AN INTRODUCTION TO THE PHYSIOLOGY OF
CROP YIELD

ROBERT K M HAY & ANDREW J WALKER

AN INTRODUCTION TO THE PHYSIOLOGY OF CROP YIELD

ROBERT K. M. HAY
Scottish Agricultural Science Agency,
East Craigs, Edinburgh
AND
ANDREW J. WALKER
Scottish Agricultural College, Auchincruive,
Ayr

AN INTRODUCTION TO THE
PHYSIOLOGY OF CROP YIELD

This book is dedicated to our parents, in gratitude

Margaret Hay   **1916–1982**
William Hay   **1912–1990**
Mary Walker
Kenneth Walker   **1920–1987**

PREFACE

As we neared the completion of this book, the population of the earth reached five thousand million (billion), double that of about 1950. World agricultural production kept pace with, or slightly exceeded, this increase, and indeed the current production of food is sufficient to provide an adequate nutrition for about six billion people (the estimated population for the year 2000). In this sense, agriculturalists have met the demands imposed on them by the increasing population. However, it hardly needs to be repeated here that the available food is unequally distributed, with surpluses in some regions and severe shortages in others. Apparently intractable social, political and economic complexities, at local, national and international levels, maintain this imbalance. The long-term solution to the problem of food shortages in many developing countries is, therefore, an increase in the production of food, for local consumption and sale, on countless small farms. The problems of agriculture in the developed world are, of course, very different, although here again agriculture cannot be considered in isolation, simply as the means of producing food. Decisions which a farmer makes about what he grows are influenced, or even dictated, by the policies of governments attempting to control their countries' political and economic machinery.

This is not the place to enlarge upon the problems of agricultural production throughout the world. Instead, we offer our belief that the introduction of improved crop plants and growing systems should play no small part in solving some of these problems. 'Improved' could mean a variety of changes specific to particular species and environments but, in general, we are referring to plants able to photosynthesize more efficiently in terms of available solar radiation, water use and fertilizer input, able to convert a greater proportion of biomass into the desired product, whether food, fibre, fuel or the precursors of medicinal drugs, or better able to withstand environmental stresses. We further believe that such changes will be brought about as a result of understanding how the plants function, both individually and as crops: 'plant physiology is to agronomy what human physiology is to medicine' (van Overbeek 1976). The rapidly developing techniques of genetic engineering, complementing traditional plant breeding, provide the means; physiology must provide the knowledge required to draw up the specifications.

We have written this book as a text for degree-level teaching, and have assumed that our readers have a basic knowledge of plant physiology, biochemistry and anatomy. We have taken pains to explain ideas which we know, from our own teaching experience, students find difficult. Some of these problems arise because students can be reluctant to accept that, because our understanding of certain topics is incomplete, some experimental observations have more than one (or no) 'explanation'. Other difficulties arise because processes at the crop level are controlled by many factors, the relative importance of which can change with time or with variations in the environment or management. The 'correctness' of different explanations may therefore change

according to circumstances. And, of course, our perception of how the crop works must be continually reviewed as new observations are made.

These complications pose problems also for the writer, who tries to be objective, but whose inevitable (but unwitting) bias in interpretation may well be shown by subsequent work to have been misjudged. This is unfortunate, but unavoidable if the work is to draw on the most recent literature, and will at least serve to reinforce the reader's awareness of the multiplicity of influences on the crop plant. However, any unintentional bias in interpretation has been superimposed upon a conscious bias in the selection of topics. Crop physiology is a vast field, and we have chosen to deal only with the above-ground processes fundamental to crop yield. Even so, in trying to keep the book to a manageable size, we have perhaps neglected work which should have been included, and it would be helpful if any such omissions, as well as errors or misinterpretations, are brought to our attention (R K M H, Chapters 2, 6, 7, 8; A J W, Chapters 3, 4, 5, 9). We are grateful to Dr Dale Walters who has collaborated in this project from the start, contributing several valuable sections on the interactions between plant disease and crop physiology.

Parts of the book have been read in draft form by Mr E J Allen, Dr L C Ho, Dr E J M Kirby, Dr P E H Minchin, Dr J R Porter, Dr M J Robson, Dr J H M Thornley and Miss J Woledge, and we are grateful for their valuable comments. Professor D A Baker kindly read the entire manuscript, and to him we are especially indebted. The exacting task of producing the diagrams in their final form fell to Jacqueline Gemmell, Felicity Walker and Euan McCall, and to them we extend our thanks. Finally, we thank our families for their forbearance during a long period of undeserved neglect.

REFERENCE

van Overbeek, J. 1976 Plant physiology and the human ecosystem, *Ann Rev Plant Physiol* **27**: 1–17

ACKNOWLEDGEMENTS

CONTENTS

CHAPTER 1 INTRODUCTION

And then a queer thought came to her there in the drooked fields, that nothing endured at all, nothing but the land she passed across, tossed and turned and perpetually changed below the hands of the crofter folk since the oldest of them had set the Standing Stones by the loch of Blawearie and climbed there on their holy days and saw their terraced crops ride brave in the wind and sun. Sea and sky and the folk who wrote and fought and were learned, teaching and saying and praying, they lasted but as a breath, a mist of fog in the hills, but the land was forever, it moved and changed below you, but was forever, you were close to it and it to you, not at a bleak remove it held you and hurted you.

(From *Sunset Song*, Lewis Grassic Gibbon 1932).

This book is an introduction to the physiological processes determining the yield which can be harvested from a stand of crop plants, processes which are common to all crop species, whether grown for direct consumption by humans (cereals, seed legumes, potatoes, vegetables), for indirect consumption via livestock (grass, forage legumes, oilseeds), or for industrial purposes (production of fibre, alcohol, fuel). Although crop physiology is firmly founded upon plant physiology and biochemistry, it has now emerged as a relatively distinct subject, for a number of reasons. First, the range of species studied is restricted, compared with that studied by plant physiologists and ecologists, with the greatest emphasis, to date, being placed upon cereals (wheat, rice, maize, barley). However, this specialization is offset by the unique depth of study of individual species at all levels from subcellular biochemistry to field-scale agronomy. Furthermore, crop physiology involves complementary studies of plants growing singly and in stands, in the field and under controlled conditions. Secondly, in the field, concepts such as leaf area index have led to the idea of the crop leaf canopy as a single functional unit, rather than an assemblage of individual plants. This, in turn, has permitted the development of new micrometeorological methods for measuring mass and energy exchange between atmosphere and canopy (e.g. canopy net photosynthesis).

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). To achieve this transformation, it is necessary for the crop to carry out the following three processes in sequence:–

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

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

$$Y = Q \times I \times \varepsilon \times H \qquad [1.1]$$

where Q is the total quantity of incident solar radiation received over the period

I is the fraction of Q which 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 radiant energy

H is the fraction of the dry matter produced which is allocated to the harvested parts. This is really the harvest index of the crop stand, although it should be emphasized that it is 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, which depends upon daylength and the diurnal pattern of irradiance, varies regularly with season and latitude, and irregularly with altitude and short-term weather factors such as cloudiness. Variation in Q is an aspect of environmental physics, and since it is admirably covered in a number of other textbooks (e.g. Monteith 1973; Woodward and Sheehy 1983), it is not studied in depth here.

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 (the canopy structure or architecture). The factors controlling leaf growth and canopy development are reviewed in detail in Chapter 2. As shown by the pioneering studies of Watson in the 1940s, 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). This is clearly illustrated by Fig. 1.1, 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 (compare with Figs 3.3 and 7.16 where the same effect is shown over the entire growing season). Thus, 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. Figs 2.13 and 2.19).

The scientific literature concerned with ε, the photosynthetic efficiency, which is reviewed in Chapters 3 and 4, is much more extensive than that dealing with leaf and canopy development, in spite of the fact that ε varies much less than I in the field. There are at least three reasons for this concentration of interest upon photosynthesis and related processes (respiration, photorespiration). First, the reactions of photosynthesis are intriguing in themselves since they are unique to green plants and are the primary source of energy for virtually all food chains. Secondly, it is important to be able to account for the fact that the rates of component processes of photosynthetic efficiency vary between species, and are influenced substantially by variation in environmental factors, whereas ε varies little between crops and species (note the linear relationships in Figs 1.1, 3.3, and 7.16). Thirdly, it has become clear that in certain crops, notably grasses, there is limited scope for improvement of yield by variation in I and H, and that increased production can come only from increases in ε.

H, the partitioning of dry matter to the harvested parts, is undoubtedly the least under-