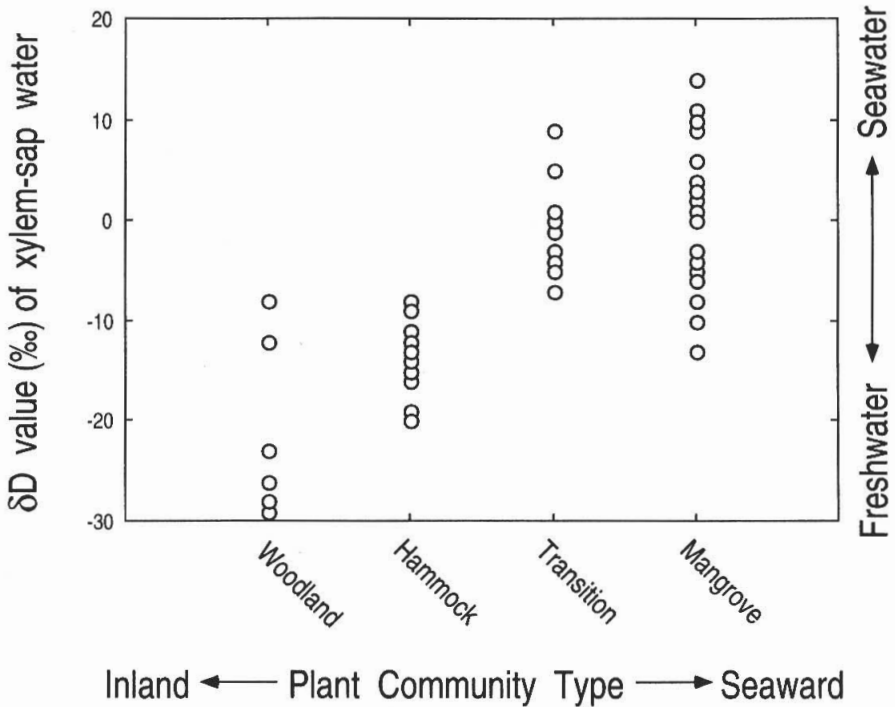


Figure 6.18. The δD of water extracted from the xylem of plants from four different coastal communities in southern Florida (USA) as a function of their position along an inland (freshwater) to seaward (seawater) gradient. Modified after Dawson (1993b); based on data in Sternberg and Swart (1987) and Sternberg et al. (1991).

Azevedo and Morgan, 1974; Harris, 1987). Much of this hydrologic input comes directly from fog-drip off of the tree foliage (Dawson, 1996 and in press). Water samples collected over the course of three years (1992 - 1994) in the redwood forests along the coast north of Arcata, California demonstrate that the plants inhabiting this region are using fog-precipitation (Figure 6.19; Dawson, 1996 and in press). Interestingly, during the summer, when fog in this region is heaviest, this water source can comprise 65% or more of the water used by many of the herbaceous and woody understory plants. In contrast, the dominant tree, *Sequoia sempervirens*, derived, on average, about 30% of its water from fog-precipitation. Ground water and deep soil water from winter rains comprised the primary water source for this tree (Figure 6.19). A similar type of process also should occur in cloud forests found in many tropical regions of the world (for example see Cavellier and Goldstein, 1989).

All of the studies cited above provide compelling evidence that the use of the stable isotopic compositions of water sources and the plants that use these sources can be a powerful tool for exploring water movement through the soil-plant-atmosphere continuum. Such studies are now forming the cornerstone for addressing current issues related to the management of water resources and have provided a solid foundation for scaling up to the entire catchment. In order to successfully accomplish this scaling effort, it is important to account for the magnitude of water flux in the soil, in surface flows and through plants inhabiting these catchments.

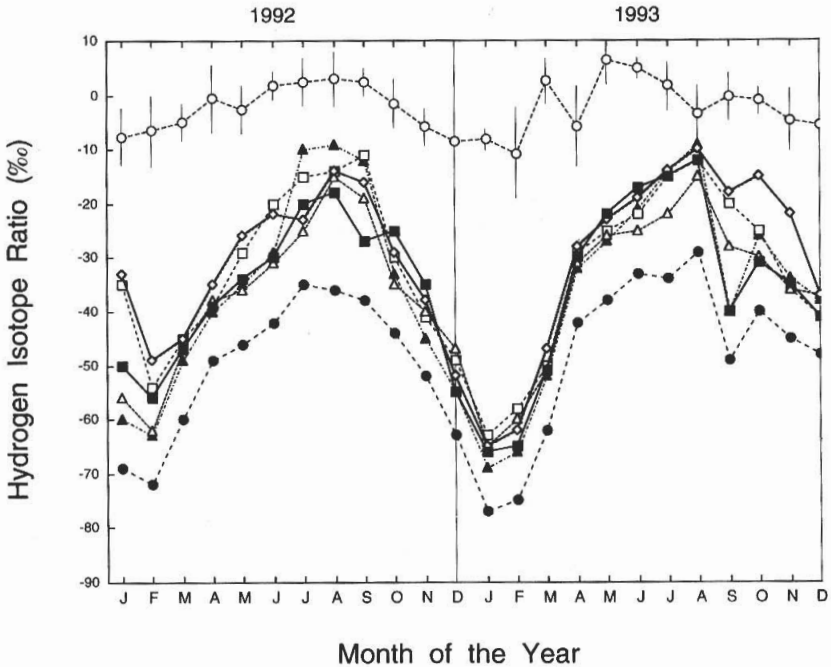


Figure 6.19. The average stable hydrogen isotope ratio (δD) of rainfall (filled circles), fog (open circles) and water extracted from the xylem of plants ($n = 15/\text{species}$) from a coastal site north of Arcata, California (USA) during the period from January 1992 through December 1993. The plants species are the coastal Redwood (*Sequoia sempervirens*; filled squares), Redwood sorrel (*Oxalis oregana*; open diamonds), California rose-bay (*Rhododendron macrophyllum*; open triangles), sword fern (*Polysticum munitum*; open squares), and salal (*Gaultheria shallon*; filled triangles). Fog was obtained from fog-collectors ($n = 10$) and from fog-drip off *S. sempervirens* foliage ($n = 7$) and pooled to obtain the mean value. Error bars on the fog data are standard deviations ($n = 17/\text{month}$). Error bars for the rainfall and plant data are not shown because they made it difficult to see the trends for each line. Variation about the mean δD values for the rainfall are $\pm 7.1\text{‰}$ in 1992, and $\pm 5.9\text{‰}$ in 1993, and $\pm 6.4\text{‰}$ and $\pm 7.4\text{‰}$ in 1992 and $\pm 8.6\text{‰}$ in 1993 for the xylem-water δD values from all of the plant species (adapted from Dawson, in press).

6.5 Current Issues Involving Plants and Catchment-Scale Hydrologic Processes

6.5.1 Invasive plants and site water balance

Increasingly, plant communities, and especially those characterized by some type of disturbance regime, are becoming dominated by invasive, highly competitive species (Heywood, 1989). Many of these species are deeply rooted (phreatophytic; literally, "well" plants), such as salt cedar (*Tamarix* spp.), that have high water requirements (Campbell and Dick-Peddie, 1964) and thus have a clear impact on many ecosystem processes, especially hydrologic processes (Vitousek, 1990). To the extent that these species continue to invade, dominate, and pre-empt water from the native vegetation, we should expect marked changes in hydrologic processes for the catchments in which they grow. In situations where these types of invaders may occur, the stable isotope analysis of source and plant waters may provide an important way for determining the potential impacts they may have on water resources and surface-subsurface

interactions at the catchment level. For example, in a recent investigation on riparian phreatophytes of the southwestern United States, Busch et al. (1992) demonstrated a close hydrologic linkage between the river, ground and soil water during the early part of the growing season and that plants used water from all of these sources. However, as drought set in, poplar and willow (*Populus fremontii* and *Salix gooddingii*, respectively) were shown to only use deeper water sources while salt cedar (*Tamarix ramosissima*) appeared to use all water sources and despite suffering greater water stress, continued to transpire (Figure 6.20). This study points out the potential of using stable isotope analysis of source and plant water in hydrologic research where there traditionally has been a strong dependence on correlative data. In this case, understanding that *Tamarix ramosissima* is a facultative rather than an obligate phreatophyte may factor prominently in management decisions that involve this invasive species. Because it uses all potential water sources, as a species *T. ramosissima* will have a significantly greater impact on catchment water balance than will any of the native plants.

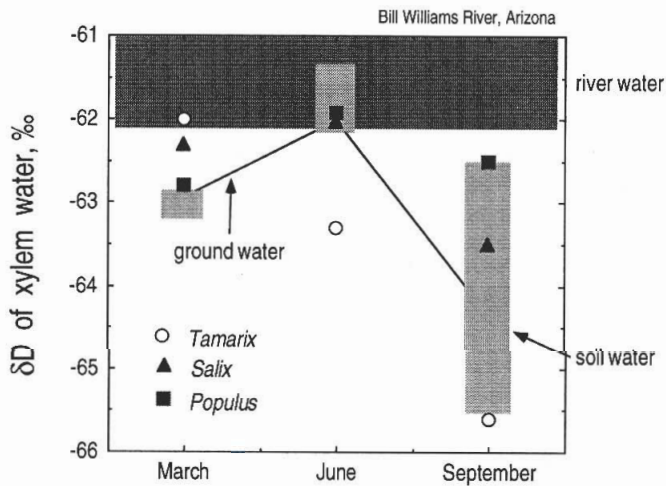


Figure 6.20. The time course of δD in the water extracted from the xylem of fremont poplar (*Populus fremontii*), willow (*Salix gooddingii*) and salt cedar (*Tamarix ramosissima*) - riparian phreatophytes - growing along the Bill Williams River (Arizona, USA; drawn from data in Busch et al., 1992). The shaded area at the top of the figure show the range of δD for river water. The stippled bars at each month is the range of δD seen for soil water at the same site. The δD of ground water is shown by the line.

6.5.2 Stream diversions and riparian manipulations

Stream diversions are an important way of providing water for human consumption and for generating hydroelectric power throughout much of the world. Work conducted by Smith et al. (1991) was designed to specifically address the effects of diverting stream water on the functional responses of riparian plants. Working at Bishop Creek along the eastern escarpment of the Sierra Nevada Mountains of California in the United States, Smith et al. (1991) evaluated the water sources used by several species over the course of the dry season and for plants growing along stream reaches where water had or had not been diverted. The δD values obtained for tree, soil, ground, and surface water suggested that early in the season trees used

water from the surface sources (soil or stream) but that as drought developed later in the season, ground water became the primary water source (Figure 6.21). In the short term, although adult trees may be able to utilize ground water if streams are diverted, juvenile trees cannot and will die. However, longer term stream diversions eventually lead to a decline in ground water levels because plants are transpiring this water source away and because the aquifer itself is not recharged annually. This will eventually lead to adult tree mortality, as well (Smith et al., 1991).

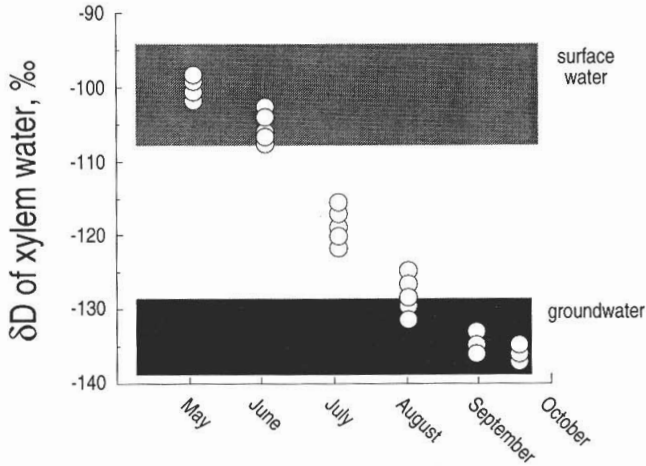


Figure 6.21. The time course of water uptake by a variety of plant species (open circles) growing along a diverted stream draining from the Sierra Nevada mountains, California (USA). The gray areas show the range of δD for surface (stream) waters and ground water (drawn from data in Smith et al., 1991).

Another example comes from the recent work along the River Murray in southeast Australia. The alteration of surface water flows and the rise of saline water tables (Jolly et al., 1993) has caused salt accumulation in the semi-arid floodplain soils in the Murray-Darling basin, Australia's largest hydrologic basin. The river red gum trees (*Eucalyptus camaldulensis*), one of the dominant trees on the floodplain, are now experiencing radical changes in water logging and salinity as a result of this altered hydrologic regime. Interestingly, isotopic evidence showed that these trees use a significant proportion of the highly saline ground water each year (Mensforth et al., 1994) and this is having a significant impact of the trees' water relations (Thorburn et al., 1994) as well as on the long-term health of the forests which live along this altered floodplain (Jolly et al., 1993). These types of investigations provide an excellent example of how powerful the stable isotope method can be for understanding how the manipulation of riparian hydrology can impact not only the water itself but also the vegetation that depends upon it.

6.5.3 Deforestation, reforestation and desertification

The loss of forest cover by either natural disturbance or human-induced deforestation causes radical changes in local and regional climatic conditions, and in the hydrology of an area once

forested (Bruijnzeel, 1991). Generally, when trees are removed from a parcel of land, the radiation and heat load increases markedly (e.g. 2.5 to 3.5EC over the Amazon Basin; Shukla et al., 1990) and, as a consequence, the water stress visited upon the remaining trees or on trees adjoining the deforested land increases dramatically (Covich, 1993). The removal of trees caused E_p , on both a catchment and on a plot basis, to decline by 30% (Shukla et al., 1990) or more due to a loss of canopy leaf area. Furthermore, as water and heat stress increase on a deforested region, the remaining trees generally close their stomata and as such E_p declines (Johns, 1992). In addition, as pointed out above, runoff will increase in deforested catchments and thus the water that would normally reside in either the soils or the vegetation is lost from the catchment.

At the regional level it is known that plant transpiration can be responsible for recycling up to 80% of the precipitation that falls on a forested region (Gleick, 1993). As a result, loss of the forest trees results in a reduction of average rainfall by 25% or more, especially in the rain forest regions of the Amazon Basin (Shukla et al., 1990) and West Africa (Fearnside et al., 1990). Deforestation also leads to a net reduction in the primary productivity of a catchment and thus directly impacts both the hydrologic and carbon cycles and indirectly impacts the mineral cycles (Likens et al., 1977). In stands of trees that can be shown to use water from a variety of sources, particularly deeper sources like ground water, tree removal should have a marked influence on the magnitude of surface/subsurface hydrologic interactions as well as the strength of hydrological linkages between surface, soil, and ground water. For example, Dawson (1993c, 1996) has conjectured that if sugar maple trees, which conduct hydraulic lift, are removed from a catchment, the subsurface waters that were once linked by this process to surface layers are now disconnected and this should have a marked influence on the remaining plants in the community (see Figure 6.16 and Section 6.4.3). The absence of hydraulic lift might, in turn, cause a decline in the biogeochemical cycling driven by this subsurface-to-surface water movement. In fact, a comparison of individual tree leaf water potential and E_p for large sugar maple trees (conducting hydraulic lift) versus small trees where there was no lift (i.e. no access to ground water) demonstrates quite clearly how important trees that have access to deeper water sources can be on the speed and magnitude of water discharge from the forest stand (Figure 6.22).

One extreme ecological outcome of deforestation and the subsequent climate changes that come with it is *desertification*, or the conversion of once vegetated land to a vegetationless state by the activities of man. Nine million square kilometers of the arid and semi-arid regions of the world have been converted to deserts by the loss of vegetation and increased aridity, salinity, and/or loss of valuable soil (Dregne, 1983; Bruijnzeel, 1991). One third of this area is in the Sahel region of Africa. The process of desertification, like deforestation, leads to a decrease in average precipitation, increased wind-induced soil loss and erosion, and an overall loss of soil water holding capacity for both crops and any remaining native plants. Although we could find no study which has investigated plant water use, stable isotopes, and desertification *per se*, such an investigation could provide important insights as to which hydrologic processes lead to this extreme alteration in landscape level water balance.

The work of Jolly et al. (1993) comes close to making this linkage. They showed a link between tree death and increasing salinity and how the modified hydrologic regime might be manipulated to slow or even reverse the desertification process. Isotopic analyses of ground and soil water were an integral part of this study and their data raised a very important issue about

reforestation of arid lands. For example, it would be interesting to know if areas that have been essentially converted to desert could be rehabilitated and revegetated by reforestation practices with extremely drought tolerant or phreatophytic plants. An analysis of plants which use deep water sources (e.g. in Section 6.5.1) and how they deal with an altered hydrologic regime (e.g. in Section 6.5.2) may be one important step in developing rehabilitation procedures. Reforestation has clearly been shown to alter and improve catchment level water balance (Swank and Crossley, 1988). Studies which attempt to merge the philosophy of ecosystem rehabilitation with research on hydrologic and plant water use using stable isotopes may hold great promise in our attempts to understand how to slow and/or reverse the processes of deforestation and desertification.

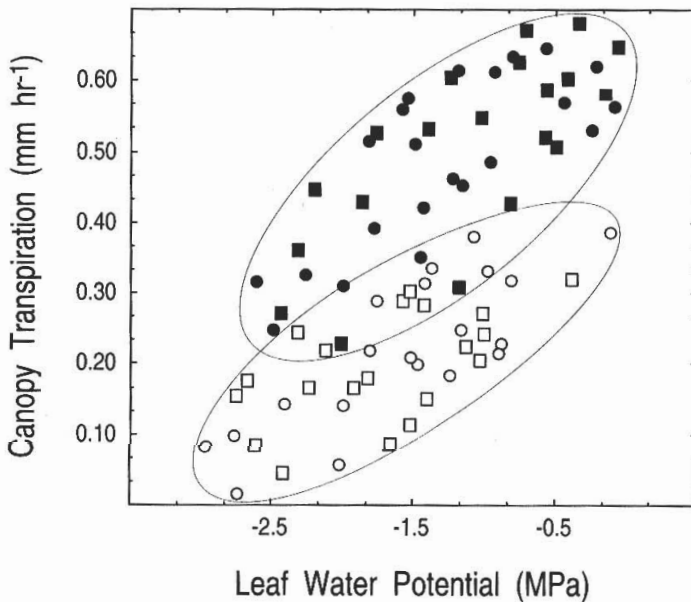


Figure 6.22. The canopy transpiration rate (E_p ; see Equation 6.4) for *Acer saccharum* (sugar maple) as a function of midday leaf water potential for large trees conducting hydraulic lift (closed symbols) or small trees which had no hydraulic lift (open symbols). The E_p data were collected from trees using sap flow, porometric and Bowen ratio methods. Circles around the points represent the ranges seen for both small and large trees (modified after Dawson, 1996).

6.6 Long-term Record of Water Use by Plants

We have shown how the application of stable isotopes can provide valuable information on the short-term dynamics of water uptake and water use by plants from a variety of different ecosystems. One of the greatest challenges, however, is understanding to what extent these short-term data can provide insights over greater lengths of time. The well established field of dendrochronology was founded on the premise that analysis of the information "recorded" in tree rings and the cellulose that composes them is a way to obtain this long-term perspective (Fritts, 1976).

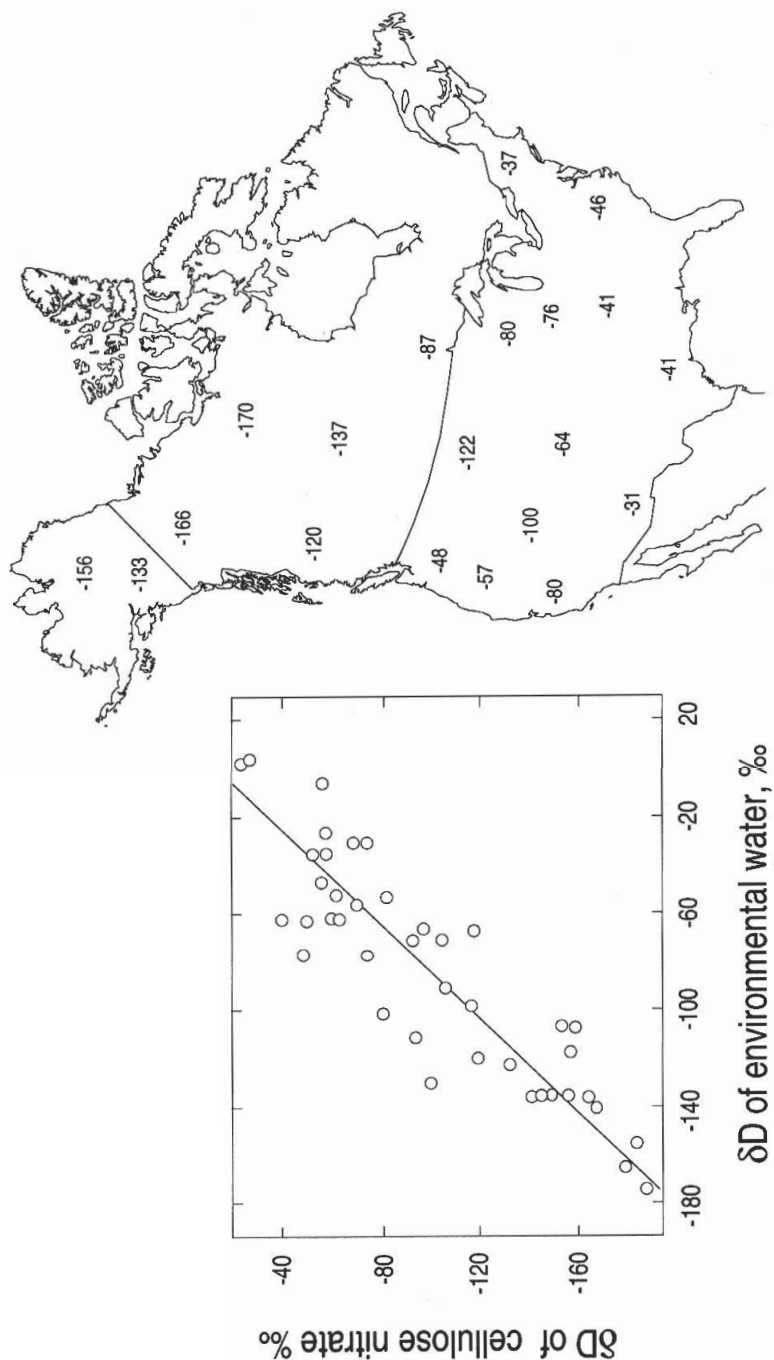


Figure 6.23. The correlation between δD of cellulose nitrate in tree rings of selected tree species inhabiting North America and the δD of the environmental water source they were using (based on a figure in Yapp and Epstein, 1982b - from Ehleringer and Dawson, 1992). The distribution of δD of cellulose nitrate in tree rings of selected tree species inhabiting North America (map at right; based on information in Yapp and Epstein, 1982a - modified from Ehleringer and Dawson, 1992).

Early investigations which used the analysis of the nonexchangeable hydrogen and oxygen isotopes in tree ring cellulose provided important information on past climates. For example, when the isotopic ratio of cellulose (which has been nitrated to remove the hydrogen isotopes that can exchange with water in the plant after the cellulose is synthesized) was determined, Yapp and Epstein (1976; 1982a, b) discovered that it was strongly correlated with the hydrogen isotopic ratio of local precipitation (or better, the meteoric water) present in the area where the trees were growing (Figure 6.23). Because there is also a significant correlation between the δD and $\delta^{18}O$ of precipitation and the temperature at the time when it fell (between 5.5 and 5.81 per °C, they used tree-ring data to reconstruct past temperatures (Yapp and Epstein, 1982a,b; Gray and Song, 1984). Thus, the potential for reconstructing past climates from the isotopic composition of tree ring cellulose was established. Yakir et al. (1994) extended this work and showed that comparison of the $\delta^{13}C$ and $\delta^{18}O$ in tamarix wood from the Roman siege rampart with present-day tamarix growing in the Masada region of Israel, indicated that ancient trees lived in a less arid climate compared to extant trees.

These studies using oxygen isotopic analyses in wood cellulose were successful because there is constant isotopic fractionation (enrichment) of 27‰ between water in the leaf and that which ends up in the cellulose (Sternberg and DeNiro, 1983; Sternberg et al., 1986; Yakir and DeNiro, 1990). A similar single fractionation factor has not been found for hydrogen isotopes in wood cellulose. In fact, the data which do exist would initially suggest little or no fractionation (Yakir, 1992; Dawson, 1993c; White et al., 1994). Instead it is more likely that there are two large fractionation events that are opposite in direction (possibly one in the leaf and another in the stem) which offset each other giving the appearance of little isotopic fractionation between environmental water and non-exchangeable hydrogens in cellulose. Yakir and DeNiro (1990) and White et al. (1994) have developed competing models to explain the environmental and biochemical factors influencing hydrogen isotope ratios in tree-ring cellulose.

Whether the mechanism proposed by either group turns out to be correct or not, using the correlation shown in Figure 6.23 still provides a very powerful tool for reconstructing the water use histories of plants. They may also provide a way to examine long-term water use patterns in forested catchments (also see Dawson, 1993b). If changes in the hydrology of a catchment influence the sources of water the trees are using, then the analysis of the hydrogen and oxygen isotopic composition of tree rings may provide a method to gain a historical perspective on the catchment water balance. The method also provides a way to integrate information on plant water use in time, just as the water uptake studies cited above provide a greater spatial perspective. Many more applications of stable isotope tree-ring analyses are likely to contribute to our long-term understanding of annual fluctuations in catchment hydrology once we have a mechanistic understanding of what influences the hydrogen isotope ratios of cellulose.

6.7 Merging the Study of Stable Isotopes in Water with Studies of Water Uptake and Water Use in Plants and the Hydrology of Catchments

In this chapter we have tried to show (1) how an understanding of the process of water transport, as influenced by plants, may be important at the catchment scale, (2) how plants use and modify soil and ground water and how they regulate water movement at the individual and stand level, and (3) how stable isotope analysis of plant- and source-waters are providing new insights into the patterns of water movement, uptake and use for a variety of ecosystems and plant types on both a short-term and long-term basis.

We know of no single study that has drawn these three areas together into an integrated perspective on the role of plants in hydrologic processes at the catchment scale. Recently, there have been a number of studies that have used a variety of isotope, energy balance, and water relations methods to gain a greater understanding of water use (E_p) in trees and forests and how it is influenced by the either water sources available to the plants or the hydrologic properties of the area they inhabit (examples are: Walker and Richardson, 1991; Calder, 1992a and references therein; Dugas et al., 1993; Thorburn et al., 1993; Dawson, 1996). An isotope tracer approach advocated by Calder (1992) and Dugas et al. (1993) is an important step towards integrating isotope tracers, measures of plant transpiration, and hydrology together. One drawback of this approach, however, is that the isotope tracer method is invasive and may influence the hydraulic conductivity of the tree and thereby the transpiration estimates (e.g. the injection method will cause air embolisms to form in the water conducting tissues of a tree and thus significantly change estimates of transpiration since the "natural" flow path has been altered; see Tyree and Sperry, 1989). Furthermore, the tracers themselves are either radioactive or enriched in stable isotopic composition and thus cannot be used in natural plant stands or compared to isotope studies at natural abundance levels. Lastly, the majority of similar work that has been done is on single trees or young, even-aged, plantation grown trees. As such, it is not clear how these methods may apply to trees growing in natural stands and non-uniform catchment terrain.

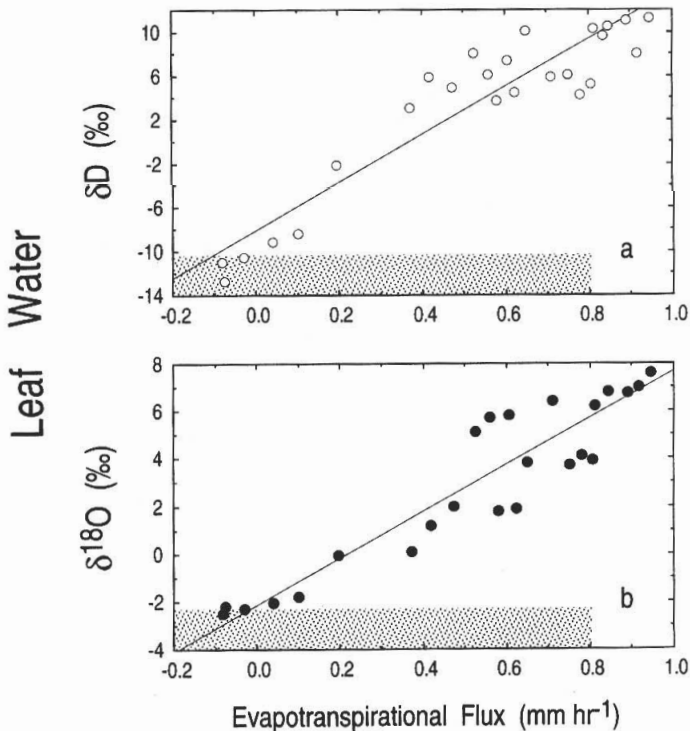


Figure 6.24. The relationship between " E_t flux" determined by aerodynamic-energy balance methods and (a) the δD and (b) the $\delta^{18}O$ of leaf water extracted from alfalfa (redrawn from Bariac et al., 1989).

A recent study by Dawson (1996) has advocated a variation on the methods used by Calder, Dugas, and others for natural forested catchments. Here, the stable isotope methods and approaches presented above were coupled with detailed analyses of evaporation (Bowen ratio) and transpiration (sap flow) measured separately and on trees growing in a defined area. As shown above (Figure 6.22), this approach allowed Dawson to simultaneously measure water loss from the stand while identifying the sources of water used by different sized trees. Ideally, this approach could be extended to also measure the isotopic composition of the water leaving the canopy or forest stand as a way to combine an understanding of the rates and magnitudes of water movement through the stand to the water sources used by trees. Bariac et al. (1989) present part of such a research program with field-grown alfalfa. By evaluating water fluxes from stable isotope information at natural abundance levels, energy budget techniques, and plant physiological measurements, in a field where soil water inputs were well known, they were able to link the daily changes in plant transpiration to a) water uptake patterns, b) water storage capacity of the plant, and c) to the fluctuations in aerodynamic regime, stomatal opening and water supply in the soil (Figure 6.24). Brunel et al. (1992), Simpson et al. (1992), and Wang et al. (1995) have applied similar methods to other crops. Such an approach should also be feasible for trees growing in well-defined catchments or regions. In fact, it is now possible to merge eddy correlation techniques used to understand forest mass and energy exchanges (e.g. Hollinger et al., 1994) with stable isotope tracer methods so that ecosystem pools and fluxes can be partitioned. This approach, called relaxed eddy-accumulation (see Pattey et al., 1993), will help in providing realistic estimates of E_p and E_t as well as identifying the water sources from which they came so that their relative importance and contribution to the hydrologic balance of the catchment will be independently measured rather than estimated by difference.

Understanding what influences the hydrologic cycle has and will continue to be important for ecological, economic and social reasons (Gleick, 1993). We believe that there is much to be gained by applying the stable isotope techniques cited above towards elucidating the role that plants play in the hydrologic cycle; such a research agenda should be part of all future hydrologic research. For this goal to be realized, however, it will be important for plant biologists and hydrologists who are employing isotope tools and tracers in their research to collaborate.

Acknowledgments

We would like to thank the editors for inviting two "outsiders" to the field of catchment and isotope hydrology to contribute our perspective to this volume. In preparing this chapter, discussions with Dennis Baldocchi, Monica Geber, Tom Hatton, Tom Hinckley, David Hollinger, Paul Jarvis, Keith McNaughton, Lisa Mensforth, John Pate, Roman Pausch, Detlef Schulze, Peter Thorburn, Riccardo Valentini, Rob Vertessy, and Glen Walker about merging the study of tree water use with forest and catchment hydrology using stable isotopes helped clarify many of the issues and our ideas. The comments of Ronald Amundson, Joel Gat, Greg Lewis, Sandy Tartowski, and Peter Thorburn were all very helpful in making revisions to an earlier draft of this chapter. We would also like to acknowledge the support of the Ecological Research Division at the Office of Health and Environmental Research, United States Department of Energy, the National Science Foundation, The Andrew W. Mellon Foundation, Cornell University, and the University of Utah.

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