

# Eco-Hydrology

Plants and water in terrestrial  
and aquatic environments

*Edited by*

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# INTRODUCTION

*Andrew J. Baird*

## WHAT IS ECO-HYDROLOGY?

Eco-hydrology, as its names implies, involves the study of both hydrology and ecology. However, before attempting a definition of eco-hydrology, and therefore a detailed description of what this book is about, it is useful to consider briefly how hydrology and ecology have been studied separately and together in the past. As a *discipline*, hydrology has a long history, which has been described in detail by Biswas (1972) and Wilby (1997a). As a *science*, its origins are more recent. Bras (1990: p. 1) defines modern hydrology as 'the study of water in all its forms and from all its origins to all its destinations on the earth.' Implied in this definition is the need to understand how water cycles and cascades through the physical and biological environment. Also implied in this definition is the principle of continuity or the balance equation; that is, in order to understand the hydrology of a system we must be able to account for all inputs and outputs of water to and from the system as well as all stores of water within the system. As noted by Baird (1997) after Dooge (1988), the principle of continuity can be considered as the fundamental theorem or equation in hydrology. The dominance of the principle is relatively recent, and it is surprising to discover that the earliest hydrologists were unable to perceive that rainfall was the only ultimate source of stream and river flow. Remarkably, it was not until the studies of Palissy (1510–1590) that it was realised that rain falling on a catchment was sufficient to sustain stream discharge (Biswas, 1972: p. 152). Much of the history of hydrology is dominated by the necessity to secure and distribute potable water supplies (Wilby, 1997a). The discipline, therefore, has an engineering background.

Today, hydrology is still in large part an engineering discipline concerned with water supply, waste water disposal and flood prediction and, as studied by engineers, has close links with pipe and channel hydraulics. This link between hydrology and hydraulics together with the practical application of hydrological knowledge often forms the focus of standard hydrology and hydraulics textbooks written for engineering students, such as Chow (1959),

Jonasson *et al.* (1997), Stocker *et al.* (1997), Bruijnzeel and Veneklaas (1998) and Hall and Harcombe (1998). However, the term 'eco-hydrology', which is used to describe the study of these links, seems to have been coined originally to describe only research in wetlands (see, for example, Ingram, 1987) and appears to have been in use by wetland ecologists for at least two decades (G. van Wirdum and H.A.P. Ingram, personal communication). In an editorial of a collection of papers on eco-hydrological processes in wetlands in a special issue of the journal *Vegetatio*, Wassen and Grootjans (1996: p. 1) define eco-hydrology purely in terms of processes occurring in wetlands:

Ecohydrology is an application driven interdisciplin [*sic*] and aims at a better understanding of hydrological factors determining the natural development of wet ecosystems, especially in regard of their functional value for nature protection and restoration.

It is instructive to read the papers in the special issue of *Vegetatio*, because they give an insight into how users of the term 'eco-hydrology' conduct their research. A recurrent theme of the papers is that hydrological, hydrochemical and vegetation patterns in the studied ecosystems are measured separately and *then* related to each other. This is particularly evident in the papers of Wassen *et al.* (1996), who compare fens in natural and artificial landscapes in terms of their hydrological behaviour, water quality and vegetation composition, and Grootjans *et al.* (1996a), who investigate vegetation change in dune slacks in relation to ground water quality and quantity. Somewhat surprisingly, manipulative experiments, whether in the laboratory or in the field, on factors affecting growth of plants do not figure highly in the research programmes presented. A second theme in the papers is that of the practical application of scientific knowledge to ecosystem management, especially for nature conservation. The compass of eco-hydrology as defined by these papers would, therefore, appear to be somewhat narrow. First, the term is used to describe wetlands research. Second, it describes predominantly field-based research where links between hydrological and ecological variables are sought; it does not appear to include manipulative experiments. Third, the term is associated with practical application of scientific ideas, especially in nature conservation. Interestingly, and somewhat confusingly, Grootjans *et al.* (1996b; cited in Wassen and Grootjans, 1996) appear to recognise that the term can be applied more widely. To them, 'ecohydrology is the science of the hydrological aspects of ecology; the overlap between ecology, studied in view of ecological problems.' Although broader, this definition still includes an emphasis on solving ecological 'problems', where presumably these are similar to the conservation problems mentioned above.

Very recently, Hatton *et al.* (1997) have used the term to describe plant-water interactions in general and suggest that Eagleson's (1978a-g) theory of an *ecohydrological equilibrium* should form the focus of eco-hydrological



research. The ideas of Hatton *et al.* on eco-hydrological modelling are discussed briefly later in this volume (Baird, Chapter 9; see also below).

## THE SCOPE OF THIS TEXT

In this book, a wider definition than either (Wassen and Grootjans, 1996; Grootjans *et al.*, 1996b) given above is used. In recognising that *eco* is a modifier of *hydrology* it could be argued that eco-hydrology should be more about hydrology than ecology. However, it is undesirable and probably impossible to consider the links between plants and water solely in terms of how one affects the other. Thus, while this book tends to focus on hydrological processes, it also considers how these processes affect plant growth. Additionally, as noted above, there is no intrinsic reason why eco-hydrology should be solely concerned with processes in wetlands. Eco-hydrological relations are important in many, indeed probably all, ecosystems. Although such linkages are very important in wetlands, they are arguably of equal importance in forest and dryland ecosystems, for example. Therefore, an attempt is made in this volume to review eco-hydrological processes in a *range* of environments, thus following the broader definition of eco-hydrology implied by Hatton *et al.* (1997). Eco-hydrological processes are considered in drylands, wetlands, forests, streams and rivers, and lakes. However, it is probably impossible to compile a volume which looks at every aspect of eco-hydrology. In recognition of this, the book focuses on plant–water relations in terrestrial and aquatic ecosystems. Thus the role of marine ecosystems in the global hydrosystem, although extremely important and acknowledged in the conclusion, is not considered in any detail. Full consideration of the topic would require a volume in its own right. For similar reasons, the role of water as an environmental factor controlling animal populations is not dealt with. Even with the focus on terrestrial and aquatic ecosystems it has been impossible to provide a comprehensive overview of all ecosystems. Thus, eco-hydrological processes in tundra and mid-latitude grasslands, for example, are not discussed. Despite this selective focus, it is hoped that the material presented herein will still reveal the key research themes and perspectives within eco-hydrology. Finally, in this volume a range of eco-hydrological research methods, including manipulative experiments, are reviewed.

Each of the five chosen environments or ecosystem types mentioned above are dealt with in Chapters 4 to 8. In Chapter 4, John Wainwright, Mark Mulligan and John Thornes consider eco-hydrological processes in drylands. The authors look at how dryland plants cope with generally low and highly variable amounts of rainfall. They consider how plants affect runoff and water-mediated erosion in drylands. The issue of scale is also dealt with. Spatially, the role of small-scale process interactions on large-scale soil–vegetation–atmosphere transfers (SVAT) in drylands is considered.

Temporally, vegetation evolution in the Mediterranean is considered in terms of climate change.

In Chapter 5, Bryan Wheeler looks at water and plants in wetlands. The bulk of the chapter considers how water levels in wetlands exert a control on plant growth and survival. Wheeler notes that it is vital to consider more than just bulk amounts of water; water level regime can exert as much control on plant growth as can absolute level. However, despite ample evidence for water levels affecting plant growth, it is clear that simple deterministic relationships between level or regime and vegetation species composition have remained elusive. Complicating factors in the relationship between vegetation composition and water levels include the source of the water, which affects its nutrient status, and the effect of water on other processes within wetland soils such as oxidation–reduction (redox) reactions. Wheeler also considers the role of plants in affecting wetland water levels, principally through their control of the structure of the organic substrate found in many wetlands.

In Chapter 6, John Roberts explores the relationships between plants and water in forests. The emphasis here is on how trees affect the delivery of water to the ground surface and how they affect soil moisture regimes through the processes of evapotranspiration. Emphasis is placed on methods of measuring and modelling the various processes considered, especially canopy interception and transpiration. Roberts focuses on processes in temperate forests and tropical rain forests, and draws comparisons between water transfer processes in the two. He acknowledges that relatively little is known about plant–water relations in boreal and mediterranean forests and that these ecosystems should form the focus of future studies of forest hydrology.

Chapter 7, written by Andrew Large and Karel Prach, considers plants and water in streams and rivers. Plants exert a considerable influence on the hydraulic properties of channels, principally through their effect on channel roughness or friction to flow. The exact effect will depend on river stage and the species composition and density of in-channel vegetation. Flow regime, in turn, has a profound effect on plant growth and survival in channels. If the flow is too powerful, plants can become uprooted from the channel substrate or cannot become established. Equally, the stability of the substrate, itself related to flow regime, can affect rooting of in-channel plants. As in wetlands, hydrological regime is as important as mean conditions, and floods and droughts can pose special problems for plants growing in channels.

In Chapter 8, Robert Wetzel examines plants and water in lakes. The role of plants in controlling lake water levels is considerable. Here it is the littoral vegetation that is most important. Although planktonic organisms can modify thermal conditions and influence evaporation, stratification and related mixing processes in open water, they are of relatively minor importance in the hydrology of lake basins as a whole. Indeed, evapotranspiration from lake-edge vegetation can be several times greater than open-water evaporation, and can

exceed other forms of water loss from lake systems. The drawdown of lakeside water tables can in turn change patterns of groundwater flow to and from a lake. Wind-generated water movements within lake waters transport sediment and nutrients and can, therefore, affect where plants are able to become established within the lake system. These water movements are also greatly affected (reduced) by the presence of littoral emergent vegetation.

To underpin and augment the thematic material on particular environments, three 'generic' chapters have been included. In the first of these, Chapter 2, Melvyn Tyree looks at the water relations of plants. The purpose of this chapter is to provide the reader with basic information on how plants use water. Many existing hydrology textbooks consider transpiration briefly, but few look in detail at the movement of water from roots to leaves and the effect of waterlogging and drought on plant growth and survival. Thus Chapter 2 provides a basic foundation for all the other chapters, but in particular Chapters 4 to 8. One theme within Chapter 2 is scale: water relations of plants are considered at the scale of the cell, whole plants and stands of plants. The theme is continued in Chapter 3, where Robert Wilby and David Schimel demonstrate how eco-hydrological relations can be considered at different spatial and temporal scales. Scale is an increasingly important theme in both hydrology and ecology, and it is important to understand how different eco-hydrological processes can be represented at different scales, from the small research plot to the regional and global scale. It is also important to consider how we can link observations made at different scales and how we can evaluate the effect of processes occurring at one scale on larger- and smaller-scale processes. In Chapter 9, Andrew Baird considers the role of models in eco-hydrology. Models are frequently used to formalise understanding of environmental processes and for theory testing. The growing importance of, and need for, eco-hydrological models is stressed. However, it is important that models are sensibly designed in order to improve scientific understanding of eco-hydrological processes. There is the persistent danger that models can become over-complex abstractions of reality that are difficult to understand and use.

The volume concludes with Chapter 10, in which Robert Wilby suggests future directions in eco-hydrological research. He returns to the theme of scale and considers the prospects for a planetary-scale eco-hydrology. He also examines the role of an experimental approach within eco-hydrology and looks at how an understanding of eco-hydrological processes can be used in the management of human-impacted ecosystems.

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# WATER RELATIONS OF PLANTS

*Melvin T. Tyree*

## INTRODUCTION

Water relations of plants is a large and diverse subject. This chapter is confined to some basic concepts needed for a better understanding of the role of plants in eco-hydrology, and readers seeking more details should consult Slatyer (1967) and Kramer (1983).

First and foremost, it must be recognised that water movement in plants is purely 'passive'. In contrast, plants are frequently involved in 'active' transport of substances; for example, membrane-bound proteins (enzymes) actively move  $K^+$  from outside cells through the plasmalemma membrane to the inside of cells. Such movement is against the force on  $K^+$  tending to move it outwards, and such movement requires the addition of energy to the system to move the  $K^+$ . Energy for active  $K^+$  transport is derived from ATP (adenosine triphosphate). While there have been claims of active water movement in the past, no claim of active water transport has ever been proved.

Passive movement of water (like passive movement of other substances or objects) still involves forces, but passive movement is defined as spontaneous movement in a system that is already out of equilibrium in such a way that the system tends towards equilibrium. Active movement, by contrast, requires the input of biological energy and moves the system further away from equilibrium or keeps it out of equilibrium in spite of continuous passive movement in the counter-direction. The basic equation that describes passive movement is Newton's law of motion on Earth where there is friction:

$$v = (1/f)F \quad (2.1)$$

where  $v$  is velocity of movement ( $m\ s^{-1}$ ),  $F$  is the force causing the movement (N) and  $f$  is the coefficient of friction ( $N\ s\ m^{-1}$ ).

In the context of passive water or solute movement in plants, it is more convenient to measure moles moved per s per unit area, which is a unit of measure called a flux density ( $J$ ). Fortunately, there is a simple relationship

between  $J$ ,  $v$  and concentration ( $C$ ,  $\text{mol m}^{-3}$ ) of the substance moving:  $J = Cv$ . Also, in a chemical/biological context, it is easier to measure the energy of a substance, and how the energy changes as it moves, than it is to measure the force acting on the substance. Passive movement of water or a substance occurs when it moves from a location where it has high energy to where it has lower energy. The appropriate energy to measure is called the chemical potential,  $\mu$ , and it has units of energy per mol ( $\text{J mol}^{-1}$ ). The force acting on the water or solute is the rate of change of energy with distance, hence  $F = -(d\mu/dx)$ , which has units of  $\text{J m}^{-1} \text{mol}^{-1}$  or  $\text{N mol}^{-1}$  (because  $\text{J} = \text{N m}$ ). So replacing  $F$  with  $-(d\mu/dx)$  and  $v$  with  $J$  we have:

$$J = -K (d\mu/dx) \quad (2.2)$$

where  $K$  is a constant  $= C/f$ . Equation (2.2) or some variation of it is used to describe water movement in soils (Darcy's law – see Chapter 9) and plants. The variations on equation (2.2) generally involve measuring  $J$  in  $\text{kg}$  or  $\text{m}^3$  of water rather than moles and measuring  $\mu$  in pressure units rather than energy units.

## WATER RELATIONS OF PLANT CELLS

The water relations of plant cells can be described by the equation that gives the energy state of water in cells and how this energy state changes with water content, which can be understood through the Höfler diagram. First let us consider the factors that determine the energy state of water in a cell.

The energy content of water depends on temperature, height in the Earth's gravitational field, pressure and mole fraction of water ( $X_w$ ) in a solution. For practical purposes, we evaluate the chemical potential of water in a plant cell in terms of how much it differs from pure water at ground level and at the same temperature as the water in the cell; i.e., we measure

$$\Delta\mu = \mu - \mu_0 \quad (2.3)$$

where  $\mu_0$  is the chemical potential of water at ground level at the same temperature as the cell. It has become customary for plant physiologists to report  $\Delta\mu$  ( $\text{J mol}^{-1}$ ) in units of  $\text{J}$  per  $\text{m}^3$  of water because this has dimensions equal to a unit of pressure (i.e.  $\text{Pa} = \text{N m}^{-2}$ ), and this new quantity is called water potential ( $\psi$ ). The conversion involves dividing  $\Delta\mu$  by the partial molal volume of water ( $\bar{V}_w$ ), i.e.,

$$\psi = \frac{1}{\bar{V}_w} \Delta\mu \quad (2.4)$$

So, in general,  $\psi$  is given by

$$\psi = P + \pi + \rho gh \quad (2.5)$$

where  $P$  is the pressure potential (the hydrostatic pressure),

$$\pi = \frac{RT}{V_w} \ln X_w$$

is called the osmotic potential (sometimes called osmotic pressure) and is approximated by  $\pi = -RTC$ , where  $C$  is the osmolal concentration of the solution,  $R$  is the gas constant and  $T$  is the kelvin temperature,  $\rho$  is the density of water,  $g$  is the acceleration due to gravity, and  $h$  is the height above ground level.

Water will flow into a cell whenever the water potential outside the cell ( $\psi_o$ ) is greater than the water potential inside the cell ( $\psi_c$ ). Let us consider the water relations of a cell at ground level, i.e., how water moves in and out of the cell in the course of a day. Water flows through plants in xylem conduits (vessels or tracheids), which are non-living pipes, and the walls of the pipes are made of cellulose. Water can freely pass in and out of the conduits through the cellulose walls (Figure 2.1A). The water potential of the water in the xylem conduit is given by:

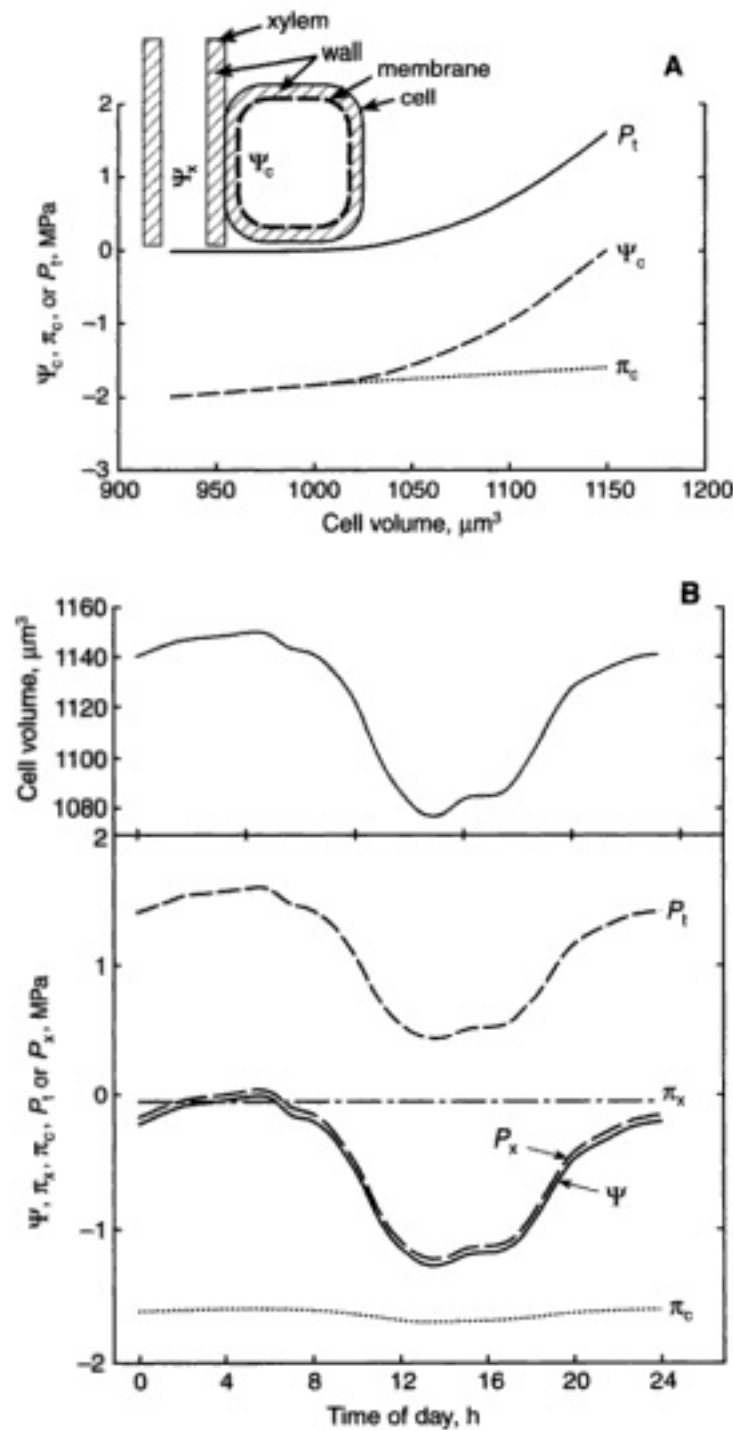
$$\psi_x = P_x + \pi_x \quad (2.6)$$

During the course of a day,  $P_x$  might change from slightly negative values at sunrise (e.g.  $-0.05$  MPa) to more negative values by early afternoon (let us say  $-1.3$  MPa) and then might return again by the next morning, as explained in 'the cohesion-tension (C-T) theory and xylem dysfunction', below. The concentration of solutes in xylem fluid is usually very low (i.e., plants transport nearly pure water in xylem) so  $\pi_x$  is not very negative (let us say  $-0.05$  MPa). So  $\psi_x$  might change from  $-0.1$  to  $-1.35$  MPa in the example given in Figure 2.1B. This daily change in  $\psi_x$  will cause a daily change in  $\psi_c$  as water flows out of the cell as  $\psi_x$  falls and into the cell as  $\psi_x$  rises.

The two primary factors that determine the water potential of a cell at ground level ( $\psi_c$ ) are turgor pressure  $P_t$  (i.e.  $P$  inside the cell) and  $\pi$  of the cell sap ( $\pi_c$ ):

$$\psi_c = P_t + \pi_c \quad (2.7)$$

Plant cells generally have  $\pi_c$  values in the range of  $-1$  to  $-3$  MPa; consequently  $P_t$  is often a large positive value whenever  $\psi_c = \psi_x$ . There are two reasons for cells having  $P_t > 0$ :



*Figure 2.1* A drawing of a living cell with plasmalemma membrane adjacent to a xylem conduit (shown in longitudinal section). The living cell is surrounded by a soft cell wall composed of cellulose, which retards expansion of the cell and prevents collapse of the cell as  $P_t$  falls. The xylem conduit is surrounded by a woody cell wall (cellulose plus lignin), which strongly retards both expansion and collapse when  $P_x$  becomes negative. A: A Höfler diagram showing how the cell water potential ( $\psi_c$ ), the cell osmotic potential ( $\pi_c$ ) and the turgor pressure ( $P_t$ ) change with cell volume. B: A representative daily time course of how cell or xylem water potential ( $\psi$ ) changes during the course of a day. The component water potentials shown are xylem pressure potential ( $P_x$ ), xylem osmotic potential ( $\pi_x$ ), cell turgor pressure ( $P_t$ ) and cell osmotic potential ( $\pi_c$ ). Also shown is how cell volume changes with time. See text for more details.



- 1 The protoplasm of living cells is enclosed inside a semi-permeable membrane (the plasmalemma membrane) that permits relatively rapid trans-membrane movement of water and relatively slow trans-membrane movement of solutes, so the solutes inside the cell making  $\pi_c$  negative cannot move out to the xylem to make  $\pi_x$  more negative.
- 2 The membrane-bound protoplasm is itself surrounded by a relatively rigid-elastic cell wall, so the cell wall must expand as water flows into the cell to accommodate the extra volume; the stretch of the elastic wall places the cell contents under a positive pressure (much like a tyre pumped up by air puts the air in the tyre under pressure). The rise in  $P_c$  raises  $\psi_c$  until it reaches a value equal to  $\psi_x$ , at which point water flow stops.

The effect of water movement into or out of a cell is described by a Höfler diagram (Figure 2.1A). Entry of water into the cell has two effects: it causes a dilution of cell contents, hence  $\pi_c$  becomes slightly less negative; and  $P_c$  rises very rapidly with cell volume. The net effect of the increase in  $\pi_c$  and  $P_c$  is an increase in  $\psi_c$  towards zero. Conversely, a loss of water makes  $\psi_c$ ,  $\pi_c$  and  $P_c$  fall to increasingly negative values. If  $\psi_c$  falls low enough, then  $P_c$  falls to and remains at zero in cells in soft tissue. In woody tissues, i.e. in cells with lignified cell walls, the lignification will prevent cell collapse and  $P_c$  can fall to negative values. The information in the Höfler diagram can be used to understand the water relations of cells in the course of a day.

A representative time course is shown in Figure 2.1B. Suppose the sun rises at 06:00 and sets at 18:00. Radiant energy falling on leaves will enhance the rate of evaporation above the rate at which roots can replace evaporated water, hence both  $\psi_c$  and  $\psi_x$  will fall to the most negative values in early afternoon (indicated by the solid line marked by  $\psi$  in Figure 2.1B). As the afternoon progresses the light intensity diminishes and the rate of water loss from the leaves falls below the rate of uptake of water from the roots; hence  $\psi$  increases. Overnight, the value of  $\psi$  will return to a value near zero in wet soils or more negative values in drier soils; in either case  $\psi$  reaches a maximum value just prior to dawn. The value of  $\psi$  prior to sunrise (called the pre-dawn water potential) is often taken as a valid measure of soil dryness ( $= \psi_{\text{soil}}$ ) in the rooting zone of the plant. In the xylem, the osmotic potential ( $\pi_x$ ) remains more or less constant and only slightly negative during the day. Therefore, all the change in  $\psi_x$  is brought about by a large change in  $P_x$ , which closely parallels changes in  $\psi$ . Similarly, in living cells, changes in  $\psi_c$  are brought about by large changes in  $P_c$ , while the cell osmotic potential ( $\pi_c$ ) changes only slightly and remains a large negative value.

The evaporative flux density ( $E$ ) of water vapour from leaves is ultimately governed by Fick's law of diffusion of gases in air. The control exercised by the plant is to change the area available for vapour diffusion through the opening and closing of stomatal pores. The value of  $E$  (mmol water per s per  $m^2$  of leaf surface) is given by:

$$E = g_L (X_i - X_o) \quad (2.8)$$

where  $g_L$  is the diffusional conductance of the leaf (largely controlled by the stomatal conductance,  $g_s$ ),  $X_i$  is the mole fraction of water vapour at the evaporative surface of the palisade and mesophyll cells, and  $X_o$  is the mole fraction of water vapour in the ambient air surrounding the leaf. The mole fraction is defined as  $X = n_w/N$ , where  $n_w$  is the number of moles of water vapour and  $N$  is the number of moles of all gas molecules, the most abundant gas molecules being  $N_2$  and  $O_2$ . The dependence of  $g_L$  on some environmental and physiological variables is illustrated in Figure 2.3.

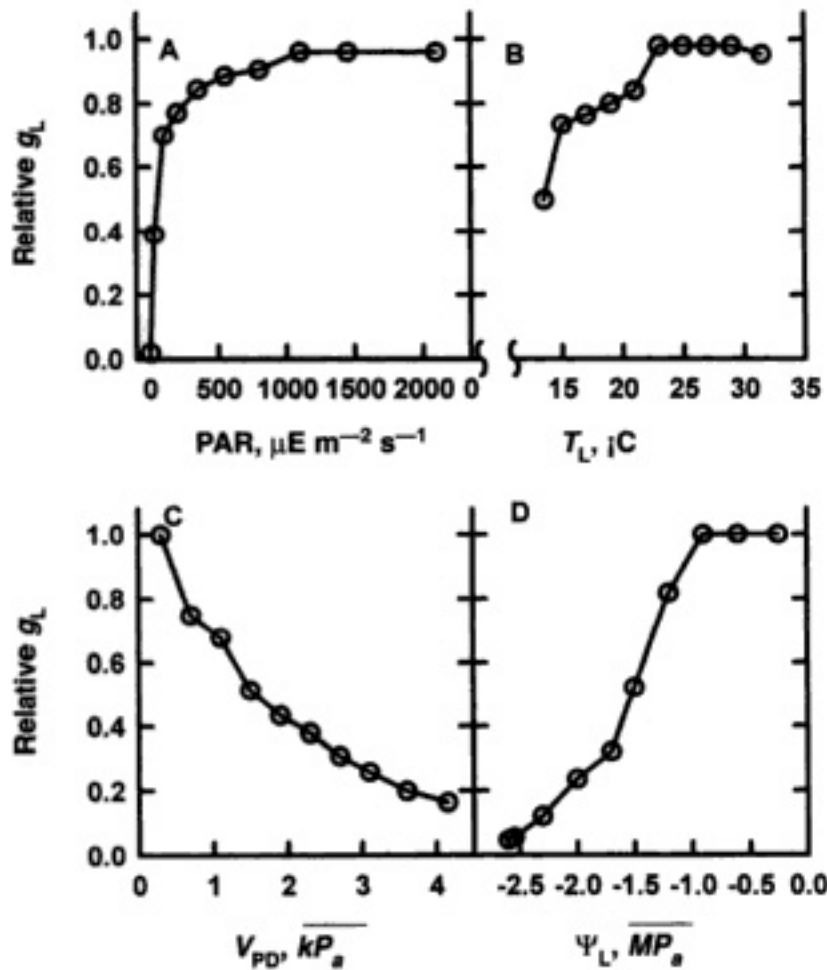


Figure 2.3 Relationship between change of  $g_L$  relative to the maximum value, i.e.  $g_L/g_{Lmax}$  and various environmental factors measured on *Acer saccharum* leaves. The environmental factors are A: photosynthetically active radiation (PAR); B: leaf temperature ( $T_L$ ); C: vapour pressure deficit ( $V_{PD}$ ); and D: leaf water potential ( $\Psi_L$ ). Adapted from Yang *et al.* (1998).

The maximum value of  $X$  occurs when RH is 100 percent, i.e. when the air is saturated with water vapour, and its value increases exponentially with the kelvin temperature of the air. The air at the evaporating surface of leaves is at the temperature of the leaf ( $T_L$ ), and  $X_i$  is taken as the maximum value of  $X$  at saturation, which we can symbolize as  $X_i = X(T_L)$ . The value of  $X_o$  depends on the microclimate near the leaf, i.e. the air temperature and relative humidity. However, the microclimate of the leaf is strongly influenced by the behaviour of the plant community surrounding the leaf, so even though the leaf has direct control over the values of  $g_s$  and  $g_L$ , it has less control over  $E$  than might appear from equation (2.8).

The qualitative aspects of how leaves influence their own microclimate is easily explained. When the sun rises in the morning, the radiant energy load on the leaf increases. This has two effects.  $T_L$  rises as the sun warms the leaves; hence  $X_i$  rises and  $g_L$  increases as stomata open. But the increased evaporation from the leaves causes  $X_o$  to rise as water vapour from the leaves is added to the ambient air. Even changes of  $g_L$  under constant radiant energy load causes less change in  $E$  than might be expected from equation (2.8). When  $g_L$  doubles  $E$  also doubles, but only temporarily. The increased  $E$  lowers  $T_L$  because of increased evaporative cooling, and the increased  $E$  from all the leaves in a stand eventually increases  $X_o$ ; hence  $X_i - X_o$  declines, causing a decline in  $E$ . Consequently, equation (2.8) is not very useful in predicting the value of  $E$  at the level of plant communities. Leaf-level behaviour can be extrapolated to the community level if we take into account leaf-level solar energy budgets using equations that describe light absorption by leaves at all wavelengths and the conversion of this energy to temperature and heat fluxes. Studies of solar energy budgets have been made at both the leaf and stand level (Slatyer, 1967; Chang, 1968).

Eco-hydrologists are primarily concerned with  $E$  expressed as kg or  $m^3$  of water per s per  $m^2$  of ground. Fortunately, most of the changes in  $E$  at the leaf level can be explained in terms of net radiation absorbed at the stand level, and net radiation absorption is relatively easy to measure. This relationship is illustrated in Figure 2.4, where daily values of  $E$  at the leaf level (kg per  $m^2$  per day) are correlated with daily values of net radiation (MJ per  $m^2$  of ground per day) measured with an Eppley-type net radiometer. Equations presented elsewhere in this volume (Chapter 6) to describe stand-level  $E$  in terms of net radiation and other factors are validated by relationships like that in Figure 2.4. The other factors most commonly included account for plant control over  $E$  through leaf area index (leaf area per unit ground area), the effect of drought on  $g_L$ , and ambient temperature (see 'Factors controlling the rate of water uptake and movement', p. 29).

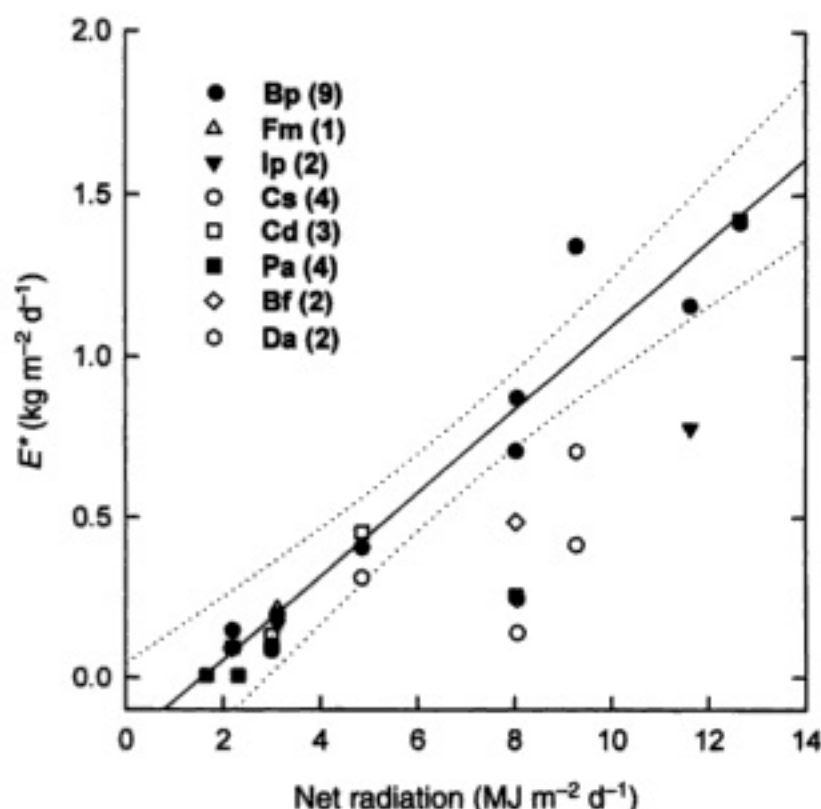


Figure 2.4 Correlation of daily water use of leaves ( $E^*$ ) and net radiation (NR). Data are from potometer experiments with nine woody cloud forest species in Panama. The number of days per species is given in parentheses. The regression (with 95 percent confidence intervals) is for *Baccharis pendunculata* (Bp) ( $E^* = -0.20 + 1.29 \text{ NR}$ ,  $r^2 = 0.92$ ). Even when the data for all species are pooled, NR proved to be a very good predictor of daily water use ( $E^* = -0.2 + 1.04 \text{ NR}$ ,  $r^2 = 0.72$ ). Other species names are *Croton draco* (Cd), *Ficus macbridei* (Fm), *Inga punctata* (Ip), *Parathesis amplifolia* (Pa), *Blakea foliacea* (Bf), *Clusia stenophylla* (Cs) and *Dendropanax arboreus* (Da). From Zotz *et al.* (in press).

## WATER ABSORPTION BY PLANT ROOTS

The primary factor affecting the pattern of water extraction by plants from soils is the rooting depth. Rooting depths can be extremely variable, depending on soil conditions and species of plant producing the roots (Figure 2.5A). Many of the early studies of rooting depth and the branching pattern of roots were performed in the 1920s and 1930s in deep, well-aerated prairie soils, where roots penetrate to great depths. At the extreme, roots have been traced to depths of 10 to 25 m, e.g. alfalfa (10 m), longleaf pine (17 m) (Kramer, 1983), and drought-evading species in the California chaparral (25 m) (Stephen Davis, personal communication). The situation is very different for plants growing in heavy soils, where 90 percent of the roots can be found in the upper 0.5 to 1.0 m.

In seasonally dry regions, e.g. central Panama, the majority of the roots may be located in the upper 0.5 m, but it is far from clear if the majority of

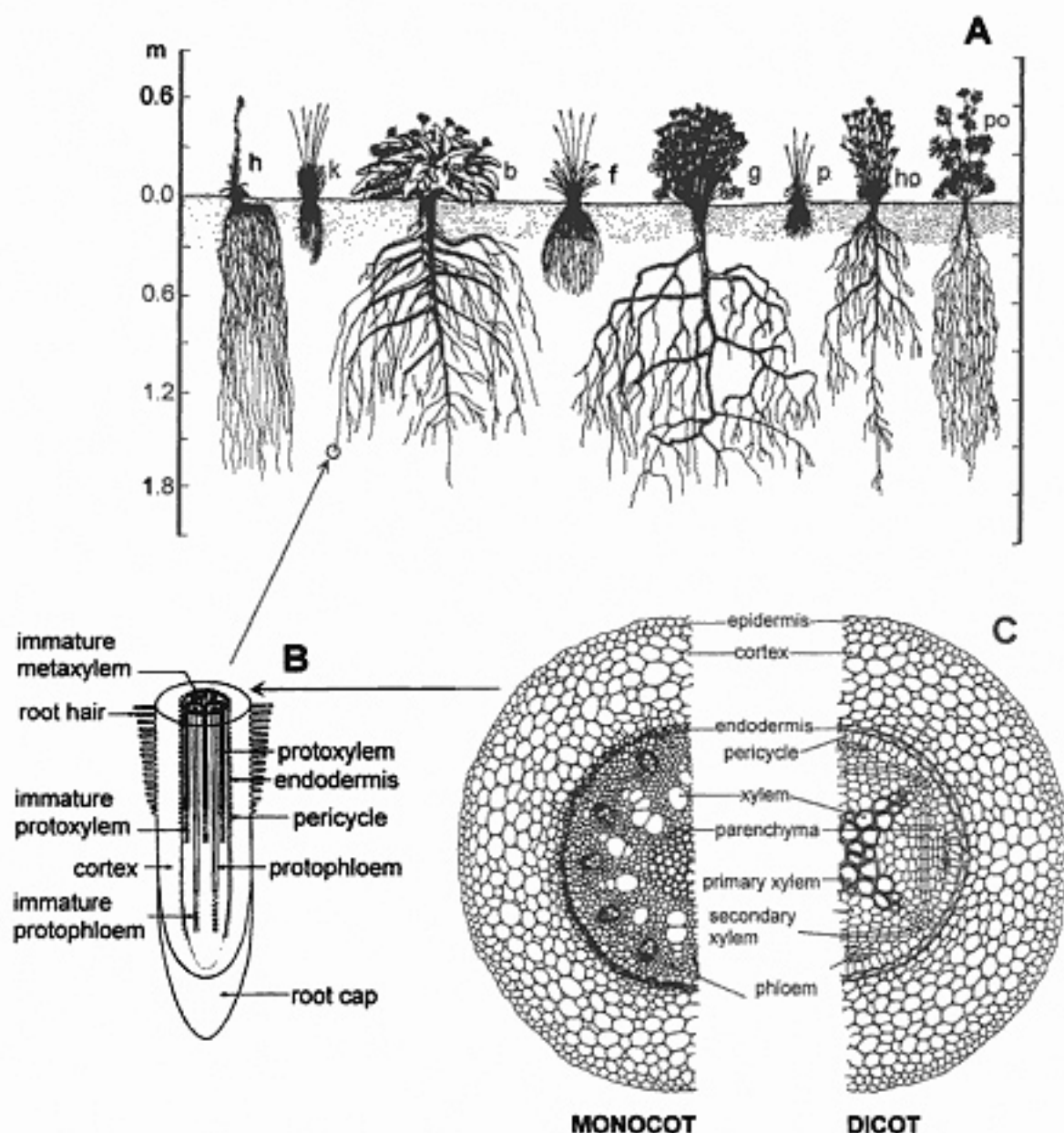


Figure 2.5 A: Differences in root morphology and depth of root systems of various species of prairie plant growing in a deep, well-aerated soil. Species shown are *Hieracium scouleri* (h), *Loelera cristata* (k), *Balsamina sgittata* (b), *Festuca ovina ingrata* (f), *Geranium viscosissimum* (g), *Poa sandbergii* (p), *Hoorebekia racemosa* (ho) and *Potentilla blaschkeana* (po). B: A dicot root tip enlarged about 50 $\times$ . C: Cross-section of monocot and dicot roots enlarged about 400 $\times$ . Adapted from Kramer (1983), Steward (1964) and Bidwell (1979).

water absorption occurs in the upper 0.5 m during the dry season. Water use by many evergreen trees is higher in the dry season than in the wet season, even though the upper 1 m of the soils has much lower potential than the leaves of the trees ( $\psi_{\text{soil}} \ll \psi_{\text{leaf}}$ ) (personal observation). Hence the role of shallow versus deep roots of woody species deserves more study. In addition, deeply rooted species may contribute to the water supply of shallow-rooted species through a process called 'hydraulic lift'. In one study, it was found that shallow-rooted species growing within 1 to 5 m of the base of maple trees



were in a better water balance than the same species growing >5 m away (Dawson, 1993). Each night,  $\psi_{\text{soil}}$  at a depth of 0.5 m increased underneath maple trees but did not increase at distances >5 m from the trees. This indicated that the deep maple roots were in contact with moist soil and were capable of transporting water from deep roots to shallow roots overnight. Since the water potential of the shallow roots exceeded the water potential of the adjacent soil, water flow from the shallow roots to the adjacent soil contributed to the overnight rehydration of shallow soils. For more on hydraulic lift, see Richards and Caldwell (1987) and Chapter 6.

Roots absorb both water and mineral solutes found in the soil, and the flows of solutes and water interact with each other. The mechanism and pathway of water absorption by roots is more complex than in the case of a single cell (see above). Water must first travel radially from the epidermis to cortex, endodermis and pericycle before it finally reaches the xylem vessels, from which point water flow is axial along the root (Figure 2.5B and C). The radial pathway (typically 0.3 mm long in young roots) is usually much less conductive than the axial pathway (>1 m in many cases); hence whole-root conductance is generally proportional to the root surface area. The radial pathway can be viewed as a 'composite membrane' separating the soil solution from the solution in the xylem fluid. The composite membrane consists of serial and parallel pathways made up of plasmalemma membranes, cell wall 'membranes' and plasmodesmata (pores <0.5  $\mu\text{m}$  diameter) that connect adjacent cells. The composite membrane is rather leaky to solutes; hence differences in osmotic potential between the soil ( $\pi_s$ ) and the xylem ( $\pi_x$ ) have less influence on the movement of water. At any given point along the axis, the water flux density across the root radius ( $J_r$ ) will be given by

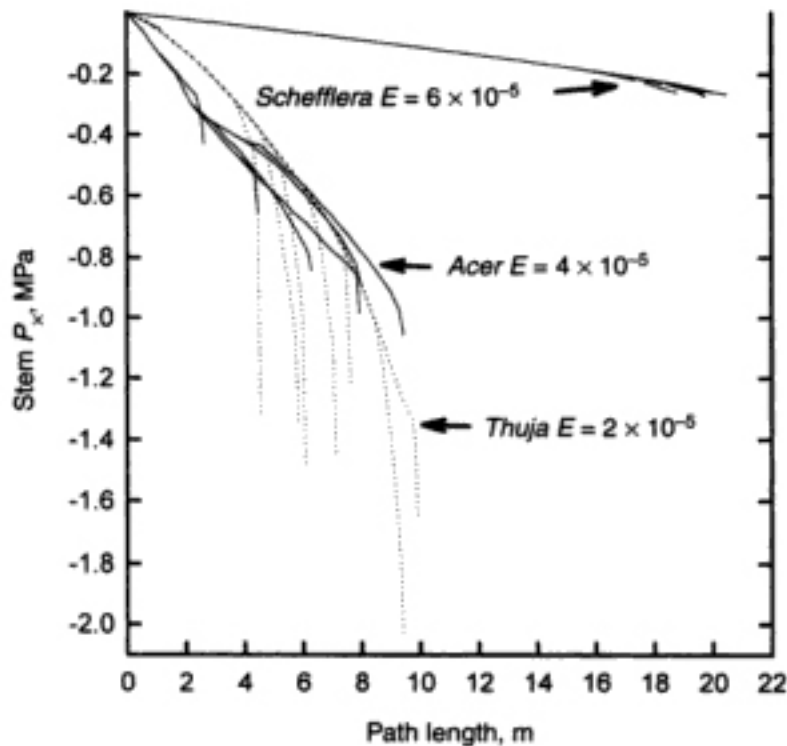
$$J_r = L_r [(P_s - P_x) + \sigma(\pi_s - \pi_x)] \quad (2.9)$$

where  $L_r$  is the radial root conductance to water and  $\sigma$  is the solute reflection coefficient. For an 'ideal' membrane, in which water but not solutes may pass,  $\sigma = 1$ . But for the composite membrane of roots,  $\sigma$  is usually between 0.1 and 0.8. The system of equations that describes water transport in roots is quite complex when, for example, axial and radial conductances, the fact that each solute has a different  $\sigma$ , and the influence of solute loading rate ( $J_s$ ) on water flow are taken into account. Water and solute flow in roots can be described by a standing gradient osmotic flow model, and readers interested in the details may consult Tyree *et al.* (1994b) and Steudle (1992).

Fortunately, the equations describing water flow become quite simple when the rate of water flow is high. The concentration of solutes in the xylem fluid is determined by the ratio of solute flux to water flux ( $J_s/J_w$ ). Solute flux tends to be more or less constant with time, but water flux increases with increasing transpiration. When water flow is high, the concentration of solutes in the xylem fluid becomes quite small and approaches values comparable

unit cross-section have larger  $K_s$  values than segments with small-diameter vessels. Another useful measure is obtained by dividing  $K_h$  by leaf area dependent on the segment to get leaf specific conductivity,  $K_L = K_h/A$ ;  $K_L$  values give the hydraulic sufficiency of stems to supply water to leaves and permit the quick computation of pressure gradients, since  $-dP_x/dx = E/K_L$  (ignoring gravity). Values of  $K_L$  and  $K_s$  are not uniform within large trees; values decline with declining diameter because small branches tend to have smaller-diameter vessels than large branches. There are also dramatic differences in  $K_L$  between species.

Values of  $K_L$  have been applied to complex 'hydraulic maps', where the above-ground portion of trees were represented by hundreds to thousands of conductance elements (Figure 2.6). Using known values of  $K_L$  and  $E$ , it is possible to calculate  $P_x$  versus path length from the base of a tree to selected branch tips. This has been done in Figure 2.7. Some species are so conductive (large  $K_L$  values) that the predicted drop in  $P_x$  is little more than is needed to lift water against gravity (see *Schefflera*). In other species, gradients in  $P_x$  become very steep near branch tips (see *Thuja*).



**Figure 2.7** Pressure profiles in three large trees, i.e. computed change in xylem pressure ( $P_x$ ) versus path length.  $P_x$  values were computed from the base of each tree to a few randomly selected branch tips. The 'drooping' nature of these plots near the apices of the branches is caused by the decline of leaf specific conductivity ( $K_L$ ) from base to apex of the trees. The pressure profiles in this figure do not include pressure drops across roots or leaves. In some species, pressure drop across leaves can be more than shown in this figure. The pressure drop across roots is generally equal to that across the shoots (including leaves).  $E$  = evaporative flux density in  $\text{kg s}^{-1} \text{m}^{-2}$ .

The major resistance (i.e. inverse conductance) to liquid water flow in plants resides in the non-vascular pathways, i.e. the radial pathway for water uptake in young roots and in the cells between leaf veins and the evaporating surfaces of leaves. Non-vascular resistances can be 60 to 90 percent of the total plant resistance to water flow, even though the total path length may be less than 1 mm. Even though water flows through distances of 1 to 100 m in the vascular pathways from root vessel to stems to leaf vessels, the hydraulic resistance of this pathway rarely dominates.

The biggest resistance to water flow (liquid and vapour) from the soil to the atmosphere resides in the vapour transport phase. The rate of flow from the leaf to the atmosphere is determined primarily by the stomata, as discussed above.

### THE COHESION-TENSION (C-T) THEORY AND XYLEM DYSFUNCTION

The C-T theory was proposed over 100 years ago by Dixon and Joly (1894), and some aspects of the C-T theory were put on a quantitative basis by van den Honert (1948) with the introduction of the Ohm's law analogue of sap flow in the soil-plant-atmosphere continuum (see page 24).

According to the C-T theory, water ascends plants in a metastable state under tension, i.e. with xylem pressure ( $P_x$ ) more negative than that of a perfect vacuum. The driving force is generated by surface tension at the evaporating surfaces of the leaf, and the tension is transmitted through a continuous water column from the leaves to the root apices and throughout all parts of the apoplast in every organ of the plant. Evaporation occurs predominantly from the cell walls of the substomatal chambers due to the much lower water potential of the water vapour in air. The evaporation creates a curvature in the water menisci of apoplastic water within the cellulosic microfibril pores of cell walls. Surface tension forces consequently lower  $P_x$  in the liquid directly behind the menisci (the air-water interfaces). This creates a lower water potential,  $\psi$ , in adjacent regions, including adjoining cell walls and cell protoplasts.

The energy for the evaporation process comes ultimately from the sun, which provides the energy to overcome the latent heat of evaporation of the water molecules, i.e. the energy to break hydrogen bonds at the menisci.

Water in xylem conduits is said to be in a metastable condition when  $P_x$  is below the pressure of a perfect vacuum, because the continuity of the water column, once broken, will not rejoin until  $P_x$  rises to values above that of a vacuum. Metastable conditions are maintained by the cohesion of water to water and by adhesion of water to walls of xylem conduits. Both cohesion and adhesion of water are manifestations of hydrogen bonding. Even though air-water interfaces can exist anywhere along the path of water



movement, the small diameter of pores in cell walls and the capillary forces produced by surface tension within such pores prevent the passage of air into conduits under normal circumstances. However, when  $P_x$  becomes sufficiently negative, air bubbles can be sucked into xylem conduits through porous walls.

This tension (negative  $P_x$ ) is ultimately transferred to the roots, where it lowers  $\psi$  of the roots below the  $\psi$  of the soil water. This causes water uptake from the soil to the roots and from the roots to the leaves to replace water evaporated at the surface of the leaves. The Scholander–Hammel pressure bomb (Scholander *et al.*, 1965) is one of the most frequently used tools for estimating  $P_x$ . Typically,  $P_x$  can range down to  $-2$  MPa (in crop plants) or to  $-4$  MPa (in arid zone species) and in some cases  $-10$  MPa (in California chaparral species). Readers interested in learning more about the cohesion–tension theory of sap ascent may refer to Tyree (in press).

In some plants, water movement can occur at night or during rain events, when  $P_x$  is positive due to root pressure, i.e. osmotically driven flow from roots. Water flow under positive  $P_x$  is often accompanied by guttation, i.e. the formation of water droplets at leaf margins. But water is normally under negative pressure (tension) as it moves through the xylem towards the leaves during sunny days. The water is thus in a metastable condition and vulnerable to cavitation due to air entry into the water columns. Cavitation results in embolism (air blockage), thus disrupting the flow of water (Tyree and Sperry, 1989). Cavitation in plants can result from water stress, and each species has a characteristic ‘vulnerability curve’, which is a plot of the percentage loss of  $K_h$  in stems versus the xylem pressure potential,  $P_x$ , required to induce the loss. Vulnerability curves are typically measured by dehydrating large excised branches to known  $P_x$ . Stem segments are then cut under water from the dehydrated branches and, for the most part, the air bubbles remain inside the conduits. An initial conductivity measurement is made and compared with the maximum  $K_h$  after air bubbles have been dissolved. The vulnerability curves of plants, in concert with their hydraulic architecture, can give considerable insight into drought tolerance and water relations ‘strategies’.

The vulnerability curves for a number of species are reproduced in Figure 2.8 (Tyree *et al.* 1994a). These species represent the range of vulnerabilities observed so far in over sixty species; 50 percent loss of  $K_h$  occurs at  $P_x$  values ranging from  $-0.7$  to  $-11$  MPa. Many plants growing in areas with seasonal rainfall patterns (wet and dry periods) appear to be drought evaders, while others are drought toleraters. The drought evaders avoid drought (low  $P_x$  and high percentage loss  $K_h$ ) by having deep roots and a highly conductive hydraulic system. Alternatively, they evade drought by being deciduous. The other species frequently reach very negative  $P_x$  for part or all of the year and are shallow-rooted or grow in saline environments. These species survive by having a vascular system highly resistant to cavitations.

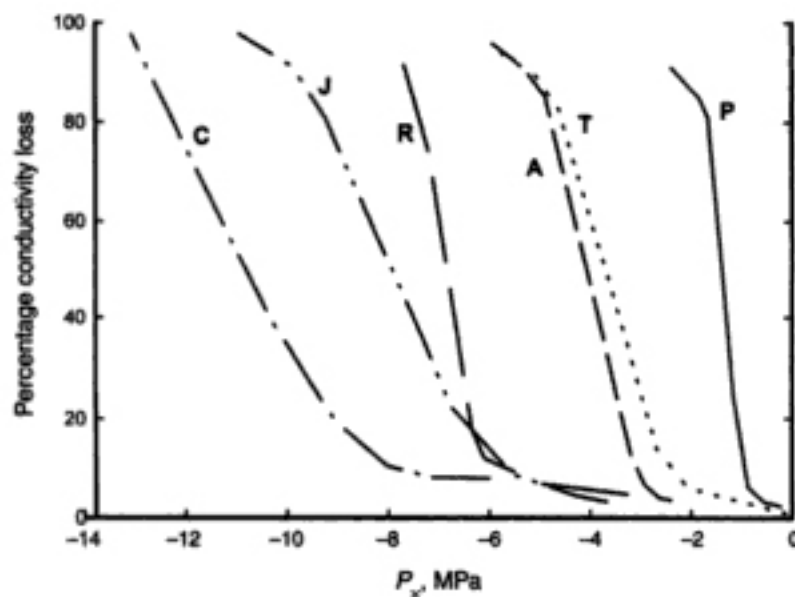


Figure 2.8 Vulnerability curves for various species. y-axis is percentage loss of hydraulic conductivity induced by the xylem pressure potential,  $P_x$ , shown on the x-axis. C = *Ceanothus megacarpus*, J = *Juniperus virginiana*, R = *Rhizophora mangle*, A = *Acer saccharum*, T = *Thuja occidentalis*, P = *Populus deltoides*.

Embolisms may be dissolved in plants if  $P_x$  in the xylem becomes positive or close to positive for adequate time periods (Tyree and Yang, 1992; Lewis *et al.*, 1994). Embolisms disappear by dissolution of air into the water surrounding the air bubble. The solubility of air in water is proportional to the pressure of air adjacent to the water (Henry's law). Water in plants tends to be saturated with air at a concentration determined by the average atmospheric pressure of gas surrounding plants. Thus, for air to dissolve from a bubble into water, the air in the bubble has to be at a pressure in excess of atmospheric pressure. If the pressure of water ( $P_x$ ) surrounding a bubble is equal to atmospheric pressure ( $P_a$ ), bubbles will naturally dissolve, because surface tension ( $\tau$ ) of water raises the pressure of air in the bubble ( $P_b$ ) above  $P_a$ . In general,  $P_b = 2\tau/r + P_x$ , where  $r$  is the radius of the bubble. According to the cohesion theory of sap ascent,  $P_x$  is drawn below  $P_a$  during transpiration. Since  $2\tau/r$  of a dissolving bubble in a vessel is usually  $<0.03$  MPa, and since  $P_x$  is in the range of  $-0.1$  to  $-10$  MPa during transpiration,  $P_b$  is usually  $\leq P_a$ , and hence bubbles, once formed in vessels, rarely completely dissolve. Repair (i.e. dissolution) occurs only when  $P_x$  becomes large via root pressure. One notable exception to this generality has recently been found in *Laurus nobilis* shrubs, which appear to be able to refill embolised vessels even while  $P_x$  is at  $-1$  MPa (Salleo *et al.*, 1996). The mechanism involved has evaded explanation.

## FACTORS CONTROLLING THE RATE OF WATER UPTAKE AND MOVEMENT

Environmental conditions control the rate of water movement in plants. The dominant environmental factor is net solar radiation, as mentioned previously. Water movement can be explained by the solar energy budget of plants. We will now take a more quantitative look at the solar energy budget of plants at both the leaf and stand level.

### Leaf-level energy budgets

Objects deep in space far away from solar radiation tend to be rather cold (about 5 K), whereas objects on Earth tend to be rather warm (270–310 K). The reason for the elevated temperature on Earth is the warming effect of solar radiation. The net radiation absorbed by a leaf ( $R_{NL}$ ,  $\text{W m}^{-2}$ ) can be arbitrarily divided into short-wave and long-wave radiation, with the demarcation wavelength being at  $1\ \mu\text{m}$ . Most short-wave radiation comes from the Sun, and most long-wave radiation comes from the Earth. As a leaf absorbs  $R_{NL}$ , the leaf temperature ( $T_L$ ) rises, which increases the loss of energy from the leaf by three different mechanisms – black body radiation ( $B$ ), sensible heat flux ( $H$ ), and latent heat of vaporisation of water ( $\lambda E$ , where  $E$  is the evaporative flux density of water due to transpiration ( $\text{mol of water s}^{-1} \text{ m}^{-2}$ ) and  $\lambda$  is the heat required to evaporate a mole of water ( $\text{J mol}^{-1}$ )).  $R_{NL}$  can also be converted to chemical energy by the process of photosynthesis and to energy storage, but these two factors are generally small for leaves and are ignored in the equation below:

$$R_{NL} = B + H + \lambda E \quad (2.13)$$

The  $B$  in equation (2.13) is the 'black body' radiation. All objects emit radiation. Very hot objects like the Sun emit mostly short-wave radiation, whereas cooler objects on Earth emit mostly long-wave radiation. The amount of radiation emitted increases with the kelvin temperature according to the Stefan–Boltzmann law: i.e.  $B = e\sigma_{sb} T_L^4$ , where  $e$  is the emissivity ( $\geq 0.95$  for leaves), and  $\sigma_{sb}$  is the Stefan–Boltzmann constant  $= 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ .

$H$  in equation (2.13) is sensible heat flux density, i.e. the heat transfer by heat diffusion between objects at different temperatures. For leaves, the heat transfer is between the leaf and the surrounding air. The rate of heat transfer is proportional to the difference in temperature between the leaf and the air, so  $H = k(T_L - T_a)$ , where  $T_a$  is the air temperature and  $k$  is the heat transfer coefficient. Heat transfer is more rapid and hence  $k$  is larger under windy conditions than in still air. But the value of  $k$  is also determined by leaf size, shape and orientation with respect to the wind direction. Readers interested in more detail should consult Slatyer (1967) or Nobel (1991).

where  $K_e$  is the eddy transfer coefficient,  $C_p$  is the heat capacity of air,  $\rho_a$  is the air density,  $\Delta T$  is the difference in air temperature measured at the two levels in Figure 2.10 separated by a height difference of  $\Delta Z$ , and  $\Delta[H_2O]$  is the difference in water vapour concentration at the two levels in Figure 2.10 separated by a height difference of  $\Delta Z$ .

It is easy to measure  $\Delta T$  and  $\Delta[H_2O]$  but difficult to assign a value for  $K_e$ , which changes dynamically with changes in wind velocity, so the usual practice is to measure the ratio of  $H/\lambda E = \beta$ , which is called the Bowen ratio (see also Chapter 6). From the equations above it can be seen that

$$\beta = \frac{C_p \rho_a}{\lambda} \frac{\Delta T}{\Delta[H_2O]} \quad (2.18)$$

Estimates of stand water use are obtained by solving equations (2.15 and 2.18) for  $E$ :

$$E = \frac{R_N - G}{\lambda (\beta + 1)} \quad (2.19)$$

An example of the total energy budget measured over a pasture is reproduced in Figure 2.11, the data in which show again that the main factor determining  $E$  is the amount of solar radiation,  $R_N$ , as in Figure 2.4. However, the leaves in a stand of plants do have some control over the value of  $E$ . As soils dry, and leaf water potential falls, stomatal conductance falls. This causes a reduction in  $E$ , an increase in leaf temperature and thus an increase in  $H$ .

Very intensive monitoring of climatic data is needed to obtain data for a solution of equation (2.19). Temperature,  $R_N$  and relative humidity have to be measured every second at several locations. Eco-hydrologists prefer to estimate  $E$  with a less complete data set. Fortunately, the Penman–Monteith formula (Monteith, 1964) permits a relatively accurate estimate of  $E$  under some restricted circumstances. The Penman–Monteith formula is derived from energy budget equations together with the assumption that some non-linear functions can be approximated as linear relations. After many obtuse steps in the derivation (Campbell, 1981), a formula of the following form results:

$$E = \frac{e' (R_N - G) + \rho_a C_p V_{pd} g_a}{\lambda \left( e' + \gamma \left[ 1 + \frac{g_a}{g_c} \right] \right)} \quad (2.20)$$

where  $e'$  is the rate of change of saturation vapour pressure with temperature at the current air temperature,  $V_{pd}$  is the difference between the vapour

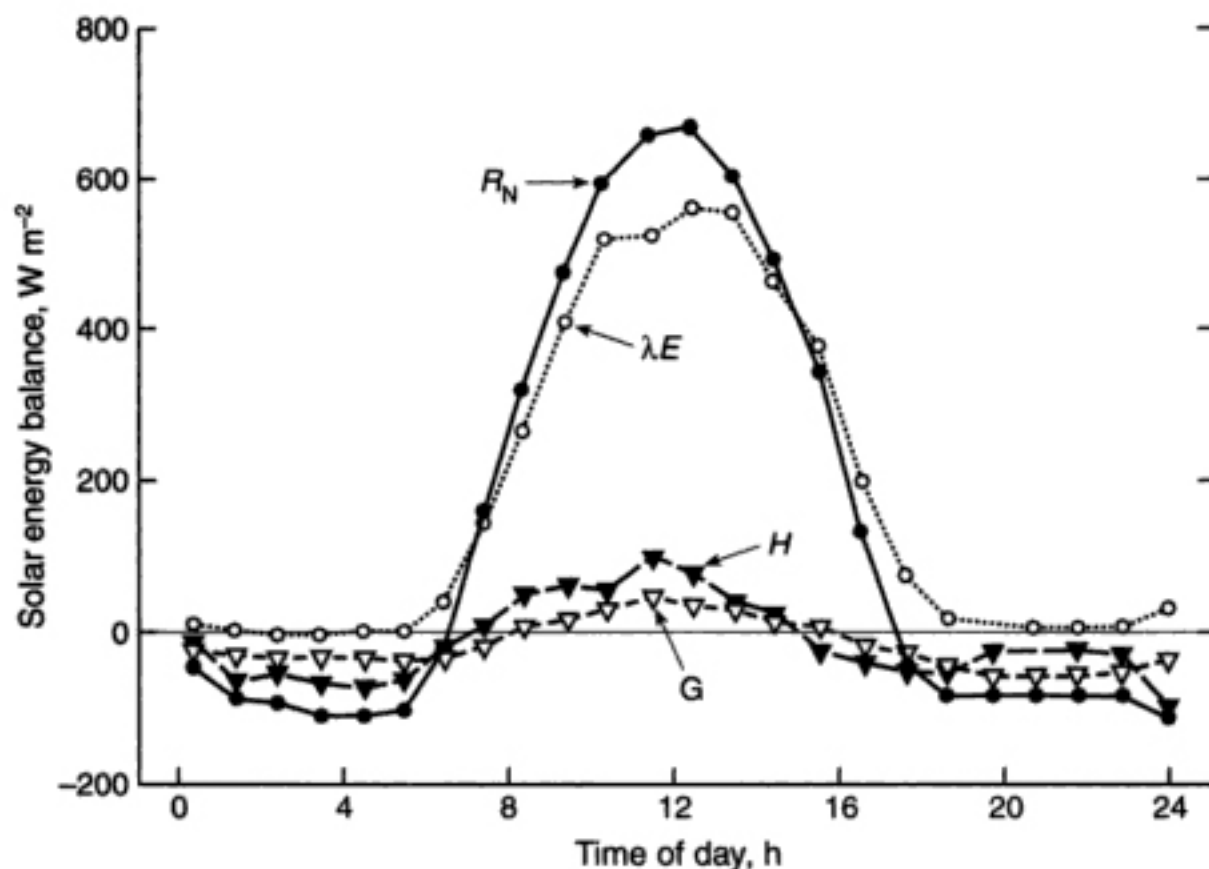


Figure 2.11 Solar energy budget values measured in a meadow.  $R_N$  = net solar radiation of the meadow,  $\lambda E$  = latent heat flux,  $H$  = sensible heat flux and  $G$  = rate of heat storage in soil. Adapted from Slatyer (1967).

pressure of air at saturation and the current vapour pressure,  $\gamma$  is the psychrometric constant,  $g_a$  is the aerodynamic conductance and  $g_c$  is the canopy conductance of the stand. The problem with equation (2.20) is that  $g_a$  and  $g_c$  are both difficult to estimate and are not constant. The value of  $g_a$  depends on wind speed and roughness parameters that describe the unevenness at the boundary between the canopy and the bulk air. Surface roughness affects air turbulence and hence the rate of energy transfer at any given wind speed. Surface roughness changes as stands grow and is difficult to estimate in terrain with hills or mountains. The value of  $g_c$  is under biological control and difficult to estimate from climatic data. In one study on an oak forest in France,  $E$  was estimated independently by Granier sap flow sensors in individual oak trees. This permitted the calculation of  $g_c$  against season, morphological state of the forest and climate (Granier and Bréda, 1996). The value of  $g_c$  was found to be a function of global radiation,  $V_{pd}$ , leaf area per unit ground area, which changes with season, and relative extractable water, which is a measure of soil dryness. Once all these factors were taken into account, equation (2.20) did provide a reasonable estimate of half-hourly estimates of  $E$  over the entire summer.

## WILTING AND WATERLOGGING

## Wilting

Wilting denotes the limp, flaccid or drooping state of plants during drought. Wilting is most evident in leaves that depend on cell turgor pressure to maintain their shape and, therefore, occurs when turgor pressure falls to zero. Many plants maintain leaf shape through rigid leaf fibre cells. 'Wilting' in these species is considered to commence at the turgor loss point. Wilted plants generally have low  $E$  because stomata are closed and  $g_s$  is very small when leaf water potential,  $\psi_L$ , falls during drought. Continued dehydration beyond the wilting point usually causes permanent loss of hydraulic conductance due to cavitation in the xylem. Complete loss of hydraulic conductance usually leads to plant death, but the water potential causing loss of hydraulic conductance varies greatly between species (see Figure 2.8). Some plants in arid environments avoid drought either by having short reproductive cycles confined to brief wet periods or by having deep roots that can access deep sources of soil water (Kramer, 1983).

As plants approach the wilting point, there is a gradual loss in stomatal conductance and, hence, a reduction in  $E$  and photosynthetic rate (Schulze and Hall, 1982). Some species are much more sensitive than others (Figure 2.12B). The short-term effects of decreased  $\psi_L$  on transpiration are less dramatic than are long-term effects (Figure 2.12A). Long-term effects of drought are mediated by hormone signals from roots, which cause a medium-term decline in  $g_s$  and by changes in root morphology, e.g. loss of fine roots, suberisation of root surfaces, and formation of corky layers (Ginter-Whitehouse *et al.*, 1983). The morphological changes to roots cause an decrease in whole plant hydraulic conductance ( $K_p$ ), so  $\psi_L$  becomes more negative at lower values of  $E$  because  $\psi_L = \psi_{\text{soil}} - E/K_p$ . Very severe drought can further lower  $K_p$  due to cavitation of xylem vessels.

## Waterlogging

Waterlogging denotes an environmental condition of soil water saturation or ponding of water, which can last for a just a few hours or for many months. Plants absent from flood-prone sites are damaged easily by waterlogging. On the other hand, plants that inhabit flood-prone sites include species that can grow actively in flooded soils or species that survive flooding in a quiescent or dormant state (see Chapter 5). Paradoxically, the commonest sign of tobacco roots having an excess of water is the development of a water deficit in the leaves (Kramer, 1983; Kramer and Jackson, 1954); but flood-tolerant species are not so easily affected.

Flooding often affects root morphology and physiology. The wilting and defoliation that is found on flooding can be traced to an increased resistance



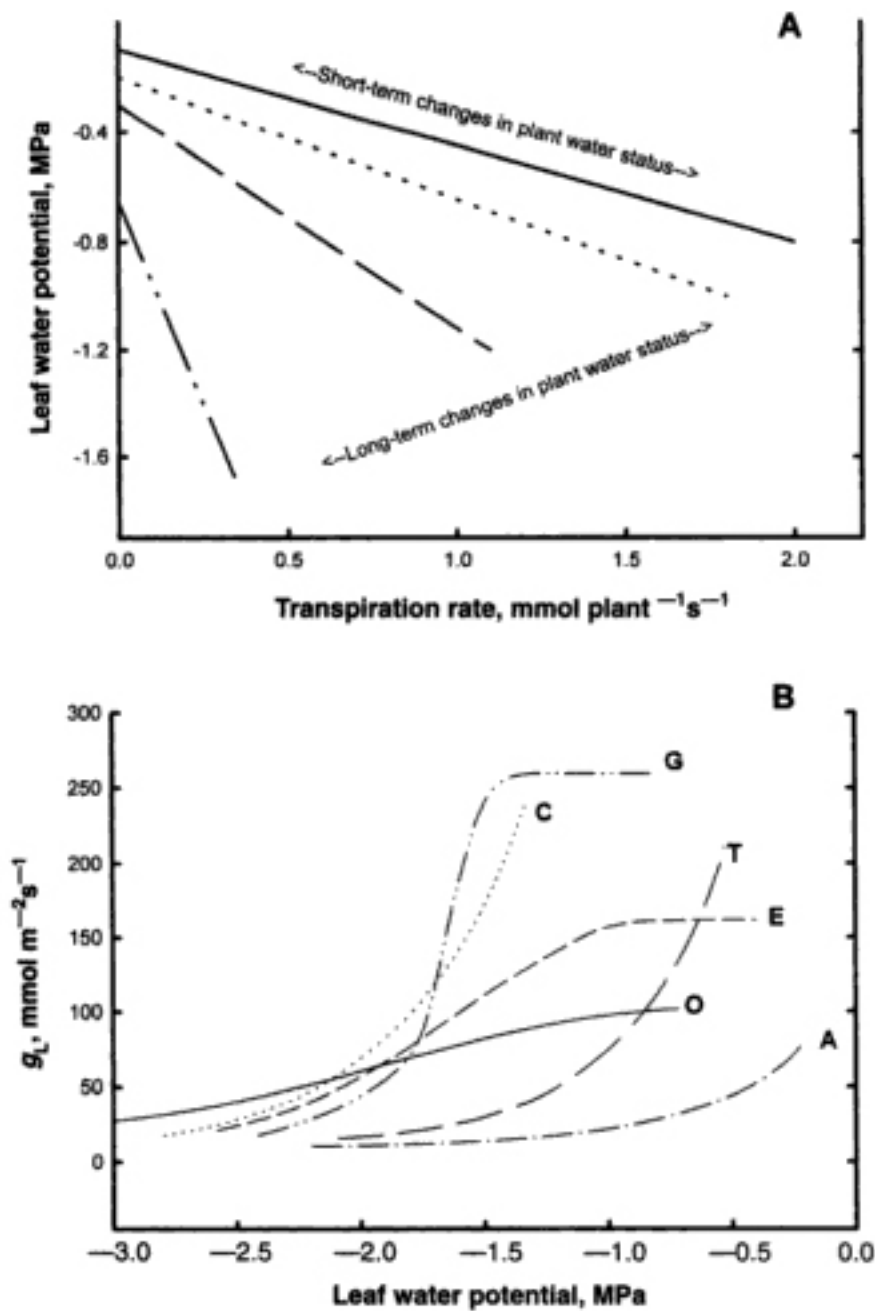


Figure 2.12 Effects of drought on transpiration, leaf water potential and stomatal conductance. A: Short-term and long-term effects of drought on leaf water potential and transpiration. The short-term effects are dynamic changes in leaf water potential that might occur in the course of one day. The long-term effects are associated with slow drying of soil over many days. B: Short-term effects of leaf water potential on stomatal conductance. Species represented: A = *Acer saccharum*, C = *Corylus avellana*, E = *Eucalyptus socialis*, G = *Glycine max*, T = *Triticum aestivum*. Adapted from Schulze and Hall (1982).

to water flux in the roots (Mees and Weatherley, 1957). In most flood-tolerant species, flooding induces morphological changes in the roots. These modifications usually involve root thickening, with an increase in porosity. The increase in porosity increases the rate of oxygen diffusion to root tips and thus permits continued aerobic metabolism in the inundated roots. In

flood-sensitive species, root and shoot growth are rapidly reduced on flooding, and root tips may be damaged. Growth of roots can be renewed only from regions proximal to the stem. The physiological responses and adaptations to waterlogging are numerous and beyond the scope of this chapter, but interested readers may get into the literature by consulting Crawford (1982).

## CONCLUSION

Water flow through plants is purely passive. Water flow through most of the plant is driven by differences in water pressure,  $\Delta P$ . According to the cohesion-tension theory of sap ascent, water movement is driven by surface tension effects at the evaporating surface of the leaf. Surface tension lowers the pressure of water at the site of evaporation, causing water to flow up from the roots.

In some cases, solutes can influence the rate of water movement. These cases occur when solutes are constrained by permeability barriers, which make water movement easier than solute movement. Water flow through plant membranes into or out of cells is driven by differences in water potential,  $\Delta\psi$ , between the inside and outside of the cell. Differences in  $\psi$  are determined by differences in pressure and solute potential –  $\Delta P$  and  $\Delta\pi$ , respectively. Water flow through roots is driven by  $\Delta P$  and more weakly by  $\Delta\pi$ , because roots are leaky to solutes. Water flow rates through roots are usually high enough to make  $\Delta\pi$  much less than  $\Delta P$ , so most of the time water flow through roots is driven by the pressure difference between the water in the soil and the base of the plant.

The rate of evaporation of water from plants is controlled by both the plant and the environment. The plant controls water movement via the stomatal physiology. Stomata respond to changes in light, temperature,  $\text{CO}_2$ , leaf water potential and humidity by increasing or decreasing leaf conductance ( $g_l$ ) to water vapour diffusion. The most important environmental factor controlling evaporation is then net radiation absorbed by plants.

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# SCALES OF INTERACTION IN ECO-HYDROLOGICAL RELATIONS

*Robert L. Wilby and David S. Schimel*

## INTRODUCTION

parameters and processes important at one scale are frequently not important or predictive at another scale, and information is often lost as spatial [or temporal] data are considered at coarser scales of resolution.

Turner, M.G. (1990)

This observation holds for all the geophysical and biological sciences, including eco-hydrology. Indeed, 'scale issues' have become the legitimate focus of a growing body of research in the environmental sciences and were even identified as a research priority by the US Committee on Opportunities in the Hydrological Sciences (James, 1995). According to Blöschl and Sivapalan (1995), the task of *linking* and *integrating* hydrological 'laws' at different scales has not yet been fully addressed, and doing so remains an outstanding challenge in the field of surficial processes. Several factors have contributed to the current awareness of scale issues in plant–water relations.

First, recent population growth, technological developments and economic activities have broadened the scale of human interference in hydrosystems. Historically, the hydrological discipline evolved from the technical demands of supplying societies with potable water for domestic and agricultural consumption, disposing of liquid wastes, and protecting land from inundations (Klemes, 1988; Wilby, 1997a). Such concerns were initially small-scale but have now attained global dimensions with respect to climate change impacts, regional land-use changes, and the potential for transboundary pollution incidents.

Second, most meteorological, hydrological and ecological processes are strongly heterogeneous in both space and time. However, our ability to observe and/or sample these processes is severely constrained by the available

technology, human and financial resources, and a general lack of standardisation in measurement techniques (Rodda, 1995). At the same time, modelling often demands long-term, spatially consistent descriptions of heterogeneous parameters such as albedo or soil hydraulic characteristics. As will be shown below, the advent of remote sensing and new technologies for visualising and handling spatial data have gone some way to addressing such needs.

Third, eco-hydrological theories and models are often highly scale-specific. Models constructed at one scale are not always transferable to a higher or lower temporal/spatial resolution, because the dominant processes may be different between the scales or because there may be strong non-linearities in the system behaviour. To date, the vast majority of eco-hydrological studies have focused on point (or plot) to catchment (or sub-regional) scale processes. Again, this is a reflection of the fact that small-scale studies are logistically easier to conduct than large-scale experiments, and that the perceived level of the anthropic impact has traditionally been hill-slope or catchment scale (Wilby, 1997b).

The following sections will elaborate upon these issues. Although the emphasis of this chapter will be upon *spatial* scales of interaction in plant-water relations, temporal scaling is implicit to all the following discussions given that small length-scale processes tend to operate at small-scale time intervals, and large length-scale processes at long time intervals. However, the primary aim of the chapter is to evaluate different methods of representing spatial heterogeneity in plant-water relations, and the extent to which these relations are transferable between plant and patch, and from patch to regional scales. Accordingly, key concepts such as characteristic process scales, heterogeneity, spatial organisation and scale interactions are introduced. These terms are discussed within the context of emerging 'spatial' technologies such as remote sensing, geographical information systems (GIS) and digital terrain models (DTMs). Three broad approaches to handling heterogeneity and linking between scales are then reviewed. First, methods of extrapolating plant-process models to patch and regional scales are considered with reference to leaf-area models and holistic scaling approaches such as fractals. Second, techniques for obtaining sub-grid-scale heterogeneity through empirical and/or statistical downscaling methods are described. Third, procedures for distributing sub-grid-scale parameters using higher-resolution, covariant properties such as topography are examined with reference to distributed eco-hydrological modelling. The concluding section briefly considers the significance of scale issues in research on regional deforestation, and studies of the potential terrestrial impacts of greenhouse-gas forcing (global warming).

# CHARACTERISTIC OBSERVATION SCALES

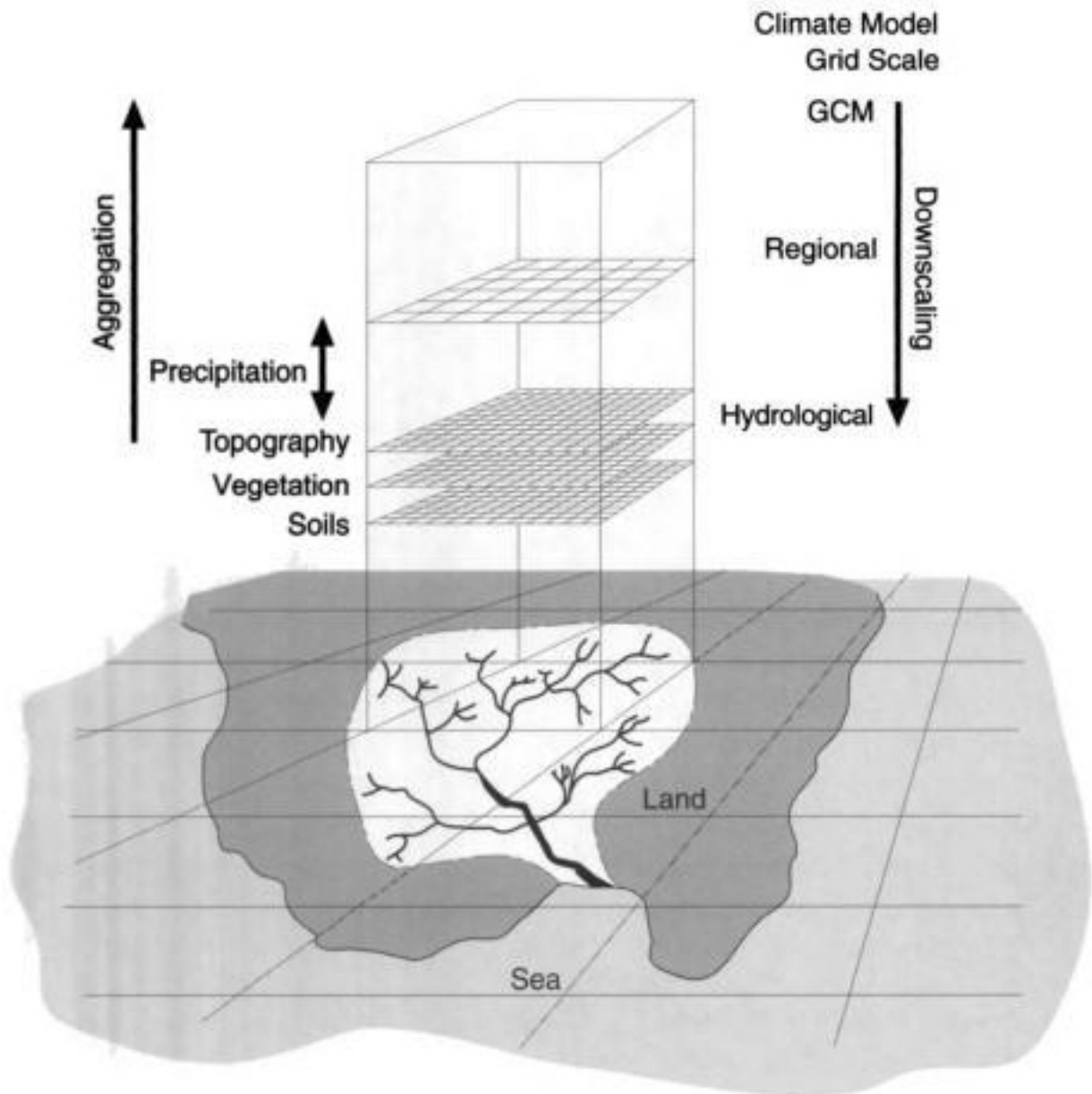
According to Dooge (1988), hydrology as a scientific discipline could theoretically span fifteen orders of magnitude (Table 3.1), ranging from the scale of a cluster of water molecules ( $10^{-8}$  m) to the planetary scale of the global hydrological cycle ( $10^7$  m). In practice, hydrological studies have traditionally favoured the catchment scale, or what Dooge refers to as the mesoscale or the lower end of the macroscale. Similarly, there has been a bias among ecologists towards experimental studies of biotic interactions within 'tennis-court-sized' field plots (Root and Schneider, 1995). Both hydrological and ecological scales of interest have, therefore, been in stark contrast to those of climatologists, who typically employ grid squares of the order  $500 \times 500$  km in their models. For example, hydrological models are frequently concerned with small, sub-catchment (even hill-slope) scale processes, occurring on spatial scales much smaller than those resolved in general circulation models (GCMs). Conversely, GCMs deal most proficiently with fluid dynamics at the continental scale, yet incorporate regional and smaller-scale processes (Figure 3.1). As Hostetler (1994) has observed, the greatest errors in the parameterisation of *both* GCMs and hydrological models occur on the scale(s) at which climate and terrestrial-impact models interface. These scale-related sensitivities and mismatch problems are further exacerbated because they usually involve the most uncertain components of climate models, namely water vapour and cloud feedback effects (Rind *et al.*, 1992). Furthermore, mismatch problems have important implications for the credibility of impact studies driven by the output of models of climate change, especially as research into potential human-induced modifications to hydrological and ecological cycles is assuming increasing significance (Ehleringer and Field, 1993).

Therefore, in order to bridge the scales between climate, hydrological and ecological models, methods for both observing and representing sub-

Table 3.1 Spatial scales in hydrology.

Class	System	Typical length (m)
Macro	Planetary	$10^7$
	Continental	$10^6$
	Large catchment	$10^5$
Meso	Small catchment	$10^4$
	Sub-catchment	$10^3$
	Catchment module	$10^2$
Micro	Elementary volume	$10^{-2}$
	Continuum point	$10^{-5}$
	Molecular clusters	$10^{-8}$

Source: Dooge (1988).



*Figure 3.1* Conceptualisation of down-scaling and aggregation between atmospheric and hydrological models (Hostetler, 1994). Reproduced with permission of Kluwer Academic Publishing.

grid-scale heterogeneity, as well as linking parameter/state variables across disparate scales, are required. However, as Beven (1995: p. 268) observes: 'Hydrological science is constrained by the measurement techniques that are available at the present time. Hydrological theory reflects the scale at which measurements are relatively easy to make.'

In other words, a distinction should be made between the characteristic 'observation scale' and the 'process scale'. Prior to the 1970s, most environmental monitoring was focused on local-scale point processes and measurements (e.g. rainfall, pan evaporation, infiltration, groundwater levels, river flows). This favoured observation scale reflects the applied tradition of hydrology, the relative ease with which such data can be collected and the available technology for data storage and interrogation (see Boucher,

1997, for an overview). With a growing appreciation of the global dimension to environmental change, there have been moves to rationalise existing monitoring networks (Rodda, 1995) and to undertake coordinated, international experiments such as the Global Energy and Water Cycle Experiment, GEWEX (Anon., 1993). At the same time, the compilation of proxy and/or palaeoenvironmental data sets has enabled the reconstruction of hydrometeorological and palaeoecological time series, and has involved a greater range of scientific disciplines in eco-hydrological research (Barker and Higgitt, 1997). Similarly, archival and documentary evidence is increasingly employed to augment instrumental records and to construct homogeneous data sets for key hydrological variables such as rainfall (Jones and Conway, 1997) and temperature (Parker *et al.*, 1992).

Despite these contributions, there is still a paucity of near-surface data for the oceans and many remote or mountainous regions of the world. However, remotely sensed (satellite and radar) information has provided hydrologists and ecologists with new opportunities to observe non-point processes at resolutions of a few metres to the global scale. Remote sensing now routinely provides data for hydrological model parameter estimation, computations of soil moisture and flow regimes, and for real-time flood forecasting (Schultz, 1988). Indeed, remote sensing is capable of quantifying all the key hydrological fluxes and storages of the water balance equation (i.e. precipitation, evapotranspiration, snow cover, runoff and soil moisture) to resolutions of 10–30 m (Engman and Gurney, 1991). This capability has facilitated what Shuttleworth (1988) terms 'macrohydrology': the study of global atmosphere–hydrosphere–biosphere relations and feedbacks. For example, Oki *et al.* (1995) used atmospheric vapour flux convergence in conjunction with atmospheric water balance calculations to estimate monthly discharge for nearly seventy large rivers and to produce global freshwater runoff volumes.

By calculating ratios of the upwelling land surface reflectance in the red and infrared portions of the electromagnetic spectrum, satellite sensors such as the Advanced Very High Resolution Radiometer (AVHRR) can also be used to derive areal averages of photosynthetically active biomass, albedo, canopy resistance, leaf area index and fractional vegetation cover (Xinmei *et al.*, 1995). For example, the normalised difference vegetation index (NDVI) (Tucker and Sellers, 1986) has been used to study vegetation phenology (Justice *et al.*, 1986) and to monitor vegetation changes over whole continents in relation to shifts in precipitation (Tucker *et al.*, 1991) or El Niño-related droughts (Anyamba and Eastman, 1996). NDVI data are also used to monitor crops, and as a major biophysical indicator in drought and famine early warning systems such as the Global Early Warning System (GEWS) of the Food and Agricultural Organisation (FAO) (Henricksen, 1986; Hutchinson, 1991).

Two technological developments have afforded visualisation and quantitative modelling of eco-hydrological problems, namely geographical



which homogeneous records seldom exceed thirty years. Although individual weather radar measurements provide superior spatial coverage (typically 100 km in the mid-latitudes), the networks are currently limited to the industrialised nations with records extending over even shorter periods (see Collier, 1991). Similarly, satellite data may potentially yield global coverage but are constrained by factors such as cost, standardisation, ground-truthing and interpretation.

According to Blochl and Sivapalan (1995), heterogeneity and variability may be described using three attributes: (1) discontinuity – the existence of discrete zones (e.g. geological or biotic) in which the properties are uniform and predictable, yet between which there is marked disparity; (2) periodicity – the existence of a predictable cycle (e.g. annual runoff regime); (3) randomness – which is predictable only in terms of statistical properties such as the probability density function. To this list a fourth category might legitimately be added: (4) chaotic – the existence of apparently random patterns that are in fact deterministically generated. Spatial properties may be described from sample measurements using geostatistics. Kriging is perhaps one of the most popular techniques (Isaaks and Srivastava, 1989). This method involves the estimation of a parameter for an unknown point given neighbouring points within a field of values. Variability within the field is determined on the basis of direction and distance and, potentially, covariates (in co-kriging). The approach works because points close together tend to show more similarity (i.e. are more correlated) than points further apart, and points along certain bearings will show less variability than equidistant points along a different bearing (Baird, 1997). Thus, kriging models not only assist in the description of physical variables in space but can also be used to speculate on the underlying causes of spatial 'structure' in environmental variables.

To illustrate this point, Figure 3.3 shows exponential decay functions fitted to individual correlation values obtained from pairs of neighbouring daily rainfall records (Osborn and Hulme, 1997). The correlation between all stations in Europe is plotted against the separation distance for winter and summer. The overall decay lengths for the region were found to be greater in winter (300 km) than in summer (204 km), indicating that the characteristic scale of precipitation-causing weather is greater in winter than summer. This is due to the fact that a higher proportion of winter rainfall is of frontal origin, whereas the dominant mechanism in summer is convective rainfall. Given the dependence of the decay lengths on the relative importance of frontal versus convective rainfall, the correlation distances were also found to vary spatially as well as seasonally. Such techniques have important applications in the validation of GCM grid-box area-average precipitation frequencies and amounts, as well as for scaling of contrasting precipitation mechanisms.

Thus, the distance at which the spatial structuring or correlation in a



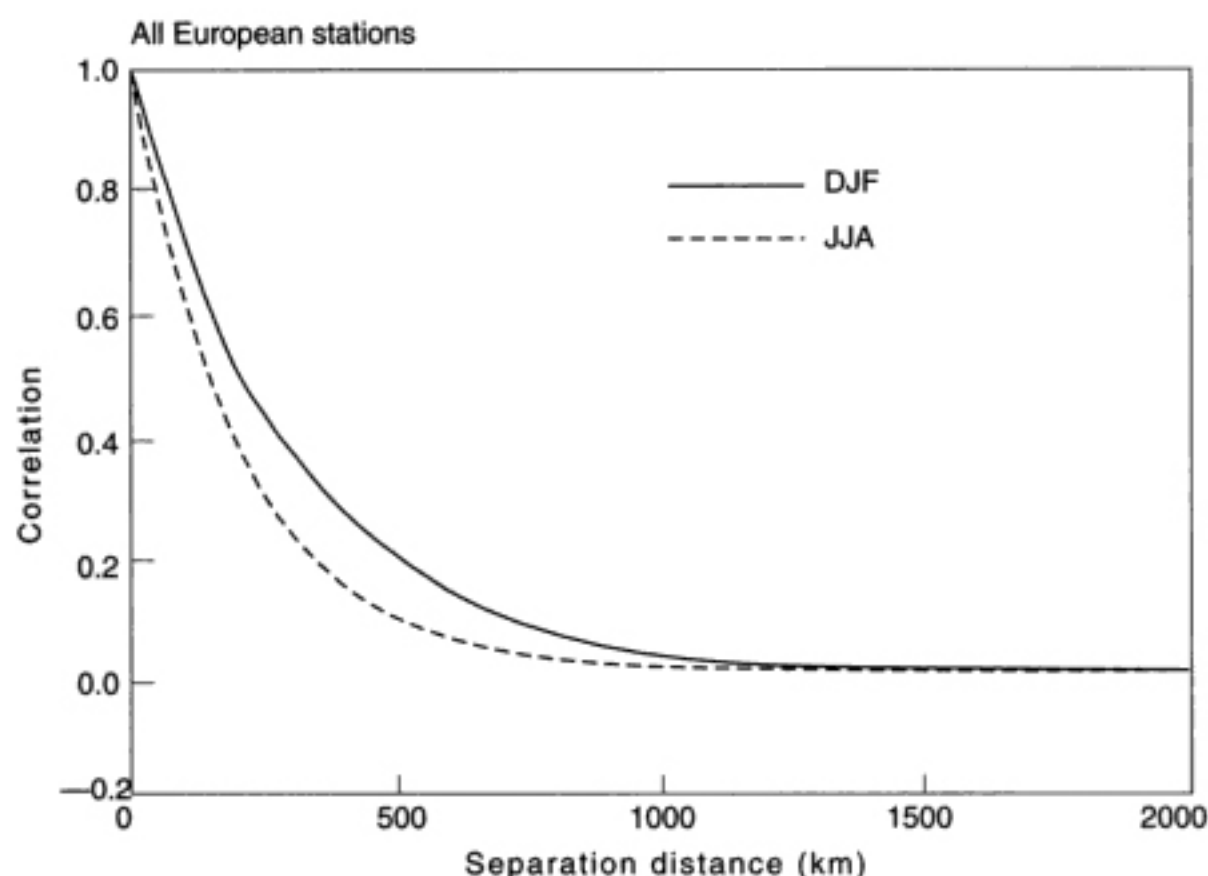


Figure 3.3 Correlation decay curves obtained for winter (DJF) and summer (JJA) daily rainfall between neighbouring stations across Europe. Adapted from Osborn and Hulme (1997).

variable breaks down can indicate that a new set of physical laws is required to describe the phenomenon at this length scale. This notion underlies the concepts of the representative elementary volume (REV) (Hubbert, 1940; Bear, 1972) (see Chapter 9) and, more recently, that of the representative elementary area (REA) (Wood *et al.*, 1988; 1990; Beven *et al.*, 1988), namely, that there exists a soil volume or spatial scale at which simple descriptions of governing processes may suffice (see also Chapter 9). Since measurements of streamflow are inherently spatial averages (Woods *et al.*, 1995), increasing the length scale (area or volume) effectively increases the sampling of hydrological forcings (rainfall and evaporation), hill slopes, soil properties and vegetation, which leads to a decrease in the difference between equivalent sub-catchment area responses (Figure 3.4). The REA is the domain scale at which the variance between hydrological responses for catchments of the same scale attains a minimum, and thus a fundamental building block for distributed hydrological modelling. At the scale of the REA, it is possible to neglect differences in spatial *patterns* of catchment properties (such as soil hydraulic conductivity), but it is still necessary to take spatial *variability* into account in terms of distribution functions (Beven *et al.*, 1988). However, as Wood (1995: p. 92) points out:

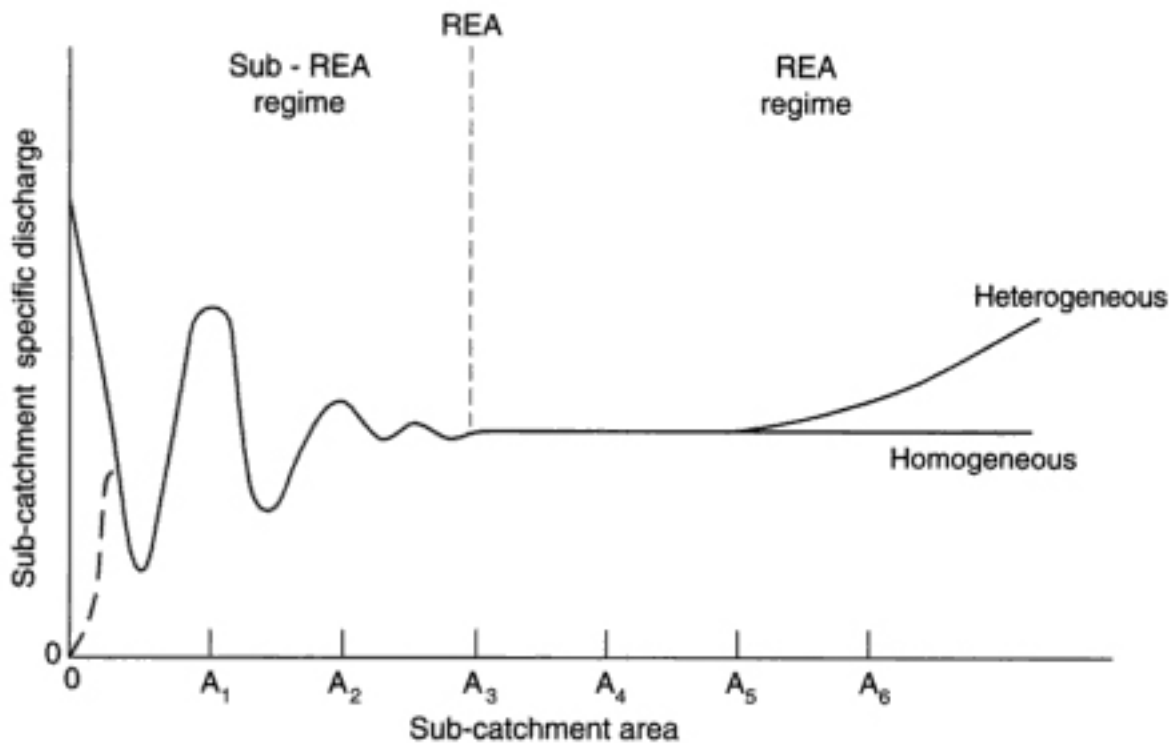


Figure 3.4 Definition of the representative elementary area (REA). In this case, the REA is  $A_3$ . Modified from Baird (1997).

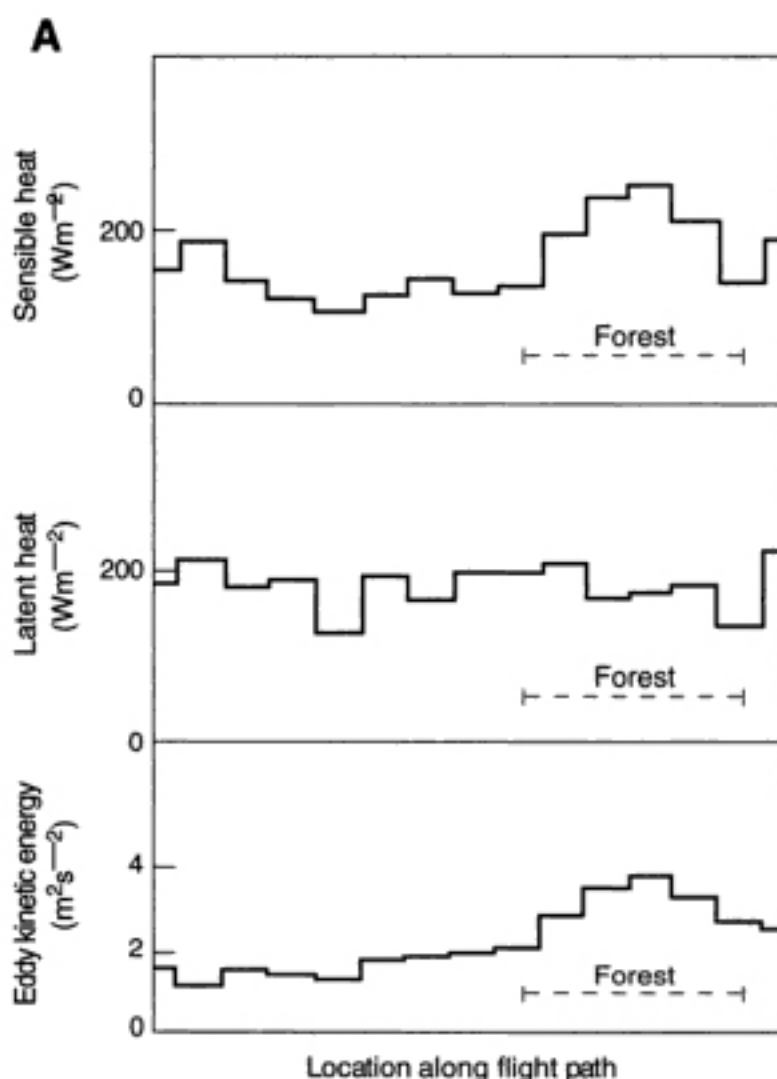
this transition in scale, where pattern no longer becomes important but only its statistical representation, may occur at different spatial scales for different processes, may vary temporally for the same parameter (except during wet or dry periods) and may vary with the scale of the 'macroscale' model. Much of the research to date may indicate that the REA for catchment modelling is . . . [in the region of] 0.1 to 25 km<sup>2</sup>.

Theoretically, an REA may be derived for any spatially averaged environmental parameter, but its precise value will be process-, region- and time-specific. For example, Blöschl *et al.* (1995) showed that the REA size is strongly governed by the correlation length of precipitation fields and by the storm duration.

The characterisation of spatial heterogeneities in land surface–atmosphere interactions at all length scales also remains a great challenge to hydro-meteorologists, because the characteristics of the atmosphere above dry and wet (vegetated) surfaces are significantly different due to the contrasting processes of energy redistribution at the ground surface. Avissar (1995) identified five land-surface characteristics that need to be specified accurately in atmospheric models, namely, stomatal conductance, soil surface wetness, surface roughness, leaf area index and albedo. Under stable weather conditions, spatial-variability of any of these characteristics of the order of 100 km was found to induce mesoscale circulations in models of the transport

of heat and moisture in the planetary boundary layer. Such circulations were observable for length scales as low as 10 km and were sufficient to promote non-linear feedbacks arising from cloud formation and precipitation. In a similar analysis, Shuttleworth (1988) made a distinction between disorganised and organised variability, also for length scales of 10 km (Figure 3.5). Under conditions of disorganised variability at length scales of 10 km or less, fluid flow and mixing processes naturally integrate the land-atmosphere feedbacks, but under conditions of organised variability at length scales greater than 10 km, there may be an organised (convective) response in the atmosphere that alters the effective value of surface properties at GCM sub-grid scales.

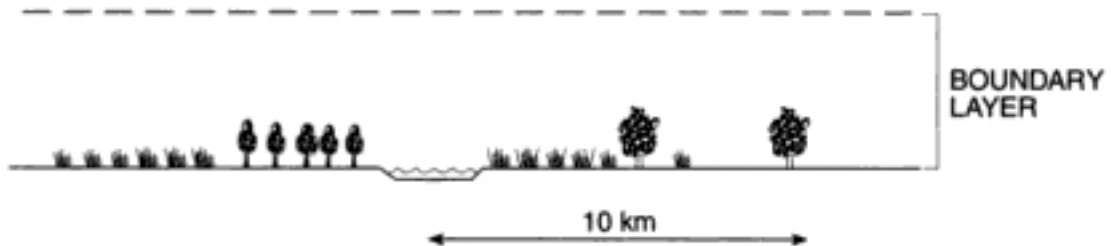
Both studies suggest that spatial variability in land-surface parameters over length scales of the order 10 km is sufficient to induce non-linear feedbacks,



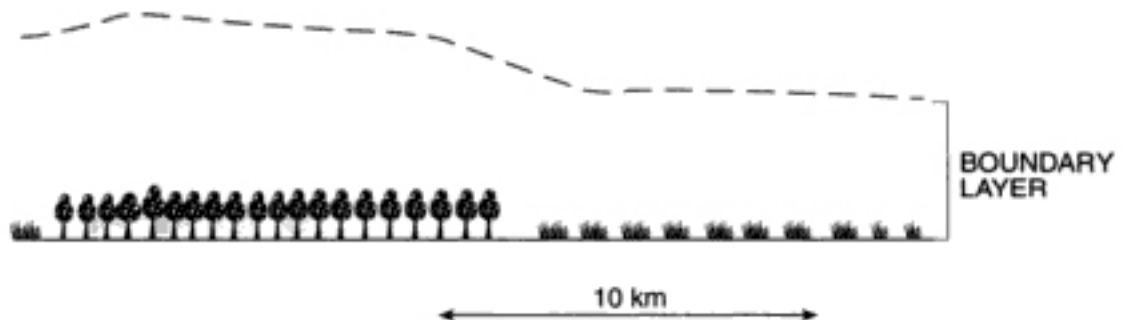
*Figure 3.5A:* Aircraft measurements of sensible heat, latent heat and eddy kinetic energy made at a height of 100 m, these being the median values for three flights between 11:45 and 15:00 GMT on 16 June 1986. The flight path was over a disorganised mixture of agricultural crops apart from the (organised) change to pine forest for the portion indicated by the broken line.

**B****Type 'A' land surface cover**

Exhibits disorganised variability at length scales of 10 km or less:  
Gives no apparent organised response in atmospheric boundary layer

**Type 'B' land surface cover**

Exhibits variability which is organised at length scales of greater than 10 km:  
may give an organised response in the atmosphere such as to alter the effective value of surface properties



Note: Surface vegetation not drawn to scale

*Figure 3.5B: A proposed classification of different types of land surface based on organisational variability of surface cover. Source: Shuttleworth (1988). Reproduced with permission of Elsevier Science.*

principally through modified spatial patterns of rainfall and surface energy redistribution. However, many state-of-the-art atmospheric models have adopted parameterisations of land-surface processes at smaller scales at which spatial homogeneity is assumed. Even statistical descriptions of heterogeneity fail to capture lateral interactions between contrasting vegetation surfaces, suggesting that mesoscale circulations must be considered explicitly (Avisar, 1995). Changed energy fluxes and wind regimes have also been associated with changes from tall evergreen vegetation to the alternating short annual vegetation and bare soils associated with agriculture. For example, Hobbs (1994) has described profound changes in nutrient, energy and water fluxes as a result of the fragmentation of native perennial vegetation in Western Australia by the introduction of predominantly annual crops and pastures.

geological or climatological controls to spatial variations in the vegetation cover evident at the regional scale (Figure 3.6A) could be inferred from the observable information at the field scale (Figure 3.6C).

Nonetheless, the most straightforward up-scaling approach is to assume that the parameters at the meso and sub-mesoscale are the same as those at larger scales. The scaling problem then becomes a matter of multiplying by the new length scale or catchment area. For example, Kuczera (1985) modelled observed reductions in river catchment runoff following bushfires in the eucalyptus forests of the Melbourne water supply district, Australia, as a function of stand age:

$$Y_t = L_{\max} K(t-2)e^{1-K(t-2)} \quad \text{if } t > 2 \text{ else } Y_t = 0 \quad (3.1)$$

where  $Y_t$  is the average yield reduction (mm) relative to mature mountain ash forests  $t$  years after the bushfire,  $L_{\max}$  is the maximum yield reduction (mm) and  $1/K$  is the time to maximum yield reduction (years). Regional relationships were then established between the two parameters  $L_{\max}$  and  $K$  using forest descriptors such as the percentage of the catchment area covered by regrowth eucalyptus forest. The model was subsequently adapted by Wilby and Gell (1994) to simulate the effect of piecemeal forest harvesting on downstream runoff yields entering a sensitive wetland site (Figure 3.7). In both cases, the simple dependence of yield reductions following either fire or

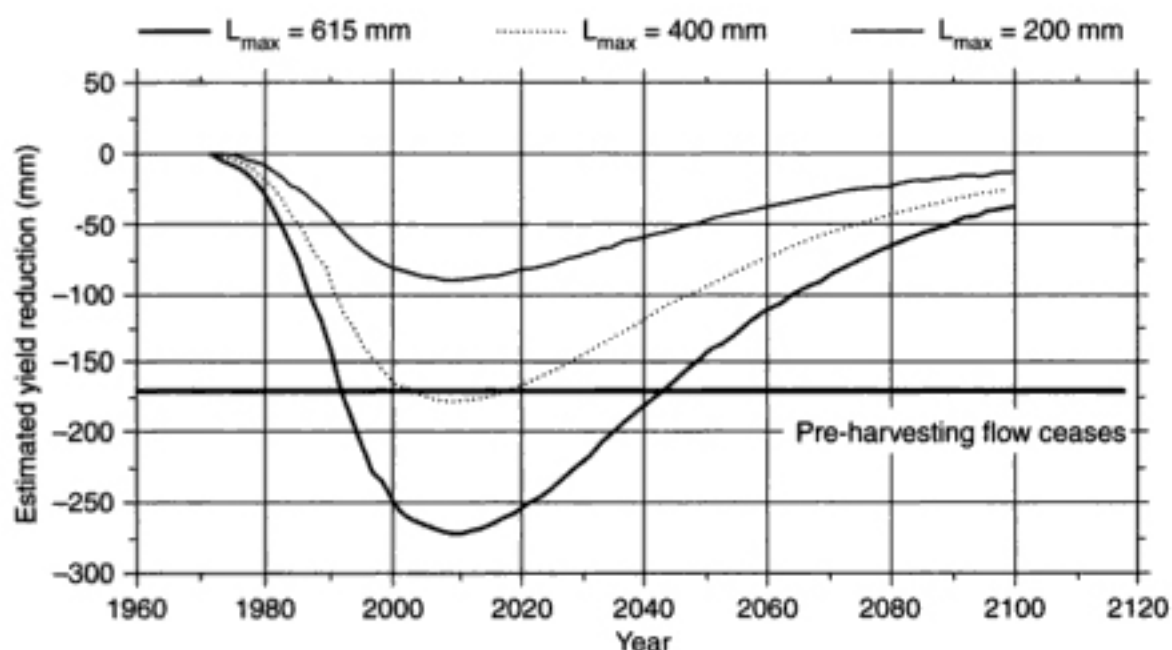


Figure 3.7 Simulated yield reduction curves for selected  $L_{\max}$  values following twenty years of eucalypt forest harvesting upstream of Tea-tree Swamp, Errinundra Plateau, Victoria, Australia. Source: Wilby and Gell (1994). Reproduced with permission of International Association of Hydrological Sciences Press.

harvesting (equation (3.1)) reflects empirical variations in sapwood area and throughfall losses with the age of forest regrowth. Field measurements of transpiration flows indicate that stand water use is strongly related to the amount of sapwood area per unit area of forest. Similarly, canopy conductance is proportional to the product of the average leaf conductance and the leaf area index (LAI, a ratio of leaf area to ground area, which is in turn a function of the stand basal area) (Rogers and Hinckley, 1979). Thus, Haydon *et al.* (1996) found that the sapwood area of eucalypt overstorey in the central highlands of Victoria, Australia, reached a peak of  $10.5 \text{ m}^2 \text{ ha}^{-1}$  at age 15 years and declined gradually to  $2.5 \text{ m}^2 \text{ ha}^{-1}$  at age 200 years, whereas the peak interception loss of 25 percent occurred at age 30 years, declining to 17 percent at age 200 years.

Hatton and Wu (1995) present an alternative scaling theory, which predicts the nature of the water vapour flux/leaf area relationship by combining elements of ecological field theory, the hydrological equilibrium theory and a standard treatment of the soil-plant-atmosphere continuum in the form:

$$Q = aIA + b\psi A^f \quad (3.2)$$

where  $Q$  is the vapour flux ( $\text{m}^3$ ),  $I$  is radiation intercepted by the canopy ( $\text{MJ m}^{-2}$ ),  $\psi$  is the soil water potential (MPa) (see Chapter 9),  $A$  is the leaf area ( $\text{m}^2$ ),  $f$  is a scaling exponent, and  $a$  and  $b$  are lumped parameter coefficients. However, the use of equation (3.2) to extrapolate individual tree water consumption to stand water consumption entails several assumptions: (1) a strong relationship is assumed to exist between the leaf area of individual trees/stands and the site water balance; (2) each tree tends towards an equilibrium between its size (leaf area) and its local environment such that at no time do resources in local abundance remain untapped; (3) the site is assumed to be homogeneous with regard to soils and climate; (4) the site is fully occupied and tending towards hydrological equilibrium between available moisture and available energy; (5) individual plants react in parallel with all others in the stand; (6) the simple demand function based on irradiance ignores advective contributions to evaporative demand. The principal advantage of the technique is that it does not assume a single fixed relationship between leaf area and water flux; instead, tree water use extrapolated on the basis of leaf area is affected by temporally variable, non-linear stress responses (Figure 3.8). The sampling variability of parameters  $a$  and  $b$  was found to depend on plot homogeneity, although there is a degree of generality of  $a$  between species. Therefore, making use of the equation to scale across heterogeneous landscapes requires spatial distributions of soil water potential and irradiance, and local leaf area distributions. As will be shown below, spatial patterns of soil and energy environments may be obtained from topographic indices.

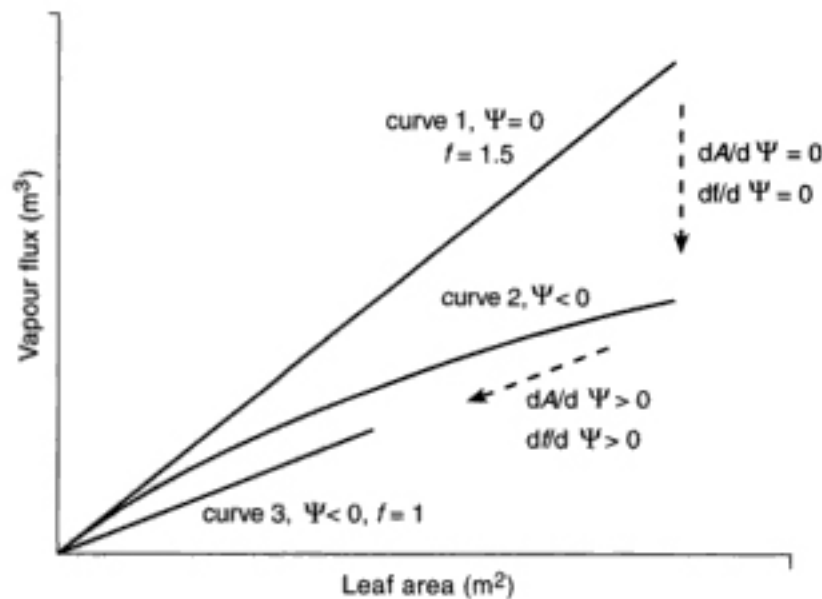


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*Figure 3.8* Forms of the theoretical scaling relationship between tree leaf area and water flux. With unlimited soil water, the relationship is linear and the slope is limited only by irradiance (curve 1). As the soil dries, the retention of leaves creates a quasi-equilibrium in which the leaf efficiency of the larger trees declines (curve 2). If a drought is of sufficient extent and duration, the trees will drop leaves such that the relationship is in a new, lower hydrological equilibrium, and the curve may once again be linear (curve 3). Source: Hatton and Wu (1995). Reproduced with permission of John Wiley & Sons Ltd.

Despite their limitations, small-scale (*c.* 0.1 hectares) field studies of plant–water relations remain appealing because this is the scale at which species interactions are most readily observable and at which data have been traditionally collected by ecologists (and hydrologists too!). Forest ‘gap’ models seek to integrate dynamic plant responses to environmental constraints defined at the level of the individual plant (Shugart and Smith, 1996). Key processes in gap models include (1) species-specific growth rates, which depend upon the net photosynthetic rate of the tree per unit area of leaves; (2) spatial positioning and competition for light between individual trees; a range of environmental constraints such as soil moisture and fertility; (3) disturbances due to fire or flooding, and light availability; (4) mortality, which is often age- or stress-related and modelled stochastically; and (5) establishment, which again is represented stochastically and may be a function of environmental constraints. Such forest patch models have been used extensively in studies of global climate change (see, for example, Lauenroth, 1996; Post and Pastor, 1996; Bugmann *et al.*, 1996).

Scaling up patch models via statistical sampling procedures assumes that a generalised patch model is able to simulate the dynamics of entire ecosystems as well as individual species. However, there is a discontinuity between patch- and ecosystem-scale models (Shugart and Smith, 1996). At the patch scale, individual plant recruitment, growth and mortality are in a state of

quasi-cyclical disequilibrium, whereas at the scale of the ecosystem the same processes are represented using mass balance approaches, which assume an equilibrium status for whole plant communities. Furthermore, at the patch scale there are feedbacks between the canopy composition and recruitment. Representation of processes such as dispersal, fire and insect outbreaks requires a spatial framework for *linking* patches. Such considerations suggest that for continental-scale applications it is desirable to replace the individual species in patch models with plant functional types that are based on life forms, physiology and rooting distributions with depth (Bugmann and Fischlin, 1996; Coffin and Lauenroth, 1996).

Jarvis and McNaughton (1986) and Schimel *et al.* (1991) have suggested that extrapolation techniques are also limited by the fact that plants do not respond uniformly to external environmental stresses, that there are feedback processes external to the leaf scale that operate at the ecosystem scale, and that there are major difficulties in forecasting the behaviour of (non-ideal) complex systems. For example, increasing concentrations of atmospheric CO<sub>2</sub> are assumed to have the dual effect of enhancing photosynthetic activity and improving the efficiency of plants' water use (Sellers *et al.*, 1996). This may be valid at the scale of individual plants, but CO<sub>2</sub> fertilisation confers advantages selectively within ecosystems, depending on species. At the forest scale, spatial and temporal variations in the microclimate (in particular the relative humidity) of the canopy will have a negative feedback on evapotranspiration rates of individual plants. This selectivity will also modify internal nutrient and water fluxes.

An alternative extrapolation philosophy is to derive scale-independent 'laws of nature' by employing dimensional analysis or self-similarity techniques (Blöschl and Sivapalan, 1995). Fractals provide a mathematical framework for the treatment of apparently complex shapes that display similar patterns over a range of space/time scales. According to Mandelbrot (1983) many attributes of nature exhibit a property known as statistical self-similarity, whereby subcomponents of an object, pattern or process are statistically indistinguishable from the whole. Fractals have found widespread application in hydrology, geomorphology and climatology (see, for example, the *Journal of Hydrology*, Volume 187, Issues 1–2, Gao and Xia, 1996; or Goodchild and Mark, 1987). It has even been suggested that fractals are indicative of underlying processes of organisation, as in the case of the geometry of drainage networks, which reflect minimum energy expenditure (Rinaldo *et al.*, 1992), and the hierarchical structuring of mid-latitude mesoscale atmospheric convective systems (Perica and Foufoula-Georgiou, 1996). However, simple fractal properties are seldom applicable across all temporal and/or spatial scales and it is unclear as to how multifractals should be interpreted relative to observable hydrological processes (Wilby, 1996).

to future climate conditions. Richardson's (1981) weather generator (WGEN) model is the most commonly used for climate impact studies: this was originally designed to simulate daily time series of precipitation amount, maximum and minimum temperature, and solar radiation for the present climate. Rather than being conditioned by circulation patterns, all variables in the Richardson model are simulated conditionally according to previous precipitation occurrence. At the heart of all such models are first- or multiple-order Markov renewal processes in which, for each successive day, the precipitation occurrence (and possibly amount) is governed by outcomes on previous days. Models such as WGEN have been adapted for a number of climate change impact studies (e.g. Wilks, 1992; Mearns *et al.*, 1996). There is also the possibility of spatially distributing WGEN parameters across landscapes, even in complex terrain, by combining interpolation techniques and DTMs (see VEMAP study below). However, the principal issue involving the application of WGEN or other stochastic weather generators to future climates has been the method of adjusting the parameters in a physically realistic and internally consistent way. For example, Katz (1996) demonstrated, using daily observations at Denver, Colorado, that when the WGEN parameters are varied, certain unanticipated effects can be produced. Modifying the probability of daily precipitation occurrence changed not only the mean daily temperature but also its variance and autocorrelation in possibly unrealistic ways.

Given the limitations of GCM grid-point predictions for regional climate change impact studies, the final downscaling option is to embed a higher-resolution limited-area climate model within the GCM, using the GCM to define the (time-varying) boundary conditions (Giorgi, 1990; Mearns *et al.*, 1995). Although limited area models (LAMs) can produce climates for 20–50 km horizontal grid spacing and 100–1000 m vertical resolution there are several acknowledged limitations of the approach. LAMs still require considerable computing resources and are as expensive to run as a global GCM. Furthermore, they are somewhat inflexible in the sense that the computational demands apply each time that the model is transferred to a different region. Above all, the LAM is completely dependent upon the veracity of the GCM grid-point data that are used to drive the boundary conditions of the region – a problem that also applies to circulation-driven downscaling methods.

As Table 3.2 indicates, the confident application of statistical downscaling techniques to the study of plant–water relations is constrained by several as yet unresolved issues. Perhaps the most serious limitation is the way in which downscaling compels the use of 'passive' atmosphere–vegetation models; current methodologies do not incorporate feedbacks between the land surface and climate, or permit scale interactions. Furthermore, the majority of downscaling tools relate point or areal averages to regional scale phenomena according to the level of data available. However, what is often required for

*Table 3.2* Outstanding challenges to the confident application of statistical downscaling techniques.

- 
- The whole ideology of downscaling presupposes that, as a result of human-induced global warming, there will be significant (and predictable) changes in the downscaling predictor variables (such as the frequencies of daily weather patterns).
  - To date, most downscaling studies have been conducted for daily or monthly precipitation in temperate, mid-latitude regions of the Northern Hemisphere; relatively few have tackled semi-arid or tropical locations. There has also been a topographic bias towards low-altitude sites.
  - There is a need for more general weather classification systems used in downscaling. Most weather classification schemes are inherently parochial because of the important controlling influences of regional- and local-scale factors such as topography or ocean/land distributions.
  - The majority of downscaling approaches generate time series of data for only a few hydrologically relevant parameters, most commonly precipitation. There is a need for techniques that downscale internally consistent multivariate data which preserve covariance among parameters and auto-correlation within time series.
  - Current downscaling approaches seldom capture climate variability at all temporal or spatial scales. For example, even within a single circulation pattern, the precipitation statistics may vary considerably from year to year.
  - This type of non-stationarity can be accounted for by developing more complex statistical models (within the constraints of model reliability imposed by data availability). This, however, puts greater pressure on the driving GCMs to provide reliable predictions for a greater range of variables.
  - Downscaling is a uni-directional modelling technique. Local- and regional-scale hydrological or ecological responses are forced by mesoscale predictor variables. Current techniques have no means of incorporating terrestrial feedbacks into the driving climate models.
- 

*Source:* Adapted from Wilby and Wigley (1997).

impact assessment is a means of interpolating between data-rich regions to data-poor sites. The remaining two sections will address these important scale issues.

## DISTRIBUTING TECHNIQUES

Some commentators have suggested that a general theory of hydrological scaling is unlikely to exist and that sub-grid-scale heterogeneity should be treated statistically (Beven, 1995: p. 278):



the hydrological system is greatly influenced by external historical and geological forcings. This greatly limits the potential for scale-invariant behaviour and it is suggested that it may be better to recognise explicitly that scale-dependent models are required in which the characterisation of the heterogeneity of responses is posed as a problem of sub-grid scale parameterisation.

As was noted earlier, hydrological and ecological measurements tend to have a coarser spatial than temporal resolution, prompting the widespread use of interpolation techniques for the space domain. Perhaps the most thoroughly discussed interpolation problem in hydrology is the spatial estimation of rainfall from point rain-gauge measurements (see, for example, Shaw, 1994; Reed and Stewart, 1994). The problem arises because the measurements on which the interpolation techniques are based are too widely spaced relative to the natural variability of rainfall. For example, the average spacing of hourly rain-gauges in the relatively dense monitoring network of the British Isles is between 15 and 30 km (Faulkner and Reynard, personal communication), whereas the length scales of individual storm cells are of the order of 10 km (see Figure 3.2). Although the UK Meteorological Office's MORECS predictions of potential and actual evapotranspiration have a grid spacing of 40 km, rainfall radar typically has a resolution of 2 km, and remotely sensed AVHRR satellite imagery pixels of 1 km, the widespread use of these data sources is constrained by their high cost and short record lengths relative to surface networks (e.g. AVHRR provides about fifteen years of data).

Given the constraints of both remote and surface monitoring systems, and the natural heterogeneity of surface processes, one solution is to correlate the variable of interest to an auxiliary variable whose spatial distribution is more readily obtained. The spatial distribution of the dependent variable is then inferred from the spatial distribution of the covariate (Blöschl and Sivapalan, 1995). To date, one of the most widely used covariates in eco-hydrology has been topography, for which data with a resolution of 50 m are often available in digital form. The availability of digital elevations and other environmental variables such as soils and geology, coupled with GIS and DTM software for manipulating data, has favoured the development of predictive mapping techniques in the last twenty years. As Table 3.3 indicates, topography can be used to infer the spatial distribution of a wide variety of secondary variables. For example, the precipitation–elevation regressions on independent slopes model (PRISM) (Daly *et al.*, 1994) simulates precipitation at 10 km grid scales by, first, dividing the terrain into topographical facets of similar aspect; second, regressing point precipitation data against elevation for each facet by region; and third, employing these regression equations spatially to extrapolate station precipitation to cells that have similar facets.

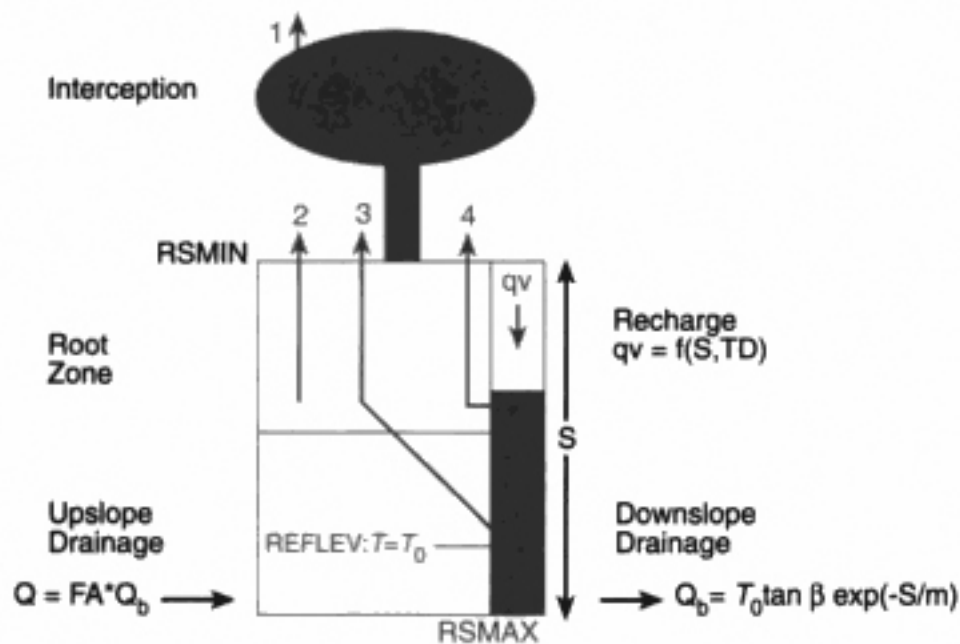
Beven's (1987) solution to the problem of sub-grid-scale hydrological parameterisation was the use of spatial distribution functions to represent



Table 3.3 Examples of topographically derived hydrometeorological variables.

- 
- *Elevation*: daily and seasonal precipitation totals; snow characteristics including snow water equivalent; wind speeds; air temperature; soil depth; air and soil water chemistry.
  - *Slope*: incident solar radiation; soil properties and preferential flow pathways; lateral subsurface flow rate; soil moisture; transpiration rates; soil water chemistry.
  - *Aspect*: incident solar radiation; precipitation totals; snow accumulation and melting; wind speeds; air temperature; soil moisture; transpiration rates; atmospheric wet and dry deposition.
  - *Upslope catchment area*: precipitation and runoff volume; soil moisture; soil surface properties; stream network order and main channel length.
  - *Slope curvature*: snow accumulation; subsurface water flow; soil moisture; soil litter accumulation; soil erosion/deposition rates; rill initiation; soil depth and texture; water-holding capacity; nutrient availability.
- 

local-scale processes governing runoff production. For example, TOPMODEL (Beven and Kirkby, 1979) simulates the scale-dependent dynamics of the storm hydrograph using the distribution function of an index of hydrological similarity,  $\ln(\alpha T_0 \tan\beta)$ , where  $\alpha$  is the area draining through a point,  $\tan\beta$  is the local slope angle at that point and  $T_0$  is the local downslope transmissivity at soil saturation. These properties, as well as the spatial distribution functions for incoming rainfall intensities, vegetation processes such as throughfall, soil properties and downslope water velocities, may all be inferred from DTM of the catchment topography. Quinn *et al.* (1995) and Beven (1995) have extended TOPMODEL to represent interactions between downslope subsurface flows and water availability for transpiration. Figure 3.10 shows the key elements of their simple patch model, which represents areas of the landscape with broadly similar responses in terms of evapotranspiration. The model differs from conventional one-dimensional surface vegetation-atmosphere models in one respect: subsurface water fluxes are able to enter and leave the patch via upslope and downslope drainage, respectively. The variability in runoff production, soil moisture and evapotranspiration is then calculated from a linear combination of patches of varying topographical, meteorological, soil, geological and vegetation characteristics. Although this allows for more realistic modelling of the patch in the context of the landscape, the spatial distribution of many of the vegetation and soil properties listed in Figure 3.10 must still be specified from the results of micrometeorological experiments and available field data. Furthermore, it must be recognised that there may be many permutations of patches that give similar hydrological responses in terms of observed evapotranspiration or runoff. This equifinality in model behaviour (see



Processes in the patch model

1. Evaporation from the interception store (canopy resistance = 0)
2. Evapotranspiration from the root zone store ( $R_{MIN} < \text{canopy resistance} < R_{MAX}$ )
3. Evapotranspiration from the water table when in root zone
4. Evapotranspiration supplied by capillary rise from the water table

Parameters of the patch model

$RA$ (s/m)	Aerodynamic resistance
$R_{MIN}$ (s/m)	Minimum dry canopy resistance
$R_{MAX}$ (s/m)	Maximum dry canopy resistance at wilting point
$MAXINT$ (m)	Interception storage capacity
$FA$	Fractional upslope area
$REFLEV$ (m)	Reference level for soil transmissivity
$T_0 \tan \beta$ (m <sup>2</sup> )	Product of saturated transmissivity at reference level and effective downslope hydraulic gradient
$m$ (m)	Transmissivity profile (and recession curve) parameter
$TD$ (h/m)	Effective wave speed per unit of deficit for recharge
$SOIL$	Soil type for capillary rise calculations

Figure 3.10 Schematic representation of a simple patch model including definitions of all model parameters. Source: Beven (1995). Reproduced with permission of John Wiley & Sons Ltd. (Please note: the model equations are not explained here and interested readers should consult the original paper.)

Chapter 9) is further exacerbated by the number and weighting of patches selected.

These parameterisation issues might be resolved by calibrating semi-distributed hydrological models such as TOPMODEL using the products of predictive vegetation mapping. Indeed, predictive vegetation mapping already embraces many of the principles inherent in topographic hydrological models (e.g. Palmer and Van Staden, 1992). Founded in ecological niche theory and gradient analysis, the approach predicts vegetation composition across a landscape given interpolated environmental variables that are related to physiological tolerances and are derived from digital soil or elevation data

SCALES AND SCALE 'MISMATCH' BETWEEN  
ECOLOGICAL AND HYDROLOGICAL  
PROCESSES

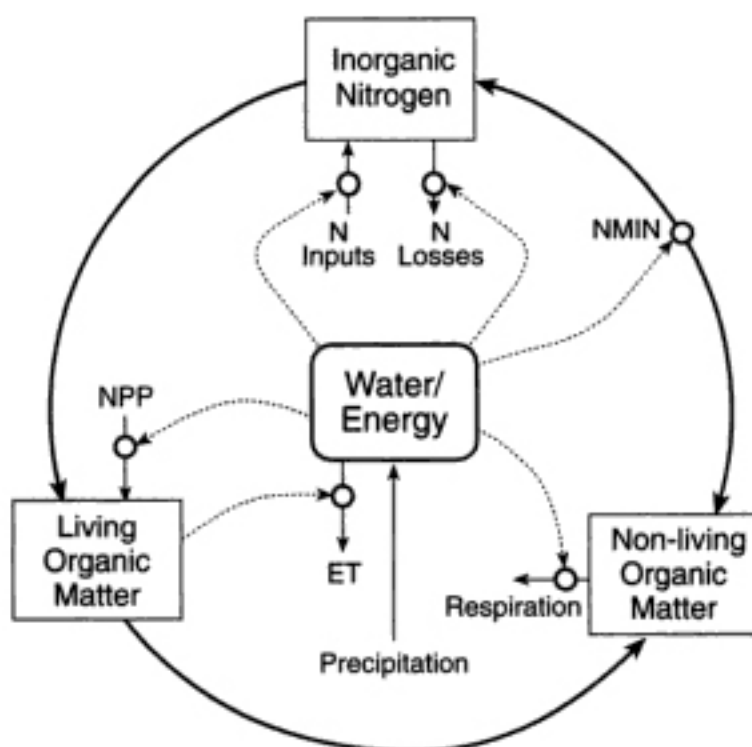
A major theme of research for the past decade has been to understand the consequences of climate variability and potential climate change on eco-hydrological systems. In any assessment of climate impacts on ecosystems, processes mediated through the hydrological cycle must come to the fore: droughts, floods and changes to moisture stress on vegetation. However, most of our knowledge of the atmosphere's spatial characteristics is of low spatial resolution (Giorgi and Marinucci, 1996). This is a classic issue in linking atmospheric GCMs to the land surface, where typical GCM grid cells represent many thousands of square kilometres, and most ecological and hydrological processes are best understood on length scales of metres to small river catchments (a few tens of square kilometres). Resolution is also an issue in analysing observations. A recent project, the Vegetation and Ecosystem Modelling and Analysis Project (VEMAP, 1995), produced a set of down-scaled climatologies for the USA as input into eco-hydrological models. The analysis was conducted on an  $0.5^\circ$  latitude  $\times$  longitude grid, quite coarse for ecosystem studies, yet resulting in over 3000 grid cells. Even in the USA, where observations are relatively dense, meteorological station densities average no more than two per grid cell. While there exist a few areas in the USA and Europe where patterns of mean climate and interannual variability may be observed directly with a resolution of a few kilometres, in most regions precipitation and surface temperatures may only be estimated from observations with length resolutions of 50–100 km. Thus, large-scale studies (e.g. biome or drainage basin scale) must rely on downscaling to account for catchment-scale influences of topography on temperature, precipitation, radiation and other terrain-dependent aspects of climate (see above). Downscaling procedures intrinsically produce a reasonable portrayal of mean conditions, which are strongly constrained by effects of elevation and orography on precipitation processes and temperature. They do a much worse job with precipitation rates, which depend upon the dynamics of atmospheric processes that intrinsically occur on scales smaller than the resolution of typical observing systems: processes on the scale of convective and precipitating cloud systems. Thus, capturing even the statistics of storm intensity at a regional scale can be challenging.

There are thus two 'scale mismatches' between climate and hydrology: first, between large-scale atmospheric features and small-scale land-surface attributes, in effect, between the resolution of climate models and observations, and the scale of topographic features. This means that terrain-dependent features of climate – adiabatic effects, inversions and precipitation – must be inferred indirectly from models and observations. Second, there is a mismatch between small-scale atmospheric features (convective and

precipitating clouds) and regional land systems, which makes capturing the occurrence and statistics of extreme events over large areas difficult.

In considering eco-hydrological systems, there are also key scale 'matches'. The river catchment or landscape has long been a scale at which both ecologists and hydrologists could work. Hill slopes provide ordered sequences of soil variability, moisture availability and vegetation that have been exploited by hydrologists, ecologists and soil scientists (Schimel *et al.*, 1985; Burke *et al.*, 1989). River catchments are a key unit in understanding hydrological processes such as evapotranspiration, runoff generation and baseflow: they are also an integrated unit for ecosystem studies, contributing to the understanding of nutrient budgets and transformations, water use, primary production and disturbance effects (Borman and Likens, 1979). Catchment studies provide both a scale at which variability within landscapes in ecological and hydrological processes may be studied (Moldan and Cerny, 1994), and through hydrological and hydrochemical gauging, an integrated scale where the aggregate interactions of climate, hydrology and ecology may be observed and modelled. For example, regional to global nitrogen studies have just begun, and it is evident that gains and losses of N are highly coupled to water budgets (via leaching) and to soil moisture variations, the key control over trace gas losses (Mosier *et al.*, 1997; Parton *et al.*, 1996; Figure 3.12). Given the crucial importance of carbon and nitrogen budgets in contemporary ecology and limnology (Schimel *et al.*, in press; Hornberger *et al.*, 1994), the catchment scale must be a central focus of research as the scale where phenomena such as leaching and soil moisture storage may be linked to the biogeochemistry of C and N.

While much of the material reported in this chapter has dealt with interpreting atmospheric information in terms of scales of hydrological and ecological processes, land-surface processes also affect climate. There is now an extensive literature documenting the effects of large-scale modification by the land surface of climate (e.g. Melillo *et al.*, 1996). Studies have indicated that deforestation may affect climate via changes to evapotranspiration and the Bowen ratio, via albedo and roughness changes, and via changes to land-surface patch structure, causing mesoscale effects (Dickinson, 1992; Pielke *et al.*, 1991; Henderson-Sellers and McGuffie, 1995). Other studies have looked at global-scale effects of the changing land surface on climate via sensitivity studies examining an artificial perturbation to surface conductance (Thompson and Pollard, 1995), simulated effects of doubled atmospheric CO<sub>2</sub> concentrations (Sellers *et al.*, 1996), and by a comparison of global 'potential natural' to actual vegetation (Chase *et al.*, 1996). Clearly, feedbacks from land-surface hydrology, especially via evapotranspiration, can have substantial effects on climate. Studies of global hydroclimatological feedbacks using models require that the surface processes be correctly forced, meaning that changes to the fluxes at the land-atmosphere interface be correct with regard



*Figure 3.12* Schematic illustration of the coupling of water, nitrogen cycling and carbon in ecosystems. Principal features of these coupled controls are that (a) water controls the inputs and outputs of nitrogen (N), (b) increasing net primary productivity (NPP) allows more of the N flux through the system to be captured into organic matter, (c) increasing organic N stocks allows for more N mineralisation, supporting more NPP, and (d) increasing precipitation allows for both more NPP and more N cycling, thus water and nutrient limitation of NPP tend to become correlated. Note that the circles indicate key water/energy-driven processes involved in the nitrogen cycle. Source: Schimel *et al.* (in press).

to the natural scale of the land surface. They also require that land-surface fluxes be correctly aggregated back to the scale of the atmospheric processes simulated, taking into account any processes that arise at sub-grid scales (Zeng and Pielke, 1995). Simulating the coupled effects of land surface and climate change will be a 'grand challenge' for interdisciplinary earth science in the twenty-first century.

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# PLANTS AND WATER IN DRYLANDS

*John Wainwright, Mark Mulligan and John Thornes*

## INTRODUCTION

It could be argued that the understanding of eco-hydrological processes is critical in drylands for two reasons. First, in most cases the aridity of the drylands means that the supply of water is the dominant control on the growth and maintenance of plants. Second, most drylands are characterised by extreme variability in water availability. Plants must adapt to use this variable source. In addition, large amounts of soil erosion during storm events can remove the uppermost, relatively fertile and moisture-retaining parts of the soil profile and thus enhance the importance of moisture availability as the dominant control on dryland vegetation. In this chapter, we will explore these interrelationships and feedback mechanisms at a number of spatial and temporal scales. In doing so, we have divided the material into three major sections.

First, we consider a number of basic eco-hydrological processes in drylands. At the largest spatial scale, we consider soil-vegetation-atmosphere transfers in drylands. This is followed by a more detailed consideration of the relationships between plants and soil water in relation to climatic controls and the processes that control the movement of water into and out of the soil. The structures and patterns of dryland vegetation that develop from these interactions are then discussed. Finally, we look at the plant controls on runoff and sediment production, which reinforce many of the patterns and processes considered earlier.

Second, the means of modelling eco-hydrology in drylands are considered. The use of models to develop and test our understanding of processes and their interactions is considered by us a fundamental part of our methodology. We consider general progress in modelling such interactions, and note some important factors that must be accounted for in developing models of dryland eco-hydrology.



static and spatially complex lithosphere. It is at the land surface that the differences between these two systems are resolved. The characteristics of the land surface determine the energy (Dirmeyer and Shukla, 1994), moisture (Walker and Rowntree, 1987; Shukla and Mintz, 1982) and momentum exchange (Sud *et al.*, 1985; Smith *et al.*, 1994) between the two systems. These exchanges can affect, and in turn are affected by, climatic and eco-hydrological processes. Since the surface is the interface between climatic forcing and eco-hydrological response, the characteristics of the surface also determine the nature and intensity of surface and subsurface hydrological processes as well as the dynamics of the vegetation cover.

The low cover of vegetation means that soil-vegetation-atmosphere transfers (SVATs) in drylands are particularly complex (Shuttleworth and Wallace, 1985; Noilhan *et al.*, 1997; Pelgrum and Bastiaanssen, 1996). SVATs in drylands are complicated in two main ways. First, the low and discontinuous vegetation cover presents the atmosphere with a very complex surface when compared with a continuous forest cover or grassland characteristic of more humid environments. Second, the boundary layer behaviour of dryland soils and dryland vegetation is quite distinct, and our understanding of hydrological and micrometeorological feedback between the two remains elementary (see Sene, 1996).

A number of crude general circulation model (GCM) sensitivity experiments in various ecosystems have suggested that the characteristics of the surface have an important influence on the medium- and long-term dynamics of the climate system (Wilson *et al.*, 1987; Meehl and Washington, 1988; Koster and Suarez, 1994; Marengo *et al.*, 1994; Eltahir and Bras, 1994; Polcher and Laval, 1994; Stockdale *et al.*, 1994). Most of these experiments have been carried out within the context of large-scale field experiments in the same ecosystem (Bolle *et al.*, 1993; Gouturbe *et al.*, 1994). Most of the early experiments of this type dealt with simple surfaces such as continuous forest cover (Blyth *et al.*, 1994; Shuttleworth *et al.*, 1991) and grassland (Betts *et al.*, 1992; Hall and Sellers, 1995). Some of the later experiments considered more complex surfaces such as North African crops and tiger-bush (HAPEX-Sahel: Gouturbe *et al.*, 1994), Mediterranean shrublands and rain-fed and irrigated agriculture (Echival Field Experiment in a Desertification-Threatened Area – EFEDA I and II: Bolle *et al.*, 1993). The early experiments looked at the impact of large-scale changes in surface cover associated with deforestation and afforestation on boundary layer structure and SVAT fluxes of water, energy and momentum. They were mainly *deforestation* experiments (O'Brien, 1996; Sud *et al.*, 1996; Lean and Rowntree, 1997). It was clear, numerically and empirically, that these gross changes had a significant impact on local, regional and, potentially, global climates.

The later experiments looked at much more subtle surface changes associated with the progressive reduction of the biological potential of the land in response to climatic aridification and agricultural intensification.

These *desertification* experiments (Gouturbe *et al.*, 1994; Bolle *et al.*, 1993; Xue and Shukla, 1996) produced evidence to support the hypothesised feedback between aridification and degradation of the land surface. Reduced vegetation cover, higher albedo, lower latent heat loss and higher sensible heat loss result from aridification and lead to less turbulence and cloud formation, in turn causing further aridification of the climate (Figure 4.1). The most significant characteristics of the vegetation cover in this process are plant albedo (vegetation type, cover, leaf area index), the degree of atmospheric coupling of the stomata (i.e. the degree to which stomatal opening is controlled by atmospheric variables as opposed to soil moisture availability; see Chapter 2) and the seasonal phenology of the vegetation cover. Anthropogenic land-use change in drylands has accelerated in recent decades and can thus have a direct impact on climate because of this climate – land-surface properties – climate feedback loop (Henderson Sellers, 1994; Dale, 1997).

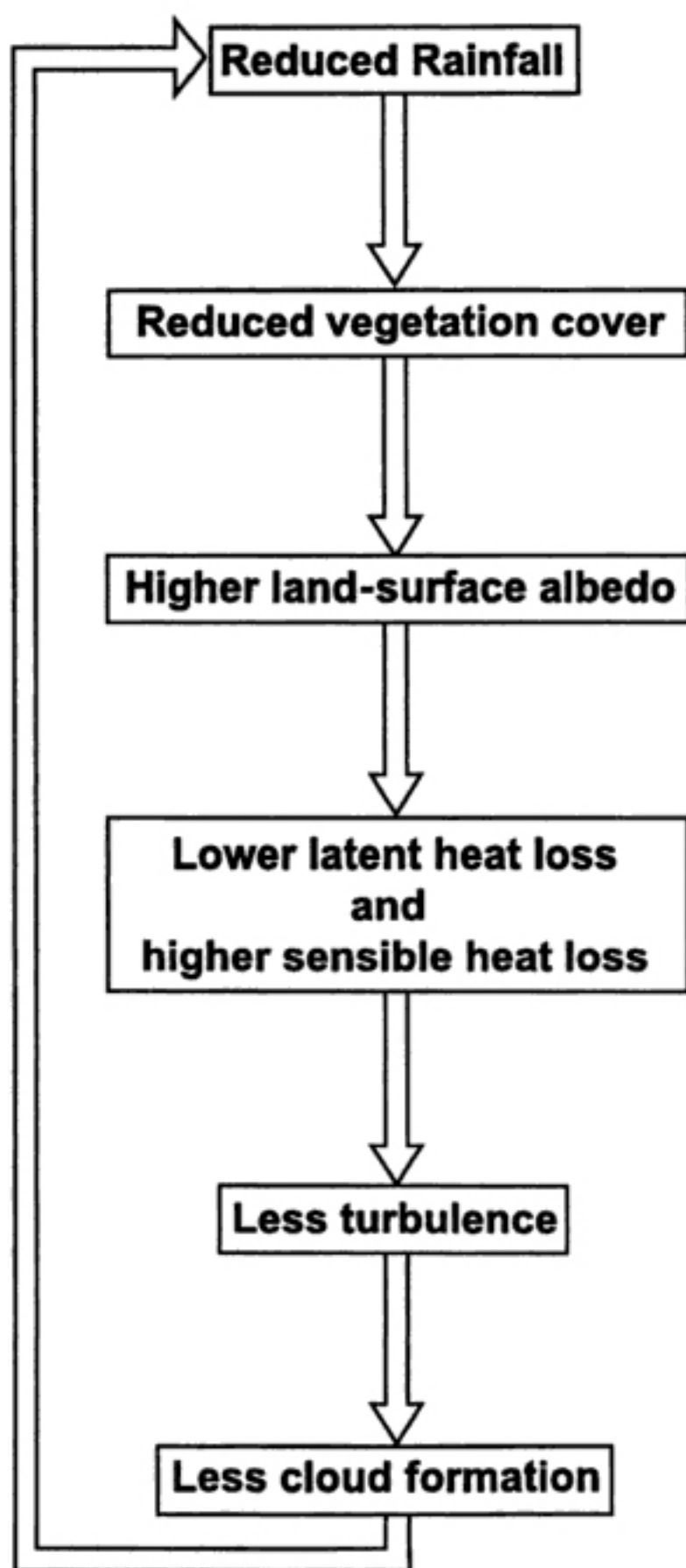
### Plant–soil–water relationships in drylands

The water budget of any part of a dryland hill slope can be expressed as the difference between water inputs at a point (precipitation, run-on and seepage) and water outputs at the same point (evapotranspiration, runoff and drainage). The most important components of the budget for most drylands are precipitation and evapotranspiration, and so the balance between the two, expressed as the ratio of precipitation to potential evapotranspiration, is a good measure of aridity.

#### *Rainfall*

Precipitation in drylands is low in volume, irregular and low in frequency, and often high in intensity. The irregularity of precipitation can be as important in controlling plant–soil–water relationships as the long-term mean total precipitation, since plants require a constant supply of water for the maintenance of biological activity, and most species have no way of storing water surpluses. The irregularity of precipitation in drylands can be expressed as the coefficient of variation of annual total precipitation, and this is commonly of the order of 30 percent for semi-arid Spain (Mulligan, 1996a), 25 percent for Mediterranean France, and around 35 percent in New Mexico (Wainwright, in press, a). In more arid areas, these values are commonly exceeded. Rumney (1968) gives values in excess of 40 percent for much of the Sudano-Saharan belt, parts of Mongolia, the southwest coast of Africa and parts of Peru, Bolivia and Argentina.

The characteristics of precipitation in drylands determine to a large extent the hydrological fate of the same precipitation. These characteristics include (1) the timing of rainfall both seasonally and with respect to previous events; (2) the intensity of rainfall relative to the rate of surface infiltration of water;



*Figure 4.1* The aridification–desertification feedback loop.

and (3) the size and duration of storms along with the pattern of intensity change through them. From an analysis of rainfall data collected using an automatic weather station (AWS) at Belmonte, central Spain, Mulligan (1996a) found that most events are of low intensity, with few of high intensity. The low-intensity events efficiently replenish soil water reserves, while high-intensity events provide more water for rapid overland flow. Mulligan (*ibid.*) also found that the great majority of storms are low in volume. Similar patterns were observed in semi-arid New Mexico by Wainwright (*in press*, a).

Of more importance to the plant–soil–water relationships are the temporal variations in rainfall receipt. Ecologically, the most significant of these are seasonality and the length of summer drought. Though rainfall seasonality is strong in drylands, it is most pronounced in mediterranean environments characterised by a cool, wet winter and a hot, dry summer. The strength of seasonality varies from year to year (Figure 4.2). Total annual rainfall itself varies inter-annually, decadally and in the longer term (Figure 4.3), and eco-hydrological processes reflect this variation.

Reynolds *et al.* (*in press*) demonstrated the importance of low-intensity events and seasonal variability of rainfall in a series of rainfall-exclosure experiments on creosote bush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*) at the Jornada Long-Term Ecological Research site in the Chihuahuan Desert, New Mexico. Both species demonstrated an ability to

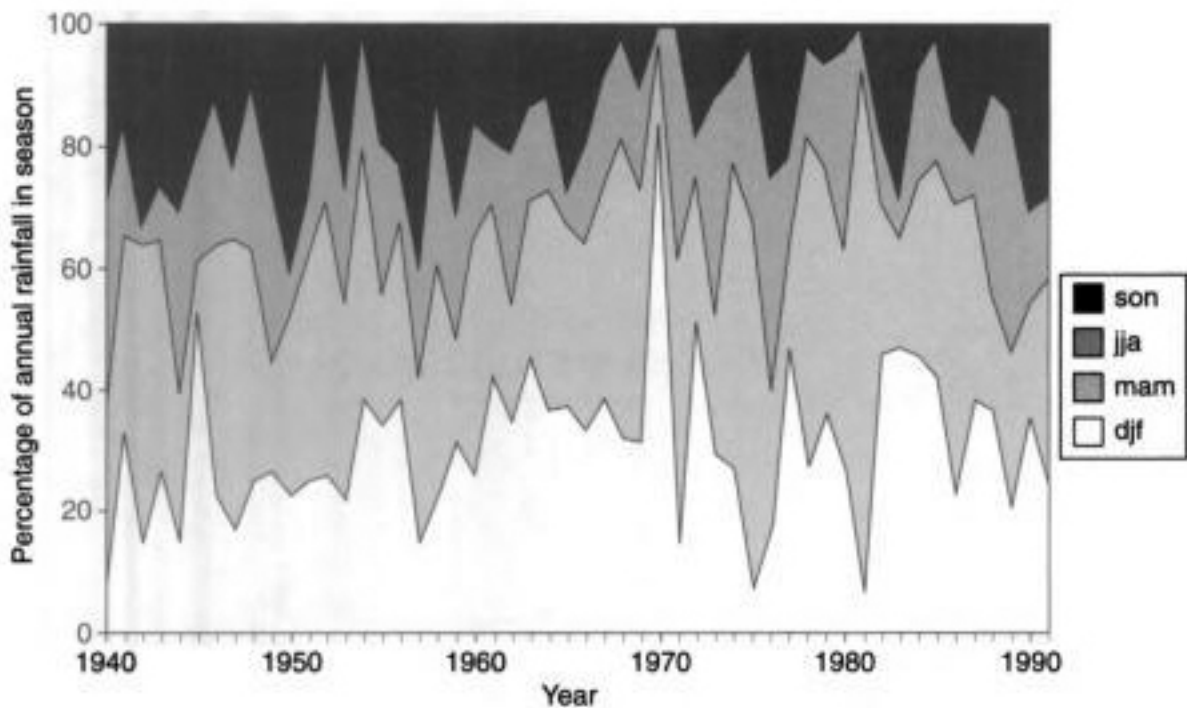


Figure 4.2 Changing seasonality of rainfall for Belmonte, central Spain, 1940–1991. Data courtesy of the Spanish National Meteorological Office. son = September, October, November; djf = December, January, February; mam = March, April, May; jja = June, July, August.

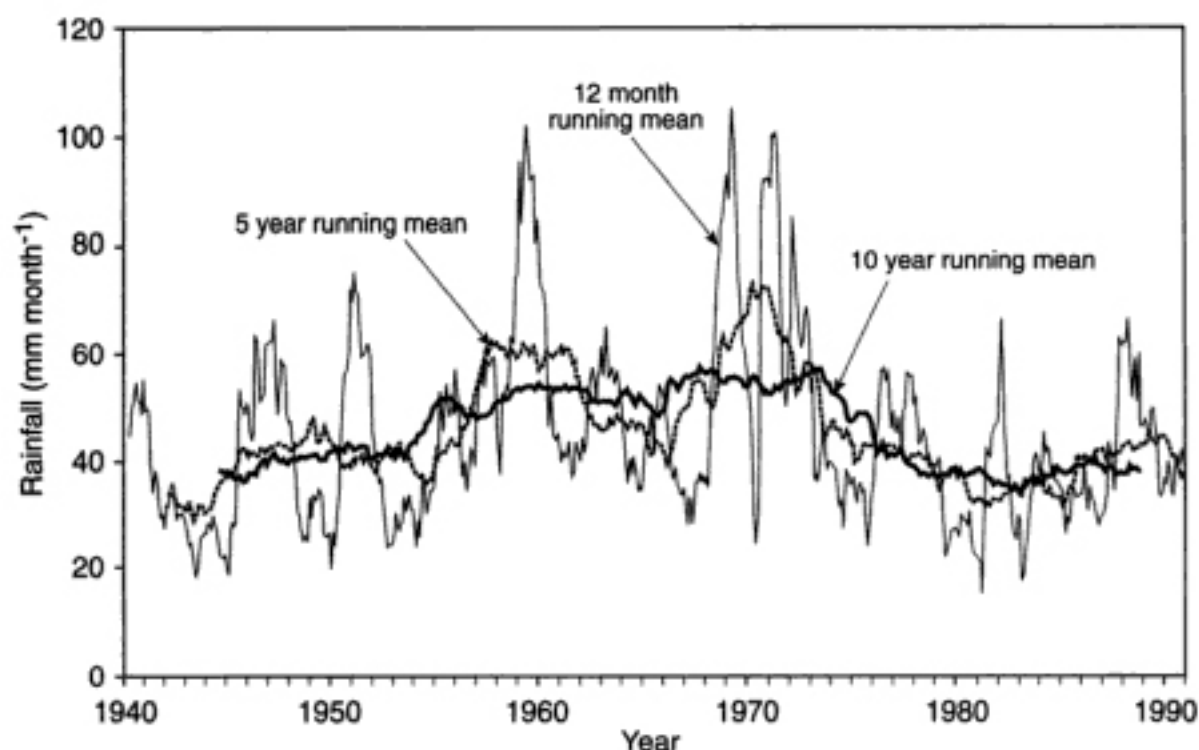


Figure 4.3 Rainfall variability for Belmonte, central Spain (1940–1991). Data courtesy of the Spanish National Meteorological Office.

compensate for summer drought by using moisture from (low-intensity) winter rainfall and for winter drought by exploiting summer rainfall. This may be one means by which shrub species are able to out-compete annuals in this environment.

### *Throughfall, infiltration and runoff*

The relationship between rainfall, soil moisture and runoff production can be considered in relation to a series of experiments carried out on semi-arid shrubland and grassland in Arizona and New Mexico. Martinez-Mesa and Whitford (1996) looked at processes of throughfall, stemflow and root channelisation of water in three shrub communities at Jornada. Throughfall in creosote bush averaged 56 percent of rainfall throughout the year with a range of values from 22 to 83 percent. The average for tar bush (*Flourensia cernua*) was 53 percent in summer and 58 percent in winter, with a range from 9 to 73 percent. Mesquite had less seasonal variability, with 64 percent of rainfall occurring as throughfall in summer and 62 percent in winter, with values ranging between 36 and 89 percent. These values seem comparable with measurements on shrub vegetation from elsewhere in the world. Martinez-Mesa and Whitford were also able to demonstrate that the percentage throughfall in all of these species increases rapidly for low rainfall rates and reaches the mean value asymptotically beyond event totals of between 2.5 and 3 mm. Their stemflow measurements show a similar

vegetation is restricted to wadis, where it can take advantage of accumulations of water at depth. At the wetter end of the spectrum, steppe (semi-desert) merges into grassland and shrubland, savannah and woodland. In all of these communities, vegetation cover and plant size are positively correlated with rainfall (Shmida, 1972; Beatley, 1974, 1976). Species diversity is also related to rainfall, with maximum species richness occurring in the semi-desert zone between desert and forest ecosystems. However, edaphic variability and ecological stability are also important – ecologically stable areas are thought to have fewer species, though this is highly contentious (Tilman, 1994; Whitford, 1997).

Evenari (1985b) describes the adaptations of plants to the desert environment. He distinguishes the poikilohydrous plants (lichens and algae) and the homoiohydrous plants. Poikilohydrous plants have a number of physiological adaptations to extreme aridity, which are outlined in Table 4.2. Lichens can be a very significant component of dryland vegetation. However, most desert plants fall into the broad class of homoiohydrous but can be further classified as arido-passive perennials, arido-passive pluviotherophytes, arido-active perennials and biseasonal annuals. These types possess a number of adaptations to aridity, which are fully described elsewhere (*ibid.*).

## Plant structures and patterns

### *Spatial structure*

Perhaps the most striking characteristic of dryland vegetation is its low cover. As one moves along a continuum of aridity from  $P/E_{tp} > 1$  down to  $P/E_{tp} < 0.3$ , the potential vegetation cover breaks up from total cover through a series of broken canopies to a situation in which vegetation cover is very patchy. The patches are characterised by a high density of stems in a small area and a consequent build-up of sediment – typically derived from rain splash or aeolian activity – and organic material beneath the vegetation (Parsons *et al.*, 1992; Sánchez and Puigdefábregas, 1994; Puigdefábregas and Sánchez, 1996;

Table 4.2 Features of poikilohydrous plants (after Evenari, 1985b).

- 
- |    |  |
|----|--|
| 1. | The capacity to take up water from rain, dew or water vapour in the air (at >70% humidity).  |
| 2. | The capacity to equilibrate with the hydration level of their environment and to survive extreme and prolonged desiccation without damage.           |
| 3. | The capacity to enter an anabiotic state (with extreme cold and heat resistance) and become metabolically inactive after desiccation without injury. |
| 4. | Rapid switching on and off of metabolic activity according to water availability.  |
| 5. | Relatively high rate of photosynthesis at low temperatures and low light intensities.  |
-



Wainwright *et al.*, 1995; in press). The resulting increase in surface elevation may prevent erosion either by diverting overland flow and/or by obstructing the flow and reducing the local slope, leading to an increase in the amounts of infiltration of water and deposition of sediment generated on bare patches upslope of the plants (Cerdà, 1997). This process enhances the soil moisture storage and the soil moisture storage *capacity* of the patches at the expense of upslope bare areas. This kind of environmental 'manipulation' has been identified in drylands from Israel (Valentine and Nagorcka, 1979) through the Mediterranean to North Africa (Lefever and Lejeune, 1997) and sub-Saharan Africa (MacFadyen, 1950; Grove, 1957; Worral, 1960), as well as in the American southwest (Schlesinger *et al.*, 1990), Patagonia (Rostagno and del Valle, 1988) and Australia (Mabbutt and Fanning, 1987) and can lead to the development of hill-slope-scale, and even regional, patterned structures on sloping terrain. Dunkerley (1997) has suggested on the basis of model simulations and evidence from eastern Australia that such patterns are relatively stable under, and may even be enhanced by, drought and/or grazing pressure. Davis and Burrows (1994) have also proposed that the repeated occurrence of fires can be an important factor in the development of vegetation patchiness in drylands.

### *Patch development*

While a number of plant-scale advantages of clumping can be recognised, the ecological mechanism for the phenomenon remains poorly understood, although recent theoretical (van der Maarel, 1988) and modelling (Sánchez and Puigdefábregas, 1994; Puigdefábregas and Sánchez, 1996; Jeltsch *et al.*, 1996) studies have helped in understanding the processes involved. In addition to increasing the available soil moisture and soil moisture capacity through overland flow trapping, clumping can have a number of other eco-hydrological impacts, some of which are presented in Table 4.3.

## **Plant controls on runoff and sediment movement**

### *General considerations*

There is a complex and often non-linear interaction between vegetation, hill-slope hydrological processes and erosion. Despite this, many forest engineers in drylands still promote the long-held, and somewhat simplistic, idea that degradation and soil erosion can be reduced and hydrological processes adjusted by encouraging the growth of forests.

The core of the forest protection approach is based on more than 100 years of paired catchment experiments in the USA and the UK and the repeated empirical observation that sediment yields are less from forested catchments and well-vegetated plots. A critical review of the confused signals coming

Table 4.3 The eco-hydrological consequences of vegetation clumping.

- 
1. Reduction of soil evaporation loss through shading of the root zone soil.
  2. Enhancement of root zone moisture supply through the concentration of stem-flow.
  3. Increase of the infiltration of direct rainfall and reduction of overland flow loss.
  4. Provision of a low air temperature and high-humidity environment around the majority of leaves, which may reduce transpirational loss.
  5. Concentration of nutrient reserves in the surface soil from (drought deciduous) leaf loss, thereby reducing nutrient losses.
  6. Reduction of grazing pressure by excluding access to all but the edge of the patch.
  7. Provision of a shaded environment for small animals, enhancing their contribution to the nutrient budget of the plant and also increasing the potential soil moisture storage by their burrowing.
  8. Reduction of the expenditure on below-ground biomass by bringing resources to the roots rather than growing roots to the resources.
- 

from this research reveals that the main causes of ambiguity have been the failure to obtain truly comparable paired catchments, the difficulty engendered by comparing different serial rainfall inputs to the catchments and the differences in both treatment and responses of the catchments. In this latter instance, Obando (1996) has shown in a modelling study of sites in southern Spain that changes in the location of matorral removal and re-establishment can have quite significant impacts on the pattern of water and sediment yield (Figure 4.4). The arguments for forest protection are well known. It is suggested that the forest canopy reduces the drop size and the energy of falling rain, both of which are correlated with erosion amounts and rates. However, Brandt (1986, 1989) was able to show, for both UK deciduous forests and Amazonian forest, that drop sizes and, in some cases, total kinetic energy at the surface can be substantially increased under forest. These results suggest that it is the protection afforded to the soil by the root matter and leaf litter layer rather than the canopy itself that reduces soil erosion. With lower-level canopies, however, Brandt demonstrated that the throughfall energy was significantly reduced when compared with rainfall energy, although certain events did still produce enhanced throughfall energies. Although throughfall in semi-arid shrubs in New Mexico was measured as being between 9 and 89 percent of the rainfall (Martinez-Mesa and Whitford, 1996: see above), the resulting energy produced was not measured. However, the results of Parsons *et al.* (1992) on differential splash rates between and under shrubs with a similar size and structure in Arizona suggest that there is a significant energy reduction in this setting. Thus the effectiveness of vegetation protection against erosion is a function of canopy size, height and spatial pattern, although more work is required to define the exact relationships.

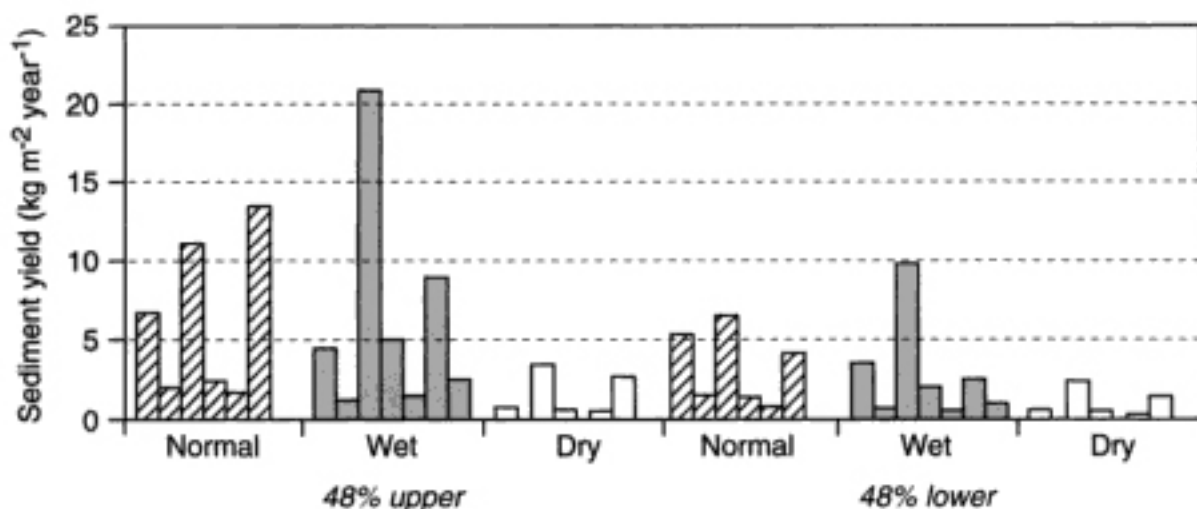
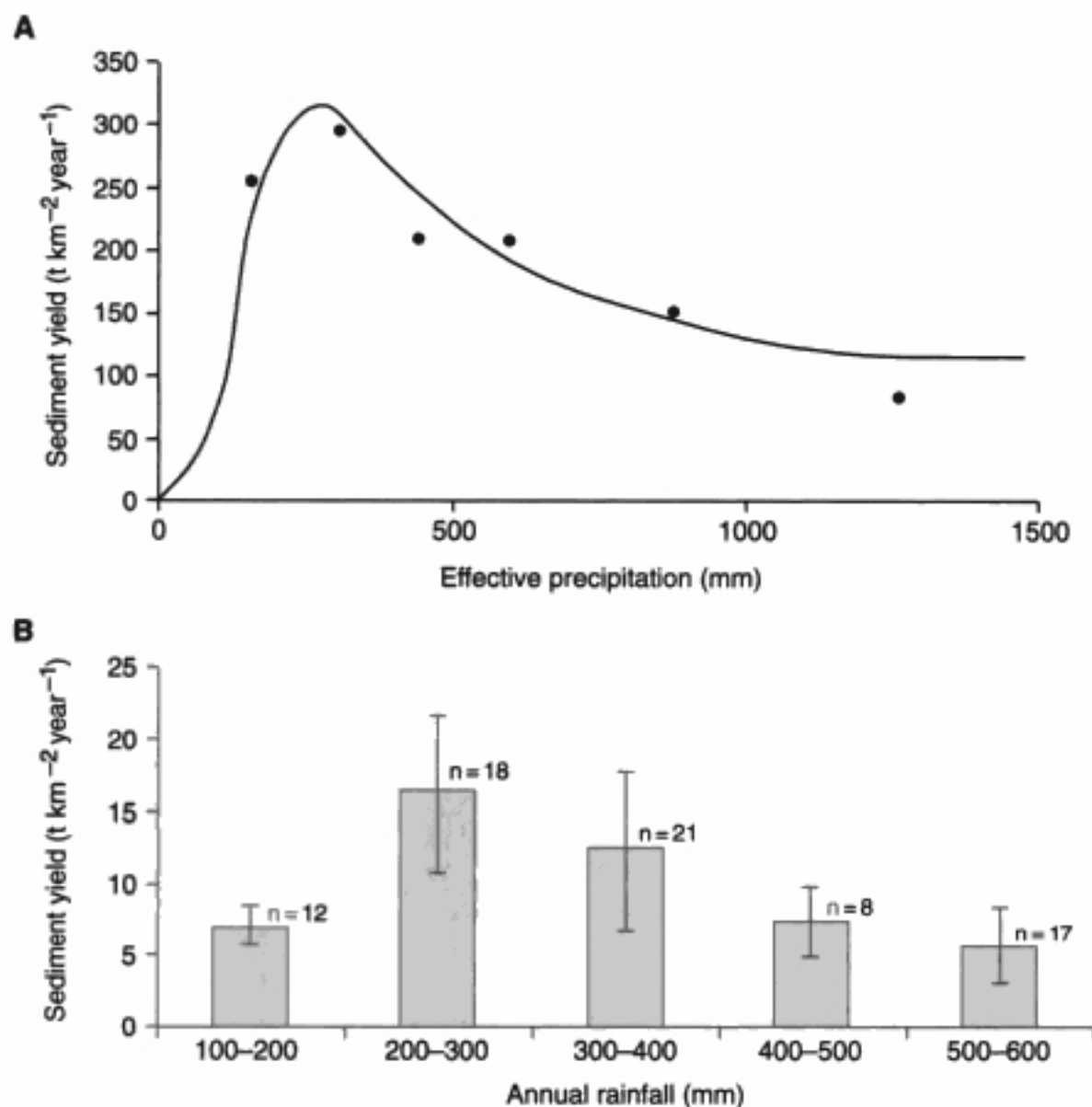


Figure 4.4 The effect of different spatial distributions of vegetation cover on predicted erosion rate in the study of Obando (1996). Both cases have a 48 percent vegetation cover of matorral, concentrated in either the upslope or downslope area.

It has been observed that lower plant life forms (algae and lichens) can have a dramatic effect on erosion rates by increasing the surface stability (Alexander and Calvo, 1990). As discussed above, such forms are an important component of many dryland ecosystems; thus this effect may be widespread. Surface stability can be quickly lost by grazing and negligent soil management. However, the debate about the impact of grazing has to be treated with caution, not least because animals are highly selective in their choice of food, and also because most of the enhanced runoff can be attributed to compaction by hooves. In addition, grazing may induce better fertilisation of soil, so that in the Sahel vegetation may be better established closer to water points than further away (Warren and Khogali, 1992). Moreover, there are some species for which grazing *improves* the cover characteristics with respect to erosion by increasing leaf density and encouraging outward growth of bushy species such as *Quercus coccifera* (Barbero *et al.*, 1990).

### Regional scale

At regional scales it is argued that, with zero rainfall, there must be zero runoff and therefore no erosion, but that as the rainfall and runoff increase, the sediment yield must also increase to a peak at *c.* 300–500 mm of effective rainfall (i.e. semi-arid environments) (Langbein and Schumm, 1958; Figure 4.5A). Further rainfall increases the vegetation cover, causing a steep slump in sediment yield (Figure 4.5A). Douglas (1967) argued that total denudation might well follow the same curve, but that in tropical climates the high solution rates and throughput of soil water would produce much higher denudation, despite the increased vegetation cover. Walling and Webb (1983) also qualified the Langbein and Schumm (1958) curve on the basis of a much greater and more carefully filtered sample size (Figure 4.6).



**Figure 4.5** Relationships between precipitation and sediment yield. A: Relationship between effective annual precipitation and sediment yield proposed by Langbein and Schumm (1958). B: Relationship between annual precipitation and sediment yield as measured on 76 Mediterranean sites under shrubland vegetation by Kosmas *et al.* (1997).

A relationship similar to that of Langbein and Schumm has recently been confirmed empirically for Mediterranean-type climates in both the Old and the New Worlds (Inbar, 1992) and for the Mediterranean by the experimental sites in the MEDALUS project (Kosmas *et al.*, 1997) (Figure 4.5B). Inbar (1992) demonstrated that the peak of the curve occurred at around 300 mm of annual precipitation for catchments in coastal Israel and Spain, with corresponding erosion rates of  $310 \text{ t km}^{-2} \text{ year}^{-1}$ . The subsequent decrease in sediment yield with increasing annual precipitation is of the order of  $50 \text{ t km}^{-2} \text{ year}^{-1}$  for each 100 mm of additional precipitation. Peak rates in the mediterranean climates of California and Chile are of the order of 500 to

reduction of vegetation produces increases in sediment yield, however, is well documented from a number of carefully carried out investigations of human clearance. Examples of clearances include those in mid-Holocene Europe (Starkel, 1983; 1987), when the Aulehm deposits were created in river valleys, and those in the Mediterranean (e.g. Laval *et al.*, 1991; van Andel *et al.*, 1986; see also below). One of the problems in providing unequivocal statements about past changes comes from the timescales of observation. As noted above, many major erosional events in a Mediterranean context occur as a result of plant die-back following drought on an annual to decadal cycle, or as a result of intense storms following a period of seasonal drought (Kirkby and Neale, 1987). However, the resolution available throughout most of the Holocene in terms of the palaeobotanical record for the region is generally of the order of centuries.

A further significant problem here is that, while the spatial character of growth under increased precipitation and its impact on vegetation can be successfully modelled (Thornes 1990), the spatial patterning of die-off is rather inadequately modelled because of the difficulty that death is often partial in plants (twigs, leaves), so that the spatial occurrence of bare patches is spotty rather than systematic in development. Thus in desertification studies, the concept of the 'rolling forward' of the Sahel as plant death occurs under stress or human management cannot be justified. More sophisticated modelling inevitably leads to more complex conclusions about the effects of climatic change on degradation. For example, Woodward (1994) has modelled the impacts of future scenarios of Mediterranean climate change on vegetation cover in the Iberian Peninsula using physically based ecophysiological models of photosynthesis, respiration, growth, allocation and death of plants on the basis of their functional type. The work produced a plant growth model that was coupled to hydrological and geomorphological models at the hill-slope scale (Kirkby *et al.*, 1996). The results indicate that the hypothesised doubling of CO<sub>2</sub> and 15 percent reduction in winter rainfall would act differentially on bushes and grasses, and that the most marginal climatic situations would experience the greatest effects (i.e. those areas having an average dry season of seven months without rain). The results indicate losses in biomass of up to 50 percent, which would be expected to produce a dramatic change in sediment yield.

### *Slope or plot scale*

At smaller scales, variability in the controls of erosion such as vegetation leads to much greater spatial and temporal variability in rates. For this reason, local-scale estimates of erosion must be based on a thorough understanding of the processes. The erosion process can be divided into three interacting elements. Erosion by splash occurs due to the impact of raindrops on the surface, which can entrain particles in droplets that rebound from the surface.

Once overland flow is generated, it can transport sediment either in a rather diffuse manner in the undissected inter-rill zone or in a more concentrated way once incision leads to the formation of rills and, ultimately, gullies.

### *Erosion by splash*

The splash mechanism is effective for soil particles less than about 12 mm in maximum dimension (Wainwright, 1992; Wainwright *et al.*, 1995). Transport distances are typically less than a metre and decline exponentially in all directions from the source although with a net downslope movement (Savat and Poesen, 1981). Parsons *et al.* (1994) demonstrated using rainfall simulations that splash rates increased and then decreased during a first rainfall event on a semi-arid grassland plot at Walnut Gulch, with peak rates of  $9.0 \times 10^{-5} \text{ g m}^{-2} \text{ s}^{-1}$ . During a second event carried out three days later, the rates continued to decline. This pattern was interpreted as relating initially to the increased wetting of the soils, facilitating their movement by reducing cohesion, followed by a subsequent decrease in available soil for transport. Thus, the importance of splash might be expected to decrease, *ceteris paribus*, during the period of a rainy season at a particular site. As noted below, there is an important interaction between splash and sparse vegetation canopies in drylands. Soil and litter can commonly be splashed underneath a shrub canopy, but the splash process is considerably reduced beneath the canopy because of the relatively small proportion of throughfall (see above), and thus little material is splashed back out into the inter-shrub areas. Through time, this build-up of soil and litter contributes significantly to the formation of mounds (Parsons *et al.*, 1992; Wainwright *et al.*, 1995; in press). The rapidity with which this occurs is partly a function of splash rates in the inter-shrub areas, which can be an order of magnitude higher than those in the grassland areas ( $7.2 \times 10^{-3} \text{ g m}^{-2} \text{ s}^{-1}$ ; Parsons *et al.*, 1991).

### *Erosion by inter-rill overland flow*

Overland flow in the inter-rill zone is able to move larger particles – Abrahams *et al.* (1988) observed movement of particles as large as 53 mm on steep slopes – typically for much greater distances than the splash process. Tracer experiments on the Walnut Gulch grassland suggested that although a large proportion of material is redeposited within 25 cm of its origin, travel distances of almost 3 m were recorded in a single event, again with an exponential decline in the amount of material transported with distance (Parsons *et al.*, 1993). These experiments suggest that the transport is intermittent and that it would take a number of events for soil particles to travel the length of the slope and enter the channel system. Abrahams *et al.* (1991) demonstrated that inter-rill erosion is determined by sediment detachment by raindrops, as the flows themselves have insufficient energy to



detach soils. The capacity to transport such detached material is then defined by the flow depth, which is itself highly variable due to the significant surface irregularities on typical dryland slopes (Abrahams and Parsons, 1991; Parsons *et al.*, 1994; 1996a). Raindrop detachment is itself a negative exponential function of flow depth (Torri *et al.*, 1981), leading to the development of spatial patterns of erosion. On both the grassland and shrubland slopes at Walnut Gulch, the erosion first increases from the slope divide as flow transport capacity increases, and then decreases as the raindrop detachment decreases, because of the general downslope increase of flow depth (Abrahams *et al.*, 1991; Parsons *et al.*, 1996a). In both cases, there are feedbacks between the vegetation, flow dynamics and erosion. On the shrubland, the high surface runoff from the inter-shrub areas increases the erosion in these areas, which accentuates the relief of the shrub-topped mounds and equally reduces the likelihood of recolonisation of the inter-shrub areas, because of the removal of water and nutrient resources (Parsons *et al.*, 1996b; Schlesinger *et al.*, in press). The grassland is characterised more by a negative feedback wherein the more diffuse distribution of grass clumps causes overland flow to be slower and less concentrated. Sediment is thus deposited behind the clumps, often forming a series of microtopographic steps, which in turn enhance the diffusion of the overland flow (Parsons *et al.*, 1996a). Thus, despite the lower vegetation cover on the grassland (33 percent compared with 44 percent on the shrubland), erosion rates are lower, with peak rates of  $0.23 \text{ g m}^{-2} \text{ s}^{-1}$  compared with  $0.53 \text{ g m}^{-2} \text{ s}^{-1}$  on the shrubland. It can be seen that inter-rill overland flow is several orders of magnitude more effective at transporting sediment than splash (see also Wainwright, 1996b and c for Mediterranean examples).

#### *Erosion by concentrated overland flow*

Erosion in concentrated overland flow occurs when the flow gains sufficient energy to detach sediment itself, thus causing incision into the soil surface, forming rills and ultimately gullies. In this case, the detachment of soil by raindrops is no longer a limiting factor. Rilling occurs on the shrubland at Walnut Gulch and is apparently controlled by the occurrence of greater extremes of flow depth in the downslope direction (Parsons *et al.*, 1996a). This is probably a further consequence of the feedback described above, where flow is increasingly constrained into the inter-shrub areas as it travels downslope. Unpublished work at the Jornada site suggests that shrub spacing is a dominant control on this process (Charlton, personal communication).

The example discussed in detail above suggests that simple models that show a negative exponential relationship between vegetation cover and erosion – as, for example, demonstrated by Elwell and Stocking (1976) for simple crops – cannot be said to hold in all cases in drylands. Rogers and Schumm (1991) have also shown experimentally that the negative

exponential relationship breaks down at vegetation covers of 15 percent or less. Morgan (1996) has discussed differences in the form of the relationship and its parameters in relation to canopy structure as part of the European Soil-Erosion Model (EUROSEM) project. It would appear that further work on this problem is required that takes account of the canopy structure of dryland plants and their spatial distribution on a slope. Given that many drylands have plant covers of less than 30 percent, as noted above, this point is of critical importance.

As with runoff production, the consequences of fire are an important consideration in relation to erosion, principally because of the increase in runoff described above, the decrease in protection of the soil surface by the vegetation canopy, and changes in the soil structure. Vega and Diaz Fiernos (1987) showed a difference of erosion rates, with only  $1.5 \text{ t ha}^{-1} \text{ year}^{-1}$  produced on a moderately burnt *Pinus pinaster* woodland, compared with  $22 \text{ t ha}^{-1} \text{ year}^{-1}$  on an intensely burnt area in northwest Spain. On *Quercus ilex* plots in Catalonia, Soler and Sala (1992) measured erosion rates of  $0.017 \text{ t ha}^{-1} \text{ year}^{-1}$  on unburnt and  $0.162 \text{ t ha}^{-1} \text{ year}^{-1}$  on burnt plots, compared with  $0.024 \text{ t ha}^{-1} \text{ year}^{-1}$  where the plots had simply been cleared. Fire can also lead to a loss of nutrients from the system by a number of mechanisms (Christensen, 1994), which, combined with soil loss, has important consequences for vegetation regrowth (Soler and Sala, 1992; Kutiel and Inbar, 1993).

## MODELLING ECO-HYDROLOGICAL PROCESSES IN DRYLANDS

### Models for understanding dryland eco-hydrology

Numerical models (see Chapter 9) are increasingly being used as an aid to field experimentation and theoretical analysis for understanding the eco-hydrological dynamics of drylands. Models are applied at scales from the GCM grid cell, such as the land-surface sensitivity experiments discussed above and in Chapter 3, through to the individual plant scale. Models are applied for time periods from a few hours for process studies and event simulation through to hundreds of years for climate change experiments. A number of hydrological (for example, Braud *et al.*, 1995, Kirkby and Neale, 1987, Kirkby, 1990), ecological (for example, MARIOLA, Uso-Domenech *et al.*, 1995) and coupled eco-hydrological models (for example, PATTERN, Mulligan, 1996a and b; MEDALUS, Kirkby *et al.*, 1996; FOREST-BGC, Kremer *et al.*, 1996; Thornes, 1990) have been developed for dryland environments.

The particular characteristics of dryland climates, surfaces and plant communities require a particular set of modelling strategies appropriate to these conditions.

*Model timesteps*

Drylands are characterised by long periods of hydrological inactivity with short, intensive events in which a great deal of change occurs. In modelling terms, this requires the specification of a high-resolution timestep (perhaps a minute or less) in order to represent accurately rapid rate processes (particularly Hortonian overland flow) during an extreme event but also low-resolution timesteps for integration of fluxes outside these periods of activity. In this way, a variable timestep rather than a fixed one is most appropriate to dryland eco-hydrological modelling. The timestep should respond to the rate of the most rapid acting flux or process so that it is inversely proportional to this rate. A variable timestep is computationally efficient and hydrologically precise.

Where ecological processes are coupled with hydrological ones, and particularly where processes of the energy budget are included, an additional, concurrent, timestep is required. The timestep should reflect the slower biological processes and is commonly of the order of hours or days. Hourly timesteps have the advantage of increased precision but require hourly data, which are often not available. Daily timesteps, on the other hand, are easier to parameterise but can lead to significant error because they do not take into account the significant differences between daytime processes and night-time processes. These can be particularly important in drylands, where dew inputs can be high during the night and where water stress changes significantly between day and night. The analysis in Table 4.4 is the result of an application of the Penman–Monteith equation (Monteith, 1973) to the same data set, which is integrated first on an hourly basis, second on a daily basis, and third on a day–night basis with one timestep from sunrise to sunset and the next timestep from sunset to the following sunrise. Clearly, there are significant differences in the calculated evapotranspiration between these situations. If we take the hourly results as those that most closely represent reality, it is clear that a day–night timestep significantly improves the accuracy of estimation of evapotranspiration when compared to a daily timestep. The accuracy of using the day–night timestep also varies through the year, as indicated by the June figures compared with those for January.

*Specific characteristics of drylands*

A number of specific physical characteristics of drylands must also be accounted for within eco-hydrological models. First, drylands tend to have an open canopy with a complex pattern of vegetated and bare patches. This makes the use of standard evapotranspiration equations developed for closed canopies difficult, and more appropriate models are those developed for sparse crops (Shuttleworth and Wallace, 1985) and patchy vegetation (Wallace and Holwill, 1997; Wood, 1997).

later *Quercus* with a dominance of steppe species in sites in the south of the country from about 3.5 Ma, suggesting the onset of environmental gradients similar to those of the present day (Levin and Horowitz, 1987). Before 3.2 Ma, the northwestern part of the Mediterranean had been characterised by tropical vegetation species such as *Taxodium*, *Myrica*, *Symplocos* and *Nyssa* in the lowlands, suggesting high moisture conditions, and lower moisture conditions in the uplands, as demonstrated by species such as *Engelbardia*, *Carya*, *Rhioptelea*, *Hammamelis* and *Embolanthera* (Suc, 1984). Similar associations are found from before the Messinian salinity crisis, suggesting a great stability in this pattern (Suc and Bessais, 1990). Mediterranean evergreen and pine species are present in the early Pliocene in southern Italy between 4.5 and 3.2 Ma, and few tropical species were found (Bertoldi *et al.*, 1989). However, the period from 2.6 to 2.2 Ma is marked by cyclic changes in vegetation groupings, with deciduous forest, tropical humid forest, coniferous forest and steppe vegetation all present (Combourieu-Nebout, 1993). Rare Taxodiaceae and subtropical species are still present in the Villafranchian type area of northern Italy between 2.9 and 2.2 Ma (Carraro *et al.*, 1996). The latter part of this sequence and those of southern France from 2.3 Ma show an increase of steppe species (Suc and Zagwijn, 1983). From 2.1 to 1.7 Ma, the first fully Mediterranean-type vegetation zonation is found in southern France. This is made up of *Olea* and *Ceratonia* with *Pistacia*, *Phillyrea* and *Myrtus* at the lowest altitudes; *Phillyrea* and *Quercus ilex* with *Olea*, *Carpinus orientalis* and *Rhamnus* at middle altitudes; deciduous oak and *Carpinus* with *Carya*, *Ulmus* and *Zelkova* at higher altitudes; and finally *Cedrus*, *Pinus*, *Abies*, *Picea* and *Tsuga* making up a mountain forest (Suc, 1984). In southern Italy and Sicily, the same period sees the final disappearance of the subtropical Taxodiaceae (Baggioni *et al.*, 1981; Bertoldi *et al.*, 1989), although they are still present in Calabria (Combourieu-Nebout, 1993) and as late as 1.3 Ma in central Italy (Rosa Attolini *et al.*, 1988), albeit most probably as relict populations in local refugia.

Thus, the major lines of the modern vegetation show a complex development over a period of two million years. The development seems to occur earlier in the east and south than in the west and north. On the general trend are superimposed a number of cycles of vegetation change. The period of time over which these changes occurred is marked by important climate changes within the region that also reflect broader global changes. Oxygen isotope data for the western Mediterranean suggest that temperatures were up to 3 °C higher than present until 3.2 Ma (Thunell, 1979) or 3.1 Ma (Vergnaud-Grazzini *et al.*, 1990), when there was a relatively sudden drop in winter sea surface temperatures of 1.2 °C (Keigwin and Thunell, 1979). This change represents the global onset of cooling and sea level fall as seen in the Pacific (Shackleton and Opdyke, 1977) and Atlantic (Clemens and Tiedemann, 1997). A second phase of cooling occurred around 2.5 Ma, with oscillations until around 2.1 or 2.0 Ma, after which there was a general downward trend