4 Water and Energy Balance

The hydrologic cycle, driven by solar energy, is the master cycle that drives all other biogeochemical cycles. This chapter describes ecosystem energy budgets and other controls over the hydrologic cycle.

Introduction

Water and solar energy are essential for life. Their uneven distribution across Earth's surface largely account for the large-scale patterns of ecosystem structure and functioning and are therefore central to an understanding of ecosystem dynamics. Water and energy cycles are so tightly intertwined that they cannot be treated separately. Solar energy drives the hydrologic cycle through the vertical transfer of water from Earth to the atmosphere via **evapotranspiration**, the sum of surface evaporation and the loss of water from plant leaves (**transpiration**). Conversely, evapotranspiration accounts for 80% of the turbulent energy transfer (i.e., latent plus sensible heat flux) from Earth to the atmosphere and is therefore a key process in Earth's energy budget (see Fig. 2.3). The hydrologic cycle also controls Earth's biogeochemical cycles by dissolving nutrients and transferring them within and among ecosystems. Water and nutrients, in turn, provide the soil resources that support the growth of organisms. The movement of materials that are dissolved and suspended in water links ecosystems within a landscape.

A Focal Issue

Human activities have substantially altered Earth's hydrologic cycle at regional to global scales. People now use about 50% of Earth's available renewable fresh water, but this proportion exceeds 100% in some dry regions (Oki and Kanae 2006; Carpenter and Biggs 2009). This human use of fresh water affects land and water management, the movement of pollutants among ecosystems, and, indirectly, ecosystem processes in unmanaged ecosystems. Land-use changes have altered terrestrial water and energy budgets enough to change regional and global climate (Fig. 4.1; Chase et al. 2000; Foley et al. 2005). In Australia, for example, a decade-long drought at the end of the twentieth century reduced water availability below levels required for agriculture, and in dry portions of the midwestern U.S., irrigated farming is drawing on "fossil groundwater" that is depleted much more rapidly than it can be replenished by rainfall in the current climate. How much precipitation is needed to meet the water needs of different crops or other ecosystem types, and how is this influenced by plant and soil properties? What determines the proportion of incoming precipitation that enters water supplies and is potentially available to support societal needs? Evaporation of water is also one of the primary fates of energy from incoming solar radiation, which affects both air and water circulation (Fig. 4.1). What happens to the energy

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Fig. 4.1 Land-use change in southwestern Australia from a dark native heath vegetation to a wheatland that reflects more incoming radiation causes greater surface heating over the heath. This causes air to rise, drawing moisture-laden air from the wheatland and forming clouds that increase precipitation over the heath. The 30% reduction in precipitation over the wheatland reduces the viability of agriculture in this dry region (see Chap. 13)

that is absorbed by an ecosystem, if there is insufficient water to cool the canopy by evaporation?

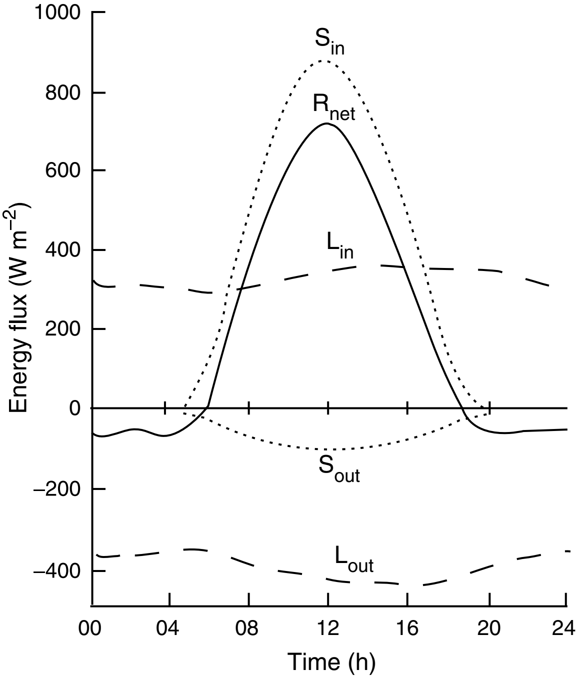
Finally, human activities alter the capacity of the atmosphere to hold water vapor. Water vapor is *the* major greenhouse gas. It is transparent to shortwave radiation from the sun but absorbs longwave radiation from Earth (see Fig. 2.2) and thus provides an insulative thermal blanket. Climate warming caused by emissions CO_2 and other greenhouse gases increases the quantity of water vapor in the atmosphere and therefore the efficiency with which the atmosphere traps longwave radiation. This **water vapor feedback** explains why climate responds so sensitively to emissions of other greenhouse gases (see Chap. 2). Warming accelerates the hydrologic cycle, increasing evaporation and rainfall at the global scale (see Chap. 14). Warming also causes sea level to rise, mainly (so far) due to the thermal expansion of the ocean and secondarily to melting of glaciers and ice caps. Rising sea level endangers the coastal zone, where most of the world's major cities are located. How much of the coastal zone or city near you is likely to be flooded with projected levels of sea level rise (e.g., http://flood.firetree.net/)? Given the key role of water and energy in ecosystem and global processes, it is critical that we understand the controls over water and energy exchange and the extent to which they have been modified by human actions.

Surface Energy Balance

Radiation Budget

The radiative energy absorbed by a surface is the balance between incoming and outgoing radiation. Here we focus on ecosystem-scale radiation budgets, although the same general principles apply at any scale, ranging from the surface of a leaf to the surface of the globe (see Fig. 2.3). The two major components of the radiation budget are shortwave radiation (K), the high-energy radiation emitted by the sun, and longwave

Fig. 4.2 Radiation budget of a Douglas fir forest during the summer. Redrawn from Oke (1987)



radiation (L), the thermal energy emitted by all bodies (see Chap. 2). **Net radiation** (R_{net}) is the balance between the inputs and outputs of shortwave and longwave radiation, measured in W m^{-2} (Fig. 4.2).

$$R_{net} = (K_{in} - K_{out}) + (L_{in} - L_{out}) \qquad (4.1)$$

At noon on a clear day, **direct radiation** from the sun accounts for 90% of the shortwave input to an ecosystem (see Fig. 2.3). Additional input of shortwave radiation comes as **diffuse radiation** that is scattered by particles and gases in the atmosphere and **reflected radiation** from clouds and surrounding landscape units such as lakes, dunes, or snowfields. Diffuse radiation becomes a larger proportion of incoming shortwave radiation on cloudy or polluted days or near dawn or dusk when sun angles are lower.

The proportion of the incoming shortwave radiation that is absorbed depends on the **albedo** (a) or shortwave reflectance of the ecosystem surface. Albedo varies at least 10-fold among ecosystems, ranging from highly reflective surfaces such as fresh snow to surfaces with a low reflectance such as wet soils or the water in lakes and the ocean (Table 4.1). Conifer canopies, for example, have a lower albedo (i.e., absorb a larger proportion of incoming radiation) than deciduous forests, and grasslands with standing dead leaves have relatively high albedo. Albedo depends not only on the reflectance of individual leaves, stems, and soil but also on ecosystem structure. A complex canopy has a lower albedo (less reflectance) than do individual leaves because much of the light reflected or transmitted by one leaf is absorbed by other leaves and stems, resulting in efficient light capture by the canopy as a whole. For this reason, deep, uneven canopies of conifer forests have a low albedo. In contrast, a relatively smooth canopy, such as a crop or grassland, reflects more of the incoming shortwave radiation from upper leaves directly back to space (Baldocchi et al. 2004).

Changes in ecosystem albedo explain in part why high-latitude regions are warming more rapidly than low latitudes. As climate warms, snow, lake ice, and sea ice melt earlier in the spring,

Table 4.1 Typical values of albedo for the major surface types on Earth

Surface type	Albedo
Ocean and lakes	0.03–0.10[a]
Bare soil	
Wet, dark	0.05
Dry, dark	0.13
Dry, light	0.40
Evergreen conifer	0.08–0.11
Deciduous conifer	0.13–0.15
Evergreen broadleaf	0.11–0.13
Deciduous broadleaf	0.14–0.15
Arctic tundra	0.15–0.20
Grassland	0.18–0.21
Savanna	0.18–0.21
Agricultural crops	0.18–0.19
Desert	0.20–0.45
Sea ice	0.30–0.45
Snow	
Old	0.40–0.70
Fresh	0.75–0.95

Data from Oke (1987), Sturman and Tapper (1996), Eugster et al. (2000), Hollinger et al. (2010)

[a] Albedo of water increases greatly (0.1–1.0) at solar angles less than 30°

replacing a reflective snow-covered surface with a dark absorptive surface (Euskirchen et al. 2007). This process, together with the resulting change in surface temperature, is referred to as the **snow (or ice) albedo feedback**. Over longer time scales, the northward movement of trees into tundra causes an additional reduction in regional albedo because the dark forest canopy masks the underlying snow-covered surface. As tree line moves north, the land surface absorbs more energy, which is then transferred to the atmosphere, causing an amplifying (positive) feedback to regional warming (Foley et al. 1994; Chapin et al. 2005). Albedo also changes in response to short-term changes in solar input. Canopies absorb a larger proportion of incoming radiation (lower albedo) at midday than at dawn or dusk and during cloudy (more diffuse radiation) than during clear conditions (Hollinger et al. 2010).

Across all vegetation types, albedo increases with increasing leaf nitrogen up to about 2.5% nitrogen and is relatively insensitive to further increases in leaf nitrogen (Hollinger et al. 2010). The increase in albedo with increasing nitrogen may result from the large surface area for gas exchange between photosynthetic cells and internal air spaces in high-nitrogen leaves (see Chap. 5; Hollinger et al. 2010). Each time radiation passes between water and air, a large proportion of the near infrared portion of the spectrum is reflected, so high-nitrogen leaves reflect more shortwave radiation than do low-nitrogen leaves. Regardless of the mechanism, this relationship suggests that, despite their low photosynthetic rates (see Chap. 5), low-nitrogen canopies absorb a larger proportion of total incoming radiation than do canopies on high-fertility sites.

The amount of longwave (thermal) radiation emitted by an object depends on its temperature and **emissivity**, a coefficient that describes the capacity of a body to emit radiation. Most absorbed radiation is emitted (emissivity of about 0.98 in vegetated ecosystems), so longwave radiation balance depends primarily on the temperature of the sky, which determines L_{in}, and the temperature of the ecosystem surface, which determines L_{out} (4.2).

$$R_{net} = (K_{in} - K_{out}) + (L_{in} - L_{out}) = (1-\alpha)K_{in} + \sigma(\varepsilon_{sky}T_{sky}^4 - \varepsilon_{surf}T_{surf}^4) \tag{4.2}$$

where α is the surface albedo, σ is the Stefan–Boltzman constant (5.67×10^{-8} W m^{-2} K^{-4}), T is absolute temperature (°K), and ε is emissivity. Clouds and water vapor are warmer than the upper atmosphere and trap longwave emissions from the surface, so ecosystems receive more longwave radiation under cloudy than clear skies and under humid conditions. This explains why cloudy nights are warmer than clear ones and why cloudless dry conditions make deserts cold at night, despite the high inputs of solar energy during the day.

Longwave radiation emitted by the ecosystem (L_{out}) depends on surface temperature, which, in turn, depends on the quantity of radiation received by the surface and the efficiency

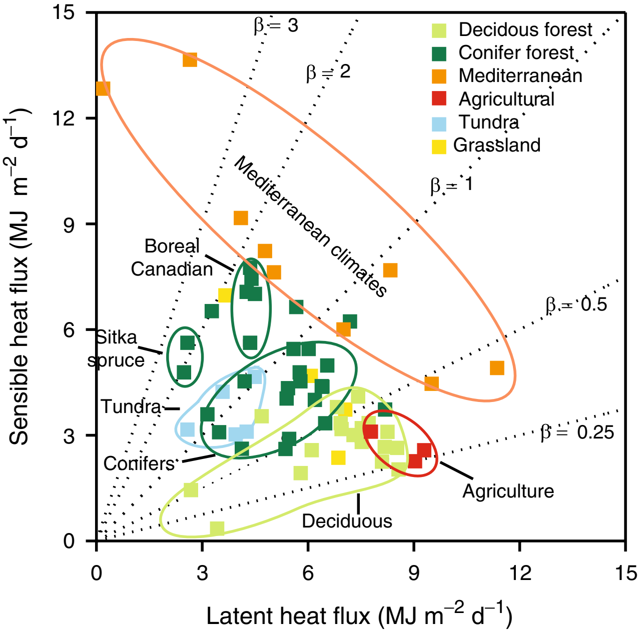


Fig. 4.3 Average daily sensible and latent heat fluxes during summer for different ecosystems measured by eddy covariance. *Dashed lines* show different Bowen ratios (β, ratio of sensible to latent heat flux). Ecosystems include deciduous forests, conifer forests, agricultural crops, tundra and grasslands. Also shown are a variety of ecosystems from a Mediterranean climate, which have high fluxes due to their high input of net radiation. Redrawn from Wilson et al. (2002)

with which this energy is transferred to the air and soil by turbulent processes, as described in the next section. Surfaces that absorb a large amount of radiation, due to high solar inputs or low albedo, tend to be warmer and therefore emit more longwave radiation. Dry surfaces and leaves with low transpiration rates tend to be particularly warm because they are not cooled by the evaporation of water. Desert sands, recent burn scars, and city pavement, for example, are generally hot (Bonan 2008). Conversely, a well-watered lawn is much cooler than an ecosystem that is dry or dominated by plants with low transpiration rates. In general, shortwave radiation input, albedo, surface roughness (see next section), and surface temperature are the parameters that most strongly influence radiation balance and therefore net radiation (4.2).

Partitioning of Absorbed Radiation

Net radiation, the radiative energy absorbed by an ecosystem, is approximately balanced by energy that is transferred out of the ecosystem by non-radiative processes. These non-radiative processes include **ground heat flux** (G), which conducts energy into the soil, and turbulent transfer of energy from the surface to the air as evapotranspiration of water (**latent heat flux**, LE) or heat (**sensible heat flux**, H). A small amount of energy (generally less than 10% of daily net radiation) may be stored (ΔS) in the ecosystem as chemical energy through photosynthesis and as a temperature increase of the plant biomass. At other times, stored energy is released by respiration and declines in biomass temperature. Although the energy trapped by photosynthesis is *the* major energetic engine that drives the carbon cycle of ecosystems, it is only a tiny part (<5%) of the total energy budget of ecosystems. Because ecosystem energy storage is usually small, energy absorbed by the surface as net radiation approximately equals energy loss by non-radiative processes over a day (4.3).

$$R_{net} = H + LE + G + \Delta S \qquad (4.3)$$

where L is the **latent heat of vaporization** (2.45 MJ kg^{-1} at 20°C), and E is the rate of evapotranspiration. As presented in this equation, R_{net} is positive when directed toward the surface; H, LE, G, and ΔS are positive when directed away from the surface. Ecosystems with high net radiation, such as those in Mediterranean climates, have higher sensible and/or latent fluxes than do ecosystems with low net radiation, such as arctic tundra or temperate rainforests (Fig. 4.3; Wilson et al. 2002).

Ground heat flux (G) is negligible over a day in most ecosystems because the heat conducted down into the soil during the day is balanced by heat conducted back up to the surface at night. The magnitude of ground heat flux depends on the thermal gradient between the soil surface and deep soils and the thermal conductivity of soils, which is greatest in soils that are wet and have a high bulk density (fewer insulating air pockets). The steepest thermal gradients and greatest ground heat flux occur in regions with permafrost. In the arctic, for example, approximately 10–20% of the energy absorbed during summer is consumed by thawing of frozen soil. This energy is released back to the atmosphere the next winter, when the soil refreezes (Chapin et al. 2000a).

Lakes and the ocean also have substantial summer "ground heat flux" because solar inputs penetrate beneath the surface, and the high heat capacity and turbulent mixing of water efficiently move heat away from the surface. In clear lakes, about half of the incoming shortwave radiation is absorbed and converted to heat in the top 10 cm, with the remaining heat conversion occurring at greater depths (Kalff 2002). Less transparent lakes convert shortwave radiation to heat closer to the surface, causing these lakes to stratify earlier in the spring and to have a colder hypolimnion than in more transparent lakes. The longer period of stratification increases the likelihood of anoxia in the hypolimnion, thereby altering all aspects of the biotic environment (Kalff 2002).

In contrast to soil heat flux, heat transfer to the atmosphere occurs primarily by **turbulence**, the irregular velocities of air movement between the surface and the **bulk air** (i.e., air above the canopy that is not strongly influenced by the canopy). Two processes generate this turbulence. **Convective turbulence** results from conduction (diffusion) of sensible heat over 1–2 mm from the surface to the near-surface air. The warm air expands, and the resulting increase in buoyancy causes this low-density warm air to rise, creating convective turbulence. A second more efficient process of energy transfer involves **mechanical turbulence**, when horizontally moving air slows down unevenly as it moves across an irregular surface. Tall uneven canopies such as conifer forests are aerodynamically **rough** compared to short smooth crop canopies. The mechanical turbulence generated by airflow across uneven topographic and vegetation surfaces creates eddies of air that sweep down into the canopy, transporting bulk air inward and canopy air out. These eddies transfer energy away from the surface and mix it with the atmosphere (Jarvis and McNaughton 1986; Bonan 2008). Conversely, air flowing across short, smooth canopies such as grasslands or crops tends to be less turbulent, so these canopies are less efficient in shedding the energy that they absorb, i.e., they are less tightly **coupled** to the bulk atmosphere. Because smooth canopies are less efficient in shedding heat, they tend to have higher surface temperatures during the day and greater longwave emissions than do forest canopies.

Turbulence transfers not only sensible heat but also the latent heat contained in water vapor that is transpired by plants or evaporates from leaf or soil surfaces. This energy is released when water vapor condenses to form cloud droplets. Dewfall represents a small latent heat flux from the atmosphere to the ecosystem at night under conditions of high relative humidity and cold leaf or soil surfaces.

Latent and sensible heat fluxes from ecosystems interact in ways that depend on surface moisture. The consumption of heat by evaporation cools the surface, thereby reducing the temperature differential between the surface and the air that drives sensible heat flux. Conversely, the warming of surface air by sensible heat flux increases the quantity of water vapor that the air can hold and causes convective movement of

Table 4.2 Representative Bowen ratios (ratio of sensible to latent heat flux) of different ecosystem types

Surface type	Bowen ratio
Desert	>10
Semi-arid landscape	2–6
Arctic tundra	0.3–2.0
Temperate forest and grassland	0.4–0.8
Boreal forest	0.5–1.5
Forest, wet canopy	−0.7–0.4
Water-stressed crops	1.0–1.6
Irrigated crops	−0.5–0.5
Tropical wet forest	0.1–0.3
Tropical ocean	<0.1

Data from Jarvis (1976), Oke (1987), Eugster et al. (2000)

moist air away from the evaporating surfaces. Both of these processes increase the vapor pressure gradient that drives evaporation. Because of these interdependencies, surface moisture has a strong impact on the **Bowen ratio**, i.e., the ratio of sensible to latent heat flux.

Bowen ratios vary by more than two orders of magnitude among ecosystems, indicating that either latent heat flux or sensible heat flux can dominate the turbulent energy transfer from ecosystems to the atmosphere (Table 4.2, Fig. 4.3; Wilson et al. 2002). In general, energy flux from wet ecosystems (e.g., open water and ecosystems whose canopy is often wet) is dominated by evapotranspiration (Bowen ratio < 0.5), whereas energy flux from other ecosystems, especially dry ones, is dominated by sensible heat flux (Bowen ratio > 0.5). Species characteristics also influence Bowen ratio, with greater evapotranspiration (lower Bowen ratio) from ecosystems dominated by rapidly growing plants with high rates of photosynthesis and transpiration (Table 4.2; see Chap. 5). Deciduous forests, for example, have higher transpiration rates and lower Bowen ratios than do conifer forests (Fig. 4.3). Strong winds or rough canopies, which generate atmospheric turbulence, reduce surface temperature, thereby reducing sensible heat flux and Bowen ratio. For these reasons, energy partitioning varies substantially both seasonally and among ecosystems. The Bowen ratio determines the strength of the linkage between the energy and water budgets of ecosystems, with wet ecosystems (low Bowen ratios) having a larger proportion of turbulent energy exchange occurring as evapotranspiration and therefore a tighter linkage between water and energy budgets (Box 4.1).

The spatial configuration of ecosystems on a landscape influences energy partitioning because heating contrasts between adjacent ecosystems create convective turbulence. This turbulence, and therefore sensible and latent heat fluxes, is greater at boundaries than in the centers of ecosystems (see Chap. 13). Most evaporation from large lakes, for example, occurs near their edges, rather than in the center, where the overlying air is so stable that it saturates rapidly and supports a relatively low evaporation rate. For the same reason, a mosaic of crops and fallow fields would support greater evapotranspiration than large homogeneous areas that contained the same proportions of crop and fallow. When ecosystem patches that differ strongly in albedo or energy partitioning are larger in diameter than the depth of the planetary boundary layer (> ≈10 km), they can modify mesoscale atmospheric circulations and cloud and precipitation patterns (Fig. 4.1; see Chap. 13; Pielke and Avisar 1990; Weaver and Avissar 2001).

Snow-covered surfaces experience threshold changes in energy exchange at the time of snowmelt. The high albedo of snow-covered surfaces minimizes energy absorption until snowmelt occurs, at which time there is a dramatic increase in the energy absorbed by the surface and transferred to the atmosphere. This often results in abrupt increases in regional air temperature after snowmelt. Leaf-out also alters energy exchange by both changing albedo and increasing evapotranspiration at the expense of sensible heat flux. Because of the dramatic difference in energy budget between snow-covered and snow-free seasons, recent advances in the date that snow melts on land or ice melts on lakes or the ocean create a strong amplifying (positive) feedback to high-latitude warming (Euskirchen et al. 2007).

Box 4.1 The Energetics of Water Movement

Water and energy participate in two of the most dynamic cycles on the planet in terms of both quantities moved and their rapidity of turnover. The energetics of water movement are critical to understanding both the linkage between these cycles and their underlying controls. Evapotranspiration is one of the largest terms in both the water and energy budgets of ecosystems, so factors governing the magnitude of evapotranspiration determine the tightness of the linkage between the water and energy cycles.

Due to its high **specific heat** – the energy required to warm 1 g of a substance by 1°C – water changes temperature relatively slowly for a given energy input. It takes four times more energy to raise the temperature of water by 1°C than an equivalent mass of air. Consequently, the summer temperature near large water bodies fluctuates less and is generally cooler than in inland areas. A wet surface also heats more slowly but evaporates more water than a dry surface.

Massive amounts of energy are absorbed or released when water changes state. It takes 580 times more energy (2.45 MJ kg^{-1}) to vaporize 1 g of water at 20°C than to increase its temperature by 1°C. Evapotranspiration therefore has a powerful cooling effect on transpiring leaves or other evaporating surfaces. Conversely, condensation of water vapor to form clouds has a powerful warming effect on the atmosphere, providing the added buoyancy that forms tall thunderheads (see Chap. 2).

Vapor pressure is the partial pressure exerted by water molecules in the air. The air immediately adjacent to an evaporating surface is approximately saturated at the temperature of the surface, for example the cell walls of a photosynthetic cell inside a leaf. The **vapor pressure deficit** (VPD) is the difference between the actual vapor pressure of air and the vapor pressure of saturated air at the same temperature. VPD is the driving force for evapotranspiration and indeed for the movement of water from soil through plants to the atmosphere. It is loosely used to describe the difference in vapor pressure between the air immediately adjacent to an evaporating surface and the bulk atmosphere, although, strictly speaking, the air masses are at different temperatures. **Conductance** of water vapor (the inverse of resistance) is the flux of water vapor per unit driving force (VPD).

Overview of Ecosystem Water Budgets

The water available to support the productivity of ecosystems depends on the balance between inputs and outputs. Water is the resource that most strongly constrains the productivity of the biosphere and therefore plays a central role in the dynamics of ecosystems. In addition, water increasingly constrains the opportunities for sustainable development of human societies in many parts of the world (Rockström et al. 1999; Vörösmarty et al. 2005; Carpenter and Biggs 2009). It is therefore important to understand water budgets to wisely manage the movement of water into, through, and out of ecosystems to meet the needs of both nature and society.

An ecosystem behaves like a bucket that is filled by precipitation and emptied by evapotranspiration and runoff. Lakes, for example, are filled by precipitation and by inflow from streams and adjacent ecosystems; water leaves by surface evaporation. When water inputs from precipitation and inflow exceed evaporation, the excess “overflows the bucket” and leaves as outflow. In many temperate lakes, evaporation is similar to precipitation, so the outflow from lakes is similar to the inflow. In warm, dry climates,

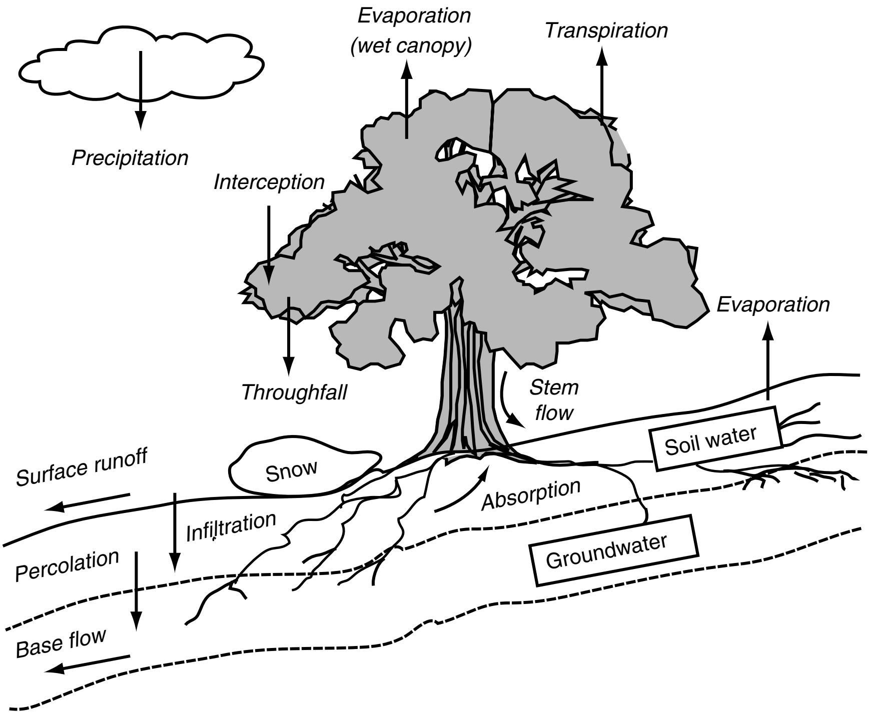


Fig. 4.4 Major water fluxes in an ecosystem

where evaporation exceeds inputs, outflow is less than inflow to lakes. Extremely dry climates, such as deserts, have such high evaporation rates that outflow seldom occurs, creating **closed-basin lakes**.

Terrestrial ecosystems also behave like a bucket in which water accumulates in the ecosystem until the water-holding capacity of soils is exceeded (Fig. 4.4). At this point, the excess water drains to groundwater or runs over the ground surface. The water losses from the ecosystem move laterally to other ecosystems such as streams and lakes. **Blue water** is the liquid water in rivers, lakes, reservoirs, and groundwater aquifers that is potentially available to society. Evaporation from the soil surface and transpiration by plants (**green water**) are the other major avenues of water loss from the soil reservoir. These processes continue only as long as the soil contains water that plants can tap, just as evaporation from a bucket continues only as long as the bucket contains water. Green water fluxes of the terrestrial biosphere exceed the blue water fluxes (Fig. 4.5; see Fig. 14.3).

Water Inputs to Ecosystems

Precipitation is the major water input to most terrestrial ecosystems. Global and regional controls over precipitation therefore determine the quantity and seasonality of water inputs to most ecosystems (see Chap. 2). In ecosystems that receive some precipitation as snow, however, the water contained in the snowpack does not enter the soil until snowmelt, often months after the precipitation occurs. This causes the seasonality of water input to soils to differ from that of precipitation.

Vegetation in some ecosystems, particularly in riparian zones, accesses additional groundwater that flows laterally through the ecosystem. Desert communities of **phreatophytes** (deep-rooted plants that tap groundwater), for example, may absorb enough groundwater that the ecosystem loses more water in transpiration than it receives in precipitation. Lakes and streams also receive most of their water inputs from groundwater or

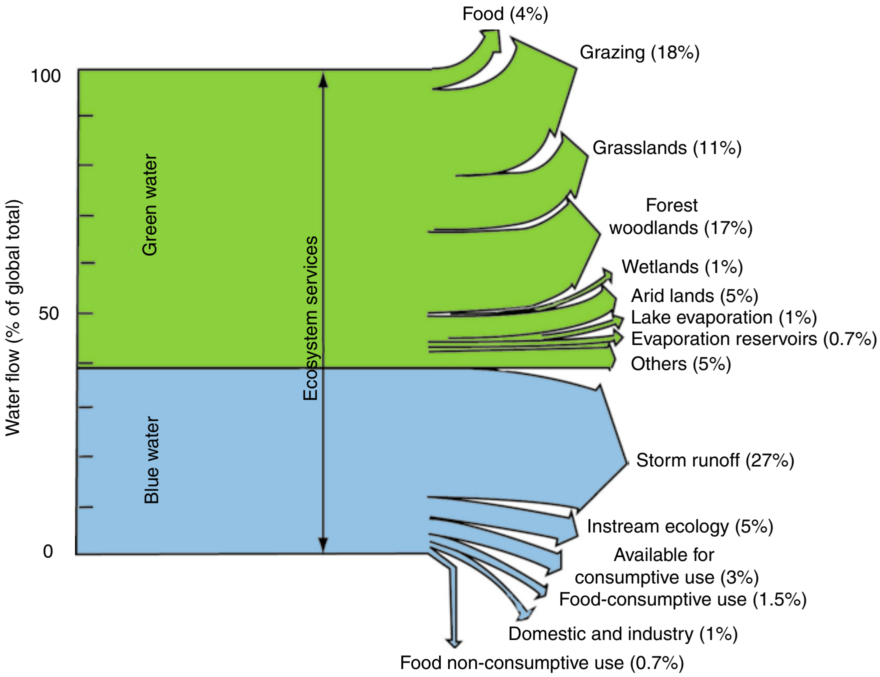


Fig. 4.5 Blue water and green water flows that support global ecosystem services. Redrawn from Carpenter and Biggs (2009) based on data from Rockström et al. (1999)

runoff that drains from adjacent terrestrial ecosystems. Water inputs to freshwater ecosystems are therefore linked only indirectly to precipitation.

In ecosystems with frequent fog, **canopy interception** of fog increases the water inputs to ecosystems, when cloud droplets that might not otherwise precipitate are deposited on leaf surfaces and drip from the canopy to the soil. The coastal redwood trees of California, for example, depend on fog-derived water inputs during summer, when precipitation is low, but fog occurs frequently (Ewing et al. 2009). Similarly, in areas that are climatically marginal for Australian rainforests, the capture of fog and mist by trees can augment rainfall by 40% (Hutley et al. 1997), just as in New Zealand high-elevation tussock grasslands (Mark and Dickinson 2008). In the absence of fog, however, canopy interception generally *reduces* the proportion of precipitation that enters the ecosystem because of canopy evaporation, as described in the next section.

Water Movements Within Ecosystems

Water Movement from the Canopy to the Soil

In closed-canopy forests, a substantial proportion of incoming precipitation lands in the canopy (Fig. 4.4). This precipitation can be evaporated directly back to the atmosphere, absorbed by the leaves, drip to the ground (**throughfall**), or run down stems to the ground (**stemflow**). **Canopy interception** is the fraction of precipitation that does not reach the ground. It is commonly about 10–20% for closed-canopy ecosystems (Bonan 2008). After light rain or snowfall, a substantial proportion of the precipitation may evaporate and return directly to the atmosphere without entering the soil. Throughfall is the process that delivers most of the water from the canopy to the soil.

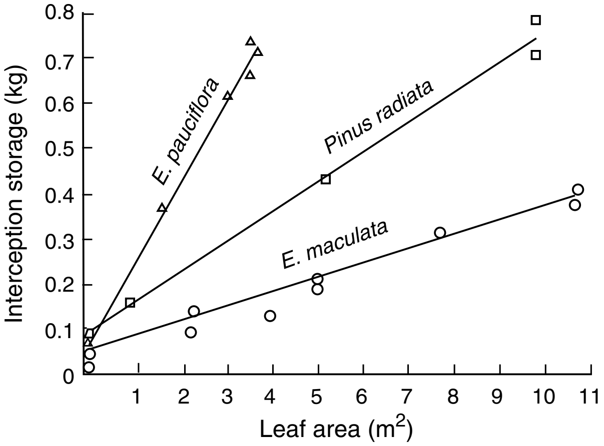


Fig. 4.6 Interception storage capacity of *Eucalyptus* species with different leaf areas. Redrawn from Aston (1979)

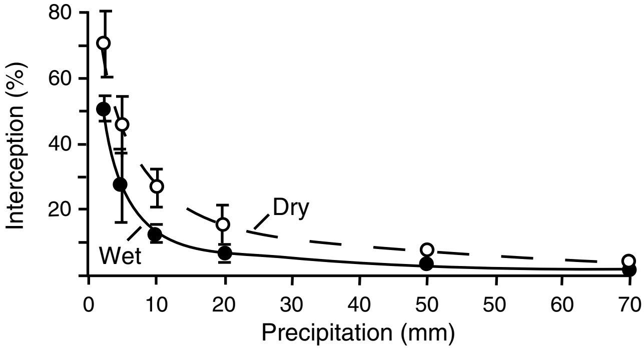


Fig. 4.7 Interception of water by dry and wet grass canopies in western Amazonia in relationship to precipitation inputs. Redrawn from Ataroff and Naranjo (2009)

The capacity of the canopy to intercept and store water differs among ecosystems. It depends primarily on canopy surface area, particularly the surface area of leaves (Fig. 4.6). Forests, for example, often store 0.8, 0.3, and 0.25 mm of precipitation on leaves, branches, and stems, respectively. Conifer forests typically store somewhat more water than deciduous forests (Waring and Running 2007; Bonan 2008). Epiphytes, which are rooted in the canopy, depend entirely on canopy interception for their water supply and increase canopy interception. Factors such as stand age and epiphyte load influence canopy interception through their effects on canopy surface area.

The bark texture and architecture of stems and trunks influences the amount and direction of stemflow. Trees and shrubs with smooth bark have greater stem flow (about 12% of precipitation) than do rough-barked plants such as conifers (about 2% of precipitation; Waring and Running 2007). In the *Eucalyptus* mallee in southwestern Australia, as much as 25% of the incoming precipitation runs down stems, due to the parachute-shaped architecture of these shrubs. The stemflow then penetrates to depth in the soil profile through channels at the soil–root interface (Nulsen et al. 1986).

In grasslands, where precipitation is generally less than in forests, interception is often 30–40% of precipitation, a larger proportion than in forests (Seastedt 1985; Ataroff and Naranjo 2009). For small precipitation events, 70% of the precipitation can be intercepted by a dry grassland canopy, with the fraction of intercepted precipitation declining with increasing event size (Fig. 4.7; Ataroff and Naranjo 2009). Factors such as grazing or burning that alter canopy structure influence the amount of water intercepted by a grassland. Burned prairies, for example, intercept about half as much of the growing season precipitation as do unburned prairies, where standing dead leaves intercept a large proportion of the precipitation (Seastedt 1985; Gilliam et al. 1987).

In general, canopy interception reduces water input to soils, especially from light rains. Only in the presence of fog does canopy interception augment water inputs to soils. However, beyond these simple generalizations, relatively little is known about variations among ecosystems in canopy effects on water inputs to soils.

Water Storage and Movement in the Soil

Soil water is stored primarily in thin water films on the surfaces of soil particles. The water-holding capacity of a soil depends on its total pore volume and the surface area of the surrounding particles (see Chap. 3). Pore volume, in turn, depends on soil depth and the proportion of the soil volume occupied by pores. Shallow soils on ridge tops, for example, hold less water than deep valley-bottom soils. Rocky or sandy soils, in which soil solids occupy much of the soil volume and particles have a low surface-to-volume ratio, hold less water than fine-textured soils.

Water moves along a gradient from high to low potential energy. The energy status of water depends on its concentration and various pressures. The pressures in natural systems can be described in terms of either hydrostatic pressures or matric forces (Passioura 1988). The major hydrostatic pressures in natural systems are: (1) gravitational pressure, which depends on height, and (2) pressures that are generated by evaporation and by physiological processes in organisms. Matric forces result from the adsorption of water to the surfaces of cells or soil particles. The thinner the water film, the more tightly the water molecules are held to surfaces by matric forces.

We can consider these forces simultaneously by expressing them in units of **water potential**, i.e., the potential energy of water relative to pure water at the soil surface. The total water potential (ψ_t) is the sum of the individual potentials.

$$\psi_t = \psi_p + \psi_o + \psi_m \tag{4.4}$$

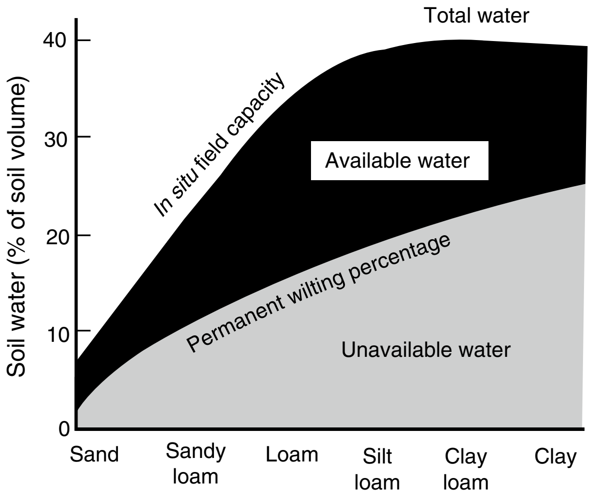
The **pressure potential** (ψ_p) is generated by gravitational forces and physiological processes of organisms; the **osmotic potential** (ψ_o) reflects presence of substances dissolved in water; the **matric potential** (ψ_m) is caused by adsorption of water to surfaces. In some treatments, matric potential is considered a component of pressure potential (Passioura 1988; Lambers et al. 2008). By convention, the water potential of pure water under no pressure at the soil surface is given a value of zero. Water potentials are positive if they have a higher potential energy than this reference or negative if they have a lower potential energy. Water potentials are negative in most parts of an ecosystem because water is held under tension in soils and stems and because it contains dissolved solutes.

Pressure gradients associated with gravity and matric forces control most water movement through soils. The rate of water flow through the soil (J_s) depends on the driving force (the gradient in water potential) and the resistance to water movement. This resistance, in turn, depends on the **hydraulic conductivity** (L_s) of the soil, and the path length (l) of the column through which the water travels.

$$J_s = L_s \frac{\Delta\psi_t}{l} \tag{4.5}$$

This simple relationship describes most of the patterns of water movement through soils, including the **infiltration** of rainwater or snowmelt into the soil and the movement of water from the soil to plant roots. Soils differ strikingly in hydraulic conductivity due to differences in soil texture and aggregate structure (see Chap. 3). For this reason, water moves much more readily through coarse-textured sandy soils than through clay soils or compacted soils. The rate of water flow in saturated soils, for example, differs by three orders of magnitude between fine- and coarse-textured soils (<0.25 to >250 mm h^{-1}).

Fig. 4.8 Plant-available water at field capacity as a function of soil texture. Redrawn from Kramer and Boyer (1995)



Infiltration of rainwater into the soil depends not only on hydraulic conductivity but also on preferential flow through **macropores** created by cracks in the soil or channels produced by plant roots and soil animals (Dingman 2001). Variation in flow paths in the surface millimeters of soil can have large effects on infiltration. Impaction by raindrops on an unprotected mineral soil, for example, can reduce hydraulic conductivity dramatically. Once water enters the soil, it moves downward under the force of gravity until the matric forces, which account for the adsorption of water to soil particles, exceed the gravitational potential. Water that is not retained by matric forces drains through the soil to groundwater and then to streams and lakes. The **field capacity** of a soil is the quantity of water retained by a soil after gravitational water has drained.

At field capacity, the water potential of a soil is about –0.03 MPa, i.e., close to the water potential of pure water (0.00 MPa). As a soil dries, the films of soil water become thinner, and the remaining water is held more tightly to particle surfaces. The **permanent wilting point** is the soil water potential (about −1.5 MPa) at which most mesic plants wilt because they cannot obtain water from soils. Many drought-adapted plants, however, can obtain water from soils at water potentials as low as −3.0 to −8.0 MPa (Larcher 2003). A second consequence of thin water films in dry soils is that water cannot move directly across air-filled soil pores but must move through water films around the edges of pores along a much longer, more tortuous path. For this reason, the hydraulic conductivity of soil declines dramatically as the soil dries. The difference in the water content between field capacity and permanent wilting point (water-holding capacity) provides an estimate of the plant-available water (Fig. 4.8), although some of this water is held in such small pores that it moves very slowly to roots. Vegetation often extracts 65–75% of the plant-available water before there are signs of water stress (Waring and Running 2007). The total quantity of water available to vegetation is the available water content per unit soil volume times the volume exploited by roots.

Water Movement from Soil to Roots

Water moves from soil to the roots of transpiring plants by flowing from high to low water potential. Water moves from the soil into the root whenever the root has a lower water potential than the surrounding soil. Movement of water into the root along a water-potential gradient causes the water film on adjacent soil particles to become thinner. This remaining water is adsorbed more tightly to soil particles and therefore has a lower water potential. The localized reduction in water potential near the root causes water to move along soil films toward the root. In this way, a root can access most available water within a radius of about 6 mm. As the soil dries, hydraulic conductivity declines, and the root accesses water less rapidly. In saline soils, the osmotic potential of the soil solution reduces total soil water potential, so roots with a given water potential can absorb less water from saline than from nonsaline soils.

A continuous pathway for water movement from the soil to the root is provided by root hairs and mycorrhizal hyphae that extend into the soil and by carbohydrates secreted by the root that maximize contact between the root and the soil. The root cannot absorb water if this root–soil contact is interrupted by the shrinking of drying soil or by the consumption of root hairs and root cortical cells by soil animals.

Rooting depth reflects a compromise between water and nutrient availability. Most plant roots are in the upper soil horizons where nutrient inputs are greatest and where nutrients are generally most available (see Chap. 9). In a given ecosystem, short-lived herbs are generally more shallow rooted than long-lived shrubs and trees and depend more on surface moisture (Fig. 4.9; Schenk and Jackson 2002). In arid ecosystems, surface evaporation and transpiration dry out the surface soils. For this reason, deserts, arid shrublands, and tropical savannas have many species with deep roots (Fig. 4.10). Phreatophytes are an extreme example of deep-rooted plants. Roots of these desert plants extend to the water table, often a depth of tens of meters. These plants have no physiological adaptations to drought and have high transpiration rates. Even wet ecosystems such as tropical rainforests have dry seasons that explain the occurrence of deep-rooted tropical trees that tap water from depths of more than 8 m (Nepstad et al. 1994). Relatively deep water (2–8 m depth) accounts for more than 75% of the water transpired by these forests. Deep-rooted plants may be more common and play a larger role in ecosystem water budgets than is generally appreciated.

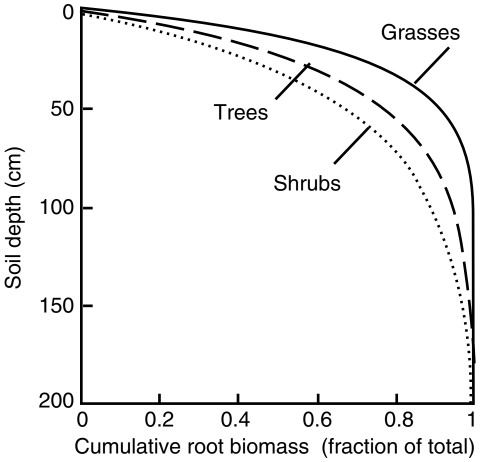


Fig. 4.9 The cumulative fraction of roots found at different soil depths for three plant growth forms averaged over all biomes. Redrawn from Jackson et al. (1996)

Rooting depth has important ecosystem consequences because it determines the soil volume that is exploited by vegetation (see Chap. 11). California grassland soils below a meter depth, for example, remain moist even at the end of the summer drought, whereas an adjacent chaparral shrub community uses water to a depth of 2 m. This greater rooting depth contributes to the longer growing season and greater productivity of the chaparral. Even in the chaparral, species differences in rooting depth lead to differences in water supply and drought stress.

Water Movement Through Plants

The vapor-pressure gradient from the leaf surface to the atmosphere is the driving force for water movement through plants. Water transport from the soil through the plant to the atmosphere takes place in a soil–plant–atmosphere continuum that is interconnected by a continuous film of liquid water. Water moves from the soil through the plant to the atmosphere along a gradient in water potential. The low water potential of *unsaturated* air outside leaves, relative to the water potential of *saturated* air inside leaves, is the major driving force for water loss from leaves

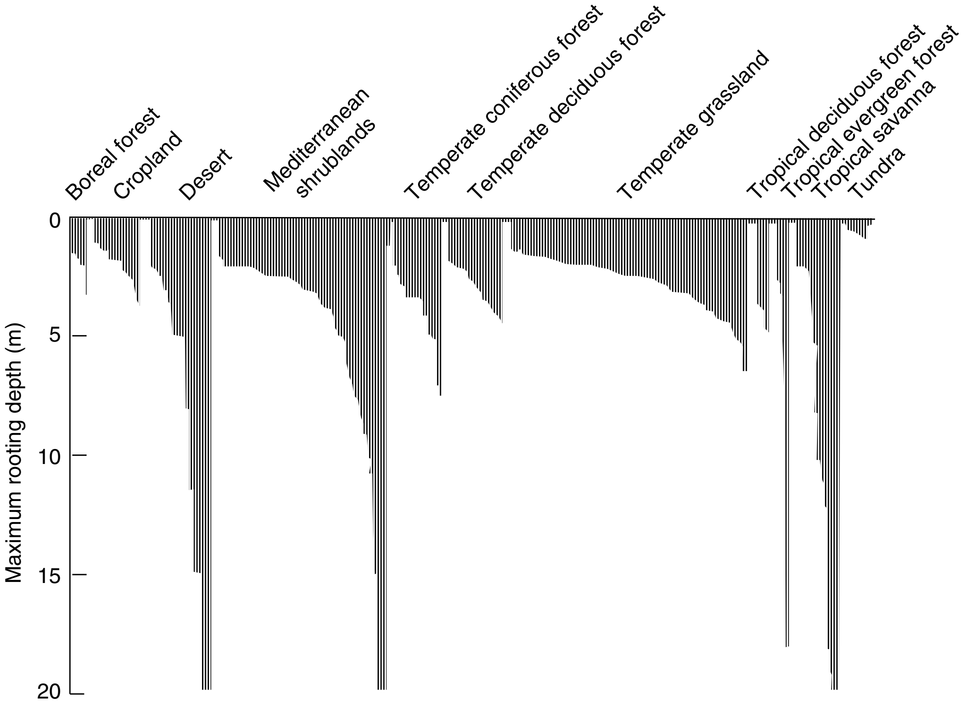


Fig. 4.10 Maximum rooting depths of selected species in the major biome types of the world. Species in each biome differ widely in rooting depth. Woody species in dry environments are often deeply rooted. Redrawn from Canadell et al. (1996)

(Box 4.1), which in turn drives water transport along a water-potential gradient from the roots to the leaves, which in turn drives water movement from the soil into the plant. Water moves through the plant under tension (negative pressure) as it is "sucked up" through xylem vessels to replace water that is lost by transpiration at the leaf surface. The rate of water movement through the plant (J_p) is determined by the water-potential gradient (the driving force; $\Delta\psi_t$) and the resistance to water movement, just as described for water movement through soils (Eq. 4.5). As in soils, the resistance to water movement through the plant depends on hydraulic conductivity (or conductance; L_p) and path length (l). The movement of water into and through the plant is driven entirely by the physical process of evaporation from the leaf surface and involves no direct expenditure of metabolic energy by the plant except to produce the roots. This contrasts with the acquisition of carbon and nutrients for which the plant directly expends considerable metabolic energy.

Roots

Water moves through roots along a water-potential gradient from moist soils to the atmosphere during the day and sometimes to dry surface soils at night. In moist soils, the cell membranes, which are composed of hydrophobic lipids, constitute the greatest resistance to water movement through roots (see Fig. 8.5). This membrane resistance to water flow is greatest under conditions of low root temperature or low oxygen, so plants that are not adapted to these conditions experience substantial water stress in cold or saturated soils. In dry soils, gaps between the root and the soil or breakage of water columns within the root, as described later, account for the greatest resistance to water flow through the plant. Plants overcome these disruptions in the water pathway from soil to leaves primarily

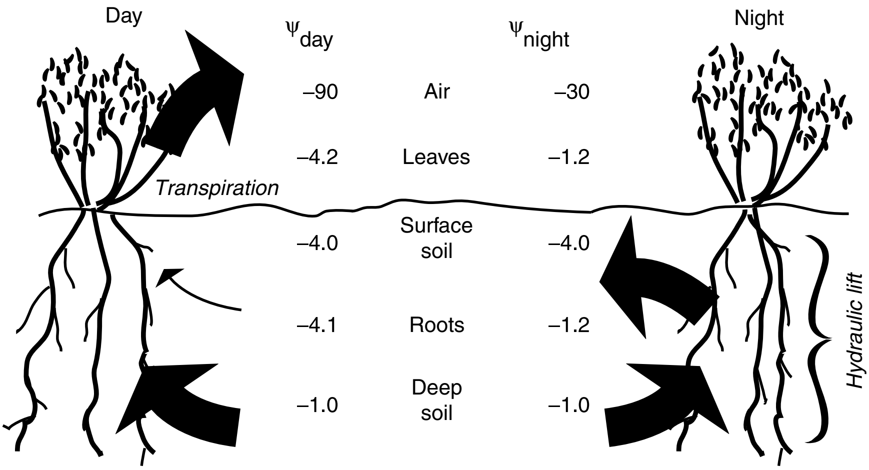


Fig. 4.11 Representative patterns of soil-water potential and water movement in arid environments during the day and at night. During the day, water moves from soils (especially deep soils) to the atmosphere in response to the strong water-potential gradient from the plant to the atmosphere. At night, when stomata are closed, water moves from wet soils at depth to dry surface soils through the root system, the process of hydraulic lift

by producing new roots, whose water transport pathway are intact and whose carbohydrates, root hairs, and mycorrhizae improve the contact with soil-water films.

In dry environments, there is a strong vertical gradient in soil-water potential due to the low water potential of dry surface soils. However, water moves slowly through the soil because of the low hydraulic conductivity of dry soils. During the day, when plants lose water through transpiration, plant-water potential is lower than soil-water potential, so water moves from the soil into the plant, particularly from deep soils where water is most available (highest soil-water potential; Fig. 4.11). At night, when stomata close and transpiration ceases, plant-water potential equilibrates with the water potential of deep soils. When surface soils are drier than those at depth, the water-potential gradient is from deep to shallow soils. Because roots have much higher hydraulic conductivity than dry soils, this gradient in water potential drives **hydraulic lift**, the vertical movement of water from deep soils *through roots* to shallow soils along a water-potential gradient (Caldwell and Richards 1989). This water movement can be documented by measuring changes in the isotopic composition of water (Box 4.2). Hydraulic lift occurs in most arid ecosystems and in many moist forests. Sugar maple trees, for example, acquire all their moisture from deep roots during dry periods, but 3–60% of the water used by shallow-rooted herbs in these forests comes from water that has been hydraulically lifted by the maple trees (Dawson 1993). In the Great Basin deserts of western North America, 20–50% of the water used by shallow-rooted grasses comes from water that is hydraulically lifted by deep-rooted sagebrush shrubs. The water provided by hydraulic lift stimulates decomposition and mineralization in dry, shallow soils, augmenting the supplies of both water and nutrients to shallow-rooted species. Because deep-rooted plants both provide water to, and remove water and nutrients from, shallow soils, hydraulic lift complicates the interpretation of species interactions in many ecosystems. When surface soils are wetter than deep soils after rain, roots provide an avenue to recharge deep soils (Burgess et al. 1998). Thus roots provide an avenue for rapid water transport from soil of high to low water potential, regardless of the vertical direction of the water-potential gradient.

Box 4.2 Tracing Water Flow Through Ecosystems

Stable isotopes are useful tools for tracing the movement of elements or compounds through ecosystems (Dawson and Siegwolf 2007). The source of water used by plants, for example, can be determined from its isotopic composition. Two isotopes of an element differ in the number of neutrons in the nucleus and therefore differ in their physical properties more strongly than their chemical properties. The ratio of the concentration of deuterium (D) to hydrogen (H) provides a useful signature of different water sources. These ratios are often expressed relative to the ratio in some standard substance (such as the ocean in the case of water). Therefore, water that has more D than ocean water has a positive value, and water with less D than ocean water has a negative value. Evaporation discriminates against the heavier isotope (deuterium), causing the isotopic ratio of D/H in water vapor to decline (become more negative), relative to the water source that gave rise to evaporation (Fig. 4.12). Condensation, on the other hand, raises the D/H ratio, causing rainfall to have a less negative hydrogen isotopic ratio than its parent air mass. The D/H ratio of water vapor remaining in the atmosphere therefore declines (becomes more negative) with sequential rainfall events. There is also a positive linear relationship between air temperature at the time of precipitation and the D/H ratio, so summer precipitation has a higher D/H ratio than winter precipitation. These changes in D/H ratio with evaporation and condensation generate characteristic signatures of different pools of water in ecosystems. During the growing season, for example, deep water is more likely to be derived from winter precipitation (low D/H ratio) and shallow water from summer precipitation (high D/H ratio). These isotopic signatures can be used to identify the sources of water used by plants (Fig. 4.13). The isotopic ratio of xylem water, for example, can show the relative proportions of deep vs. shallow water used by plants and therefore their dependence on winter vs. summer precipitation. Similarly, D/H ratios show that some plants such as redwood trees derive most of their water from fog, whereas others use soil water or ground water (Dawson 1993; Limm et al. 2009). D/H ratios of stream water identify the relative contributions of soil water from recent precipitation

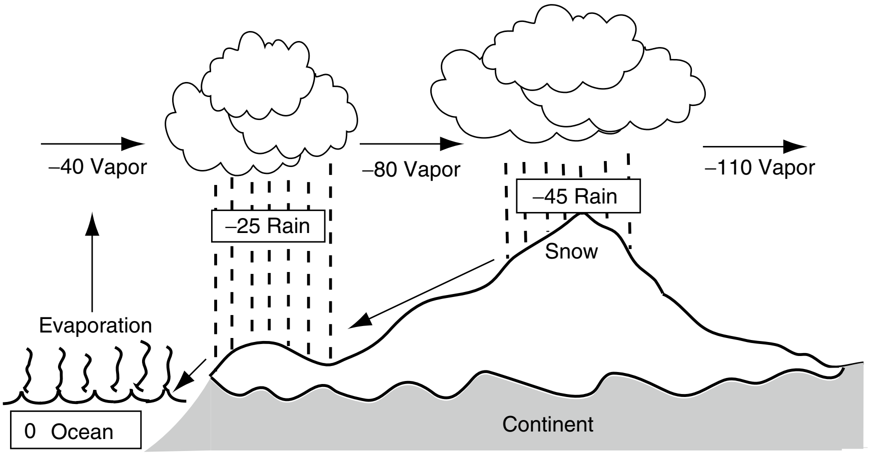


Fig. 4.12 The effect of evaporation and subsequent condensation during rainfall on the ratio of hydrogen isotopes. Redrawn from Dawson (1993)

(continued)

Box 4.2 (continued)

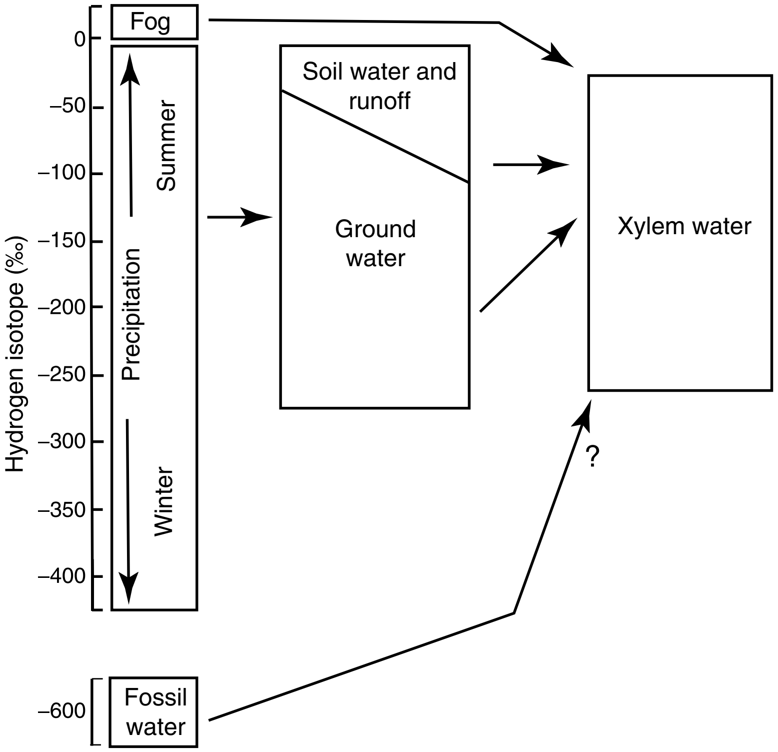


Fig. 4.13 Isotopic signature of water from various sources. By sampling the water in the xylem of plants, one can determine the main water supply used by a plant. Redrawn from Dawson (1993)

events vs. ground water. Oxygen isotope ratios in water show patterns of variation similar to those of hydrogen and have been particularly useful in estimating the atmospheric temperatures associated with the snowfall that produced glacial ice in the distant past (see Fig. 14.2).

Stems

Water moves through stems to replace water lost by transpiring leaves. The water-conducting tissues in the xylem are narrow capillaries of dead cells that extend from the roots to the leaves. Water is "sucked up" through these capillary tubes in response to the water-potential gradient created by transpirational water loss. The cohesion of water molecules to one another and their adhesion to the walls of the narrow capillary tubes allow these water columns to be raised under tension (a negative water potential) as much as 100 m in tall trees.

There is a tradeoff between hydraulic conductivity of xylem vessels and their risk of **cavitation**, i.e., the breakage of water columns under tension (Jackson et al. 2000; Sperry et al. 2008). Hydraulic conductivity of stems varies with the fourth power of capillary diameter, so a small increase in vessel diameter greatly increases hydraulic conductivity. For example, vines, which have relatively narrow stems and rely on other plants for physical support, have large-diameter xylem vessels. This allows rapid water transport through narrow stems but increases the risk of cavitation and may explain why vines are most

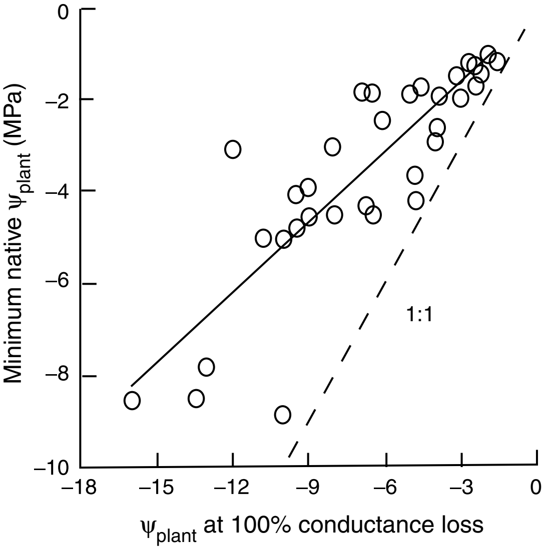


Fig. 4.14 The relationship between the water potential at which a plant loses all xylem conductivity due to cavitation and the minimum water potential observed in nature. Each data point represents a different species. The 1:1 (*dashed*) line is the line expected if there were no safety factor, i.e., if each species lost all conductivity at the lowest water potential observed in nature. Species that naturally experience low water potentials exhibit a greater margin of safety (i.e., a greater departure from the 1:1 line). Redrawn from Sperry (1995)

common in moist environments such as tropical wet forests. The stems of tropical vines, for example, have hydraulic conductivities and velocities of sap flow that are 50- to 100-fold higher than those of conifers (Larcher 2003). Broad-leaved deciduous trees are intermediate. Many plants in moist environments, particularly herbaceous plants, function close to the water potential where cavitation occurs, suggesting that they invest just enough in water transport tissues to allow water transport for the growing season (Sperry 1995; Sperry et al. 2008). Plants from dry environments produce stems with a larger safety factor, i.e., stems that resist cavitation at much lower water potentials than the plants commonly experience (Fig. 4.14).

Fine roots appear to be even more prone to cavitation than are stems due to their relatively large vessel diameters (Jackson et al. 2000). Due to the greater root surface area than stem cross-sectional xylem area, however, these two organs probably limit water transport to a similar degree at the whole-plant level (Craine 2009).

Plants in cold environments suffer cavitation from freezing. Trees adapted to these cold environments typically produce abundant small-diameter vessels that can, in some species, refill after cavitation (diffuse-porous species). In contrast, many trees in warm environments produce small-diameter vessels as well as large-diameter vessels that cannot be refilled after cavitation and therefore function for only a single growing season (ring-porous species).

The water transported by a stem depends on both the hydraulic conductivity of individual conducting elements and the total quantity of conducting tissue (the **sapwood**). There is a strong linear relationship between the cross-sectional area of sapwood and the leaf area supported by a tree (Fig. 4.15). However, the slope of this relationship varies strikingly among species and environments. Drought-resistant species generally have less leaf area per unit of sapwood than do drought-sensitive species because of the small vessel diameter (lower conductance) of drought-resistant species. The ratio of leaf area to sapwood area, for example, is generally more than twice as great in trees from mesic environments as in trees from dry environments (Margolis et al. 1995). Any factor that enhances the productivity of a tree increases its ratio of leaf area to sapwood area. This ratio increases, for example, with improvements in nutrient or moisture status and is greater in dominant than subdominant individuals of a stand.

Water storage in stems buffers the plant from imbalances in water supply and demand.

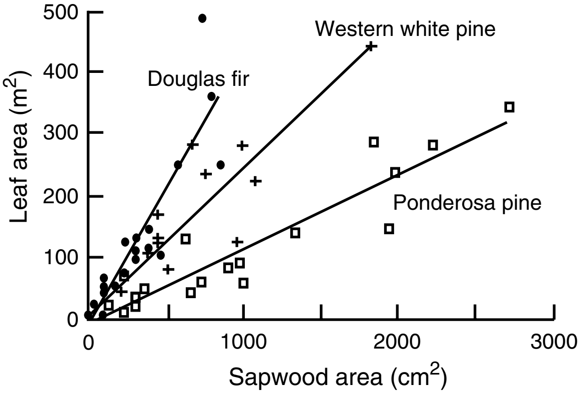


Fig. 4.15 Leaf area vs. sapwood cross-sectional area for three forest trees. Ponderosa pine, which typically occupies dry sites, has smaller vessels and therefore supports less leaf area per unit sapwood than does Douglas fir from moist sites. Redrawn from Monserud and Marshall (1999)

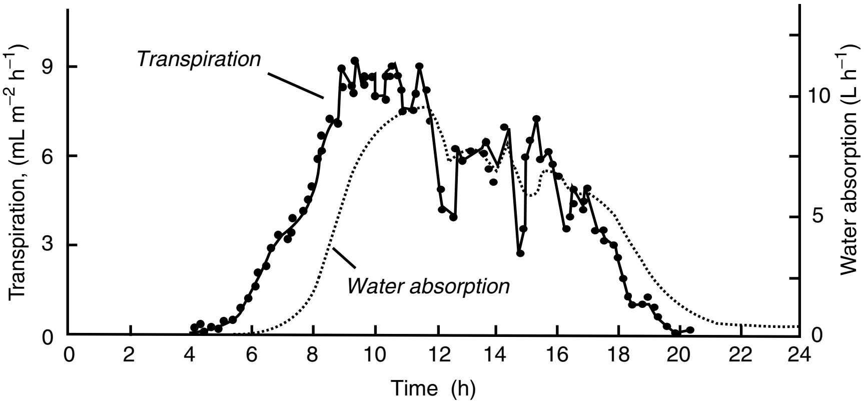


Fig. 4.16 Diurnal time course of water absorption and water loss by Siberian larch. During morning, transpiration is supported by water loss from stems, creating a lower water potential in stems and roots, which generates the water-potential gradient to absorb water from the soil. Absorption is measured as vertical transport through the stem, and water loss as transpiration per unit leaf area. The water stored in stems is replenished at night. Redrawn from Schulze et al. (1987)

The water content of tree trunks generally decreases during the day, causing water absorption by roots to lag behind transpirational water loss by about 2 h (Fig. 4.16). The quantity of water stored in sapwood is substantial, equivalent to as much as 5–10 days of transpiration. This sapwood water, however, exchanges relatively slowly, so stores of water in sapwood seldom account for more than 10% of transpiration. In tropical dry forests, where trees lose their leaves during the dry season, this stored water is critical to support flowering during the dry season. Trees with low-density wood and large stem water storage can flower during the dry season, whereas trees with high-density wood and low stem water storage can flower only during the wet season (Borchert 1994). Water stored by desert succulents may allow transpiration to continue for several weeks after water absorption from the soil has ceased.

Leaves

Water loss from leaves is controlled by the evaporative potential of the air, the water supply from the soil, and the stomatal conductance of leaves. Soil water supply and the evaporative potential of the air are the major environmental controls over water loss from

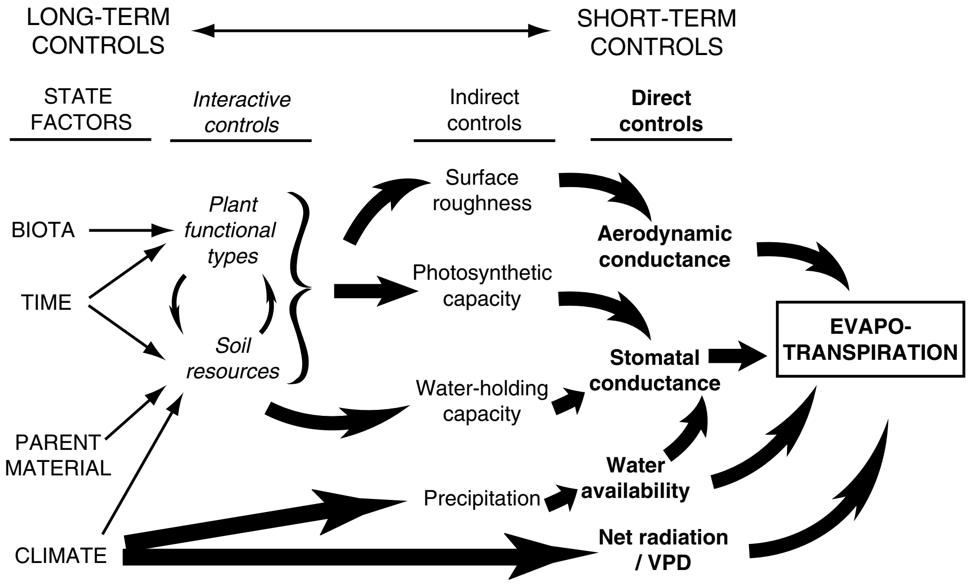


Fig. 4.17 The major factors governing temporal and spatial variation in evapotranspiration from a plant canopy. These controls range from the proximate controls, which determine the diurnal and seasonal variations in evapotranspiration, to the interactive controls and state factors, which are the ultimate causes of ecosystem differences in evapotranspiration. The thick *arrows* indicate that all these controls are important, with stomatal conductance most important in dry conditions and aerodynamic conductance in moist conditions. Net radiation is the strongest driver of evapotranspiration for smooth canopies and VPD for rough canopies

leaves (Fig. 4.17). **Stomata** (or stomates) are pores in the leaf surface that can be opened or closed by the plant to regulate the rates at which CO_2 enters the leaf and water is lost (the process of transpiration). Stomata determine the **conductance** of water vapor between the plant and the air, i.e., the flux of water vapor per unit driving force (vapor pressure gradient). When the stomata are open, leaves have a high conductance, and water vapor is rapidly lost. When stomata close, conductance declines to very low levels, and little water loss occurs. In dry soils, the low hydraulic conductivity of the soil minimizes the amount of water that can move directly from soil to the air by surface evaporation. The extensive root systems of plants and the high hydraulic conductivity of plant xylem make plants an effective conduit for moving water from the soil to the atmosphere. Plants adjust the size of stomatal openings to regulate the loss of water from leaves. Because stomatal conductance also determines the rate of CO_2 entry into leaves, there is an inevitable tradeoff between carbon gain and water loss by leaves (see Chap. 5).

Diurnal and climatic differences in air temperature and humidity determine the driving force for transpiration. Air inside the leaf is always saturated with water vapor because it is adjacent to moist cell surfaces. On a sunny day, air temperature rises to a maximum shortly after midday, allowing the air to hold more water. This rise in air temperature and the radiation absorbed by the leaf increases the temperature of the leaf and therefore the water vapor concentration of air spaces inside the leaf. The water vapor concentration of the external air increases less than that inside the leaf. The resulting increase in the gradient in water vapor concentration (i.e., VPD, Box. 4.1) between the inside and the outside of the leaf increases the transpirational water loss from the leaf. In the evening, the temperature decreases, causing a decline in the water vapor concentration inside the leaf and a decline in transpiration. Variations in weather or climate that cause an increase in air temperature or a decrease in atmospheric moisture content also enhance the driving force for transpirational water loss. The evaporative potential of desert air is therefore extremely high because it is both hot and dry. Cloud forests generally have low evaporative potential because the air is saturated and clouds reduce radiation input. Cold climates have low evaporative potential because cold air holds relatively little water vapor.

Stomatal conductance is *the* major control that plants exert over water loss from a leaf. Some plants reduce stomatal conductance when leaves are exposed to warm, dry air that would otherwise cause high transpirational water loss. Species differ considerably in their sensitivity of stomatal conductance to the evaporative potential of the air. Both the mechanism and ecological patterns in the sensitivity of stomatal conductance to atmospheric humidity are poorly understood.

Stomatal conductance declines in response to drought because plants sense the soil moisture content of their root systems. Roots exposed to low soil moisture produce **abscisic acid** (ABA), a hormone that is transported from roots to leaves and causes a reduction in stomatal conductance. The degree of coupling between soil moisture and stomatal conductance depends on specific plant adaptations. **Isohydric** plants, which tend to grow in moist environments, close their stomata at relatively high soil moistures before they experience large changes in plant-water potential. This stops photosynthesis, so they must rely on stored reserves to meet their energy demands during dry periods, but it prevents hydraulic failure. In contrast, **anisohydric** plants, which tend to grow in dry sites, show less response of stomatal conductance to soil drying and therefore continue to photosynthesize and to absorb and lose water as the soil dries (McDowell et al. 2008). These plants therefore maintain greater physiological activity in dry soils than do plants adapted to moist habitats, and, in the process, they transfer more water to the atmosphere under dry conditions. Although anisohydric plants are relatively drought tolerant, they are predisposed to hydraulic failure under extreme drought because they operate closer to their safety limits under these conditions. This in turn reduces their resistance to insect outbreaks and other indirect effects of drought (McDowell et al. 2008).

Species differ in stomatal conductance under favorable conditions. Stomatal conductance is highest in rapidly growing plants adapted to moist fertile soils (see Chap. 5; Körner et al. 1979; Schulze et al. 1994).

Water Losses from Ecosystems

Water input is the major determinant of water outputs from ecosystems. The water loss from ecosystems equals the input in precipitation (P) adjusted for any changes in water storage (ΔS). The major avenues of loss are evapotranspiration (E) and runoff (R).

$$P \pm \Delta S = E + R \tag{4.6}$$

Just as in the case of carbon and energy, the changes in water storage are generally small relative to inputs and outputs, when averaged over long time periods (multiple years). In ecosystem comparisons therefore the quantity of water entering the ecosystem largely determines water output, just as GPP (carbon input) is the major determinant of ecosystem respiration (carbon output; see Chap. 7).

The route by which water leaves an ecosystem depends on the partitioning between evapotranspiration and runoff. This partitioning has a critical impact on regional hydrologic cycles because green water that returns to the atmosphere is available to support precipitation in the same or other ecosystems. In contrast, runoff supplies the blue water input to aquatic ecosystems and provides most of the water used by people (Fig. 4.5). In a sense, runoff is the “left-overs” of water that entered in precipitation and was not transferred to the atmosphere by evapotranspiration. In summary, controls over evapotranspiration largely determine the partitioning between evapotranspiration and runoff.

Evaporation from Wet Canopies

Evaporation of water intercepted by the canopy is greatest in ecosystems with a high surface roughness. Forests have high rates of evaporation from wet canopies, primarily because the efficient mixing that occurs in rough forest canopies promotes rapid evaporation from each leaf (Kelliher and Jackson 2001). The large water storage capacity of forest canopies is less important than its **surface roughness** (vertical irregularities in the height of the canopy surface) in explaining the quantity of water evaporated from wet canopies. The evaporation rate from a wet canopy depends primarily on the climatic conditions that drive evaporation (primarily VPD) and the degree to which environmental conditions in the canopy are coupled by turbulence to conditions in the atmosphere. Turbulence, in turn, is greatest in ecosystems with a tall, aerodynamically rough canopy. In forests, which are tightly coupled to atmospheric conditions, wet canopy evaporation is largely independent of net radiation and is similar during the day and night. In grasslands, which are less tightly coupled to the atmosphere, wet canopy evaporation depends on net radiation as well as VPD and is greater during the day than at night. Due to differences in canopy roughness, forests have greater wet-canopy evaporation than do shrublands or grasslands, and conifer forests evaporate more water from wet canopies than do deciduous forests.

Climate is the other factor that governs evaporation from wet canopies. Climate determines the frequency with which the canopy intercepts precipitation or dew and the conditions that drive evaporation. Ecosystems in wet climates generally have greater canopy evaporation because of the more frequent capture of rainfall by the canopy, even though the low VPD of wet climates causes this evaporation to occur slowly. The *frequency* of rainfall and dew formation is generally more important than total precipitation in governing the annual flux of wet-canopy evaporation (Rutter et al. 1971). The canopy acts like a bucket that stores water from a given rain or dew event until its storage capacity is exceeded, at which point water moves to the ground as throughfall or stem flow. Canopy evaporation increases exponentially with air temperature because of the temperature effects on VPD (Box 4.1; McNaughton 1976), so ecosystems generally lose more intercepted water through canopy evaporation in warm than in cold climates. Despite these generalizations, the interactions among multiple controls over wet-canopy evaporation are so complex that they are best addressed through physically based models that consider all these factors simultaneously (Waring and Running 2007; Monteith and Unsworth 2008).

Canopies that intercept precipitation as snow or ice often store twice as much water equivalent as when precipitation is received in liquid form. Snow interception and subsequent **sublimation** (vaporization of a solid) from the canopy is greatest in ecosystems with a high **leaf area index** (LAI, the leaf area per unit ground area). Most snow usually falls to the ground, however, where low net radiation and low wind speeds minimize sublimation. In tundra, where there is no canopy in winter to shade the snow, or in continental boreal forests with low precipitation and low wind speeds, sublimation can account for 30% and 50%, respectively, of winter precipitation (Liston and Sturm 1998; Pomeroy et al. 1999; Sturm et al. 2001).

Evapotranspiration from Dry Canopies

Water moves from a dry canopy to the atmosphere above the canopy in two consecutive steps: diffusion and turbulent mixing. These two steps in the hydrologic pathway are controlled by quite different processes. **Surface conductance** determines the flux of water vapor from inside the leaf or soil to the near-surface air and is controlled primarily by leaf stomata and soil surface properties, respectively. **Aerodynamic conductance**, also termed boundary-layer conductance, determines the flux of water vapor from the air near the leaf or soil surface to the bulk air above the canopy and is controlled primarily by turbulent mixing within the canopy. Ecosystem structure and soil moisture determine the relative importance of these two controls.

Vegetation structure and climate govern evapotranspiration rate when soil moisture is adequate. Under moist-soil conditions, turbulent mixing between bulk and canopy air largely determines the rate of water loss because open stomata and soil evaporation allow rapid diffusion of water vapor to the air immediately above these surfaces. The aerodynamic conductance, which defines the potential for turbulent mixing, depends on wind speed and the size and number of roughness elements, such as trees. Aerodynamic conductance is greatest when surface turbulence mixes large quantities of air from the bulk atmosphere with air inside the canopy and couples the evaporation at the leaf or soil surfaces with the atmospheric moisture content above the canopy. Ecosystems such as forests with tall, aerodynamically rough canopies therefore have a higher aerodynamic conductance and reduce soil moisture more rapidly than do grasslands or crops (Mark and Dickinson 2008).

Vegetation structure also determines which climatic variables regulate evapotranspiration. In aerodynamically rough, well-coupled canopies, the moisture content of canopy air is similar to that above the canopy, so the moisture content of the bulk air is the main determinant of evapotranspiration (Waring and Running 2007). In canopies that are short, smooth, and weakly coupled, by contrast, the air adjacent to leaves mixes less readily with the bulk air, so evapotranspiration moistens the canopy air and reduces the driving force for diffusion through stomata. In these smooth canopies, evapotranspiration is determined more by net radiation than by the moisture content of the bulk air because net radiation determines surface temperature and therefore the driving force for water vapor diffusion through stomata to the near-surface air. The **decoupling coefficient**, which indicates the degree of canopy decoupling from the bulk air (Table 4.3; Jarvis and McNaughton 1986), is determined primarily by canopy height. In summary, the moisture content of the bulk air (as measured by VPD) is the dominant control in tall, well-coupled canopies, whereas net radiation is the dominant driver of evapotranspiration in short, weakly coupled canopies (Waring and Running 2007). These patterns of environmental control over evapotranspiration from ecosystems with moist soils and dry canopies are identical to those that we described earlier for wet-canopy evapotranspiration.

Table 4.3 Decoupling coefficient of vegetation canopies in the field under conditions of adequate moisture supply

Vegetation	Decoupling coefficient[a]
Alfalfa	0.9
Strawberry patch	0.85
Permanent pasture	0.8
Grassland	0.8
Tomato field	0.7
Wheat field	0.6
Prairie	0.5
Cotton	0.4
Heathland	0.3
Citrus orchard	0.3
Forest	0.2
Pine woods	0.1

Data from Jarvis and McNaughton (1986) and Jones (1992)

[a] A completely smooth surface has a decoupling coefficient of 1.0, and a canopy in which the air is identical to that in the atmosphere has a decoupling coefficient of zero

Under moist conditions where turbulent mixing within the canopy is the rate-limiting step, ecosystem differences in surface conductance are surprisingly small (Kelliher et al. 1995). In sparse vegetation, evaporation from the soil surface is the major avenue of water loss. As leaf area increases, transpiration increases (more leaf area to transpire), which is counteracted by a decrease in soil evaporation (more shading and less turbulent exchange at the soil surface). Consequently, surface conductance is relatively insensitive to the quantity of leaf area present. Vegetation affects maximum surface conductance primarily through its effects on stomatal conductance (Kelliher et al. 1995). However, even this effect is often relatively small. Maximum stomatal conductance of individual leaves is relatively similar among natural ecosystems (Körner 1994; Kelliher et al. 1995). Woody and herbaceous ecosystems, for example, have similar stomatal conductance of individual leaves (Körner 1994) and similar surface conductance of entire ecosystems (Kelliher et al. 1995). Crops, however, which have about 50% higher stomatal conductance

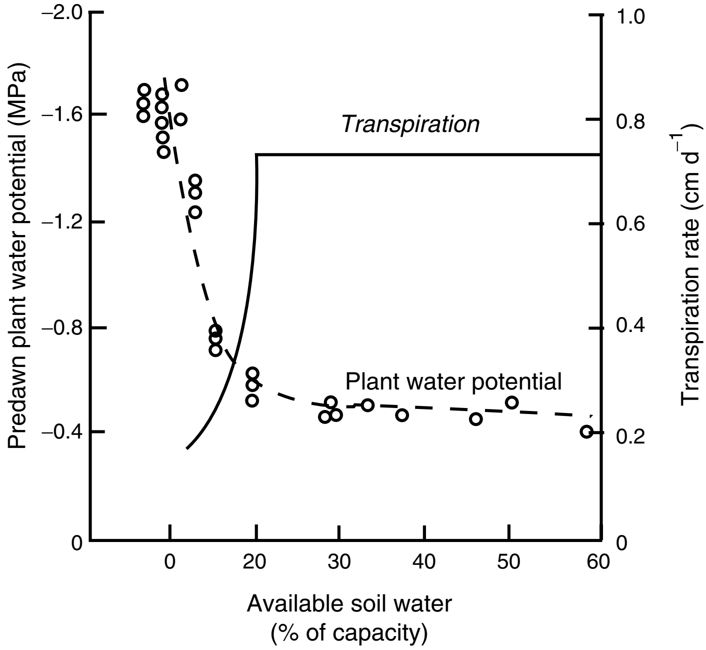


Fig. 4.18 Response of plant-water potential and transpiration to soil moisture (Sucoff 1972; Gardner 1983; Waring and Running 2007). Soil moisture has little effect on plant-water potential or transpiration until about 75% of the available water has been removed from the rooting zone

than does natural vegetation, also have about 50% higher surface conductance (Schulze et al. 1994; Kelliher et al. 1995). In summary, under moist-soil conditions, evapotranspiration is controlled much more strongly by surface roughness effects on aerodynamic conductance than by leaf area or maximum stomatal conductance.

As soil moisture declines, the control over evapotranspiration shifts from canopy structure to soil moisture. Plant-water potential and transpiration rate are surprisingly insensitive to water availability until plants have depleted about 75% of the plant-available soil water (Fig. 4.18). Evapotranspiration from dry canopies is therefore relatively insensitive to precipitation over a broad range of soil moisture (Fig. 4.19). Over this range of soil moisture, aerodynamic conductance remains the primary control over evapotranspiration. As soils continue to dry, however, their hydraulic conductivity declines. This creates a relatively abrupt threshold of soil moisture, below which the rate of water supply to roots declines, and plants experience water stress (low water potential; Fig. 4.18). Under these circumstances, plant stomata close, reducing surface conductance and evapotranspiration below their physiological maxima, just as described earlier for individual leaves. Under these dry-soil conditions, surface conductance limits water movement from the ecosystem to the atmosphere and is controlled primarily by the effects of soil moisture on stomatal conductance, as described earlier.

In summary, aerodynamic conductance, which depends on plant height and the number of roughness elements, is the main control over evapotranspiration from dry canopies under conditions of adequate water supply. Stomatal conductance exerts an increasingly important control over evapotranspiration as soil moisture declines below the point where soil hydraulic conductance is substantially reduced. In other words, stomatal conductance (and therefore surface conductance) accounts for *temporal* variation in evapotranspiration in response to soil drying, but surface roughness (and therefore aerodynamic conductance) is the major factor explaining *ecosystem differences* in evapotranspiration under *moist* conditions.

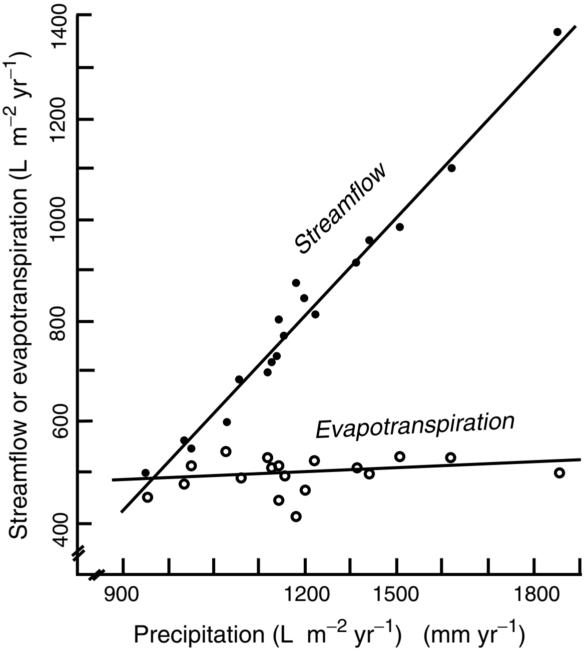


Fig. 4.19 Relationship between annual water input (precipitation) and output (evapotranspiration and streamflow) from a temperate forest watershed (Hubbard Brook in the U.S.) over a 19-year period. In this moist forest, evapotranspiration varies little among years, whereas streamflow is quite sensitive to the quantity of precipitation. Redrawn from Bormann and Likens (1979)

Changes in Storage

Water inputs that exceed outputs replenish water that is stored in soil and groundwater. Water that enters the soil is retained until the soil reaches field capacity. Additional water moves downward to groundwater. In cold climates in winter, most of the precipitation input is stored above ground in the snowpack. The snowpack substantially increases the quantity of water that an ecosystem can store and the residence time of water in the ecosystem. Stored water supports evapotranspiration at times when evapotranspiration exceeds precipitation; the declines in soil moisture during these times draw down water storage. The seasonal recharge and depletion of stored water are important controls over evapotranspiration and NPP in many ecosystems.

Groundwater, i.e., the water beneath the rooting zone, is a large pool that is inaccessible to plants in many ecosystems. The size of this pool depends on the depth to impermeable layers and the porosity of materials in this layer. Porosity governs the pore volume available to hold water and the resistance to lateral drainage of water. The groundwater pool has a relatively constant size, so, when new water enters groundwater from the top, it displaces older water that drains laterally to streams, lakes, and the ocean. The time lag between inputs to groundwater and outputs can be substantial (months to millennia) because of the large size of this pool.

People modify groundwater pools by changing the vegetation and associated rooting depth and by tapping groundwater to support human activities. Introduction of deep-rooted exotic species in arid regions as shade trees often allows the ecosystem to tap groundwater that was previously inaccessible. This can cause the water table to drop. The introduction of deep-rooted *Tamarix* in North American deserts, for example, caused the water table to drop so much that desert ponds have dried, endangering endemic fish species (Berry 1970).

Removal of vegetation causes the water table to rise because surface water is no longer tapped to support evapotranspiration. The clearing of heathlands for agriculture in Western Australia, for example, reduced the depth of the rooting zone, causing naturally saline groundwater to rise close to the surface. This reduced the productive potential of the crops, further reducing evapotranspiration and the depth to groundwater. Finally, evaporation from the soil surface increased soil salinity to the point that soils no longer supported crop growth in many areas nor could they be recolonized by native heath vegetation (Nulsen et al. 1986). Planting of salt-tolerant eucalypt forests in these saline soils increased evapotranspiration and reduced the height of the water table, thereby reducing soil salinity within and adjacent to forests (Jackson et al. 2005). In these ways, human modification of vegetation substantially alters the hydrologic cycle and all aspects of ecosystem structure and functioning.

Expansion of human populations into arid regions is often subsidized by tapping groundwater that would otherwise be unavailable to surface organisms. Irrigated agriculture often uses 80–90% of the water and is highly productive because of warm temperatures and high solar radiation, when the natural constraints of water limitation are removed (see Fig. 14.1). These irrigated lands are important sources of fruits, vegetables, cotton, rice, and other high-value crops. Conversion of arid regions to irrigated agriculture, however, reduces the amount of water available for runoff. Human use of water in the arid southwestern U.S., for example, converted the Rio Grande River from a major river to a small stream with intermittent flow during some times of year. Irrigation also increases soil evaporation, which increases soil salinity in a fashion similar to that described for Western Australia.

In cases where evapotranspiration of irrigated agriculture exceeds precipitation, there is not only a decrease in runoff but also a depletion of the groundwater pool. The Ogallala aquifer in the north-central U.S., for example, accumulated water when the climate was much wetter than today. Tapping of this "fossil water" has increased depth to water table substantially. Continued drawdown of this aquifer cannot be sustained indefinitely because current water sources cannot replenish it as rapidly as it is being depleted to support irrigation.

Runoff

Runoff from terrestrial ecosystems is the difference between precipitation inputs, changes in storage, and losses to evapotranspiration (4.6). Average runoff (or **discharge**) from a drainage basin depends primarily on precipitation and evapotranspiration because long-term changes in storage are usually negligible. Runoff responds to variation in precipitation much more strongly than does evapotranspiration (Fig. 4.19) because runoff constitutes the leftovers after the water demands for evapotranspiration and groundwater recharge have been met. Runoff is therefore greater in wet than in dry climates or seasons. Over hours to weeks, runoff generally increases after rainfall events and decreases during dry periods. Changes in water storage buffer this linkage between precipitation and runoff. The recharge of soil moisture in grasslands, shrublands, and dry forests, for example, may prevent large increases in streamflow after a rain when soils are dry, whereas streamflow may increase rapidly after a storm when soils are wet or shallow (Jones 2000). In ecosystems with a small capacity to store water such as deserts with coarse-textured soils and a calcic layer or ecosystems underlain by permafrost, runoff responds almost immediately to precipitation, and rainstorms can cause flash floods. Conversely, slowly draining groundwater provides a continued source of water to streams (**base flow**) even at times without precipitation. In this way, water balance determines the distribution and abundance of freshwater ecosystems and their temporal variability (Kalff 2002).

In ecosystems that develop a snowpack in winter, precipitation inputs are stored in the ecosystem during winter, causing winter stream flows to decline, regardless of the seasonality of precipitation. During spring snowmelt, this stored water recharges aquifers or moves directly to streams, causing large spring runoff events. Glacial rivers, for example, have greatest runoff in midsummer, when warm temperatures cause greatest melting, whereas non-glacial rivers in the same climate zone have peak flow in early spring after snowmelt. When climate warming changes snowfall to winter rains, this increases winter runoff and reduces the spring snowmelt pulse and summer runoff, which are important water sources for many cities.

River flow integrates the precipitation, evapotranspiration, and changes in storage throughout the drainage basin. In large rivers, the seasonal variations in flow often reflect patterns of precipitation and evapotranspiration that occur upstream, hours to weeks previously. These integrative effects of runoff from large drainage basins make runoff a good indicator of long-term changes in the hydrologic cycle.

Seasonal variations in streamflow are a major determinant of the structure and seasonality of ecosystem processes in streams and rivers. Periods of high flow in streams and rivers, for example, scour stream channels, removing or redistributing sediments, algae, and detritus (Power 1992a). In undammed rivers, high flow events may lead to predictable patterns of bank erosion and deposition. Life histories of river biota are adapted to natural flow regimes (Poff et al. 1997; Lytle and Poff 2004). Dams that reduce the intensity or seasonality of high-flow events therefore dramatically alter the natural disturbance regime and functioning of freshwater ecosystems.

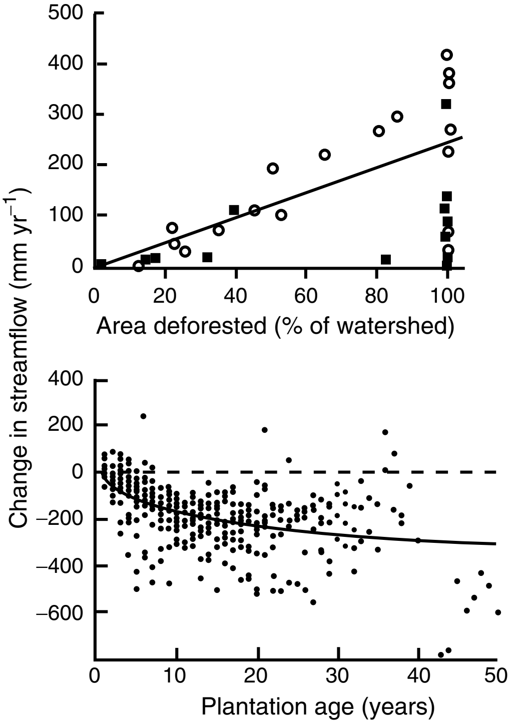


Fig. 4.20 Influence of removal (*top*) or planting (*bottom*) of trees on changes in streamflow. Streamflow in the southeastern U.S. (*open symbols*) and the more arid southwest (*closed symbols*) increases linearly with the proportion of the drainage basin that is deforested. Increased streamflow after forest harvest is least pronounced in arid ecosystems. Data from NRC (2008). Conversely, planting trees in previously unforested watersheds reduces stream flow almost immediately in watersheds sampled throughout the world. Redrawn from Jackson et al. (2005)

Vegetation strongly influences the quantity of runoff. Because evapotranspiration is such a large component of the hydrologic budget of an ecosystem, any vegetation change that alters evapotranspiration inevitably affects runoff. Deforested drainage basins, for example, exhibit increased annual runoff, although this often lasts only a few years (Fig. 4.20; see Chap. 12; Trimble et al. 1987; Moore and Wondzell 2005). In contrast, planting of new forests reduces runoff (Jackson et al. 2005; Mark and Dickinson 2008; NRC 2008). Planting forests to sequester carbon can therefore have unintended side effects of reducing water yields and availability of freshwater (Jackson et al. 2005; Mark and Dickinson 2008). On average, plantation forests have 38% less runoff than the non-forest vegetation they replace, and in 13% of the cases, streams dried up completely in at least 1 year (Jackson et al. 2005). More subtle vegetation changes also alter runoff. Conifer forests produce less runoff than deciduous forests because of their greater leaf area for interception and their longer season for evapotranspiration (Swank and Douglass 1974; Jones and Post 2004). Changes in climate, fire regime, insect outbreaks that alter vegetation structure and composition generally have predictable effects on evapotranspiration and runoff (NRC 2008).

Vegetation also influences the seasonality of runoff. Deforestation, for example, typically increases overland flow and reduces infiltration, causing larger peak flows of streams during storms and reduced flow between precipitation events. This increases the risk of flooding and reduces water flows during dry periods.

Summary

The energy and water budgets of ecosystems are inextricably linked because net radiation is the major driving force for evapotranspiration, and evapotranspiration is a large component of both water and energy flux from ecosystems. Net radiation is the balance between incoming and outgoing short- and longwave radiation. Ecosystems affect net radiation primarily through albedo (shortwave reflectance), which depends on the reflectance of individual leaves and other surfaces and on canopy roughness, which depends on canopy height and complexity. Most absorbed energy is released to the atmosphere as latent heat flux (evapotranspiration) and sensible heat flux. Latent heat flux cools the surface and transfers water vapor to the atmosphere, whereas sensible heat flux warms the surface air. The Bowen ratio, i.e., the ratio of sensible to latent heat flux, determines the strength of the coupling of the water cycle to the energy budget. This coupling is strongest in moist ecosystems.

Water enters terrestrial ecosystems primarily as precipitation and leaves as evapotranspiration and runoff. Water moves through ecosystems in response to gradients in water potential. Water enters the ecosystem and moves down through the soil in response to gravity. Available water in the soil moves along a film of liquid water through the soil–plant–atmosphere continuum in response to a gradient in water potential that is driven by transpiration (evaporation from the cell surfaces inside leaves). Evapotranspiration from canopies depends on the driving forces for evaporation (net radiation and VPD of the air) and two conductance terms, the aerodynamic and the surface conductance. Aerodynamic conductance depends on the degree to which the canopy is coupled to the atmosphere, which varies with canopy height and aerodynamic roughness. Surface conductance depends on the stomatal conductance of leaves in the canopy and on soil evaporation in sparsely vegetated ecosystems. Stomatal and surface conductances are relatively similar among natural ecosystems, but are somewhat higher in crop systems. Climate influences evapotranspiration both directly and through its effect on soil water availability, which determines stomatal conductance. Vegetation influences evapotranspiration through its effect on plant height and canopy roughness (which govern aerodynamic conductance) and on stomatal conductance (which influences surface conductance and the plant response to soil moisture).

The partitioning of water loss between evapotranspiration and runoff depends primarily on water storage in the rooting zone and the rate of evapotranspiration. Runoff is the leftover water that drains from the ecosystem at times when precipitation exceeds evapotranspiration plus any increase in water storage. Human activities alter the hydrologic cycle primarily through changes in land cover and use, which affect evapotranspiration and soil-water storage.

Review Questions

1. What climatic and ecosystem properties govern energy absorbed by an ecosystem?
2. What are the major avenues by which energy absorbed by an ecosystem is exchanged with the atmosphere? What determines the total energy exchange? What determines the relative importance of the pathways by which energy is exchanged?
3. What are the consequences of transpiration for ecosystem energy exchange and for the linkage between energy and water budgets of an ecosystem?
4. How might global changes in climate and land use alter the components of energy exchange in an ecosystem?
5. What determines the balance among the major pathways of water movement in an ecosystem, for example between evaporation, transpiration, and runoff? How do climate, soils, and vegetation influence the pools and fluxes of water in an ecosystem?
6. What are the mechanisms driving water absorption and loss from plants? How do plant properties influence water absorption and loss?

7. How do the controls over water loss from plant canopies differ from the controls at the level of individual leaves?
8. Describe how grassland and forests differ in properties that influence wet-canopy evaporation, transpiration, soil evaporation, infiltration, and runoff. What will be the consequences for runoff and for regional climate of a policy that encourages the replacement of grasslands with forests so as to increase terrestrial carbon storage?

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