Section One

Plant Ecophysiology

1

An Introduction to Biogeography: Broad-Scale Relationships Amongst Climate, Vegetation Distribution and Vegetation Attributes

This chapter provides a broad-scale overview of the patterns of global distribution of rainfall, temperature and evaporative demand. In addition it provides an introduction to some of the causes of inter-annual variability (including the El Niño Southern Oscillation, the North Atlantic Oscillation and the Southern Annular Mode) in weather patterns. Examination of the impacts of inter-annual variability of rainfall and temperature is a recurrent theme in studies of vegetation ecophysiology, modelling of landscape function and the application of remote sensing to investigate landscape structure and function. This chapter describes how climate variables were originally used to classify vegetation assemblages into biomes but also discusses the concept of plant functional types and shows how these are increasingly used in the disciplines of modelling and remote sensing as a means of representing biomes. Finally, leaf and whole-plant attributes that are deemed important in land surface models and remote sensing are discussed and recent developments in the interpretation of plant functional types are presented.

1.1 Large-Scale Patterns in Climate

1.1.1 The Solar Constant and the Earth's Tilt

Directly above the equator, at noon, about 1367 watts of solar energy per square metre (1367 W m^{-2}) are received at the outer edge of the atmosphere. This is termed the solar constant, although the sun's output is not constant with time because of changes in solar activity, including the 11-year sunspot cycle. About 7 percent of solar radiation is ultraviolet, about 41 percent is in the visible range (0.4–0.7 μm) and 51 percent has a wavelength > 0.7 μm (near infrared). The global annual average receipt of solar radiation at the edge of the atmosphere is, however, about 342 W m^{-2}, that is, one quarter of the solar constant. This is because the surface area of a sphere (assuming the earth is a sphere) is four times larger than the surface area of a disc of the same radius and thus solar energy is spread across an area four times larger than if the earth were a simple flat disc.

The amount of solar radiation reaching the earth's surface can be calculated from Equation 1.1:

$$S_h = (S_c/r^2)\cos(Z) \tag{1.1}$$

where S_h is the amount of solar radiation received on a horizontal surface (in W m^{-2}) at the earth's surface (assuming the atmosphere doesn't attenuate the solar radiation at all), S_c is the solar constant, r is the radius vector, and Z is the zenith angle. The zenith angle is the angle between a line perpendicular to the earth's surface and the sun. A zenith angle of 10° means the sun is very low in the sky (morning or evening) while a zenith angle of 80° means the sun is close to solar noon. The radius vector is the ratio of the actual distance of the earth from the sun at any given date to the annual average distance of the sun-to-earth. Since the earth's orbit is not circular but elliptical, the sun-to-earth distance is largest in July (northern summer) and smallest in January (southern summer). However, the difference in solar receipt at the earth's surface because of this is relatively small (about 3.3% less in July than January). Seasonality in temperatures arises because of the tilt of the earth's axis (about 23.4° from the vertical). During the northern hemisphere summer, the northern hemisphere is tilted towards the sun and therefore is warmed more than the southern hemisphere, which is tilted away from the sun and is therefore in its southern winter. The lower angle of the sun in winter and the shorter day length both combine to make winters colder than summers in both hemispheres. The tilt of the earth also explains why the largest solar radiation receipt on the summer solstice (June 21/22) is not seen at the equator because the equator is south of the solar declination angle (23.4°) which means that the equator is not receiving solar radiation perpendicular to the earth's surface; solar radiation that is perpendicular to the earth's surface occurs at 23.4° N latitude in the northern summer.

Clouds, aerosols, dust and gases within the atmosphere interact with solar radiation by absorbing (water vapour and other diatomic gases absorb radiation), scattering or reflecting light. Two types of scattering occur: Rayleigh and Mie. The former occurs when airborne particles have a radius of about one tenth of the wavelength of light and explains why the sky is blue on a cloudless day (blue wavelengths are scattered more because they have a shorter wavelength than the other colours). Rayleigh scattering is responsible for the creation of the diffuse beam fraction of solar radiation. Mie scattering occurs when photons interact with larger particles (approximately the same size as the wavelength of light) as opposed to particles that are much smaller (= Rayleigh). Mie scattering is responsible for the grey/white colour of clouds, as the water droplets are a comparable size to the wavelengths of visible light.

1.1.2 Latitudinal Gradients in Temperature

At the North and South poles (90°N and 90°S, respectively), mean annual temperatures are sub-zero, with mean monthly temperatures ranging from about zero to about –27°C. The coldest temperature ever recorded on the earth's surface (–89.2°C)

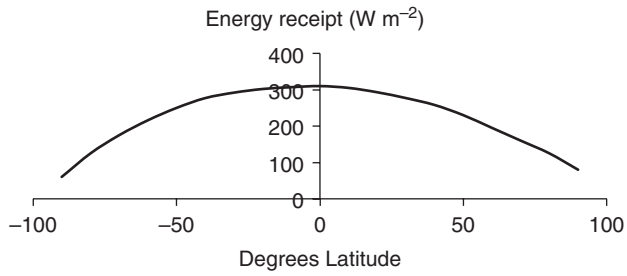

Figure 1.1. Energy receipt per square metre of land surface increases as latitude decreases (i.e., as we move towards the equator).

was recorded at Vostok Station, Antarctica. The three reasons for the poles being the coldest regions at sea-level are first, no solar radiation is received for six months of every year during winter and the ice-surface radiates heat to outer space (radiative cooling: the process of losing heat and hence cooling of a surface through loss of infra-red radiation to space); second, the sun's angle, is so oblique, even in summer, that the transfer of energy from solar radiation to the ice surface is much less efficient than in tropical regions where the solar angle is much closer to perpendicular at the ground surface; and, third, when the sun does irradiate the poles, the surface is covered with ice and snow which have a very high albedo (that is, reflect a large proportion of incoming solar radiation), thereby reducing the warming potential of the sun's rays. Note that for a zenith angle of 60° (30° from the horizontal) the area illuminated by a beam of light is double that (so the energy receipt per unit area is half) for a zenith angle of 0° (that is, perpendicular to the surface).

Total annual receipt of solar radiation (i.e., energy input) per square metre of land surface increases towards the equator (decreasing latitudes; Fig. 1.1). Consequently mean annual temperatures increase towards the equator. Annual solar radiation (energy) receipt increases because the sun's angle to the land surface increases towards the equator and therefore tends to the perpendicular.

Pole-to-equator temperature gradients are pronounced across all continents and reflect the gradient of annual solar radiation with latitude. The two following maps illustrate this (Fig. 1.2) using annual maximum temperatures (Australia) or annual mean temperatures (USA). This gradient in temperature is one of the three principle climatic determinants of the distributional patterns of vegetation. The other two climatic determinants are rainfall and potential evapotranspiration (the rate of evapotranspiration that would occur if water availability was unlimited; that is, the rate of evaporation that occurs at a site given the amount of solar radiation and atmospheric demand for water at that site, assuming water supply is not limiting to the rate of evaporation).

Coastal regions of the five continents tend to receive more rainfall than interior regions because of the close proximity to a source of water (and hence water vapour) on the coast. This is clearly seen in the rainfall maps for Australia and the United States (Fig. 1.3). Also apparent is the trend for east coasts of Australia and North

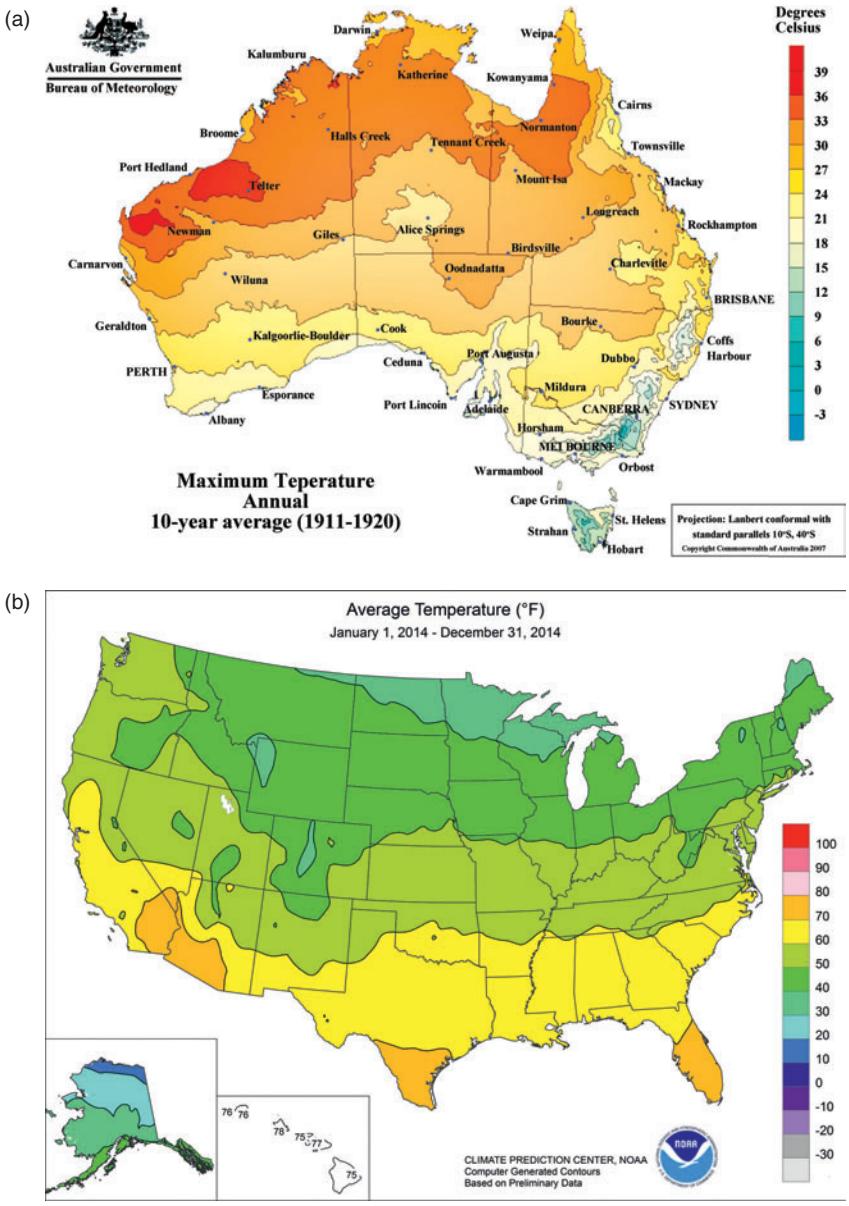

Figure 1.2. Maps of maximum annual temperature for Australia, and mean annual temperature for continental United States demonstrating the global trend of increasing temperatures towards the equator. Australian Bureau of Meteorology.

and South America to be wetter than west coasts because: (a) the prevailing wind directions bring moisture-laden wind off oceans onto the east coasts of these continents; and, (b) east coast water is warmer than land in summer but for the west coasts water is warmer than land in winter. In contrast, it is the western coast of Europe that receives the most rain because of the dominance of westerly winds bringing moisture laden air from the Atlantic Ocean, and Mediterranean, Adriatic, and Black Seas.

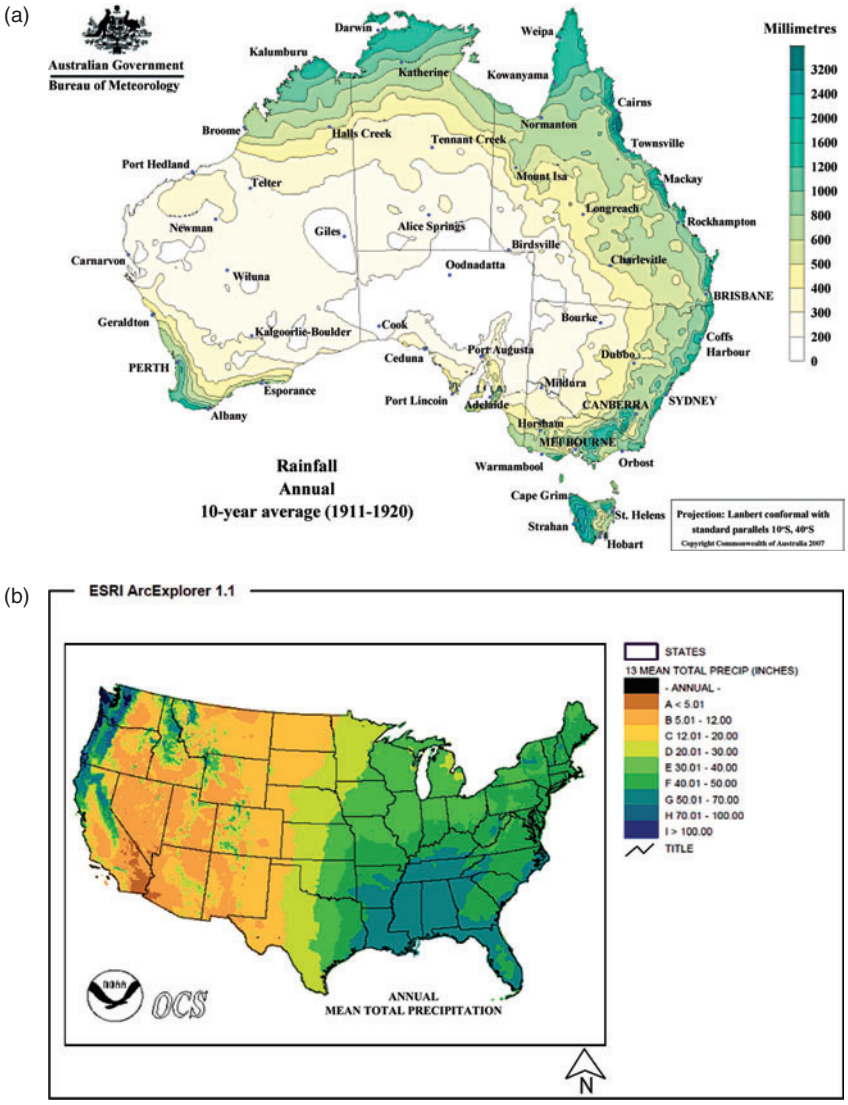

Figure 1.3. Maps of average annual rainfall for Australia and continental United States demonstrate the general trends of (a) coasts receive more rainfall (Australian Bureau of Meteorology); and (b) the east coast is wetter than the west coast (exceptions are discussed in the main text).

Notable exceptions to the trend for coastal regions to be wetter than the interiors of continents are the western coastal regions of the Sahara Desert in northern Africa and the western coastal edge of the Mojave Desert in the south western United States. These exceptions are caused by the influence of cold water off the coast which reduces evaporation and hence reduces the off-shore formation of moisture-filled clouds. Generally, however, there are gradients of rainfall from coastal to inland sites, although the presence of mountains can alter this broad pattern (for example, the Alps in south west Europe).

A key feature of rainfall with respect to vegetation distribution and function is seasonality. Rainfall that is received evenly across the whole year has a different effect on vegetation than the same amount of rainfall that falls only during a 6-month wet season (for example in the wet-dry tropics). The case studies chapters discussing the Amazon, savannas, tropical montane forests and arid-zone grasslands highlight the importance of the timing of rainfall in addition to the amount of rainfall, in influencing vegetation structure and function.

1.1.3 Evaporative Demand and the Water Balance Coefficient

In addition to consideration of the amount and timing of rainfall, it is important to consider the evaporative demand of the atmosphere. Rates of pan evaporation are the rates of evaporation that occur from an open water surface and reflect the influence of humidity, air temperature and prevailing wind speed. Annual pan evaporation rates can be larger or smaller than annual rainfall. This is clearly seen when comparing the map of rainfall for Australia (Fig. 1.3) or Europe (Fig. 1.5) with the map of pan evaporation rates for Australia or Europe (Figs. 1.4, 1.5). Pan evaporation rates are largest in tropical regions because temperatures are largest in these regions.

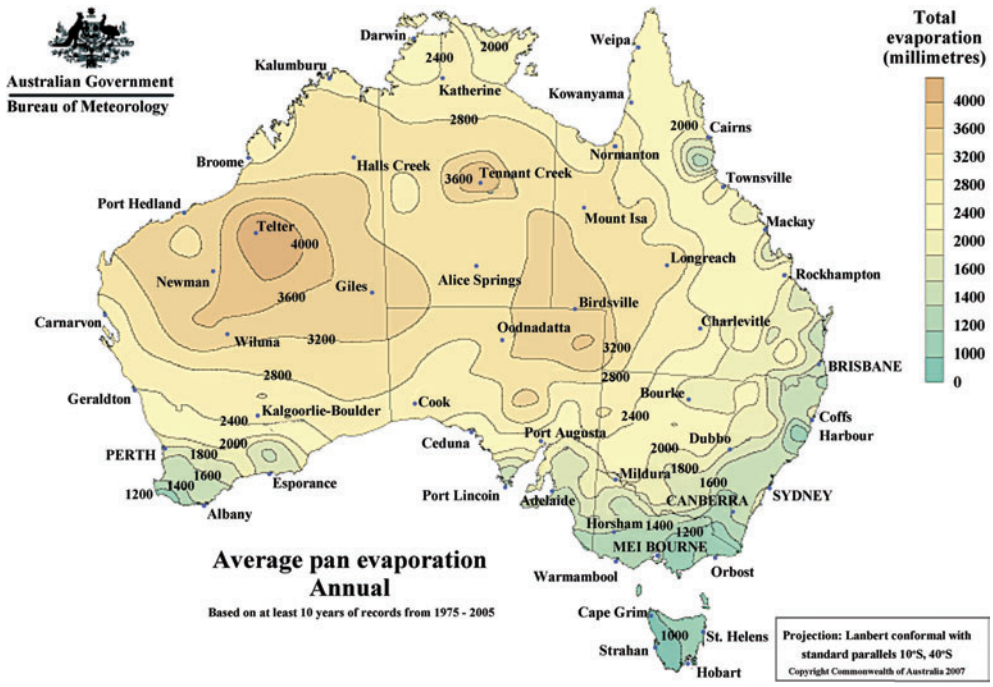

Figure 1.4. Average annual Australian pan evaporation rates. Northern, central and north-western regions display large rates; low rates occur in eastern and south-eastern regions. Annual pan evaporation rates exceed rainfall for most of Australia (refer to Fig. 1.3). Australian Bureau of Meteorology.

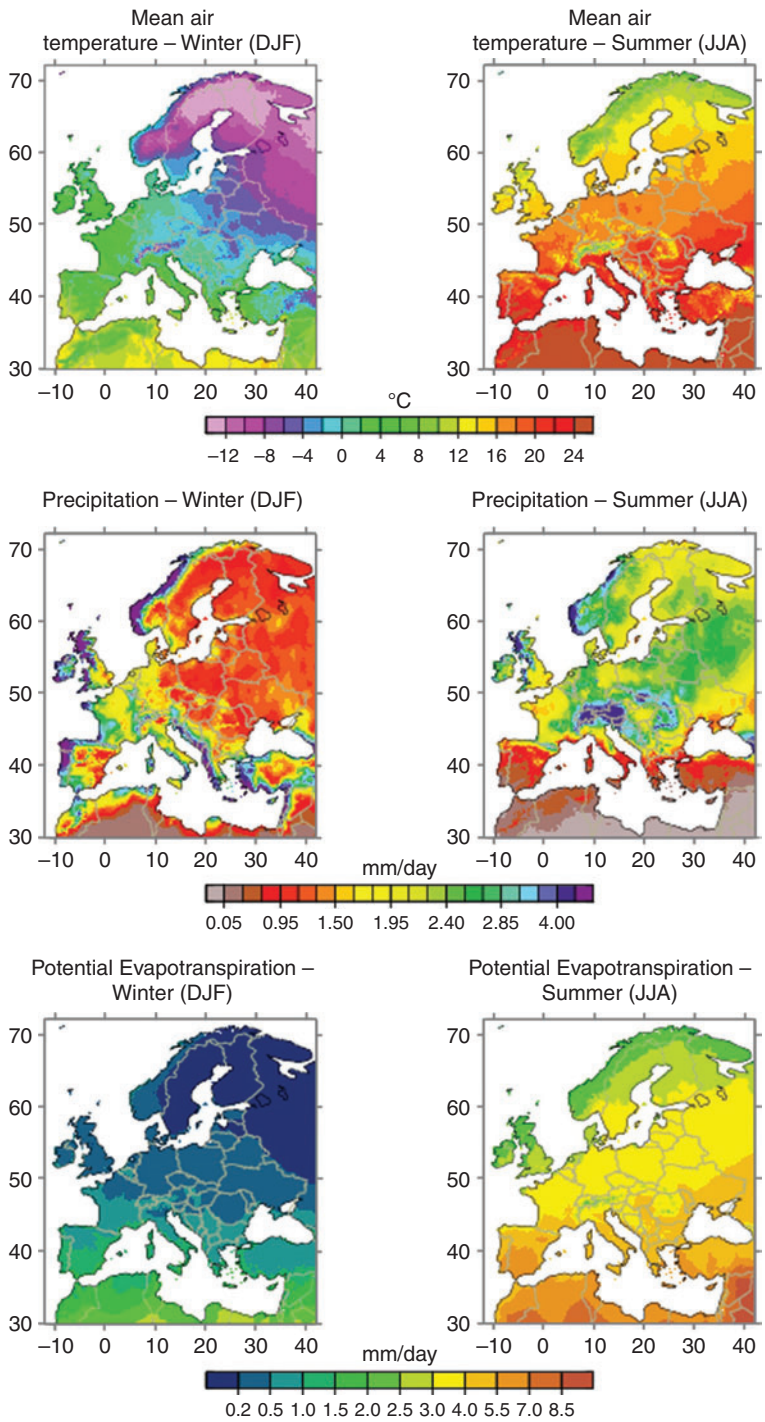

Figure 1.5. Mean air temperature, rainfall and potential evapotranspiration for summer and winter in western Europe. In summer, rates of potential evapotranspiration exceed rainfall for much of Central Europe. Note the different scale for the rainfall and potential evaporation. From the Climate Research Unit: http://www.cru.uea.ac.uk/projects/ecochange/climatedata/desc/

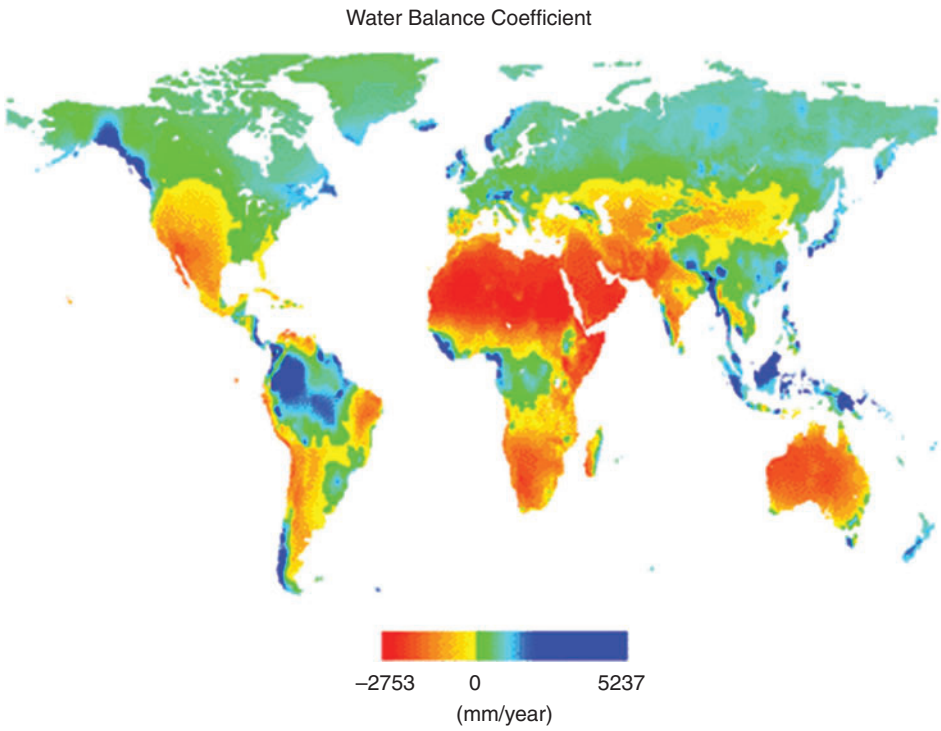

Figure 1.6. Water balance coefficient computed as the difference between annual precipitation and potential evapotranspiration. This coefficient was calculated at each 0.5° × 0.5° longitude/latitude grid cell. Potential evapotranspiration computed by the Priestley-Taylor method using the Cramer and Leemans (1991) global climate databases. From the IGBP Global Analysis, Integration and Modelling program of the IGBP: http://gaim.unh.edu/Products/Reports/Report_6/NPP.html

The water balance coefficient is the difference between annual rainfall and either pan evaporation or potential evapotranspiration rates. When annual rainfall exceeds annual potential evapotranspiration or pan evaporation rates the water balance coefficient is positive. Vegetation that has evolved in regions with a negative coefficient (rainfall smaller than evaporative demand) display very different ecophysiological attributes to that which has evolved in regions with a positive coefficient.

Figure 1.6 shows the global distribution of the water balance coefficient. Most of Australia, northern and southern Africa and the south west and central regions of the United States have strongly negative coefficients while northern Europe and Canada and northern South America have a strongly positive coefficient. Low temperatures limit evapotranspiration in northern Europe and Canada and this contributes to the positive balances in these regions.

1.2 Climate Classification Systems

Broad geographic patterns in rainfall, temperature and evaporative demand have been formalised and form the basis of the Koppen climate classification system, which has