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An Introduction to the Botany of the Major Crop Plants

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Foreword

Dr A. M. M. Berrie's book is the first in this Plant Science Series. It is the intention of the Series to provide authoritative accounts of specific areas of plant studies, each volume being written by one or more authors expert in selected topics. Most of the texts in the Series are designed with the undergraduate and graduate student in mind, and they seek to give an introduction in those areas that hitherto have been largely neglected by the written word or teaching course.

The study of plants should not require justification on intellectual and economic grounds, yet there is still a lack of appreciation prevalent even amongst scientists of related disciplines. Paradoxically, in many parts of the world mankind struggles to produce enough food for survival; in such regions botany has basic significance to those without formal education. Sometimes, a lack of realization about the vagaries of food production diminishes the value of learning about plants. Every aspect of botany urgently requires attention if sincerity is to be implied in statements concerning the undesirability of starvation.

Undoubtedly, responsibility for the state of plant studies rests collectively on those of us in its employ. In a vast subject where the languages of mathematics, chemistry and physics are becoming prerequisites in a search for precision, many areas have become esoteric and apparently unimportant. Other topics are distinctly practical but often do not enjoy the respect of the scientific community. The titles in this Series will eventually reflect the diverse nature of botany, although the bias is unashamedly towards the applied part of the subject. We shall attempt to apply a rigorous scientific approach to themes that should occupy teaching time in courses on plants in centres of advanced learning. It is indeed fitting that the series should begin with a book on the major crop species.

J. R. Hillman

Preface

There are many texts which undertake to present the agronomy of the crop plants and, in doing so, consider to varying degrees, the botany of the species. It is difficult to give equal botanical treatment to each of the crop species for much more has been done on the botany of those species of considerable economic importance than on the minor types. In this text this is reflected, perhaps even more so.

Prior to the publication of J. W. Purseglove's *Tropical Crops: Dicotyledons* in 1968 there were few suitable modern texts dealing with the extensive range of crop plants found in the tropics. Those interested in temperate crops were not much better served, and though a little outdated J. Percival's intermediate text on *Agricultural Botany* was hardly equalled. As an *ad hoc* solution I prepared a set of work sheets, which included descriptions of the main crop families, for my class in Agricultural Botany. The originals, with revision, have been used for ten years and I was persuaded to make further revision, increase the content, and provide illustrations. The result of this persuasion is the present text.

Since it developed from work sheets the presentation is somewhat dogmatic and while such, the statements are not definitive. In the areas of morphology, anatomy, and systematics the specialist appreciates the development of an interpretation, or the delegation to a particular taxon by means of logical argument, but I have found that the junior student seems to come to an understanding more rapidly if the presentation is unequivocal. That has been the approach here, but the reader should be conscious that in addition to errors of omission and commission any text can err by the presentation leading to misrepresentation. This book will be no exception and I accept responsibility for all such shortcomings.

The order of the chapters reflects the level of commercial importance of the family as determined by an author located on the north-west corner of Europe. Since there has not been any attempt to include a general treatment of plant structure and plant classification this text is intended for students who have completed an elementary course in general botany, and as such the reader can start with any chapter, and read through in any order. Indeed the reading order will be related to any specific course and will depend on the availability of living material.

Any real appreciation of crop plants can only be obtained by the student examining material of the plants in question. In certain climatic zones this demands considerable effort and the teacher will depend on his colleagues in botanical and experimental gardens. My course could not be conducted, and this text would never have been produced, were it not for the contributions made by the staff of the Glasgow Botanic Gardens and the Department of Botany's Experimental Garden of the University of Glasgow. My thanks are also extended to Dr J. R. Hillman who read the text and served as a moderator of my direct approach, and to the large number of remembered and forgotten undergraduates who have made me realize that we know only in part.

Glasgow
November 1976

A. M. M. Berrie

Contents

CHAPTER 1

The Gramineae: The Grasses

When we look at the plants around us it would appear that most of them are grasses, or plants that look very much like them. In fact there are some 650 genera, with over 10 000 species in this family and so well represented is it in the world's vegetation that it has given its name to one of the main types of plant community—the grasslands.

If any family can be said to be truly cosmopolitan it is this one with members distributed from the tropics almost to the poles, and from sea level to altitudes as high as plants can grow. This success in distribution is mirrored in the grasses' success in competing with other plants, and it is probably true that there are as many individual grass plants as the others put together. This widespread and abundant distribution implies that the grasses possess characteristics which confer upon them an ability to compete with other plants, to withstand deprivation by foraging animals, and also to be able to survive infection by various parasites.

With many plants the grazing animal is deterred from eating it if the plant has developed spines or bristles. Not many grasses exhibit morphological modifications of this type. Other plants produce poisonous, or bitter, or otherwise distasteful principles. Few grasses are poisonous, although some are bitter. In the absence of such obvious adaptations what is it that has conferred upon grass its capacity to succeed? It is the habit of the plant which gives it this capacity and at the same time a plant form which can be exploited by man to provide him with food and a number of other useful commodities. By husbanding grasses and grassland man can also keep animals able to consume parts of the grass which do not provide him with a food he himself can eat and digest.

Grass fruits are the largest single source of carbohydrate eaten by man. Wheat, rice, maize and sorghum provided Western, Eastern, South American, and African societies with most of their dietary requirement for carbohydrate. With the migrations of man and his cultures, the use of the indigenous grass to the exclusion of all others is no longer found. In Africa maize is as important as sorghum, and wheat now contributes as much to the diet of some Asiatic societies as rice. At one time the grains produced in the temperate zones of the world—wheat, barley, oats, and rye along with rice—were known as the *cereals* while those produced in the tropics and which include maize and sorghum were called the *coarse grains*. This distinction should be thought of as a convenience for traders of these products and not to be based on any botanical differences which might exist. In the temperate regions there is a tendency for the coarse grains to be used as animal feeds.

When the vegetative part of the grass is used to feed animals the species which are grown are called *forage grasses*. These forage grasses can be consumed as they grow, grazed, or harvested and preserved to be used when growth is not occurring in the field because of low temperatures and/or shortage of water. Preservation is either by drying to make hay, or by ensiling. A grass may be dual-purpose, grown either for its grain or as forage. Maize may be grown either for the production of silage or for grain.

The grasses have not only provided us with our major food crops but also with some that are significant in world markets though the product can be considered as non-essential. The major crop which comes into this class is sugar cane. Refined sugar does have some dietary value but because only carbohydrate is ingested; sugar cannot be considered a high quality food stuff. Man's sweet tooth has ensured that there will be a profitable market for this product and in the sugar cane we find the most efficient plant for the production of domestic sugar.

In some regions grasses are grown deliberately for their essential oils (e.g. citronella and oil of vetiver).

The greatest versatility of any of the grasses is shown by the bamboos which, in the tropics, provide structural materials, which can be no more elaborate than the seasoned stem, or processed into planks, gutters, drain pipes and innumerable structural components of houses. Fibres are extracted, but only locally, though some bamboos are used for the production of paper.

To conclude this brief summary of grass products two more items obtained from grains should be mentioned. Maize can have moderately high levels of oil, and as a result of selection there are varieties which contain sufficient to warrant extraction of a highly desirable edible oil much used in cooking and the manufacture of margarine. The other product that may be obtained from the grain is only available after the grain has been fermented. Any grain rich in starch can be used to produce alcohol. In any part of the world we usually find that the local grain is used to give a fermentable liquor when ground and mixed with water. The technique of producing alcohol by distilling the fermented liquor is a relatively recent development in human society and in many societies the distillate is potable, and is called *grain spirit*. Grain spirit which is drunk has an alcohol content of 30–50%. A different type of fermentable liquor is obtained if the grain is allowed to germinate before it is ground and mixed with water. In Scotland the germinated grain is dried before the liquor is made, and this dried germinated material, from barley, is called malt. The distillate eventually obtained from the fermented malt is, after a period of storage in wooden casks, malt whisky. Whole economies rest on this secondary product from the grass. Industrial alcohol is normally produced from cheaper sources of carbohydrate.

If the fermented malt liquor is stored, and treated with materials to curtail unwanted microbial activity, it gives rise to beers, ales and lagers. Barley, rice and sorghum are the grains most often used for beer production but any grain could be the source of the malt.

The annual world production of grain is substantial. In 1974 more than 1.1×10^9 tonnes were produced and one country, the USA, was responsible for about 20% of that total. Sugar cane gives us more than half the world's supply of sugar—about 4.8×10^7 tonnes of a total of 8.0×10^7 tonnes. It is not possible to estimate the world's annual production of forage grasses but it must be higher in gross weight than grain levels. In approximate monetary terms for those grass products which could have reached the commodity markets directly, the value of the grass in 1974 was at least £6.7×10^{10}. Any estimate of the value of all grass products is conjectural but if the last figure were multiplied by three the resulting total may be thought of as a reasonable estimate. It is easy to see that we must understand how a grass develops, and how one grass is related to another, in order to be able to grow the plants well and possibly, bv understanding them better, produce better crops.

The Grass Grain

In farming or commerce that part of the grass most often handled is the so-called seed. This reproductive structure in the grass is in strict botanical terms not a seed but either a fruit, or a fruit further protected by parts of the floral apparatus that remain when the fruit is shed. The botanically non-committal term *grain* should be used for this structure.

The wheat grain is a naked fruit, and indeed the fact that the fruit is not surrounded by inert coverings makes the utilization of wheat easier than it might otherwise be. The grain is called a *corn*, from the Teutonic *korno*, and the word corn is applied to the major indigenous grain of the district. Corn, in England, refers to wheat, in Scotland to oats, in the United States to maize, and so on throughout the English-speaking world. The wheat grain is approximately 7 mm long and 4 mm wide though the grains may be lean or plump with the general form being that of an oblate spheroid. The dorsal side, or back of the grain is smoothly convex but the ventral surface has a deep groove along its length. At the base or proximal end of the grain on the dorsal surface there is a small, distinct patch shaped like a shield. This region contains the *embryo*, and while only comprising about a tenth of the grain, it is the vital component. The remainder is the *endosperm* which is the food reserve used by the young seedling during and after germination. At the top, or distal end, of the grain there is a characteristic mass of long hairs called the brush.

Maize is larger than wheat, being 12 mm long by 6 mm wide and wedge- or tooth-shaped, the narrower end being the proximal part of the grain. There is no ventral groove, and the embryo at the base of the dorsal surface can occupy as much as a third of the whole. There are no hairs on maize.

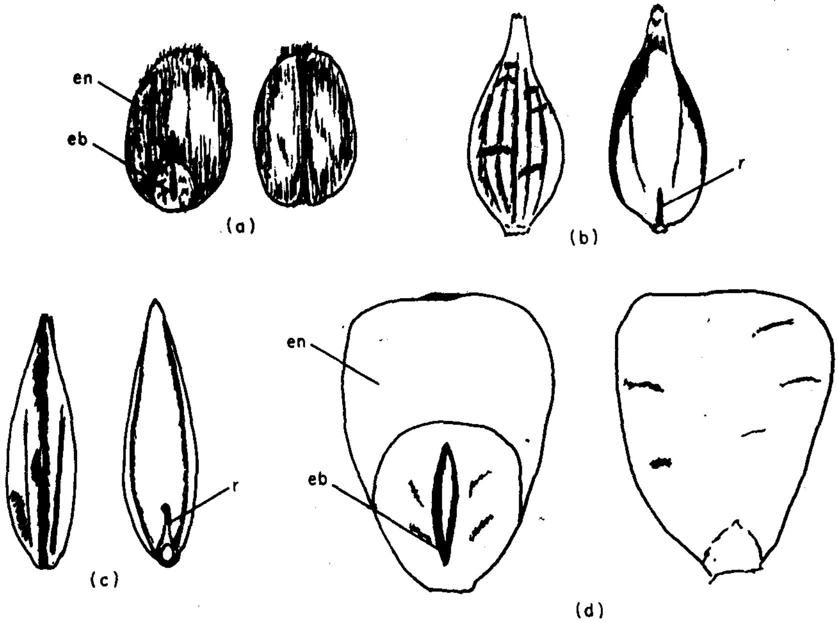

Fig. 1. Dorsal and ventral views of grains of (a) wheat (b) barley (c) oat and (d) maize: eb, embryo; en, endosperm; r, rachilla.

These fruits are characterized by having a single seed and in their development the seed coat, the *testa*, fuses to the fruit wall, the *pericarp*. A fruit of this type with fusion of the testa and pericarp is called a *caryopsis*. All the grasses encountered in temperate zones have caryopses as their fruits but amongst the bamboos we encounter as well as this distinctive fruit, nuts and berries. Bamboos seldom fruit.

Of the other grains rye, and some of the millets, are caryopses, but oats, barley and rice have the caryopsis covered by husks. These are fibrous, with little if any nutritional value, and are usually removed before the grain is milled or prepared for cooking. When the husks are removed the kernel is left. In barley the normal situation is that the husks are fused to the kernel which makes their removal a difficult process, but in the oat the husks are free. When used for animal food or for the production of malt the husks are usually left. The grains of the forage grasses are like those of oat, with a few exceptions.

The dry grain can be stored for lengthy periods and if kept dry and cool wheat grains have been known to remain viable for up to ten years. Even if the viability is lost the grain is still nutritious. When a viable seed is allowed to take up water at normal temperatures it begins to germinate. The first evidence that this is happening is a swelling of the seed and an increase in its moisture content from around 10–12% to 60%.

This embryo is associated with a shield-shaped tissue, the cells of which do not contain starch (Fig. 2). This tissue is called the *scutellum* and the embryo is

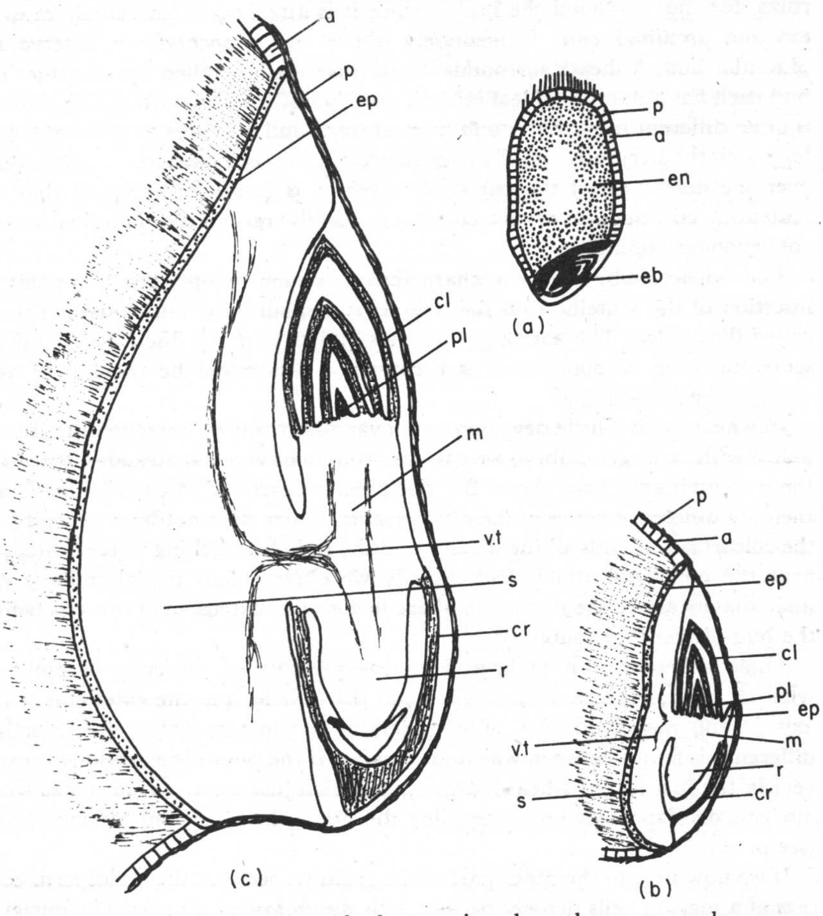

Fig. 2. (a) Longitudinal section of wheat grain: eb, embryo; en, endosperm; a, aleurone layer; p, pericarp+testa. (b) Longitudinal section of wheat embryo: ep, epiblast; cr, coleorhiza; cl, coleoptile; m, mesocotyl; pl, plumular bud; r, radicle; a, aleurone layer; ep, epithelial layer; p, pericarp+testa; vt, vascular traces; s, scutellum. (c) Longitudinal section of embryo of maize; named as for wheat.

attached to it by a peg, arising from its central region. The outer layer of cells of the scutellum where it is in contact with the endosperm are modified and have prominent nuclei and dense cytoplasm. These cells constitute the epithelial layer and it is thought that in the post-germination phase they are concerned with the mobilization of the food reserves from the endosperm to the embryo.

The embryo itself is straight and can be considered as a simple axis. Where the scutellar peg meets the axis it is called the *mesocotyl*. The axis below the mesocotyl, pointing towards the proximal part of the grain is the radicle, which is covered by a protective structure, the *coleorhiza*. Note that in wheat the coleorhiza does not surround the radicle since it is attached to the scutellum at its extreme proximal end. Immediately above the mesocotyl we observe the plumular bud. A sheath surrounds it and this sheath is called the *coleoptile*. The bud itself has a number of leaf initials, usually not more than five. This embryo is quite different from that found in most seeds and attempts to provide homology with the structures usually encountered in the seed have led to controversy over the derivation of the parts. However, it is generally accepted that the scutellum corresponds to the cotyledon readily recognized in other monocotyledonous families.

The wheat embryo has a characteristic structure opposite the point of insertion of the scutellum on the axis. It is a small tongue-like mass of tissue called the *epiblast*. The homology of this is subject to much discussion but if the scutellum is to be considered as a cotyledon this might be thought of as a vestigial second seed leaf.

In wheat there is little development of vascular tissue in the scutellum, but in maize with its larger embryo we can see prominent vascular strands connecting the scutellum and the embryo. But this greater degree of vascularization is not the only difference between these two grains. Maize does not have an epiblast, the coleorhiza extends all the way around the radicle attaching to the scutellum near the mesocotyl attachment. Finally we observe that the plumule is not immediately above the mesocotyl, there being some extension of the axis before the bud proper is encountered.

These differences in embryo features—presence or absence of epiblast, whether the coleorhiza extends all round the radicle, and the extension of the axis at the mesocotyl—are of considerable taxonomic value. One further difference is found between wheat and maize. If the plumule is sectioned transversely the first leaf of wheat has margins which just meet, but in maize these margins overlap. This character, like the other three, is used taxonomically (see p. 22).

If we now turn to the other part of the grain we see that the endosperm consists of a mass of cells densely packed with starch grains (Fig. 3). The nuclei of these starch-filled cells have disappeared during development so we can assume that these cells have no function other than for food storage. Not all endosperm cells are full of starch and enucleate. The exceptions are those on the periphery of this tissue. Usually there is a single row of columnar cells of quite distinct form

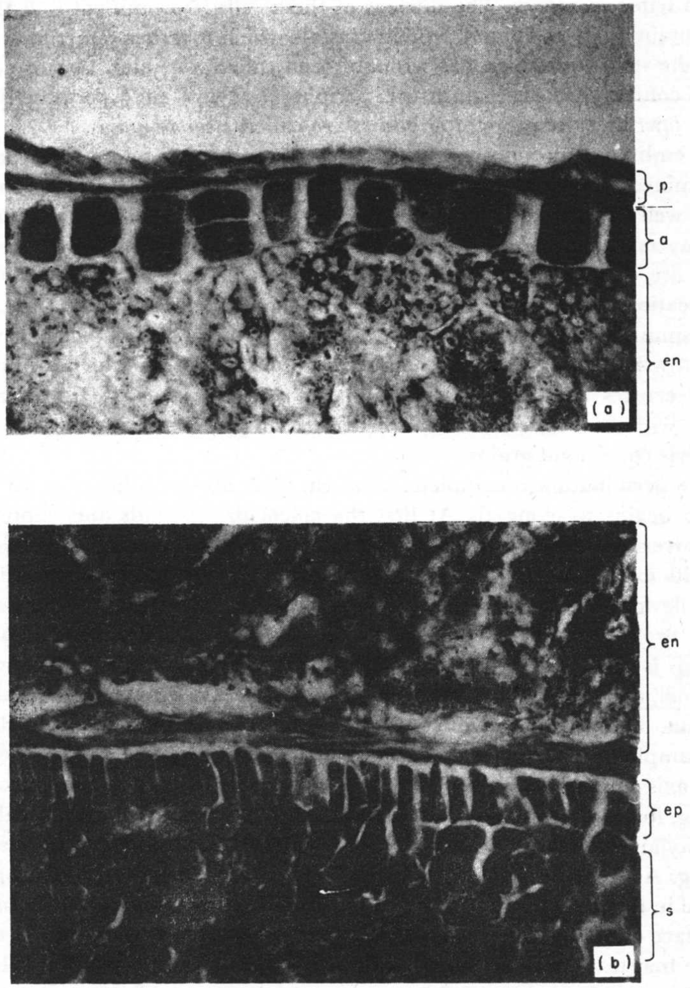

Fig. 3. (a) Section through outer layers of wheat grain: pericarp + testa, p; aleurone layer, a; endosperm, en. (b) Section through inner endosperm of embryo region of wheat: endosperm, en; epithelial layer, ep; scutellum, s. (From a slide prepared by the late J. R. Ashby).

under the coverings of the grain, but very occasionally the layer may be double or even triple in places. The nucleus of these cells is prominent and the cells also contain oil globules and protein crystals which together sometimes make a composite structure which has wrongly been called a crystal. Because of their unique contents we distinguish this peripheral row of endosperm cells as the *aleurone layer* and the protein/oil bodies are called *aleurone grains*.

The embryo and endosperm are covered by the fused testa and pericarp. As examined in sections of the type we have been describing the outer coverings are not well structured. If the grain is broken up and treated with acid and base these layers can be seen in surface view. These cells, along with the starch grains, are characteristic for a species and can be used diagnostically in the identification of the components of a feeding stuff. Starch grains are of two types: simple, ellipsoidal grains with a single growth centre (*hilum*) and with clear growth zones with distinct striae; and compound, in which a number of growth centres constitutes a unit and each centre gives rise to an angular growth without defined striae. Wheat has simple grains in two sizes while maize has compound grains.

When germination is complete, in wheat after about 20 hours at 20 °C, the embryo begins to elongate. At first the coleorhiza extends and ruptures the outer coverings. Almost as soon as these coverings are pierced, the coleorhiza ceases its extension and in turn is penetrated by the radicle. Growth of the coleoptile follows and this structure can enlarge considerably. The pericarp/testa is broken by the growing coleoptile adjacent to the embryo, but if the caryopsis is surrounded by husks the coleoptile often grows between them and the kernel, and does not become evident until it breaks through the distal end of the grain. The coleoptile will continue its growth while it remains in darkness and examples of coleoptiles 20 cm long are known. In some species the region of the axis immediately above the mesocotyl will extend as the coleoptile is growing, for example in oats, while in others e.g. wheat, this region, called the mesocotylary internode, does not begin to extend until the coleoptile has ceased growing. As the coleoptile pushes upwards, it being negatively geotropic, the first leaf in the plumular bud also grows within the coleoptile tube. On breaking the surface of the soil the coleoptile stops extending, due to the stimulus of light, but the first leaf continues to grow to break through the tip of the coleoptile. Other leaves follow, but at this stage no other region of the axis, except in specific instances the mesocotyl, extends.

After a little while the first and second internodes elongate but do not bring their associated nodes above ground. The remainder of the axis is small and the net result of this is that the apical bud is at or about ground level. Leaves will continue to be produced and some slight internode extension occurs but at this stage in development the growing point remains close to the ground (Fig. 4).

The radicle does not remain the only root produced by the developing seedling. Soon after the radicle emerges we find that there grows from the axis a set of roots, each clothed in its own coleorhiza. These roots arise from initials present

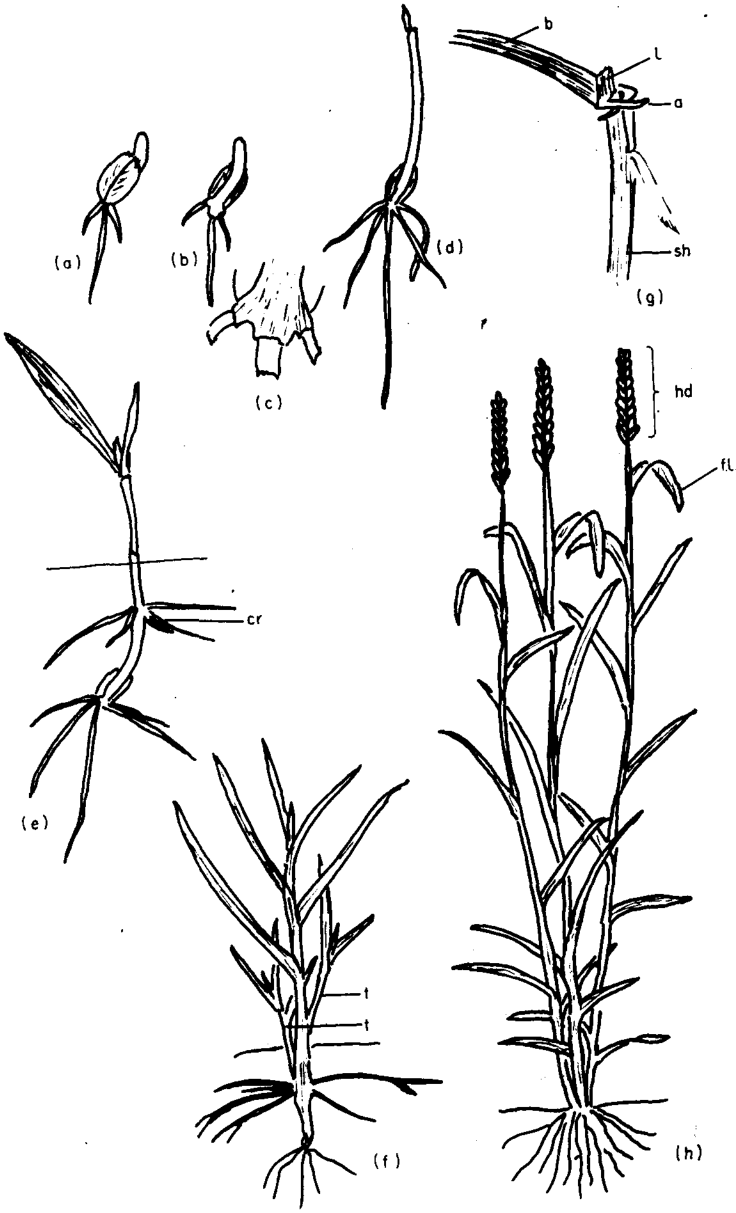

Fig. 4. Diagrammatic representation of the life cycle of a cereal (after wheat) (a) Ventral view. (b) Dorsal view of germinated grain with seminal roots and extended coleoptile. (c) Enlargement of basal region to show coleorhiza surrounding each seminal root. (d) Older seedling with full complement of seminal roots, and tip of first leaf rupturing coleoptile. (e) Expansion of leaves and development of coronal roots, c.r. (f) Tiller production, t. (g) Detail of part of an adult leaf: a, auricles; l, ligule; sh, sheath; (h) Adult plant; hd, head; fl, flag leaf.