

Chapter 1

Introduction

1.1 | Appreciating plants

During a public open day at a university, a child trying to look at a botanical exhibit was dragged away by an impatient parent with the words ‘Come on – we can’t spend all day looking at dull green things!’

There is a tendency to consider plants as somewhat dull, passive and inactive. Yet plants face and overcome the same problems as animals: how to obtain nutrients and water, how to survive extreme environmental conditions, how to ensure reproduction and the survival of the next generation. The photosynthetic mode of life has conditioned plants to evolve as sessile organisms; their basic necessities – light, carbon dioxide, water and mineral ions – are ubiquitous and there has therefore been no selection pressure for mobility. An animal may obtain its nutrients and water by skilfully stalking its prey, and learning the path to a pool; this catches human attention as interesting behaviour. A flowering plant obtains nutrients and water by millions of minute root tips constantly growing through the soil, and by pumping ions across root cell plasma membranes with molecular-sized pumps. This is plant behaviour: **plant physiology is plant behaviour**. It need not be considered dull because it is less spectacular to the eye than what is called animal behaviour. The subsequent hauling up of the absorbed water and minerals to the top of a tree, 100 metres high, might indeed be considered a quite spectacular feat (imagine doing it with a bucket!). Without stirring from the spot, flowering plants are unceasingly monitoring their environment and responding to environmental signals. For them as for us, light is an information medium; they contain optical sensors (pigments) with which they perceive and respond to light direction, wavelength composition (i.e. colour) and the duration of daylight. They are sensitive to touch, with some responses as fast as animal movement: a Venus flytrap leaf snaps shut in a second or two to catch (and digest!) insects as big as wasps or small moths. Pea tendrils are a bit slower to react, but can be seen curling around a support within minutes of making contact. Plants respond also to the direction of gravity; it is the continuous responses to gravity and light that are largely

responsible for plants growing ‘the right way up’, and with roots, branches and leaves orientated at various angles. Temperature changes are sensed. Signals with a regular annual variation – such as the changes in daylength – enable plants to synchronize their life cycles with the seasonal cycles in their environment. Even the embryo in a dormant seed, apparently quite inactive in its coat, is able to receive specific signals that stimulate it to commence germination at the appropriate season. Flowering plants, when looked at from the physiologist’s point of view, are not merely alive, they are very lively. We hope that the readers of our book will be led to appreciate how marvellous and varied in their activities flowering plants are.

There are other reasons, too, for studying flowering plants. We are utterly dependent on them. Being the dominant plants in present-day terrestrial (land) vegetation, they are the primary producers, by photosynthesis, of organic material – food – on which all other terrestrial organisms including ourselves rely. We moreover need plants for wood, textiles, drugs, and hundreds of household chemicals; their very presence gives us joy, even comfort. Gardens are a main source of pleasure for many individuals; windowsills get filled with house plants, floral baskets are hung from balconies of high-rise flats. Animals not only feed on plants, but live in them, on them and under them. The oxygen we breathe is formed as a by-product of photosynthesis. Soil and climate, too, are influenced by plants; vegetation may for instance stabilize soil against physical erosion. Thus the importance of understanding the activities of flowering plants cannot be overemphasized. With the changes currently being imposed on the biosphere of this planet by human activities, it has become more imperative than ever to study the physiology of plants, if there is to be any hope of predicting how vegetation, all-important for life on earth, might respond to such changes in the environment. An understanding of flowering plant physiology is also vital for any attempts to improve plant productivity.

1.2 | What kind of plant physiology?

Plant physiology is the functioning of plants. This can be studied at several levels of complexity and organization, as indicated by such terms as *metabolic physiology*, *cellular physiology*, or *whole-plant physiology*. The aim of the current text is to give an account of the physiology of flowering plants mainly from the **whole plant** or **organismal** point of view. Moreover, since an organism functions within its environment, and by virtue of its physiological activities continuously interacts with its environment, plant–environment interactions are emphasized throughout the book. But many plant life processes are carried out at the level of the individual cell, even of the individual organelle. Physiological processes of plants can therefore be described only to a limited degree without reference to activities at

the cellular or subcellular level. Water movement through an intact plant is a whole-plant level process; for some specified ecophysiological project, it may be adequate to discuss it, say, in terms of quantities of water absorbed by the roots, and the amounts lost by transpiration from the leaves. If, however, one wishes to understand the control exerted on the process by the plant, one is soon involved with the cellular physiology of the stomatal guard cells, which move to open and close the stomatal pores through which most of the transpiration occurs. Equally relevant to an understanding of physiological processes is a knowledge of cellular structure. To continue with the example of stomata, the opening and closing movements are also dependent on the shapes of the guard cells and on the pattern of their cell wall thickenings, right down to the precise arrangement of the cellulose microfibrils. Whilst the goal of this book is to promote the understanding of flowering plants as organisms, one cannot escape consideration of information from the realms of cellular physiology, biochemistry, cell structure and ultrastructure, and molecular biology. In this respect we have had to exercise our judgement about the depth to which such information should be presented, and the extent to which it might be taken for granted. In fact an elementary knowledge of basic metabolism, biochemistry, plant anatomy and plant cell structure has been assumed. Textbooks listed at the end of this chapter as **Complementary reading** will serve to fill in the background for readers who find this necessary, and will enable all interested readers to extend their knowledge of the more cellular aspects of plant physiology, and of plant structure, beyond this text.

1.3 | Molecular biology and plant physiology: the integration of disciplines

References to molecular biology will be found to figure liberally in parts of the text. The discipline of molecular biology embraces the study of **genes**: their isolation and identification, analysis (molecular sequencing) and their manipulation, i.e. modification and introduction of selected genes into cells at will. Gene expression, their 'switching on and off', can also be manipulated. This is a branch of science that is enabling biologists to identify and study the roles of specific genes in specified activities.

Molecular biology techniques have led to considerable advances in the understanding of plant physiology, particularly of development and differentiation. Every activity of a living organism can ultimately be traced to control by some gene(s) at some stage of its life history; the entire blueprint for everything that a flowering plant is capable of performing is inscribed in the DNA of the single-celled zygote from which it develops. Some physiological functions can be discussed with minimal reference to genetic activity. These include

numerous aspects of the processes of nutrition and transport described in the first part of this book. Such processes may also show some short-term, quantitative, reversible responses to environmental factors, which are not mediated at the genetic level. When one comes to the physiology of growth and differentiation, however, as covered in the second part of the book, the need arises to refer constantly to genetic control. One tends to think of growth as a **quantitative** increase in mass. Growth is, however, almost always accompanied by **differentiation**, a change of form and/or physiological activity, and this results in the process termed development:

development = growth + differentiation

The growing seedling, for instance, does not become an enlarged version of the embryo in the seed, it develops into the adult form of the plant. Differentiation means **differential activity of genes**, i.e. activation and suppression of specific (sets of) genes at particular developmental stages. Developmental processes all involve qualitative as well as quantitative changes in response to environmental conditions. Environmental factors act as specific stimuli calling forth specific and generally irreversible changes in physiological activities and morphology. This applies to such events as the onset of reproductive growth, and reactions to environmental stresses. Such processes are the result of interactions between the external factors and the genome of the plant, and our understanding of such processes is dependent on studies of gene activity. Paradoxical as it may seem at first sight, it is the most conspicuously organism-oriented activities, such as the onset of flowering – which entails profound changes in the physiology of the whole plant – that need the molecular biology approach to the greatest extent. These are the processes which are most strongly under control at the genetic level.

We started this chapter with a very wide view, considering the overall role of flowering plants in the biosphere. We now have reached consideration of the finest, ultimate level of biological analysis – the individual gene. Flowering plants, like any other organisms, are complex entities and understanding of them as organisms can be achieved only by studying them at various levels of organization and integrating knowledge obtained by numerous biological disciplines, from molecular biology to ecology. The division of biology into various disciplines is an artificial one, made for the convenience of handling a vast field of knowledge; no such division exists in the plant. We hope that we have been able to keep the organism, the ‘whole’ plant, in sight throughout this text, even when interpreting events in terms of molecular biology.

Plant physiology also has something to offer to molecular biologists. The science of molecular biology has led to applications known under the general term of genetic engineering, i.e. the production of transgenic (transformed) organisms, containing selected genes which may come from other species. Basic gene structure being identical in

all organisms on planet earth, genes from animals and even from prokaryotes can be inserted into the flowering-plant genome. Flowering plants possess great regenerative powers; single cells from vegetative organs are able to grow into fully formed plants. This makes them ideal subjects for genetic transformations. Some transgenic crop plants are already being grown commercially and many more potential transformations are being investigated. While some scientists see genetic engineering as a wonderful tool for improving plants as economic resources, many people regard transgenic operations with strong reservations, fearing that, accidentally or deliberately, new and dangerous organisms might be let loose upon the world. There can be no scientific safeguards against the deliberate misuse of genetic engineering. The defence against accidental disasters lies in knowledge and understanding. For successful engineering of 'plants for the future', it is imperative that the physiology of plants should be understood, and moreover understood at the organismal level. A particular transformation may be undertaken with one single activity in mind; but that activity needs to be studied in the context of the plant as a whole if one is to have a reasonable chance of predicting the result of the operation.

1.4 | Outline of the text

The book falls essentially into two parts: **Nutrition and transport** (Chapters 2 to 5) and **Growth and development** (Chapters 6 to 13).

Flowering plants are essentially autotrophic, photosynthetic organisms, with basic requirements of light, CO₂, water and some 17 elements as inorganic mineral ions. The survey of plant physiology accordingly begins with **photosynthesis** (Chapter 2), detailing how the flowering plants obtain and process the first two necessities listed above, light and CO₂. This is followed by **respiration**, the process providing energy and intermediates for metabolism. Next it is considered how they obtain and transport **water** (Chapter 3), and then how **mineral ions** are absorbed and assimilated (Chapter 4). The **translocation of organic materials**, the products of photosynthesis, is covered in Chapter 5, completing the first part of the book.

The second part of the text starts with treatment of **growth as a quantitative process** and covers some simple mathematical analysis of growth (Chapter 6). Then we proceed to discussions of the physiology of growth and development, beginning with surveys of **plant growth hormones** (Chapter 7) and **cell growth and differentiation** (Chapter 8). These are followed by consideration of **vegetative development**, **photomorphogenesis**, **reproductive development**, and **growth movements** (Chapters 9 to 12). Finally, in Chapter 13, the reactions of flowering plants to some **environmental stresses** are discussed.

Complementary reading

- Anderson, J. W. & Beardall, J. *Molecular Activities of Plant Cells*. Oxford: Blackwell, 1991.
- Dennis, D. T., Turpin, D. H., Lefebvre, D. D. & Layzell, D. B., eds. *Plant Metabolism*, 2nd edn. Harlow: Addison Wesley Longman, 1997.
- Gunning, B. E. S. & Steer, M. W. *Plant Cell Biology, Structure and Function*. Sudbury, MA: Jones & Bartlett, 1996.
- Lea, P. J. & Leegood, R. C., eds. *Plant Biochemistry and Molecular Biology*, 2nd edn. Chichester: Wiley, 1999.
- Mauseth, J. D. *Plant Anatomy*. Menlo Park, CA: Benjamin/Cummings, 1988.
- Mauseth, J. D. *Botany: an Introduction to Plant Biology*, 2nd edn. Sudbury, MA: Jones & Bartlett, 1998.
- Taiz, L. & Zeiger, E. *Plant Physiology*, 3rd edn. Sunderland, MA: Sinauer, 2003.
- Troughton, J. & Donaldson, L. A. *Probing Plant Structure*. London: Chapman & Hall, 1972.

Part I

Nutrition and transport

Chapter 2

Flow of energy and carbon through the plant: photosynthesis and respiration

2.1 Introduction

All living organisms need a supply of raw materials from which their bodies can be constructed, and a supply of energy. This energy is needed for growth, i.e. for the formation of their bodies, also for the maintenance of their bodies, and for all the various types of work, chemical and mechanical, that are carried out by living systems.

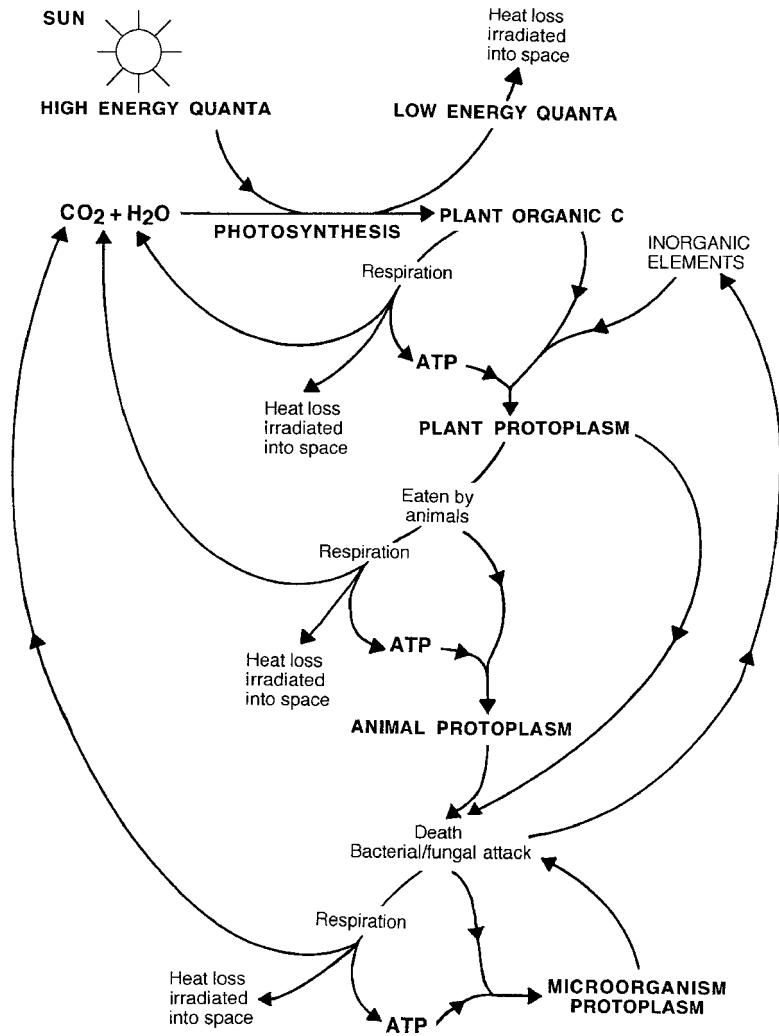
Life as we know it is based on organic compounds of **carbon** (C). This element accordingly occupies a central place among the raw materials and it is found on earth abundantly in its inorganic forms as carbon dioxide (CO_2), carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-). The ultimate energy source for most life forms on earth is the thermo-nuclear energy of the sun, transmitted to earth as electromagnetic radiation, light. **Photosynthesis** is the process by which the solar light energy is transformed into the chemical bond energy of organic carbon compounds. Photosynthesis is thus simultaneously a process of energy transduction, and a process by which inorganic carbon is converted to organic form and incorporated into living organisms. Chemically it is a reductive process. **Respiration** is the process of oxidative breakdown by which the energy stored in the organic products of photosynthesis is tapped for driving metabolism, for growth, for movements, and by which the C is returned to inorganic form again as CO_2 .

2.2 Energy flow and carbon turnover in the biosphere

2.2.1 Plants and the biosphere

The flow of energy and the turnover of C in the biosphere are illustrated in Fig. 2.1. Photosynthesis utilizes relatively high energy quanta, 'light', from the electromagnetic spectrum and these quanta energize the combination of hydrogen from water with CO_2 to organic compounds. In flowering plants, the first *stable* photosynthetic products are predominantly sugars. These sugars form the starting point of other plant constituents, including the

Fig. 2.1 The flow of carbon and energy through the biosphere. The term 'plant' is used here to denote all photosynthetic autotrophs and 'protoplasm' for all parts of an organism. The energy that is lost as heat is irradiated into space as infrared (long wavelength) radiation and cannot be recycled, but the C and other elements recycle as indicated.



macromolecules which are the units of cellular architecture. The sugars and polysaccharides (sugar polymers), sometimes also lipids, form a store of potential energy for plant cells. This store is continuously being drawn upon during respiration. The substrates are oxidized to CO_2 and water again, while some of the potential energy of the sugar molecules is transferred to molecules of ATP (adenosine triphosphate). This extremely reactive compound has been termed the energy currency molecule of living cells and its potential energy can be harnessed for cellular work – biosynthesis, growth, membrane transport, movement. During biosynthesis, other elements (Chapter 4) may be incorporated into organic combination. In the course of these activities the ATP is broken down to ADP or AMP (adenosine di- or monophosphate) respectively and it must be unceasingly resynthesized. In photosynthetic cells in the light, some cellular work may also be driven by photosynthetically formed ATP (see Section 2.3.2) without the intervention of respiration.

Photosynthesis is carried out by virtually all land plants. The only exceptions are some non-green parasitic or saprophytic species. The algae are also photosynthetic and land plants plus algae are sometimes collectively referred to as 'the green plants'. The green plants are **photoautotrophic** (literally 'light-self-feeding'), needing only light and inorganic compounds: CO₂, water and mineral ions. There are also photosynthetic bacteria (although some of these are photoheterotrophic, i.e. they need a supply of organic C compounds). The photoautotrophs are the **primary producers** and they form the basis of food chains. Plant organic matter is ingested as food by animals, fungi and other microorganisms. Any organic material synthesized by these non-photosynthetic organisms is regarded as **secondary** production, being derived from the photosynthetic products. As indicated in the lower part of Fig. 2.1, the cycles of biosynthesis and respiration are repeated in the secondary producers. Secondary producers in turn feed on each other and the cycles are multiplied, until ultimately microorganism action, decay, returns the last of the elements again to their inorganic forms of CO₂, water and mineral ions. The chemicals are recycled, although the recycling may take a long time. A living tree may retain organic materials in its body for thousands of years. Carbon fixed by the Carboniferous forests over 300 million years ago is only now being returned to the atmosphere by the burning of coal. *The energy, however, cannot be recycled.* In every process illustrated in Fig. 2.1, there occurs some energy loss as heat; this is in due course irradiated back into space as infrared radiation, low-energy quanta which can never drive photosynthesis again. The laws of thermodynamics make this energy loss inevitable: reactions are possible only if they proceed with an overall free energy loss.

Photosynthesis means a steady input of energy into the biosphere, vital for the continuance of most life. Hence photosynthesis occupies a central position, not only in the life of the green organisms which carry it out, but for life on earth in general. (An exception is provided by chemosynthetic bacteria.) On dry land, flowering plants are responsible for the major proportion of photosynthesis.

The global turnover of carbon

It is estimated that around 10¹¹ tons of C are fixed annually in photosynthesis, representing a primary production of some 1.7 × 10¹¹ tons of dry matter, while the total C held in the earth's biomass at any one time amounts to about 5.6 × 10¹¹ tons. This, however, is a minute fraction of the C present on earth. Much of this C is present as carbonates in rocks and as sedimentary organic material in the deep oceans, unavailable for photosynthesis. But even the available stores are enormous: atmospheric CO₂ holds 7.5 × 10¹¹ tons of C, and the oceans, which equilibrate with the atmosphere, contain in their upper, accessible, layers some 420 × 10¹¹ tons as dissolved CO₂, carbonate and bicarbonate.