Principles and Measurements in Environmental Biology

F I Woodward

J E Sheehy

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F I Woodward
Department of Botany, University of Cambridge

J E Sheehy
Grassland Research Institute, Hurley, Maidenhead

Butterworths
London Boston Durban Singapore
Sydney Toronto Wellington

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Foreword

This book was written to provide students with an understanding of some important physical principles and of how to apply them in environmental biology. In particular, a major aim was to describe how instruments utilizing those principles can be used to measure environmental and biological processes and their interactions. We have tried to provide a conceptual link between theory and experimental practice in a single text.

Often when attempting to test a hypothesis concerning a biological process, the difficulty of deciding precisely which measurements to make is matched by that of deciding how to make them. Usually, biological processes are strongly dependent on environmental conditions and both may be modified by the measuring instruments. We hope that we have been able to integrate the physical, biological and instrumental concepts, to provide guidance for deciding how, when and where measurements may be taken.

Chapter 1 provides a brief review of the influences on plants and animals of climatic variables: solar and terrestrial radiation, temperature, water, wind speed, carbon dioxide and pressure. The simple physics of these variables is described in Chapters 2 to 4, which also contain examples of environmental and biological interactions. The whole of Chapter 5 is devoted to the micrometeorology of plant communities.

The chapters dealing with sampling and errors (Chapters 6 and 7) introduce a logical and constructive framework for experimental design and the treatment of variability.

Instruments and suitable recording devices are always necessary, and Chapters 8 and 9 review the mechanism of operation and typical errors associated with recent instrumentation, as well as referring to earlier techniques and instruments.

The gap between theory and practice often appears wide. Chapter 10 gives selected examples of studies in order to demonstrate an obvious framework linking theory and practice.

Some of the examples in this book are concerned with rate processes affecting plants, such as photosynthesis. The interpretation and success of such studies often require parallel observations on plant growth. The general techniques of growth analysis have therefore been covered in the final chapter. This may direct readers to consider the wide gulf in knowledge between observations of growth, the environment and the actual biological mechanisms of interaction.

Numerous important environmental processes occur in the soil; although many of the principles and instruments described in this book may be used in that environment no direct reference is made to it. This in part reflects the authors' field of experience and the fact that there are many excellent texts specifically dealing with problems in that area.

The policy of modern scientific writing has been to use units of measurement which conform to the Système International d'Unités (SI), and the fundamental approach adopted in this book has been no different. However, we felt it important to demonstrate, in examples, the techniques of converting various units of measurement to their SI equivalents. Often no precise conversions from one set of units to another can be made. Nevertheless, approximations can be extremely useful in making calculations and so where possible, such approximations have been given.

F. I. Woodward
J. E. Sheehy

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F.I.W.
J.E.S.

Contents

Chapter 1

Introduction to the effects of the environment on biological organisms

'But pleasures are like poppies spread—
You seize the flow'r, its bloom is shed;
Or like the snow falls in the river—
A moment white—then melts for ever;
Or like the Borealis race,
That flit ere you can point their place;
Or like the rainbow's lovely form
Evanishing amid the storm.'
Tam o' Shanter, Robert Burns, 1759–1796.

Solar radiation

The sun emits radiation over the whole of the electromagnetic spectrum from gamma rays to radio waves. The greater part (98%) of this radiation is emitted in the waveband 0.25–3.0 μm. This waveband is used generally to define the limits of solar radiation that are of importance in biology. The extraterrestrial radiant flux from the sun (*Figure 1.1*) has an energy spectrum characteristic of a radiator or emitter with a temperature of 6000 K (5727 °C), with a peak emission at 0.48 μm. The physical properties of solar radiation can be fully explained only if radiation is considered in two quite distinct manners. Direct radiation (S_b in *Figure 1.1*) is scattered and absorbed by the atmosphere on its path to the earth's surface. The scattering varies with wavelength, as described by Rayleigh's law (*see* Chapter 2), and radiation at 0.4 μm (blue light) is scattered nine times as much as is radiation at 0.7 μm (red light). The diffuse radiation flux (S_d in *Figure 1.1*) derived in this way has a different spectral composition from the direct flux and causes the blue coloration of clear skies. This property of scattering can be explained only if solar radiation is considered to have a wave-like character.

The human eye can detect solar radiation in the waveband 0.4–0.7 μm. This process is called *vision* and solar radiation in this waveband, when concerned with vision, is called *light*. The process of vision depends on the excitation of the pigment rhodopsin by light. The process of excitation depends on the capture of light by the pigment, followed by the transfer of this energy to an electron that may change its orbit or orbital velocity, within certain limits. Only light within the 0.4–0.7 μm waveband has the correct energy content for this process. The electron will subsequently return to its original level, releasing energy that can be used to drive a biochemical reaction. This property of radiation cannot be explained in terms of a wave-like character but can be understood if radiation is considered as discrete particles, each with a specific energy content that is inversely proportional to the wavelength of the radiation. (This dual nature of radiation is considered more fully in Chapter 2.) Discrete particles of radiation are termed *quanta* and a quantum of light is called a photon. A photon of radiation with a wavelength of 0.46 μm has an energy content of 4.3×10^{-19} J, while a photon with a wavelength of 0.69 μm has a quantum energy of 2.9×10^{-19} J.

Solar radiation controls life by heating the earth and atmosphere and by providing the energy required in photosynthesis, for the conversion of carbon dioxide and water into the primary source of food: carbohydrates. The food chains of the world are all based on these photosynthetic products, which have been estimated to provide 3×10^{21} J of energy annually or 2×10^{11} tonnes of carbon (Hall and Rao, 1977).

The waveband and energy content of solar radiation have been effective constraints in the evolution of photobiological processes. The majority of these processes have action spectra limited to the 0.3–0.95 μm waveband (*Figure 1.1*) and the effectiveness of solar radiation in these processes is determined by the quantum energy content and the flux density of radiation in the waveband.

Photosynthesis is an important example of a biochemical process which can only be driven by the high energy content of solar radiation. It is powered by radiation in the 0.35–0.95 μm waveband (including bacterial). The production of carbohydrates from carbon dioxide and water requires an energy input of 477 kJ for every mole of carbon dioxide fixed. This is supplied by photosynthetically active radiation (PAR) at an average

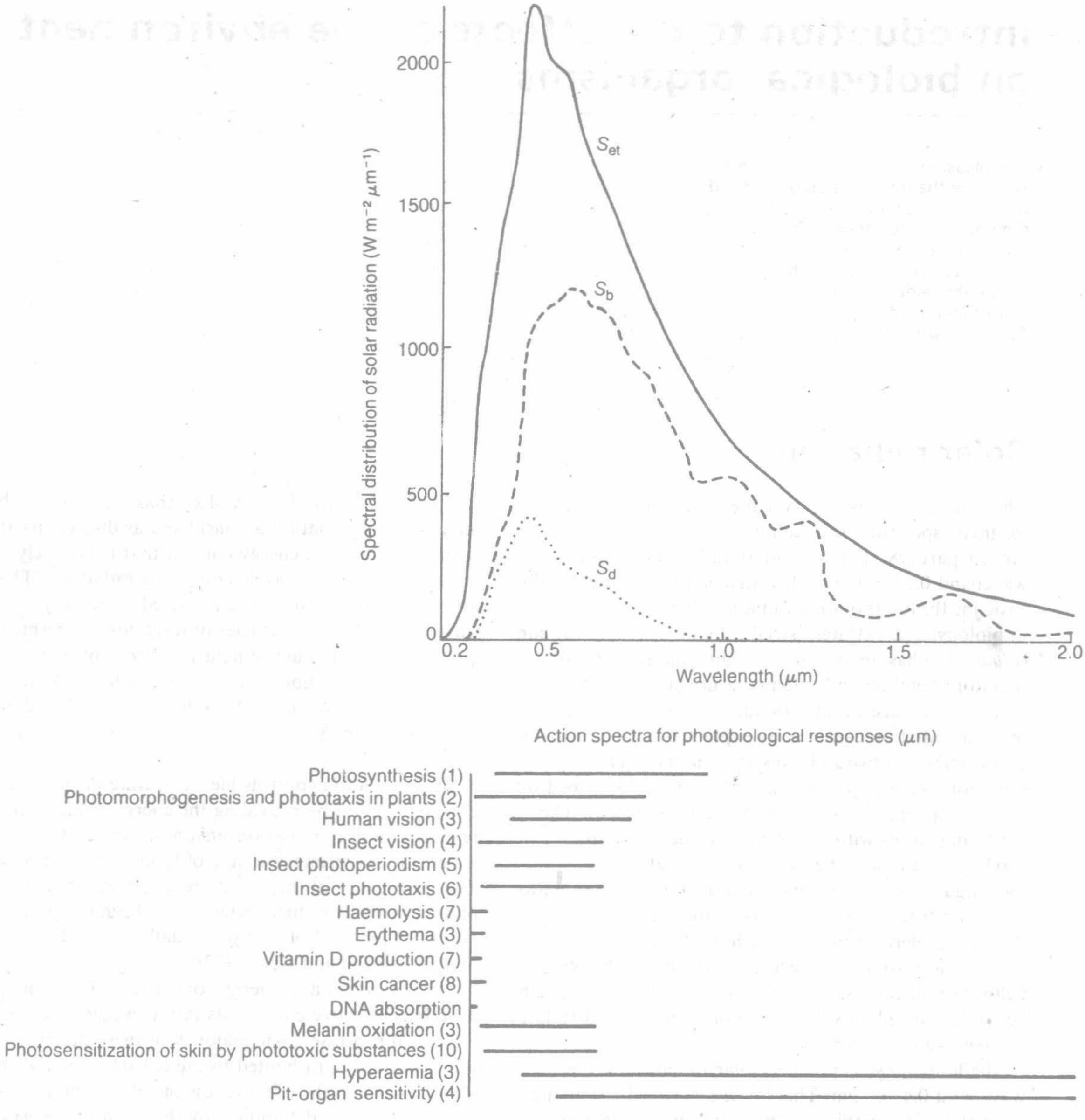

Figure 1.1 Spectral distribution of solar radiation and action spectra of photobiological responses. Data for spectral distribution from Koller (1965) and Szeicz (1974). Data for photobiological responses from: 1, Hall and Rao (1977); 2, Mohr (1972); 3, Koller (1965); 4, Ricklefs (1973); 5, Goldsmith (1973); 6, Dethier (1963); 7, Robinson (1966); 8, Epstein (1970); 9, Caldwell (1971); 10, Giese (1971).

S_b = direct irradiance on horizontal surface
S_d = diffuse irradiance
S_{et} = extraterrestrial irradiance

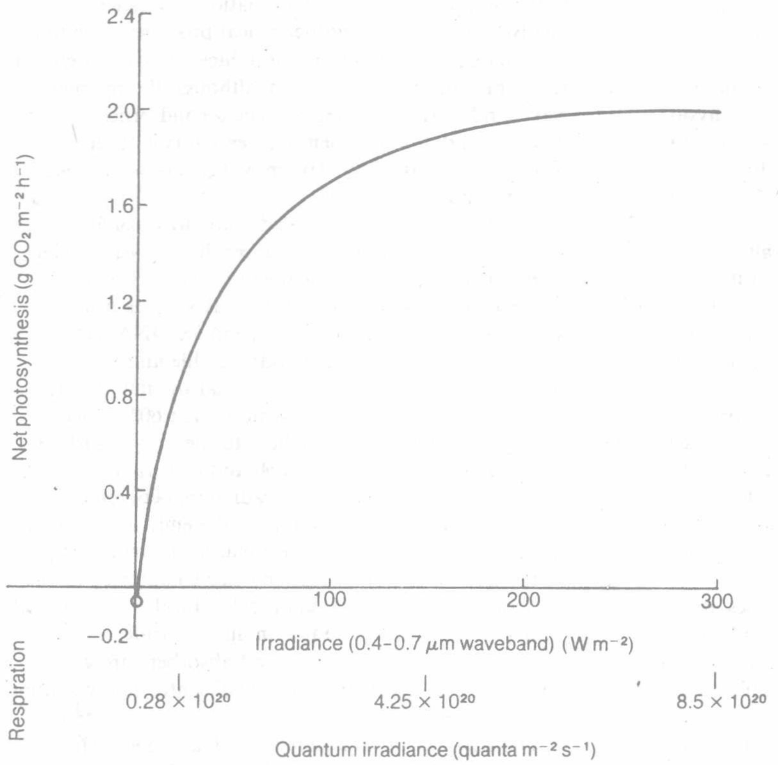

Figure 1.2 Apparent photosynthetic rate of a leaf of *Lolium perenne* (perennial ryegrass) at different irradiances

efficiency of 5% for an individual leaf. At a temperature of 25 °C the proportion of molecules with sufficient energy for this reaction is a very small fraction, of the order of 1.4 × 10^{-21}, indicating that the reaction would be very unlikely to occur without the high energy of solar radiation.

The photons of radiation required to drive photosynthesis are absorbed by pigment molecules such as chlorophylls, carotenes and phycobilins, each with specific wavelengths of peak absorptivity. Chlorophyll a, for example, has two characteristic absorption bands at 0.42 and 0.66 μm. These bands are defined by the specific quantum energy contents of the photons of these wavelengths. This precise packet of energy is required to elevate the energy potential of an electron, which in turn can be raised within a certain energy range only if it is to be coupled to the biochemical reactions of photosynthesis. Photosynthesis is also controlled by the flux density or rate of photon delivery of solar radiation within the required waveband. The general term applied to the radiant flux density incident on a unit surface is *irradiance*. *Figure 1.2* shows the relationship between the photosynthetic rate, measured by carbon dioxide uptake, irradiance and photon flux density. The greatest photosynthetic efficiency, in terms of radiation conversion, is achieved in the initial slope of the curve. Here about 14 photons of radiation are required to fix 1 molecule of carbon dioxide. On the plateau of the curve 14 photons are still required to fix 1 molecule of carbon dioxide; however, a further 100 photons are absorbed by the leaf, causing its temperature to rise. At very low irradiances there is a net loss of carbon dioxide by respiration.

The wide range of photobiological processes in the plant and animal kingdoms is shown in *Figure 1.1* with specific action spectra. The diagram illustrates the effective spectral range of particular processes; however, it is important to note that the responses are not generally equal across the whole active range. For example, the sensitivity of the human eye is optimal at 0.55 μm and is reduced to approximately 90% of this value at 0.65 μm, although vision is still possible.

Some photobiological processes are based on photochemical reactions that transform biologically inactive compounds into active compounds, or vice versa. In plants the chromoprotein *phytochrome* occurs as either a biochemically active form, phytochrome P_{fr}, or an inactive form, phytochrome P_r. These two forms can be interconverted by solar radiation at two specific wavelengths as shown in equation 1.1 (from Mohr, 1972).

$$\text{Phytochrome } P_r \xrightleftharpoons[\text{far-red light } (0.73\ \mu m)]{\text{red light } (0.66\ \mu m)} \text{Phytochrome } P_{fr} \tag{1.1}$$

Experiments in controlled-environment conditions have demonstrated that phytochrome P_{fr} is the physiologically active form which may, for example, stimulate germination, leaf growth and flower induction, after the plant has been exposed to red light at the wavelength 0.66 μm. Exposure of plants to far-red light (0.73 μm) converts phytochrome P_{fr} to the generally inactive form phytochrome P_r. In the natural situation it is the ratio between the flux densities of radiation of 0.66 μm and 0.73 μm that can determine the plant response, an example being the growth responses of plants under shade conditions (Morgan and Smith, 1978).

Ecologically, responses such as photomorphogenesis, phototaxis and vision are important in providing information for the sensing organisms. The detection of time, the direction of movement and the transfer of visual information to the brain are used to control and coordinate the basic processes of development, movement and reproduction.

The spectral responses of these processes are confined to the 0.35–0.73 μm waveband where irradiances are high and the quantum energy content is sufficient to carry out the high-energy-requiring photochemical reactions.

The response curves of hyperaemia (the accumulation of blood in a tissue), the reddening of human skin (erythema), and the pit-organ of pit vipers, such as the rattlesnake, extend into the infra-red region of the solar spectrum. These processes are essentially temperature-controlled processes dependent only on the total energy absorbed and independent of wavelength. This is not entirely true for the pit-organ, which is apparently insensitive to wavelengths less than 0.55 μm. Hyperaemia is caused by the temperature excess of the blood in the blood vessels of the skin. The pit-organs of the pit vipers are sensitive radiation thermometers (with a sensitivity of 0.002 °C) and are used to detect radiation emitted and reflected by prey.

Ultra-violet radiation (0.27–0.4 μm) has a higher quantum energy content than any other waveband of solar radiation and is capable of driving a range of photochemical reactions requiring very high energy.

Particularly important for human health is the conversion of certain sterols in the skin to vitamin D. Better known is the induction of erythema or sunburn, which may be seen to occur after periods of exposure of pale skin to the summer sun. This painful process is generally followed in light-skinned humans by increased pigmentation of the skin—tanning (at present a socially desirable response). Tanning is caused by the formation and migration of the dark pigment melanin to the superficial layers of the skin. This is a protective response that effectively reduces the transmission of harmful UV radiation into the skin. The formation of pigment involves two distinct photochemical processes. The first stage, melanin formation, can be induced by wavelengths of radiation from 0.25 to 0.65 μm, although the optimal waveband is in the UV region. The second process of melanin oxidation (pigment darkening) is induced by wavelengths in the 0.3–0.66 μm waveband, with a peak at approximately 0.45 μm.

Many of the effects of UV radiation are harmful to organisms, for example skin cancer, haemolysis, nucleic acid damage and bactericidal effects. The processes of damage are complex but in some cases it has been suggested that UV radiation may induce DNA damage. The nucleic acids carry the codes for life and it is fortunate for the evolution of life that the flux of ultraviolet radiation is reduced by more than 60% in its passage through the atmosphere to the earth's surface.

All materials on earth absorb and emit radiation at longer wavelengths than solar radiation, between approximately 3 and 100 μm. The flux of the emitted long-wave (infra-red) radiation is proportional to the temperature of the body and to its emissivity (*see* Chapter 2). In the waveband from 3 to 100 μm most natural objects absorb nearly all the incident radiation and are called *black bodies* in the waveband. All good absorbers are good emitters of radiation and so will efficiently emit radiation in this waveband.

The sun may be considered as a black body which absorbs and emits radiation efficiently. The peak wavelength of emitted radiation (0.48 μm) is related to its absolute temperature (6000 K) as described by Wien's law (*see* Chapter 2). The same law applies to terrestrial objects and so an object at 293 K (20 °C) will have a peak emission at 9.89 μm.

A terrestrial body will always be absorbing and emitting long-wave radiation, even when solar radiation is absent. Long-wave radiation transfer is important in determining the thermal or temperature relationships of organisms in their environment. As an example, the walls of the room in which you may be reading this book will be exchanging long-wave radiation with your body. In the absence of a large influx of solar radiation, heat from heating supplies and wind movements (and ignoring the effect of evaporation), long-wave radiation will be exchanging between your body and the walls and will determine your level of comfort.

The atmosphere is differentially transparent to long-wave and to solar radiation, being highly transparent to solar radiation and partly opaque to long-wave radiation. The opacity of the atmosphere to long-wave radiation is due to the absorptivity of water vapour, liquid water and carbon dioxide for long-wave radiation. However, at wavelengths between 10 and 12 μm the absorptivity of water and carbon dioxide is very low and so the atmosphere is effectively a 'window' to long-wave

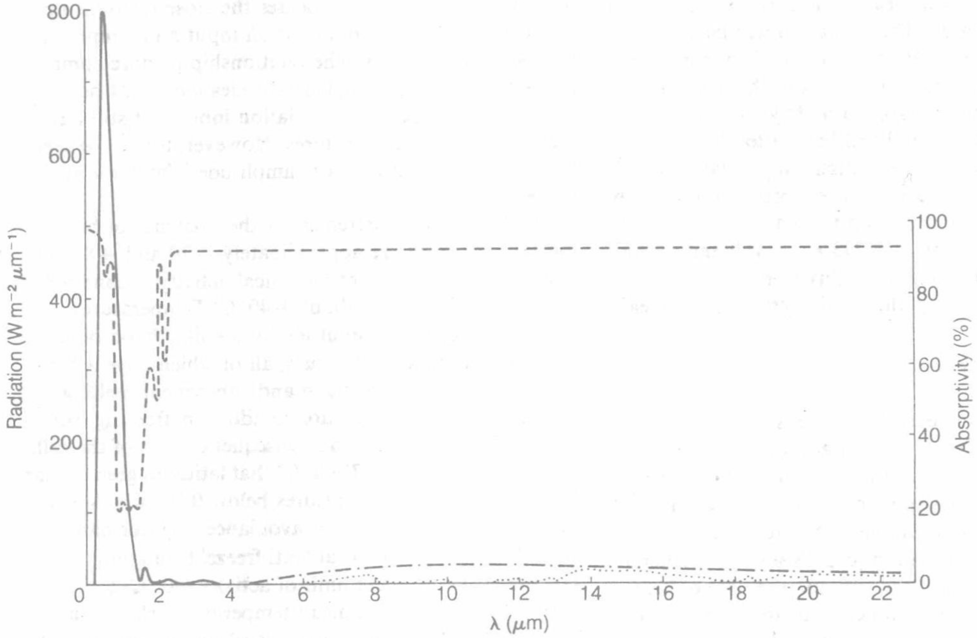

Figure 1.3 Wavebands of solar and long-wave radiation and radiation characteristics of a typical plant leaf. (————) Solar radiation at sea-level; (·······) atmospheric long-wave emission (263 K); (—·—·—) leaf long-wave emission (288 K); (– – – –) leaf absorptivity. (From Gates, 1962)

radiation in this waveband. The temperature of the clear atmosphere is very low, temperatures as low as −80 °C being possible, and the atmosphere will represent a sink for long-wave radiation emitted by warmer terrestrial organisms. The waveband of the window also coincides with the peak emission of many terrestrial organisms and so there will be a long-wave flux from the organisms through this window.

The influence of the window can be felt by humans on clear nights, which feel cold, in contrast to cloudy nights which, even at the same air temperature, feel warmer. On cloudy nights the clouds are at a higher temperature than the cloudless atmosphere and emit a greater downward radiant flux. This effect is quantified in *Table 1.1* for a range of different cloud types.

Table 1.1 Net radiation loss from the earth's surface with different cloud cover

Cloud type	*Net long-wave radiation flux (Wm^{-2})*	*Mean height of cloud base (km)*
Nimbostratus	−3 to −14	1.5
Altocumulus	−7 to −28	3
Cirrus	−70 to −91	6
Cloudless atmosphere	−84 to −126	
Transparent atmosphere	−350	

From Van Wijk and Scholte Ubing (1963)

The table indicates that the net loss of radiation (hence the negative signs) is diminished with decreasing cloud base, indicating the importance of the downward flux of radiation from the clouds. The cloud temperature is also inversely related to the height of the cloud base.

The importance of both solar and long-wave radiation to biological organisms is demonstrated by *Figure 1.3*. It may be seen that the leaf strongly absorbs solar radiation to approximately 0.75 μm, the longest effective wavelength for higher-plant photosynthesis. Between 0.75 μm and 2.1 μm the leaf absorbs solar radiation weakly, thereby escaping the radiation load from solar radiation, which in this waveband is not effective in photosynthesis. At wavelengths greater than 2.1 μm the leaf strongly absorbs radiation; however, the solar radiation flux density and the flux from the atmosphere are both low in this region. These two sources of radiation will not cause much radiative heating of the leaf, which would be the case in the 0.25–1.5 μm waveband. The importance of the high absorptivity of the leaf in the long-wave region is due to the correlation between emissivity and absorptivity, as described by Kirchhoff's law (Chapter 2). Thus bodies with high absorptivity have high emissivity and vice versa. At a temperature of 293 K (20 °C) the leaf will have a peak emissivity at 9.89 μm, which is in the long-wave window of the atmosphere.

On a clear sunny day the leaf will absorb solar radiation in the 0.4–0.7 μm region. This radiation will be used in photosynthesis but will also cause the leaf temperature to rise. The long-wave radiant flux from the leaf will increase with temperature (approximately 30% from 283 K (10 °C) to 303 K (30 °C) and will be emitted from the leaf to the atmosphere, thereby dissipating a large proportion of the heating effect of the absorbed solar radiation. The emitted long-wave flux from the leaf is large, with a typical value of 390 W m^{-2} at 293 K (20 °C), indicating the importance of the long-wave flux in reducing the energy load, and therefore the heating effect, on the leaf.

Temperature

The temperature of the earth's surface is primarily controlled by the influence of the sun and the properties of the atmosphere discussed in the previous section. The earth is an approximately spherical body at a large distance from the sun and so the sun has different apparent elevations when viewed from the earth's surface at different latitudes. The elevation of the sun and the time of year act in combination to determine the temperature of the earth. The temperature zones of the earth are generally defined by latitude, and for the Northern Hemisphere the relationship between latitude, solar elevation, solar radiation, day length and mean temperature can be seen in *Table 1.2*. This table indicates the close relationship between solar elevation, radiation input and temperature for the winter months. The relationship is more complex in the summer as the higher latitudes have a 24 hour day and the largest solar radiation input, but still have the lowest mean temperatures. However, it may be seen that the annual temperature amplitude is greatest at the highest latitudes.

Table 1.2 The relationships between latitude, solar elevation, solar radiation, day length, temperature and season at sea level in the Northern Hemisphere

Latitude (°N)	*Maximum solar elevation (degrees)*	*Mean irradiance (W m^{-2})*	*Day length (h)*	*Mean temperature (°C)*
Summer				
0	65	417	12.1	27
10	75	422	12.7	29
20	86	451	13.4	32
30	84	465	14.1	31
40	74	470	15.0	27
50	64	470	16.4	18
60	53	465	18.8	14
70	43	490	24.0	9
80	33	509	24.0	0
Winter				
0	65	411	12.1	27
10	55	359	11.6	26
20	46	296	10.9	19
30	37	228	10.2	10
40	28	150	9.4	5
50	16	87	8.1	−1
60	6	24	5.9	−10
70	0	0	0	−25
80	0	0	0	−30

From Boucher (1975) and List (1966)

The temperature extremes for the existence of biological organisms are approximately −70 and +85 °C, although the majority of biological activity is confined to a narrower zone of about 0–40 °C. Temperatures below 0 °C physically limit life by the likelihood of ice formation in biological tissues, all of which have a high water content. Ice formation and subsequent melting usually disrupt cell structure; in addition, freezing can lead to the desiccation and subsequent death of the cell.

It may be seen from *Table 1.2* that latitudes greater than 40°N have winter temperatures below 0 °C, which is a strong selective pressure for avoidance (e.g. dormancy) or acclimation (e.g. natural 'anti-freeze' formation). The upper temperature limit of activity (40 °C) is greater than any of the mean temperatures shown in *Table 1.2*. Temperatures at this level and above may be commonly experienced in the warmer latitudes of 0–30°N during hot summer days. Temperatures above 40 °C can lead to protein denaturation in cells, and once again avoidance or acclimation may be necessary to prevent this.

Biological organisms can be considered as systems of ordered series of biochemical reactions. The limited temperature range for biological activity effectively limits the potential of temperature for increasing the rate of chemical reactions. Chemical reactions generally proceed slowly over the temperature range normally encountered. Biological systems have solved the problem and overcome the likely limitations of slow reaction rates by evolving biological catalysts—enzymes. Enzymes allow reactions to proceed at appreciable rates under normal temperature conditions, by reducing the activation energy requirements of the chemical reactions. The reduction of hydrogen peroxide is a simple example. At 20 °C the reaction has an activation energy of 75 kJ mol^{-1}. In the presence of the enzyme, liver catalase, the energy requirement is reduced to 23 kJ mol^{-1}. Each biochemical reaction will require a specific enzyme and the continued existence of an organism is governed by the balance of rates and temperature sensitivities of all the biochemical reactions.

The available range of mean temperature conditions for biological colonization is shown in *Table 1.2*. This range constrains the development and evolution of organisms to those with the most efficient biochemical processes suited to the local temperature conditions. *Tables 1.3* and *1.4* demonstrate this relationship for photosynthesis by

Table 1.3 The temperature optima of photosynthesis for plants from different climatic zones

Species	*Temperature optimum*	*Climatic zone of distribution*
Oxyria digyna	12 °C	Cold Arctic
Fagus sylvatica	15 °C	Cool temperate
Citrus limon	24 °C	Warm Mediterranean
Acacia craspedocarpa	35 °C	Hot semi-arid
Tidestromia oblongifolia	43 °C	Very hot arid

From Larcher, Heber and Santarius (1973)

Table 1.4 Oxygen consumption for the Goby fish, *Gillichthys mirabilis*, from different latitudes

Latitude	Q_{10}, *10 °C to 17 °C*	Q_{10}, *24 °C to 31 °C*	*Climatic zone*
37°N	2.42	1.27	Cool
33°N	2.64	1.45	↓
31°N	1.60	1.66	
28°N		1.43	Warm

From Barlow (1961)

plants and the Q_{10} of oxygen consumption by animals. Q_{10} is the factor by which a reaction velocity changes following a rise in temperature of 10 °C. Thus a Q_{10} of 2 indicates the doubling of a rate over a 10 °C range. *Table 1.3* indicates the manner in which plants have evolved their photosynthetic temperature optima to suit the prevailing temperature conditions during the growing season. This type of relationship is not easily shown for animals. In the case of the Goby fish, *Gillichthys mirabilis* (*Table 1.4*), population from low (warm) latitudes show a low Q_{10} for oxygen consumption over a wide temperature range while populations from high (cool) latitudes have a high Q_{10} in their typical temperature range and a low Q_{10} at higher temperatures. The response of the warm-latitude populations is thought to be related to the wider range of temperature conditions which will be experienced by the fish.

Biochemical processes of individual organisms are also able to respond to changing temperature conditions during the life of the organism. This response constitutes acclimation. For example, biochemical acclimation to water temperature is shown by *Salmo gardnerii* (trout) (Prosser, 1973). The enzyme acetylcholinesterase can occur in two isozymes in the trout brain. One form occurs after acclimation at 2 °C and the other after acclimation at 17 °C. The maximum affinity of each isozyme for the substrate is also optimal at the respective acclimation temperature. Similarly in plants the temperature minimum of photosynthesis declines with the annual fall in air temperature in temperate regions. Thus *Viscum album* (mistletoe) has a photosynthetic minimum of −3 °C in summer and −7 °C in winter (Pisek *et al.*, 1973).

It is easy to define the temperature response of a simple, isolated biochemical process. The response of the whole organism to temperature in terms of reproduction, growth, development and adaptation results from the activities of many biochemical processes with different temperature optima and responses. The multicompartmental nature of organism function, with a large capacity for variations, explains how organisms can survive and occupy specific habitats all over the world. Changes in the responses of individual processes in turn affect the relationships and responses of other processes, ultimately affecting the functioning and optimum requirements of the whole organism.

The temperature responses of whole organisms, such as germination, growth and seed production in plants and feeding, growth, movement and reproduction in animals, are extensively documented elsewhere (e.g. Precht *et al.*, 1973; Prosser, 1973) and are beyond the scope of this book.

Describing any one air temperature and relating this to organism behaviour and temperature is complex in that plants and animals (poikilothermic or cold-blooded animals and homeothermic or warm-blooded animals) will develop different body and surface temperatures in identical environmental conditions. The differences are caused by variations in heat fluxes due to changes in transpiration, convection, conduction, radiation emission and metabolism. These differences are crucial to the performance and existence of the particular organism.

Figure 1.4 demonstrates the differences in body and surface temperatures of three terrestrial organisms: a plant, an insect and a fair-skinned human. The diagram compares the effect of two different inputs of solar radiation, 200 W m^{-2} and 75 W m^{-2}, on surface and body temperature, with identical conditions of air temperature, relative humidity and wind speed.

The temperature of the plant and insect varies locally over the organism and particularly in response to increased solar radiation. Leaf position (in the plant) and proximity to the substrate (for the insect) also affect the response. The relatively large volume of the insect allows a temperature gradient to develop between the exoskeleton and the body tissue owing to evaporational cooling. Only very small gradients can develop between the upper and lower surfaces of the very thin transpiring leaf.

The insect body temperature rises above air temperature, at the lower irradiance, through metabolic heat production and the radiation load. The plant temperature is either equal to or less than air temperature in the lower irradiance, with differences between leaves resulting primarily from cooling by transpiration, convection, conduction and radiation. Evaporational cooling by the insect is less efficient than for a leaf and so high surface temperatures are characteristic at the high irradiance.

The response of the homeotherm to solar radiation is quite different from that of the poikilotherm. Body

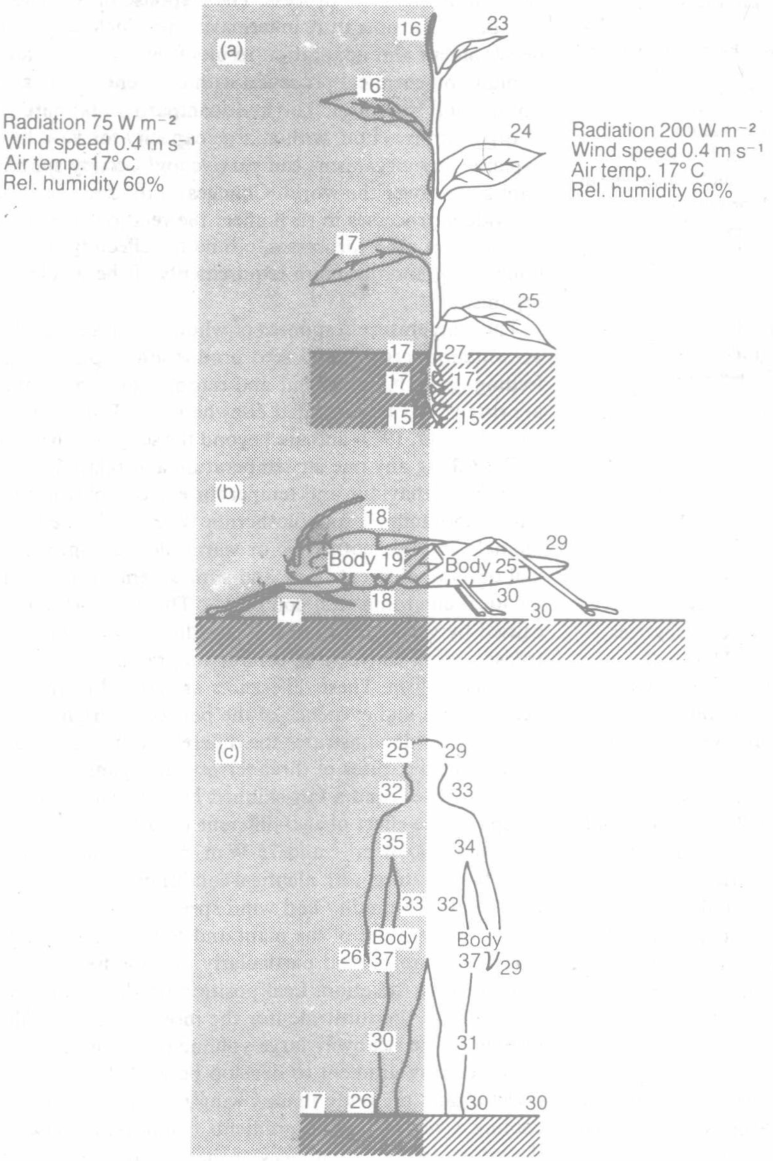

Figure 1.4 Influence of solar radiation on the body and surface temperature of (a) a plant, (b) an insect and (c) a fair-skinned human. Temperatures in °C

temperature is strictly controlled by metabolic heat production and on an equal body weight basis the basal metabolic rate of the homeothermic animal is greater than for a poikilothermic animal. Differences in surface temperature are observed, particularly at the body extremities such as the hands, feet and head (hair). These respond to the higher solar radiation load by increases in temperature. However, other regions, such as the small of the back and under the arms, fall in temperature with increasing solar radiation because of increased evaporative cooling by sweating.

Other methods of body temperature control are shown by both poikilotherms and homeotherms. One way poikilothermic animals may control their body temperatures is by controlling the absorption of solar radiation through correlated orientational change. Rapid muscular activity, such as in winged flight, can also lead to temperature increases of up to 10 °C. Basal metabolism can produce only small increases in body temperature above ambient, although large insects such as the locust can raise the resting body temperature by as much as 3 °C. Homeotherms, on the other hand, exert a very high degree of body temperature control by varying the metabolic heat production in relation to ambient conditions.

Both plants and animals, including certain homeotherms, can avoid extremes of temperature by hibernation or dormancy. In all these cases body activity is vastly reduced and the tissue temperature may fall to just a few degrees above freezing point during cold periods.

If the cell contents of a plant freeze, desiccation may result and also, subsequent warming and ice melt will lead to cell disruption. However, many plants can withdraw water from the cell. In these cases water will freeze extracellularly. A combination of this response and the supercooling of water in the cell will lead to a protection where, typically, frosts to −12 °C are prevented from freezing the cell contents, or at least freezing is delayed. Beyond this temperature plant death may occur. Frosts of −14 °C have been noted as causing the death of *Umbilicus rupestris* (pennywort) and *Ilex aquifolium* (holly), while at about −12 °C damage is insignificant. Evergreen plants may be naturally prehardened so that they are able to withstand very low temperatures, beyond those normally experienced. An extreme example is shown by the leaves of *Pinus strobus* (Eastern white pine), which are able to withstand cooling to −189 °C (Parker, 1960) without subsequent observable damage.

Animals are equally capable of acclimation to extreme low temperatures. As in plants, osmotically active cell constituents may be increased in amount. For example, the larvae of the parasitic wasp *Bracon cephi* can undergo supercooling of the body to −47 °C without damage (Salt, 1958), and *Anguilla aceti* (vinegar eel) can survive temperatures of −190 °C (Luyet and Hartung, 1941).

Certain plants are also capable of surviving high temperatures. Many subtropical higher plants (e.g. many succulents) are able to withstand temperatures up to 50–60 °C. Bacteria from hot springs are capable of withstanding temperatures of up to 70–90 °C (Larcher, Huber and Santarius, 1973).

The upper limit for the body temperature of poikilotherms is generally in the range 45–50 °C.

In many cases high body temperature may be due to a high radiant load and the animal may be able to move to shade conditions. Avoidance is therefore a crucial response to near-lethal temperatures.

Homeotherms are generally more restricted than poikilotherms in their ranges of temperature tolerance. Fit humans can endure an ambient temperature range of approximately −30 to +50 °C for limited periods of time. The maximum recorded range of body temperatures for living humans is 19–42 °C (Altman and Dittmer, 1966). The body temperatures of hibernating mammals fall considerably and temperatures of 6 °C have been recorded for *Erinaceus europaeus* (European hedgehog) (Altman and Dittmer, 1966).

Ecologically the differential species response of growth, development, reproduction, etc. over the normally encountered temperature range may be more important in limiting species distribution than extremes of temperature. For example, a change in air temperature of only 1.6 °C over the temperature range of 10.2–11.8 °C, effectively limits the distribution of the plants *Sedum telephium* (orpine) and *S. rosea* (rose-root). *S. telephium* is limited to regions with a mean growth-period temperature of 11.8 °C or greater, while *S. rosea* is limited to regions with mean temperatures of 10.2 °C or less (Woodward, 1975). *Balanus amphitrite* (acorn barnacle) has a northern latitudinal distribution controlled by its inability to survive average monthly temperatures below 7.2 °C and by its failure to reproduce when the average monthly temperature in summer falls below 18.3 °C (Crisp and Southward, 1958).

Water

Water is an important component of the environment in its three forms: water vapour, liquid water and ice. Water vapour is a variable component of the atmosphere with an approximate range of concentration from 0.01% to 5% by volume. It has already been seen that the presence of water vapour in the atmosphere has important consequences for the long-wave radiation balance of the earth. This is through water vapour's capacity for absorbing radiation, with absorption bands at 1.4 μm, 1.9 μm, 2.4 μm, 2.7 μm, 6.3 μm and >22 μm. Liquid water and ice in clouds influence the flux of incoming solar radiation by scattering, reflecting and absorbing the solar beam.

Water is continually cycled through the atmosphere by evaporation, condensation, rainfall, ice melt and water flow. Whereas it was explained earlier that temperature limits the major climatic zones of the world, rainfall is also an important determinant of climatic and particularly vegetational zones. The most extreme and obvious contrasts are desert and tropical rain-forests, which may occur at similar latitudes, or potentially similar temperature zones.

Water is an essential component of all living organisms. Although it has only a small molecular weight (18), water is a liquid between 0.1 and 99.9 °C because of the extensive hydrogen bonding which occurs between contiguous H_2O molecules. The hydrogen bonds are effective in determining the high surface tension, cohesive force and tensile strength of water. These properties are important for the water-carrying xylem vessels where water is under a tension or 'suction', or a negative water potential. Water columns have been observed to withstand large 'suctions' of approximately -300×10^5 Pa

(1 bar = 0.99 atm = 10^5 Pa) before rupture, well within the requirements of raising water to the top of the highest tree. Water is also capable of rising against the forces of gravity in capillary tubes by adhesive forces between the water and the molecules of the tube wall.

The effectiveness of water as a thermoregulatory medium is also related to the presence of hydrogen bonds. Over the temperature range 0–50 °C the energy of a hydrogen bond is approximately 20 kJ mol^{-1} compared with 200–400 kJ mol^{-1} for a covalent bond. The bond is therefore weak and may be broken. The energy required to evaporate water, i.e. to convert water from the liquid to the vapour phase, is greater than for substances of similar molecular weights because the hydrogen bonds in the liquid must be broken before transition to the vapour phase. The evaporation of 1 g of water extracts 2.4 kJ from the surrounding medium, at 25 °C. The importance of this heat extraction, or cooling, can be realized by comparison with the radiation received by an organism. An organism can receive a maximum of 1 $\text{kJ m}^{-2}\text{s}^{-1}$ of radiant energy. Plants have the capacity of dissipating up to 250 $\text{J m}^{-2}\text{s}^{-1}$ of the radiant energy by transpiration (0.1 $\text{g m}^{-2}\text{s}^{-1}$ in terms of the weight of water lost), indicating the importance of water in the energy balance relationships of organisms. Animals are also efficient at dissipating energy by evaporation and man, for example, is capable of dissipating up to 375 $\text{J m}^{-2}\text{s}^{-1}$ (0.15 $\text{g m}^{-2}\text{s}^{-1}$) of energy by sweating.

The reverse process of evaporation, namely condensation, can occur during the night as in the formation of dew. This process transfers heat to the organism, increasing its temperature. A maximum of 40 $\text{Jm}^{-2}\text{s}^{-1}$ (0.02 $\text{g m}^{-2}\text{s}^{-1}$) can be transferred in this way (Monteith, 1973). Energy transfer by dew formation occurs on clear nights when radiative cooling takes the temperature of an organism below the dewpoint temperature of the air.

Chemically, water has a polar characteristic and is effective in dissolving polar substances. Its high dielectric property also causes it to be an effective ion solvent. Thus in both plants and animals mineral nutrients and many organic products of biochemical processes can be transported in the efficient water (aqueous) transport system.

Carbon dioxide and oxygen have to be transported to and from living cells for the processes of respiration and photosynthesis. A large part of the pathway is in the gaseous form, when diffusion is rapid, but ultimately the gases must dissolve in water and be transported in solution to, for example, the chloroplasts (in plants) and mitochondria of the cell. Diffusion in solution is slower than in air, and the solubilities of carbon dioxide and oxygen are both low (*see* p. 20). This part of the diffusion pathway will limit biochemical processes; however, these gases are soluble enough and the diffusion rates high enough to allow the evolution of biological organisms. Within the plant cell, water is used both as the source of the photosynthetically produced oxygen and the hydrogen required for the reduction of carbon dioxide to carbohydrates.

All biological organisms (except viruses) are constructed on a cellular basis, with an external wall of skin. The separation between the internal cell environment and the external environment can allow the two environments to maintain different water contents, when the cell skin has a finite resistance to water flow.

In a living cell the water is held and contained in the cell by a 'suction force' at a negative water potential (*see* p. 82). This water can be removed by a greater suction force (more negative) from the outside of the cell.

Water may be held in the cell by an osmotic (solute) potential, which results from the presence of dissolved solutes in the cell solution or sap. Increasing the concentration of solutes within the cell causes the water to be held under a greater suction within the cell. As a positive pressure has to be applied to remove this water the water must therefore be under a negative potential and so osmotic potentials are assigned a negative value.

The effect of the negative potential of aqueous solutions of solutes can be observed experimentally in the traditional osmosis experiments. In these experiments pure water at an osmotic potential of zero always moves across a boundary, defined by a semipermeable membrane, to the more concentrated solution with an osmotic potential less than zero.

The cell volume increases as water is taken in by osmosis. This change in volume can cause a stretching of the cell wall and this stretching force is termed a *turgor* or hydrostatic or pressure potential. This pressure potential works in opposition to the negative osmotic potential and is therefore positive in sign. In plant cells this pressure may be large because the thick cellulose cell wall can withstand large pressures. Animal cells have no such wall and only a thin, weak membrane acts as the cell skin. In these cells the pressure potential is very small and close to zero.

From the point of view of plant and animal cells, water is retained internally by a 'suction' at a negative potential. Different external environments have different water potentials, and *Table 1.5* outlines the average potentials of a range of inhabited environments.

In soil and in deep water the depth of water over an organism will exert a positive hydrostatic or pressure potential. The hydrostatic potential increases by 0.106×10^5 Pa per 1 m increase in depth. This increasing pressure effectively limits the occurrence of certain species. Man for example cannot swim at depths below approximately 115 m, or a hydrostatic potential of 12×10^5 Pa. Deep-sea fish can be found at depths of