1

A quantitative approach to plant–environment interactions

Contents

Progress in environmental plant physiology, as in other scientific disciplines, involves repeated cycles of observation or experimentation followed by data analysis and the construction and refining of hypotheses concerning the behaviour of the plant–environment system. This process is illustrated in very simplified form in Figure 1.1. At any stage the information and hypotheses may be qualitative or quantitative, and there may be more or less emphasis on the use of controlled experiments for providing the necessary data.

The initial stages of an investigation tend to provide a more qualitative description of system behaviour: much early ecological research, for example, was concerned with the description and classification of vegetation types, with a relatively small proportion of effort being devoted to understanding the underlying processes determining plant distribution. Further improvements in the understanding of any system, however, require a more quantitative approach based on a knowledge of the underlying mechanisms.

It is at this second level that this book is aimed: I have attempted to provide an introduction to environmental biophysics and to the physiology of plant responses that can be used to provide a quantitative basis for the study of ecological and agricultural problems. Further information on specific topics may be found in specialised texts referred to throughout the book.

For the convenience of the reader I have included at the end of this book an extensive set of appendices that outline the SI system of units as used throughout the text (Appendix 1); tabulate important physical properties of air, water and other materials (Appendices 2, 3, 4 and 5); give values for a range of useful physical constants (Appendix 6); outline the calculation of solar geometry and leaf boundary layer conductance (Appendices 7, 8); provide the derivation of Eq. (9.9) (Appendix 9); and provide answers to the questions posed at the end of each chapter (Appendix 10).

1.1 Modelling

Mathematical modelling provides a particularly powerful tool for the formulation of hypotheses and the quantitative description of plant growth and function. As modelling techniques are being used increasingly in all areas of plant science, and because they are used throughout this book, it is necessary to start with a simple introduction to mathematical modelling. Mathematical models provide simplified

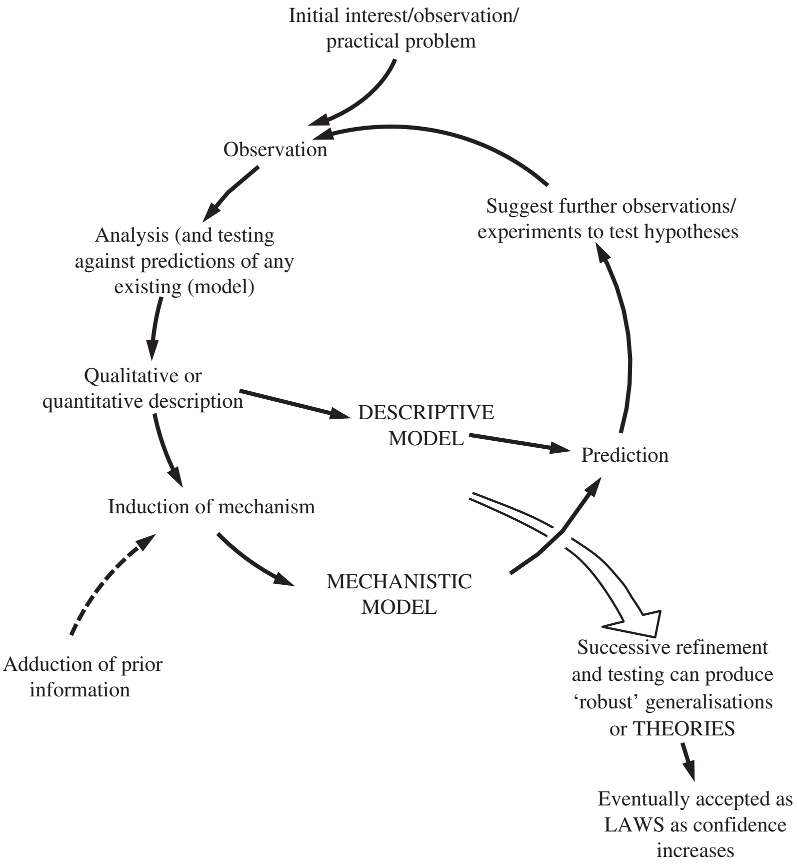

Figure 1.1 The role of models in scientific method.

descriptions of a real system (e.g. of a plant or of a process such as photosynthesis) by a series of equations that allow one to predict the development of the system over time or response of the system to external perturbations (e.g. changing temperature or water supply in the case of a plant). This predictive ability of mathematical models contrasts with other types of model, which include physical models (i.e. replicas such as model aeroplanes), conceptual models (verbal descriptions of systems) or pictorial models (illustrations and diagrams).

In the present context, a model is any representation of a real system, such as a plant, that can be used to simulate certain features of the more complex real system. For example light penetration in plant canopies is extremely complex (Chapter 2), but useful advances have been made by setting up the rather simple model where the actual canopy with its individual leaves is replaced by a layer of homogeneous absorber. This model can be either an actual object (e.g. a solution of chlorophyll) whose properties can be studied empirically, or a mathematical abstraction that simulates those properties. A mathematical model, therefore, can constitute a concise formulation of a hypothesis (in this case that light penetration through a canopy is the same as through a homogeneous absorber). As such it can be readily used to generate testable predictions (e.g. of the effect of altering the angle of incident radiation). The results of these tests can then be used to refine, confirm or refute the initial hypothesis (Figure 1.1). In the present example, the accuracy with which the equations for a homogeneous absorber predict the penetration of light in a real canopy would be used to determine the adequacy of the model.

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There are some areas of study where experiments are not possible; these include for example many studies of climate change, where it is not possible, or not ethical, to undertake the key experiments to test hypotheses. It would not be reasonable, for example, to attempt some of the major geo-engineering experiments that have been suggested as ways of combating global climate change. In such cases the only tools available are to model the system using our best understanding of the component processes and then to use predictions from the model to guide any management responses.

Because biological systems are so complex, one can rarely achieve complete mathematical descriptions of their behaviour. It is necessary, therefore, to make simplifying assumptions about the system behaviour and concerning the relevant components for inclusion in any study. This selection of variables is perhaps the most difficult task in the development of any mathematical model. An equally important step, however, in the development of useful models is their validation and testing. Some of the main advantages of mathematical models and the ways in which they can be used are summarised below.

1. They constitute precise statements of our hypotheses.
2. They are inherently testable.
3. They can 'explain' or describe a large number of separate observations in concise form.
4. They help to identify those areas where knowledge is lacking and further experiments or observations are required.
5. They can be used to predict system behaviour in untried combinations of conditions – this is particularly important in situations where experimentation is prohibitively expensive (large-scale field experiments) or inherently not possible (for example in the study of global climate or astronomical systems).
6. They can be used as management tools, for example in decision support systems for scheduling crops and management operations so as to maximise profit.
7. They can be used in diagnosis, for example in identifying crop diseases.

These last two applications have only been developed relatively recently with the advent of 'expert systems' and their use in 'decision support'. These attempt to encapsulate the knowledge of human experts into a set of rules that can be applied, among other things, to the diagnosis of disorders. A feature of this approach is that it can take account of uncertainty in any of the answers and weight them accordingly in coming to a conclusion. Although mathematical modelling has been widely used in the more physically based sciences, such as meteorology, it has, at least until recently, been underutilised in physiological and ecological studies.

Useful discussion of distinctions between different crop modelling approaches, their uses and misuses, and their relative advantages and disadvantages may be found in a series of reports arising from a symposium on crop simulation models (Boote *et al.*, 1996; Passioura, 1996; Sinclair & Seligman, 1996).

1.1.1 Types of model

Various types of mathematical model will be encountered throughout this book. These vary from relatively untested hypotheses (such as the models used in studies of 'optimum' stomatal behaviour – see Chapter 10), through partially tested models (i.e. theories), to well-tested models (i.e. laws – such as those dealing with well-known physical processes such as diffusion) where, given certain conditions, one can say with some certainty that a particular consequence will always ensue.

The majority of models can be separated into one of two groups: those that aim to improve our understanding of the physiology of crops and of their interactions with the environment; and those that aim to provide management advice to growers and farmers. The former approach requires a *scientific* or *mechanistic* approach, while the latter is usually based on more or less robust *empirical* relationships

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between plant responses and the main environmental variables. In empirical models no attempt is made to describe the mechanisms involved and minimal information is used a priori in their development. Mechanistic models, on the other hand, are developed using knowledge from previous work. A mechanistic model usually attempts to explain a phenomenon at a more detailed level of organisation. The choice of modelling approach depends on the particular research objective. Although both types of model may be used for predictions, the mechanistic approach probably has greater scope for generalised application and can lead to important advances in understanding. The large-scale dynamic crop simulation models discussed in Chapter 12 are examples where the model construction is usually based on mechanistic understanding, though they may involve a number of empirically fitted components. In the long run they are also likely to provide the more accurate predictions of system behaviour under a wide range of conditions. Nevertheless there is always a need for some care when attempting to use any model outside the range of conditions under which it was developed, and this should never be done for purely empirical models.

An example of the empirical approach is the use of relatively objective statistical regression techniques to describe and predict variation in crop yield in terms of weather variation from year to year (an example is given in Chapter 9 for hay yields in Iceland). This type of model can provide a useful description of the system by using routine techniques without the need for any physiological knowledge. The approach can, however, be made significantly more efficient with input of physiological knowledge to select the weather variates studied and to suggest appropriate forms for the relationships. It follows, therefore, that this approach is not completely distinct from the mechanistic approach, and indeed many empirical models tend to develop into more mechanistic ones as they are refined.

In addition to being empirical or mechanistic, models may be either *deterministic* or *stochastic*, and *dynamic* or *static*. In deterministic models, the output is defined once the inputs are known, while stochastic models incorporate an element of randomness as part of the model. Most models in physiological ecology are deterministic, mainly because of their greater simplicity and convenience, but some stochastic models have been used, for example to simulate random weather sequences, light penetration in canopies, spread of pathogens or ovule fertilisation (see Jones, 1981c).

Dynamic models include treatment of the time dependence of a process and are therefore particularly appropriate for simulating processes such as plant growth and yield production that integrate developmental and environmental changes over long periods. Many large-scale dynamic ecosystem and crop simulation models (see Chapter 12) have been developed, while the models used in climate modelling are also of this type. These complex computer simulations, however, can rarely be tested in the sense that physicists use the word, because of the large numbers of variables and assumptions used in their construction. They can, nevertheless, provide useful information on the sensitivity of crops or other systems to environmental variables.

Static models, in contrast to dynamic models, are used for steady-state systems or for simple descriptions of a final result. For example, many of the transport models described in this book consider only the steady state, so can be regarded as static models, as can those yield models where final yield is predicted by means of a simple regression equation between yield and certain weather variates during the season.

In addition to mathematical models, there are several examples where physical models can be used. For example, electrical circuits can be used to model diffusion and other transport processes, and with complex systems they may be easier to use than the corresponding mathematical abstractions.

Another class of models, which although not necessarily quantitative can contribute greatly to the development of understanding, are what might be termed conceptual models. These include general concepts such as the classification of plants into

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'pessimistic' and 'optimistic' on the basis of their response to drought (Chapter 10), or more generally the development of what has been termed 'plant strategy theory' (Grime, 1979). This approach provides a valuable method for rationalising the vast array of evolutionary and ecological specialisations in plants and involves the assumption that there is a limited number of what have been called 'primary strategies' available to plants. In this case one type of specialisation for one type of existence and habitat condition tends to preclude success in other environments. The 'competitor–stress tolerator–ruderal' (CSR) model is a particularly powerful example of the application of this approach and can explain and predict stress responses very successfully (Grime, 1989). Although primarily a conceptual model it is amenable to quantitative analysis, since the equilibria between competition, stress and disturbance in vegetation may be readily quantified and represented graphically.

There has been particular interest in recent years in the development of 'virtual' plants in computers or what has become known as *functional–structural plant models* (FSPM; see Vos *et al*., 2007). Functional–structural plant models combine architectural or structural models with process-based models (PBMs) to analyse problems where the three-dimensional spatial structure contributes essentially to any explanation of system behaviour. The process-based components include models of plant phenology, partitioning of carbohydrate between organs, and models of crop photosynthesis and growth. Effective simulation of crop photosynthesis, for example, requires not only the simple process-based relationship between photosynthesis and intercepted light, but also information on the geometric arrangement of leaves in space to allow calculation of the illumination on each leaf. Simulation of plant architecture was greatly stimulated by the development of L-systems by Lindenmayer (see Prusinkiewicz & Lindenmayer, 1990). This approach provided an iterative procedure for growing semi-realistic visualisations of plants based on a limited number of elements and sets of simple rules for their sequential addition. Functional–structural plant models are particularly useful for studies of phenomena such as competition between and within species where they offer opportunities to investigate interactions and feedbacks operating at the local (e.g. leaf) and global (e.g. canopy) scales. Similarly FSPMs provide tools for plant breeders to investigate plant ideotypes (see Chapter 12) that optimise photosynthesis and hence yield and growth.

In simple mathematical models a response is defined as a more or less complex function of a series of driving variables scaled by a number of fitted constants or *parameters*. In more complex models, however, the distinction between driving variables and responses may become blurred with complex feedbacks occurring and it may be the overall system response that is studied.

1.1.2 Fitting models and parameter estimation

Any observations that one makes need reducing to a simple framework, if they are to be of value in the development of a hypothesis or for predicting future behaviour of the system. Some form of curve-fitting or *calibration* procedure is necessary in order to derive a concise mathematical summary of the data. The summarising equation can be used to predict further values, as well as providing information to confirm or refute a theoretical model.

If, for example, a series of observations of photosynthetic rate at different irradiances has been made, a first step in the analysis might be to plot a graph of photosynthesis (on the ordinate, since it is likely to be the dependent variable) against irradiance (on the abscissa). One could then attempt to fit a line through the observations assuming that the points are particular examples of a general relationship. It is, however, unlikely that all points will fall on the line because some other factor (such as temperature) is also varying. The equation to the best-fit line (together with some description of the error) provides a useful mathematical summary of the

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observations. Multiple regression allows one to fit several x-variables at once.

For any particular set of points there may be an infinite number of equations that fit them and, although many may be far too complex for serious consideration, there may be several simple types that fit the observations satisfactorily. However, one must bear in mind Occam's razor (the principle that 'hypotheses must not be multiplied beyond necessity'). That is, when faced with the choice between two equally adequate models or hypotheses, one should take the simpler.

Useful introductions to the techniques for fitting curves may be found in appropriate statistical textbooks (e.g. Box *et al.*, 2005; Sokal & Rohlf, 2012), while appropriate computer packages for performing the necessary analyses include GenStat (VSN International, Hemel Hempstead, UK), Minitab (Minitab Ltd., Coventry, UK) and SPSS (IBM, Armonk, New York).

Further details of modelling techniques and their application to plant physiological problems may be found in appropriate books and reviews (Rose & Charles-Edwards, 1981; Teh, 2006; Thornley & France, 2007; Vos *et al.*, 2007). Specialised modelling platforms are available that facilitate the generation of FSPMs; these include the GroIMP platform (Kniemayer *et al.*, 2007) and the GreenLab methodology (Kang & de Reffye, 2007) and their subsequent developments.

1.1.3 Validation of models

It is often argued that crop models and other models need to be *validated*, or *verified*, before use, but this is not strictly possible as they generally do not represent a single falsifiable hypothesis, but rather a collection of separate hypotheses. Therefore strict validation, as one might use for a physical law, is not possible – only their fit to a limited set of imprecise experimental data can be tested and quantified.

It is worth noting that there are two general components to the error in model predictions: the first arises from errors in estimating the necessary parameters during the model calibration process, and the second relates to those errors arising from a failure of the model itself (whether as a result of oversimplification or as a result of incorrect understanding of the process). The latter may frequently bias the result while the former largely affect the spread of predictions (Passioura, 1996).

1.2 Use of experiments

The observational and experimental phases of research are equally important as the modelling phase. Purely observational studies, of the type that has characterised much ecological research in the past, where one relies on natural variation in the environmental factors of interest, can be restrictive and difficult to interpret. This is because of the inherent complexity of the natural system and the tendency for correlations to occur between factors such as temperature and sunshine. For this reason it is usually necessary to be able to manipulate the various environmental factors independently in controlled experiments.

It is possible to perform experiments with either more or less interference with the natural environment (Table 1.1) and either more or less precise control of certain variables. In general there is a trade-off between good control of environment and minimal interference with the natural environment, with combinations nearer the top left in this table providing more precise, but not necessarily more accurate, information on plant response to individual factors. Field experiments may suffer from poor environmental control but, because the conditions are likely to be closer to natural than those in glasshouses or controlled environment chambers, any results obtained in the field are generally more likely to relate to the plant's behaviour in natural conditions. For this reason there has been increasing interest in recent years in conducting experiments where possible under conditions as near as possible to natural conditions; the best example of this has been the study of potential impacts of elevated atmospheric CO_2

Table 1.1 Differing degrees of experimental modification of root and aerial environments (modified from Evans, 1972). The symbol × indicates impractical combinations.

		Wholly artificial		*Aerial environment*		*Wholly natural*
		Controlled environments	*Daylit cabinets*	*Glasshouse compartments*	*Shelter, neutral screens*	*Field*
Wholly artificial	Nutrient solution	✓	✓	✓	✓	×
Root environment	Inert base + nutrient solution	✓	✓	✓	✓	×
	Soil in pots	✓	✓	✓	✓	✓
	Field with fertilisation or irrigation	×	×	✓	✓	✓
	Transplant experiments	×	×	✓	✓	✓
Wholly natural	Natural	×	×	✓	✓	Observation only

concentrations using free-air carbon dioxide enrichment (FACE) systems (Long *et al.*, 2004). Unfortunately it is more difficult to modify air temperatures in natural systems, and although soil warming can be applied relatively easily, economic modification of the critical aerial environment while retaining natural variation in other environmental variables is more difficult (Aronson & McNulty, 2009).

In addition to varying degrees of modification of the physical environment, the results obtained depend to some degree on the biotic environment (competition, pathogens, etc.). Most of the studies described in this book can be classified as *autecological*, that is they consider the behaviour of one species in isolation. Although much valuable ecological information can be obtained from such studies, they can only go part way towards an 'explanation' of any ecological phenomenon. At least in many important agricultural ecosystems, the most important type of biological competition is that from plants of the same species, while other biotic factors such as pests and diseases may be effectively controlled.

In practice, the choice of experimental system depends on the specific objectives. The more detailed a mechanistic explanation or model that is required for any phenomenon, the greater will be the need for controlled experiments. However, it then becomes important to minimise the interference with normal plant growth, or to become skilled in what Evans (1972) has called 'plant stalking'. It is usually necessary to carry out a range of types of experiment, from those in tightly controlled conditions to some in the field. The latter are necessary to confirm any model derived in controlled environments. Several examples of the dangers of relying too much on controlled environments will be encountered in what follows, with studies on antitranspirants (Section 10.3.7) providing a particularly good example of the problems. There is now extensive evidence that field-grown material behaves very differently from that grown in controlled environments and only in a few cases is the reason for this difference fully understood. One example is provided by the very different stomatal response to plant water potential shown by field- and controlled environment-grown plants (see Chapter 6).

The problems caused by the different ‘coupling’ of plants to their environment in controlled environments and in the field, and the consequences for studies of the control of evaporation by stomata, are discussed in Chapter 5. Plant morphology is also markedly different between these environments as a result of different irradiances and spectral distribution (see Chapter 8). Another example, as yet unresolved, is my own unpublished observation that certain genotypes of wheat showed marked leaf rolling in a dry season in the field. Attempts to investigate this phenomenon in controlled environments have not been successful, apparently because of differences in leaf morphology in the two environments.

Some features of the environment are easier to control than others. Field studies on plant nutrition and water status, for instance, have been conducted for over a hundred years, but it is only in the last 20 or so that any useful attempts have been made to control temperature in the field. But even now, temperature studies involve enclosing the plant canopy and altering a wide range of other factors at the same time. The use of reciprocal transplant experiments, such as those conducted at the Carnegie Institution’s research gardens (Björkman *et al.*, 1973) and those of Woodward and Pigot (1975) provide a powerful technique for studying the effect of the aerial environment without using controlled environments. Growing material at all sites in soil from the same source maximises the potential for studying the aerial environment in this type of experiment.

Whether, however, one should attempt to use controlled environments to mimic all the features of the natural environment is still controversial. Many elaborate systems have been set up to simulate the detailed daily trends of temperature and radiation (e.g. Rorison, 1981), but their advantages have not been demonstrated convincingly. The increased environmental complexity tends to negate the main advantage of a controlled environment.

2

Radiation

Contents

2.1 Introduction

There are four main ways in which radiation is important for plant life:

1. *Thermal effects*. Radiation is the major mode of energy exchange between plants and the aerial environment: solar radiation provides the main energy input to plants, with much of this energy being converted to heat and driving other radiation exchanges and processes such as transpiration, as well as being involved in determining tissue temperatures with consequences for rates of metabolic processes and the balance between them (see particularly Chapters 5 and 9).
2. *Photosynthesis*. Some of the solar radiation absorbed by plants is used to generate 'energy-rich' compounds that can drive energy-requiring (endergonic) biochemical reactions. These energy-rich compounds include those derived by dehydration (e.g. in the reaction of inorganic phosphate and ADP to form ATP) or reduction (e.g. of $NADP^+$ to NADPH). This harnessing of the energy in solar radiation in photosynthesis is characteristic of plants and provides the main input of free energy into the biosphere (see Chapter 7).
3. *Photomorphogenesis*. The amount, direction, timing and spectral distribution of shortwave radiation also plays an important role in the regulation of growth and development (see Chapter 8).
4. *Mutagenesis*. Very shortwave, highly energetic radiation, including the ultraviolet, as well as X- and γ-radiation, can have damaging effects on living cells, particularly affecting the structure of the genetic material and causing mutations.

This chapter introduces the basic principles of radiation physics that are needed for an understanding of environmental physiology, and describes various aspects of the radiation climate within plant stands. The latter part of the chapter goes on to describe in more detail the inversion of remote sensing observations of plants and plant canopies for the estimation of critical biophysical properties of plant stands such as leaf area index and leaf angle distribution.

The extreme complexity of the radiation climate means that inevitably much of the treatment is concerned with the derivation of useful simplifications or models that can be used by ecologists or crop scientists. More detailed discussion of aspects of radiation physics and the radiation climate may be found in Jones *et al.* (2003) and in texts such as those by Campbell and Norman (1998), Coulson (1975), Gates (1980), Liang (2004), Monteith and Unsworth (2008), Jones and Vaughan (2010) and Rees (2001).

2.2 Radiation laws

2.2.1 Nature of radiation

Radiation has properties of both waves (e.g. it has a wavelength) and of particles (energy is transferred as discrete units termed quanta or photons). The wavelengths of radiation that are of primary concern in environmental plant physiology lie between about 300 nm and 100 μm and include some of the ultraviolet (UV), the photosynthetically active radiation (PAR, which is broadly similar to the visible) and the infrared (IR) (see Figure 2.1). The UV is conventionally split into the UV–C (<280 nm), the UV–B (280–315 nm) and the UV–A (315–400 nm), while the IR may be split into the near infrared

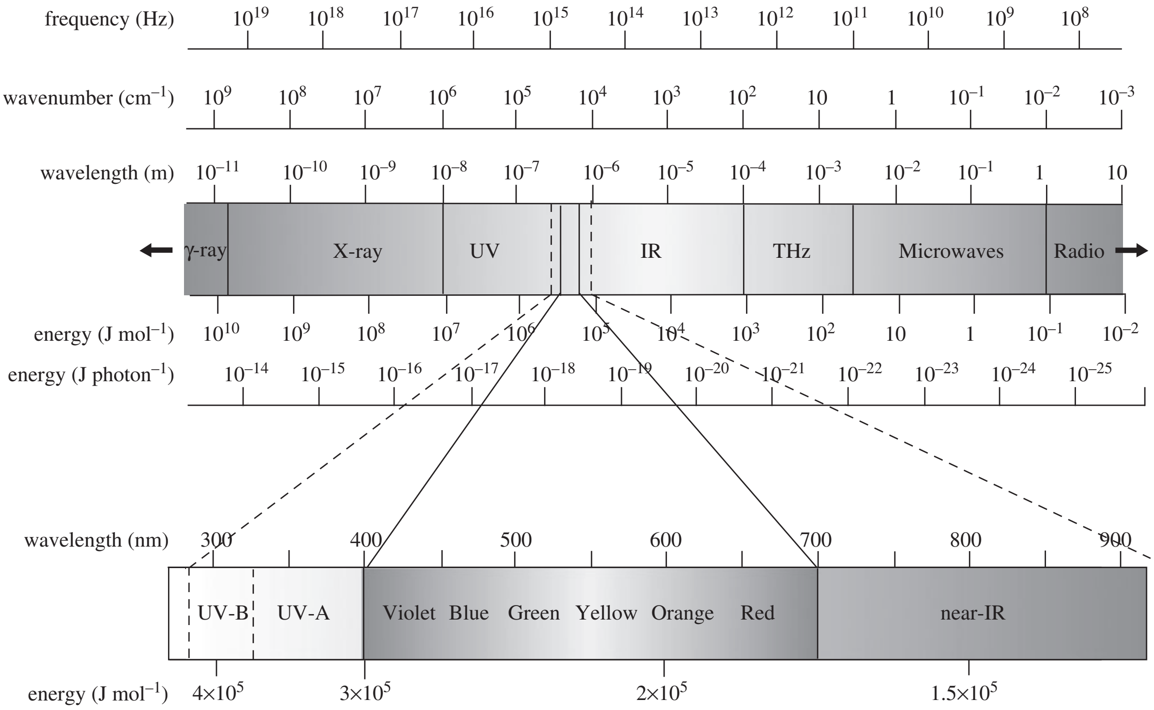

Figure 2.1 The electromagnetic spectrum: note that energy is given in J mol^{-1} (to convert to J photon^{-1} it is necessary to divide by Avogadro's number (6.022×10^{23}) so a photon of red light contains 2.84×10^{-19} J (from Jones & Vaughan, 2010).