Chapter 1

Introduction

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When an organism interacts with its environment, the physical processes involved are rarely simple and the physiological mechanisms are often imperfectly understood. . . . (environmental) physicists are trained to use Occam's razor when they interpret natural phenomena in terms of cause and effect: they observe the behaviour of a system and then seek the simplest way of describing it in terms of governing variables.

(Monteith and Unsworth 1990)

This book is about the physiological processes determining the yield that can be harvested from a stand of crop plants; these processes are common to all crop species, including those grown for direct human consumption (cereals, grain legumes, potatoes, vegetables), for indirect consumption *via* livestock (grass, forage legumes, oilseeds), or for industry (fibre, alcohol, fuel). Although crop physiology is founded on plant physiology and biochemistry, in the last fifty years it has emerged as a distinct subject, supporting major advances in food production.

The range of species studied by crop physiologists is a small subset of the plant kingdom, with emphasis being placed on the major crops (wheat, rice, maize, barley, soybean, potato, and a narrow range of pasture grasses), but there is increasing interest in applying the principles of crop physiology to minor and novel species. However, this specialisation is offset by the unique depth of study of individual species at all levels from subcellular biochemistry to field scale agronomy; until the selection of *Arabidopsis* as the model species for plant molecular genetics, wheat was probably the most intensively studied plant species on Earth.

Crop physiology is distinct in that, to provide useful information, it must involve complementary studies of plants growing singly and in stands, under controlled conditions and in the field. This distinction, although important, should not be overstressed as there is much to be learned from autecological and population biological studies of wild plants. The approach has led to concepts such as leaf area index, which considers the crop leaf canopy as a single functional unit, rather than an assemblage of individual plants. This, and the parallel development of robust instruments for sensing the field environment, has resulted in the evolution of new micrometeorological methods for measuring exchanges of mass and energy between atmosphere and canopy (e.g. canopy net photosynthesis).

The primary requirement for the success of a crop in a particular area is that its phenology fits the environment. For example, grain crops that give high yields of biomass but remain vegetative because their reproductive development does not respond appropriately to photoperiodic signals can be as unproductive as crops that set grain but run out of time or water before grain filling is complete. Chapter 2 reviews the approaches to charting and quantifying phenology, and other aspects of development, providing powerful tools for the interpretation of crop yield; for screening new varieties; and for the construction of predictive models.

Growing a crop is an exercise in energy transformation, in which incident solar radiation is converted to more useful forms of chemical potential energy located in the harvested parts (e.g. starch in cereal grains and potato tubers; lipids in oilseeds). In the crop stand, this transformation involves three processes in sequence:

- interception of incident solar radiation by the leaf canopy;
- conversion of the intercepted radiant energy to chemical potential energy (conveniently expressed in terms of plant dry matter); and
- partitioning of the dry matter produced between the harvested parts and the rest of the plant.

The yield (Y) of a crop, per unit area, over a given period of time can, therefore, be expressed by the equation:

$$Y = Q \times I \times \varepsilon \times H \tag{1.1}$$

where:

Q is the total quantity of incident solar radiation received over the period,
I is the fraction of Q that is intercepted by the canopy,
ε is the overall photosynthetic efficiency of the crop (i.e. the efficiency of conversion of radiant to chemical potential energy), commonly expressed in terms of the total plant dry matter produced per unit of intercepted radiation,
H is the harvest index of the crop (the fraction of the dry matter production that is allocated to the harvested parts, normally expressed in terms of above-ground production excluding the root system).

The amount of solar radiation incident upon unit area of cropland (Q) per day, determined by daylength and the diurnal pattern of irradiance, varies regularly with season and latitude, and irregularly with weather factors such as cloudiness. For example, Figure 1.1 shows the diurnal trend in irradiance on three almost cloudless days in January, June and September at Rothamsted in Central England. In Figure 1.2, the upper envelopes of the two datasets show the seasonal trends in maximum daily irradiance and in the total daily receipt of

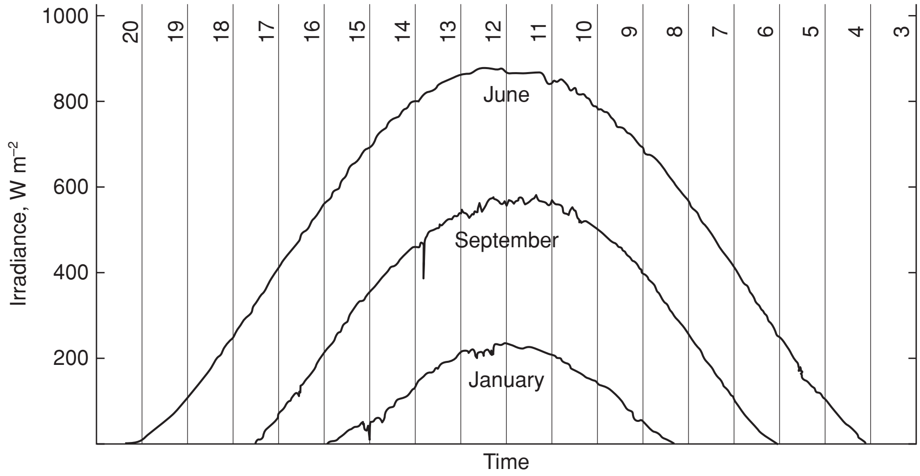

Figure 1.1 Receipts of total solar radiation on three cloudless days at Rothamsted in Central England. The numbers indicate the progression of each day in hours from right to left (from Monteith and Unsworth 1990).

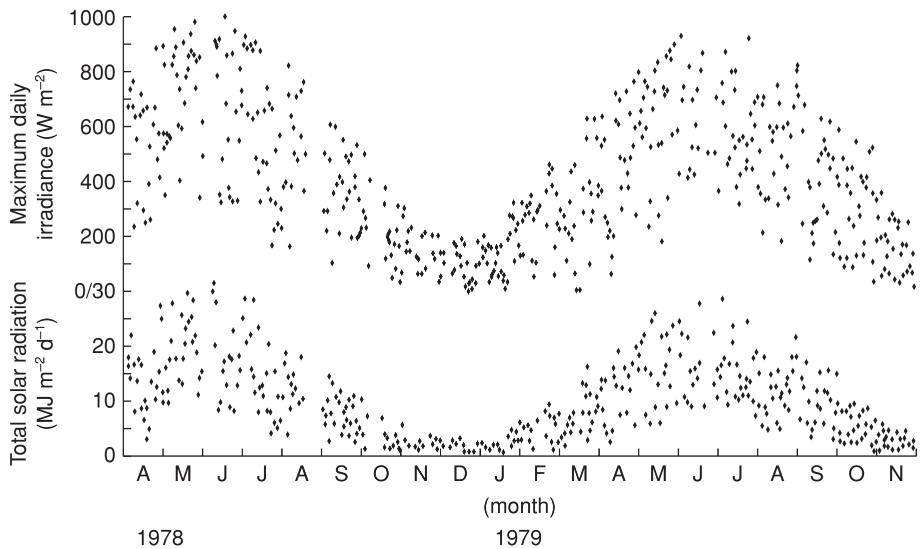

Figure 1.2 Daily records of maximum irradiance and the total quantity of incident solar radiation (0.35–2.5 μm) over two growing seasons in the north-west of England (from Hay 1985).

solar radiation, in England over two growing seasons. These confirm that, even at midsummer, the maximum potential irradiance (approaching 1000 W m^{-2}) can be seriously attenuated by cloud. Of the total solar radiation received, approximately half is photosynthetically active (PAR; 400–700 nm, Chapter 4). Diurnal and seasonal patterns of irradiance for a range of latitudes can be found in sources such as Geiger (1965) and Woodward and Sheehy (1983).

The extent to which the canopy intercepts the available radiation (I) depends not only upon the crop leaf area displayed per unit of soil surface area (leaf area index) but also upon characteristics such as leaf angle and the arrangement of the leaves in space (canopy structure or architecture). The factors controlling leaf growth and canopy development are reviewed in Chapter 3. As shown in the pioneering studies of Watson in the 1940s (Watson 1947), variation in I accounts for most of the differences in yield between sites and seasons in temperate regions, because ε and H are relatively constant in the absence of severe stress (drought, disease etc.). This is clearly illustrated by Figure 1.3, which shows that the total dry-matter production of three contrasting crop species, on a weekly basis, was linearly related to the quantity of radiant energy intercepted during that week (see also Figures 4.2, 6.7). Thus, for example, since canopy development is limited primarily by temperature, potential yield is lost in spring simply because the temperatures during the preceding weeks have been too low for the development of leaf area to intercept the available radiation (e.g. Figures 3.15, 3.25).

Even though ε varies less than I, in the field, many more resources have been expended on studying ε, resulting in a very extensive literature, which is reviewed in Chapters 4 and 5. There are at least three reasons for this concentration of interest upon photosynthesis, respiration and photorespiration. First, the reactions are of considerable intrinsic interest since they are unique to green plants and are the primary source of energy for virtually all food chains on Earth. Second, it is necessary to be able to account for the fact that the rates of component processes of photosynthetic efficiency vary among species, and are influenced by environmental factors, but ε varies little among crops and species. Third, it is becoming clear that, for many crop species, the potential yield gains by improving I and H may shortly be exhausted, and increased production can come only from increases in ε.

H, the partitioning of dry matter to the harvested parts is the least understood of the factors in Equation 1.1. Much of the work on this topic, reviewed in Chapter 6, has been aimed at establishing the fundamental physiology of assimilate translocation, but the ‘rules’ for the allocation of dry matter among the various competing sinks (storage in leaves, roots, stems and propagules, as well as in growth, maintenance of mature tissues and defence against stress and disease) are now generally understood. Such rules are widely applied in simulation models (Chapter 9). Harvest index, the net result of assimilate partitioning, is a crucial characteristic. For example, the steady increase in the grain yield of wheat and barley during the twentieth century is now seen to be the consequence of a progressive increase in harvest index, with little or no increase in total biomass production. This has important implications for breeding programmes since the indices of the most recent cultivars are approaching the theoretical maximum.

Chapters 3–6 complete the analysis of crops where yield is limited by the interception of solar radiation – a common situation in intensive temperate agriculture. However, in many other parts of the world, yield may be limited by other factors, notably water or nitrogen, and, in the pursuit of ‘sustainability’, more controlled use of such resources is necessary to prevent both waste and pollution in all countries. In Chapter 7, the approach adopted for crop yields limited by radiation (resolution into resource capture, resource use, and dry-

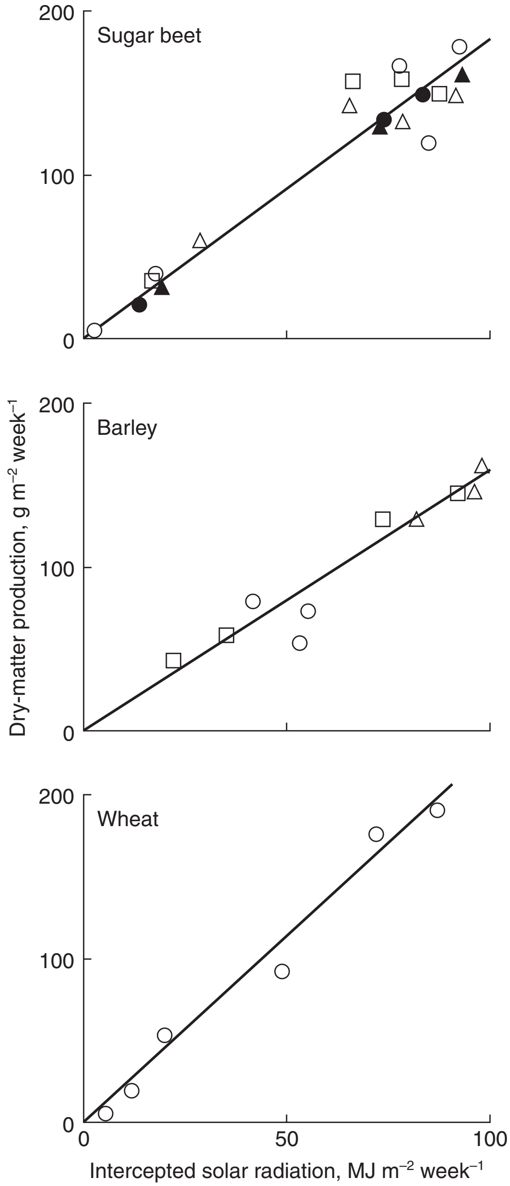

Figure 1.3 Relationships between dry-matter production and intercepted solar radiation, based on weekly measurements, for three crop species grown in the Midlands of England. The different symbols indicate different crops (from Biscoe and Gallagher 1977).

matter partitioning) is applied to water and nitrogen. Although there is a shortage of relevant data, the general conclusion is that resource capture is the most important component of yield. In Chapter 8, physiological aspects of crop quality are considered, including the widely observed inverse relationship between quality and yield; such issues are of considerable importance for the nutritional value and safety of food supplies worldwide, but they also have increasing relevance where customers are applying quality criteria in choosing food items.

The contents of the preceding chapters are drawn together in Chapter 9, which presents the theory and practice of crop modelling, describing, in detail, three widely-used models of wheat, maize and soybean. Crop models can be valuable tools in crop husbandry, but a major benefit of modelling is the identification of areas of incomplete knowledge in crop development and physiology, and in related areas of meteorology and soil science. Progress in crop physiology, therefore, requires continued collaboration between field physiologists and crop modellers, drawing heavily on recent advances in laboratory-based disciplines, such as molecular genetics. The book is rounded off in Chapter 10, by a forward look at the challenges crop physiologists may have to face in coming decades.