CEREAL DEVELOPMENT GUIDE

2nd Edition

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CONTENTS

1. INTRODUCTION

From germination until harvest the cereal plant develops through an orderly series of phases. The timing of these phases depends on the environment and variety, and cannot be predicted with precision. Only direct observation of the shoot apex or developing ear of a plant allows precise identification of the stage of development. As cereal farming becomes more sophisticated the benefits which accrue from the correct timing of cultural operations increase. This is especially true for some herbicides and for nitrogen fertiliser, where their application needs to be related to stage of plant development. For example hormone-type herbicides must be applied to the plant after the double-ridge stage or the developing ear may be malformed.

An understanding of cereal plant development can give extra insight into other aspects of crop production and may help to explain and predict the effects on yield of stress occurring at certain times during the life cycle. This is because there are clearly defined phases of plant development, during which each of the yield components is determined. Thus, in wheat, the embryo ear has its full complement of spikelets well before the ear emerges from the flag leaf sheath and any treatment which hopes to increase spikelet number per ear must be formulated with regard to this. An example of the relation between stress and plant development has been shown by research on the effects of drought on cereals. At a certain stage in the development of the floret a series of cellular changes occurs during the production of pollen and the female reproductive cells. Drought at this stage can reduce yields by causing floret sterility.

There is now much interest in the possibility that nitrogen fertiliser could be used more efficiently if applications were timed on the basis of plant developmental stage. Research workers need to use standard methods to describe development, such as those laid down in this guide. The implementation of a scheme for improved timing of nitrogen fertiliser application would also require farmers to use the same method for identifying the appropriate stage of plant development.

The embryo in a cereal seed contains up to four leaf primordia and a shoot apex. After germination further leaf primordia are produced and later the spikelet primordia are formed. Each structure of the plant originates from a single primordium formed by cell division in the shoot apex or growing point. In the young plant the shoot apex is small and hidden within enfolding leaves and special techniques and equipment are needed to observe it. The purpose of this guide is both to illustrate the development stages of the apex and to help those who wish to make observations of cereal development. It is intended for use at the laboratory bench or in the field and it is recommended that living plants taken from the field be used to follow the stages whilst studying the guide.

Much of the information in this guide is available in specialised scientific publications and we have drawn on many sources to provide a comprehensive guide suitable for the cereal grower, his advisors, and for students. It has been necessary to use a number of technical terms in the description but a glossary has been provided to explain them. A short list of references at the back of the guide will provide a starting point for those who wish to study cereal development further.

All weights and measurements given in this guide are in metric units.

We are grateful to our colleagues for their help and advice, particularly to Dr. R.B. Austin who made valuable comments about several aspects of the guide, and to the Cereal Unit of the Royal Agricultural Society of England who arranged for its publication.

Introduction to second edition

In addition to minor changes, some sections (Chapters 6, 8 and 9) have been rearranged and expanded, partly to incorporate an explanation of the botanical basis of some stages which have particular agronomic significance. The final chapter (Chapter 11) has been added in response to several requests to relate plant developmental features to growth stage scales.

As with the first edition we received support from our colleagues at the Institute. We thank Dr. D. Tottman, Weed Research Organisation, Yarnton, Oxford, for making valuable suggestions about the revisions, particularly with regard to the definitions in Chapter 8. We also thank Miss Catherine More and Mr. M. Saull, Arable Unit, National Agricultural Centre, Stoneleigh, for their help in producing this guide.

2. FACTORS AFFECTING DEVELOPMENT
The need for this guide

Cereal plants develop and grow at different rates depending on their environment. Development is an increase in complexity of form, and is measured as the time taken to reach defined stages, for example the double ridge stage or terminal spikelet stage. Growth is the increase in dry matter and is measured in units such as kilograms per square metre per day or grams per plant per day. The main factors which influence development are **temperature, daylength** and **variety**. The environment a crop experiences is affected by husbandry decisions such as date of sowing, which governs to a certain extent the daylength and the temperature during the growing period. Varieties differ in their response to these factors; winter and spring types develop differently from each other and in the early stages barley develops faster than wheat.

Development depends strongly on temperature and generally the higher the temperature the faster the rate of development; during the winter months it proceeds at a slow rate or may even stop. In the case of winter varieties of both barley and wheat exposure to cold is also important for normal development. The effect of low temperature on development is called vernalisation, and unvernalised plants, not subjected to low temperature, develop slowly and do not normally produce ears.

Daylength also has a strong effect on development. Cereals are 'long day' plants and progress towards flowering is faster the longer the day in which they are growing. Development may be twice as fast in a plant growing in an 18 h day than in a 12 h day at the same temperature.

Because all the factors discussed here affect the rate of development, and may vary between seasons, no calendar dates are given in this guide. If this were not so and stages of development were reached on specific dates regardless of variety, date of sowing or temperature, there would be no need for this guide.

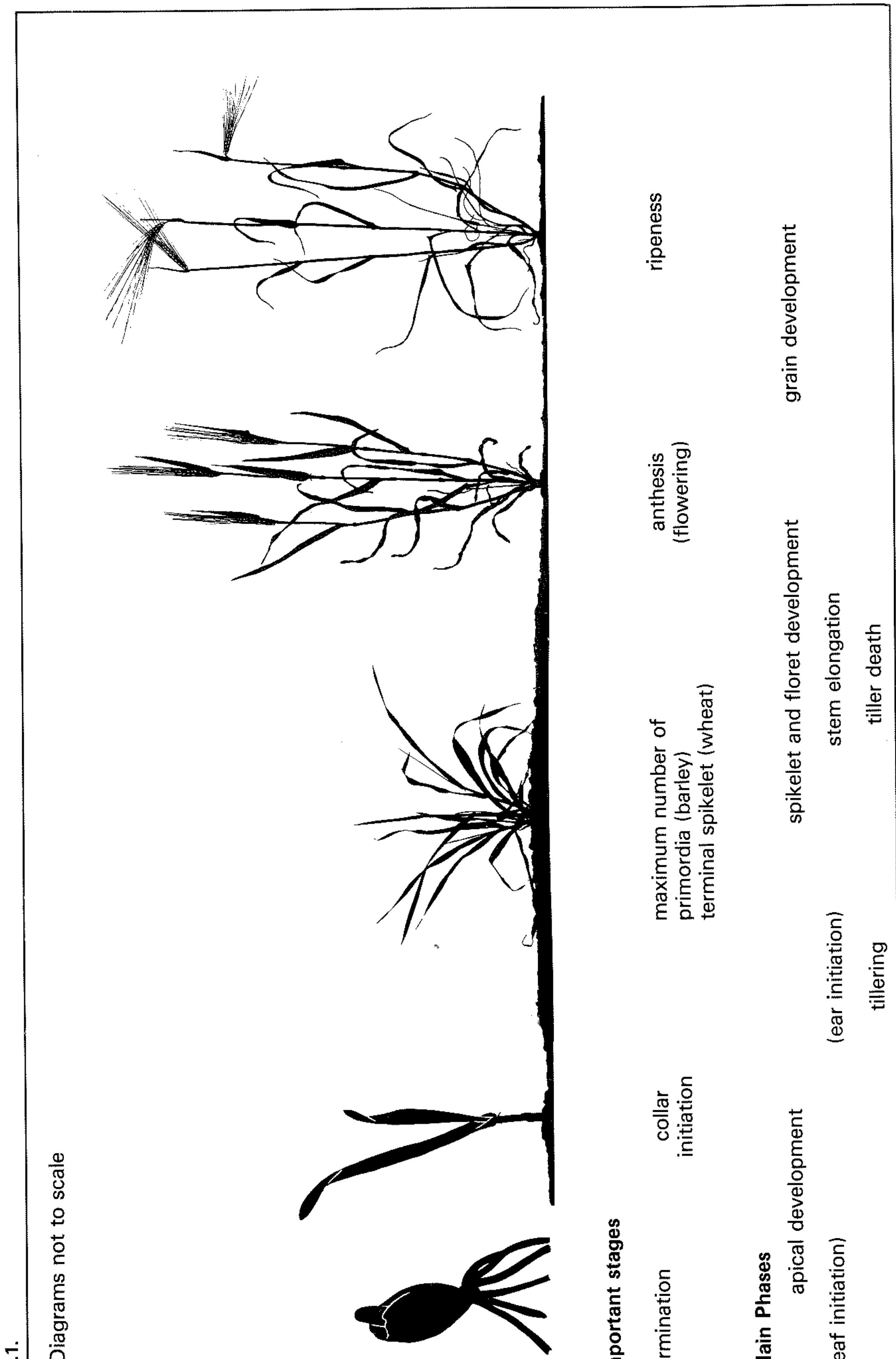


Fig. 2.1.

Layout of the Guide

The life cycle of a cereal plant can be divided into a series of clearly defined phases (Fig. 2.1). A number of distinct stages, approximately delimiting these phases, can be recognised and the external appearance of the plant at each stage is illustrated in the diagram. The changes which occur during each of these phases are described in the following chapters. In some sections barley and wheat are dealt with separately; in others, e.g. tillering, where the difference between the species is small, a general account is given. No distinction is made between the development of winter and spring barley or between winter and spring wheat, for although there are differences in size and number of parts, and the time at which changes occur, the differences are not important in the recognition of different stages.

In Chapter 4 the germination of the plant is described. During this phase of the life cycle the crown of the plant develops just below soil level. The shoot apex or apical meristem is a region where there is active cell division which initiates (or produces) 'primordia' or 'initials' of the various organs of the plant. The primordia develop and grow into leaves, tillers or the ear, depending on where and when they are formed.

Because of the importance of the shoot apex its development during the phases of leaf and ear initiation is fully described in Chapter 5. At the end of this phase the embryo ear has a full complement of potential spikelets, but is still at about soil level. Only after this does vigorous stem elongation begin to carry the ear upwards, eventually to emerge from the ensheathing flag leaf (Chapter 8).

At the same time as the ear is forming, tillers are also developing. Their origin and orderly sequence of emergence is described in Chapter 6.

After the formation of the ear is complete and stem elongation begins, development enters a new and important phase, during which some of the spikelets or florets die at a young stage. Chapter 7 describes this and also follows the development of a single spikelet or floret as the stamens and the carpel develop ready for anthesis.

Anthesis (Chapter 9) is a short phase lasting two hours or less in an individual floret and only a few days in the crop as a whole. However, the behaviour of the florets during this time is crucial for successful pollination and the structure of the ear and the changes in a floret at this time are described. The subsequent growth and development of the grain is described in Chapter 10.

In the final chapter 'Monitoring Crop Development' (Chapter 11) we point out the variation which may occur in the timing of developmental events. This variation makes it impossible to schedule certain important agronomic operations by the calendar and we consider how the various critical stages of plant development may be recognised. We make a comparison of the developmental stages described in this book with the growth stages defined by the Zadoks and other scales. The strengths and weaknesses of the various systems are reviewed and some important developmental stages which may be useful for recording and for other purposes are proposed. We conclude with some speculations about possible applications of this technology in the future.

3. DISSECTION TECHNIQUE

Before the shoot apex can be examined it must be dissected free from a number of ensheathing leaves. The techniques to do this can be mastered by anyone with suitable basic equipment, but a degree of persistence may be necessary to overcome initial clumsiness. The beginner is advised not to start with very young plants, but to begin with one which has about five or six exposed leaves on the main shoot, (maximum number of primordia stage in barley (Fig. 5.31) or terminal spikelet stage in wheat (Fig. 5.32)). At these stages the tissues are stronger and do not break easily; the shoot apex is about 3 or 4mm long and easier to find.

Equipment

For dissection of the early stages a binocular stereoscopic microscope (a 'dissecting' microscope) is essential (Fig. 3.5). Dissecting microscopes are usually fitted with a turret of interchangeable lenses or a zoom lens system and a range of magnifications from x 5 to x 50 is suitable for shoot apex dissection. If measurements are to be made, a microscope with fixed magnifications (e.g. x 6, x 12, x 25 and x 50) is preferable to one with a zoom system giving variable magnification. Some form of artificial lighting is necessary. A low voltage lamp with a focusing condenser, transformer and rheostat so that the light intensity can be varied is best (Fig. 3.5). This can be moved to give the optimum angle of illumination to show details of the structure to be distinguished. It should be fitted with a heat filter to retard drying out of the apex. Other methods of lighting such as fibre optics or a fluorescent ring illuminator are also suitable.

A sharp, mounted needle is necessary to remove young leaves. The most satisfactory type is a fine sewing needle fixed in a craft tool holder (e.g. Uno Neatrim Cutter). A small pair of scissors is useful for cutting off roots. Modelling clay (e.g. Plasticine) is ideal for holding the small shoot while the youngest leaves are removed from the apex (Fig. 3.6) and the apex can be readily manipulated to establish the stage of development.

Sampling

Apex development may vary from plant to plant in the crop because of differences in sowing depth, clumping of seeds by the drill, etc. To obtain a reliable estimate a minimum of five plants should be examined, taken at random from different areas of the field, to give a representative sample. Avoid double-sown parts of the headland and other non-typical areas.

Fig. 3.1.

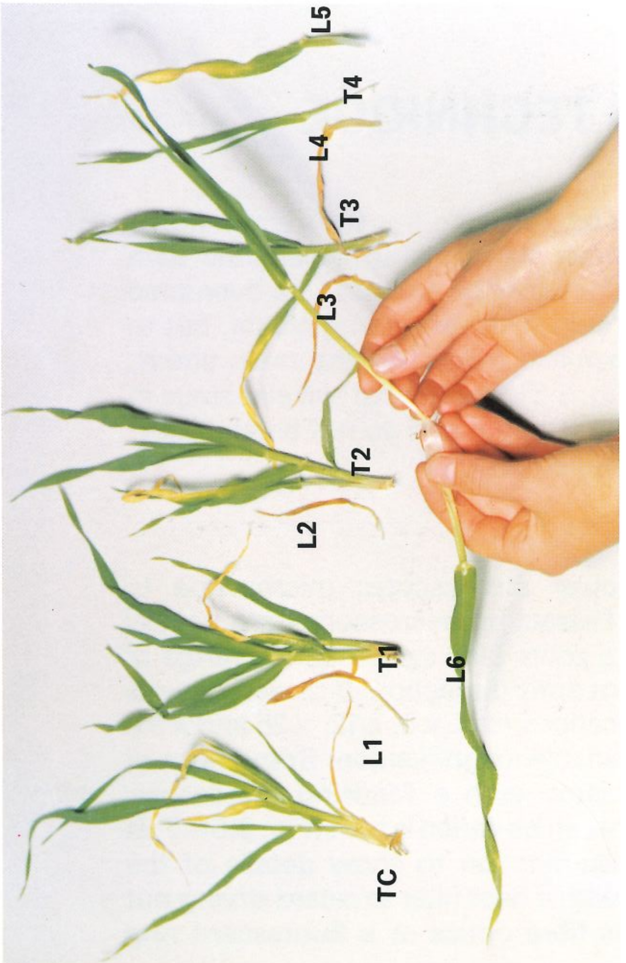
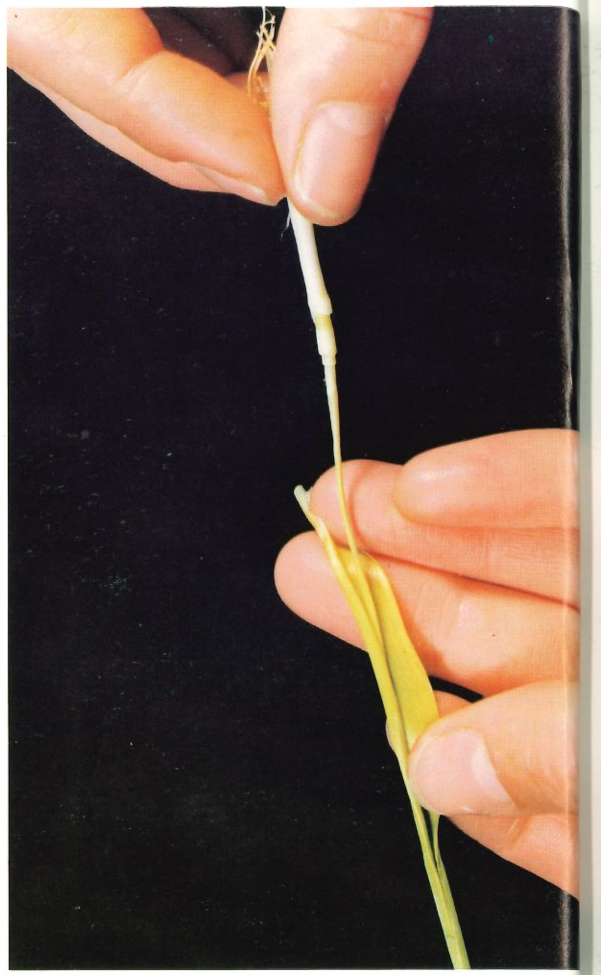
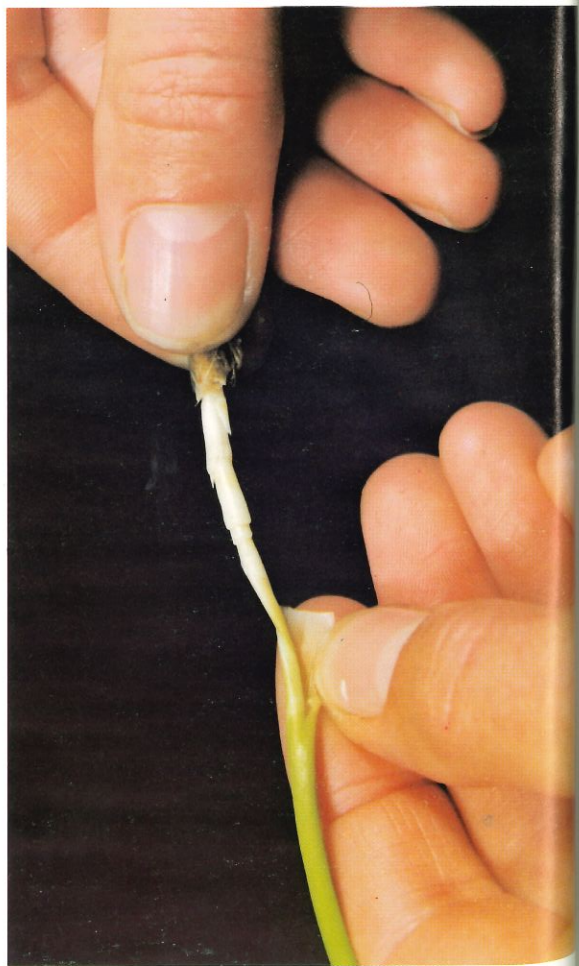


Fig. 3.2.





3. DISSECTION TECHNIQUE

Procedure

1) Examine the plant and identify the tiller groups and main shoot. Figure 3.1 illustrates the analysis of a winter barley plant. The operator has identified the group of tillers at the coleoptile position (see Chapter 6 - identification of tillers) which is held in the left hand. The tiller 1 group is on the right side, over the index finger and the blunt tip of leaf 1 can be seen on the knuckle of the index finger.

If counts or notes are to be made it is helpful to lay out the leaves and tillers in sequence (Fig. 3.2). The operator has laid out, from left to right, the TC group, leaf 1, T1 group, leaf 2, T2 group, leaf 3, T3, leaf 4, T4 and leaf 5. Leaf 6 is being removed with the left hand from the main shoot which is held in the right hand.

2) After the mature leaves have been removed the younger leaves and the shoot apex will be found to be tender and easily broken. The young exposed leaf should be supported while the margin of the leaf is found and the next leaf is freed (Figs. 3.3, 3.4). The zone of growth of the leaf is at the base and the leaf will usually break away from the stem easily and cleanly.

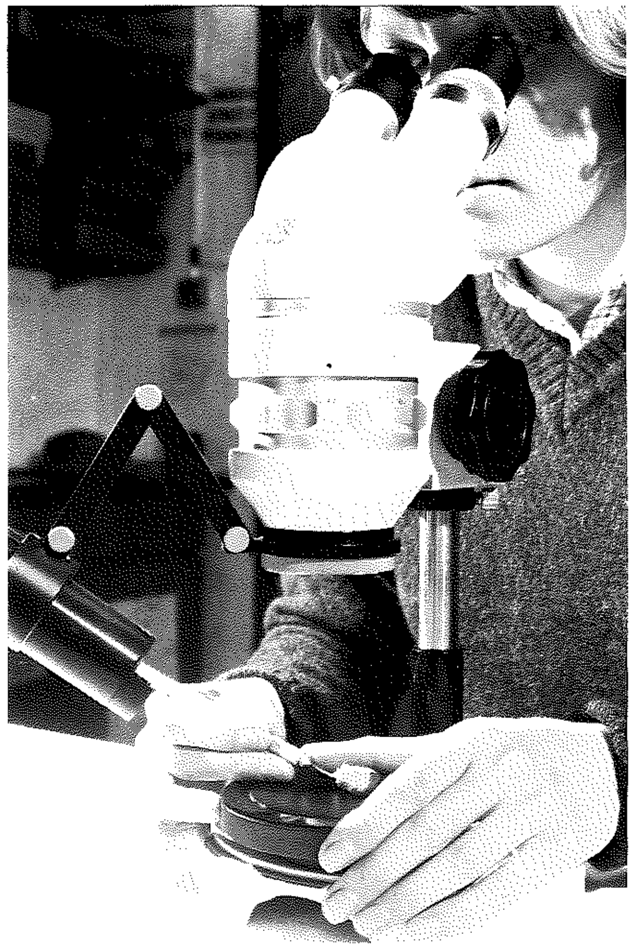


Fig. 3.5.

Fig. 3.6.

3. DISSECTION TECHNIQUE

3) When the exposed leaf is about 30mm or less long, transfer to the dissecting microscope (Fig. 3.5). At this stage the base of the plant may be held in Plasticine and fixed to the microscope stage for further dissection. (For information on choice of a microscope see Appendix II).

4) Insert the point of the needle under the leaf margin and break off the young leaf (Fig. 3.6). If any portion of the base of the leaf remains, clear it away with the needle. Expose the shoot apex, identify the profile and face planes and compare with stages illustrated in the guide. At this stage the apex will lose water and quickly shrivel, particularly if it is damaged during dissection, so quick, precise work is important.

The **profile** view is seen when the apex is viewed from the direction at right angles to the plane of the leaves. The ranks of primordia on both sides of the apex can be seen (e.g. Fig. 5.3).

The **face** view is seen when the apex is rotated at 90° to the profile view and viewed along the plane of the leaves (e.g. Fig. 5.4).

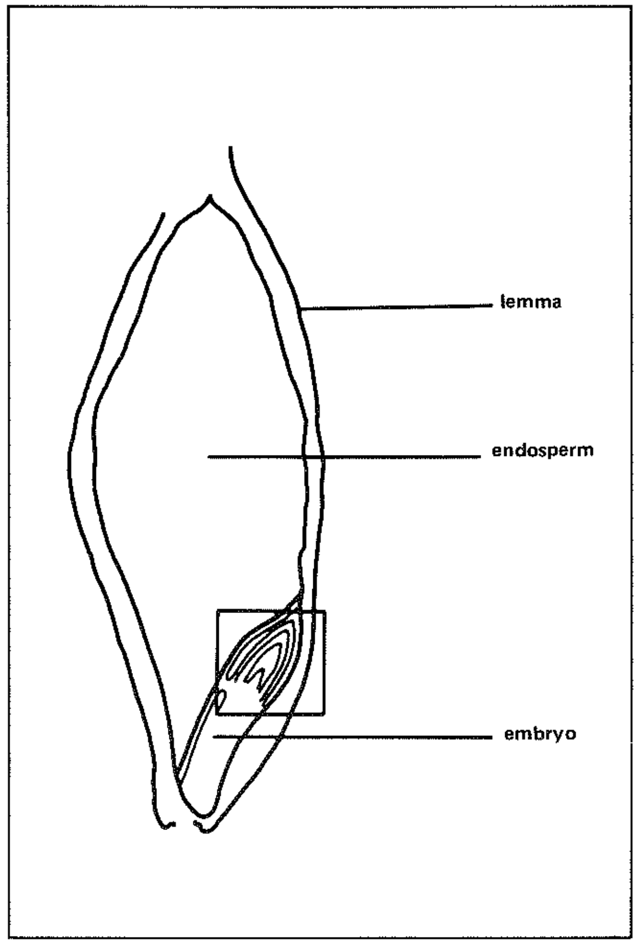


Fig. 4.1a

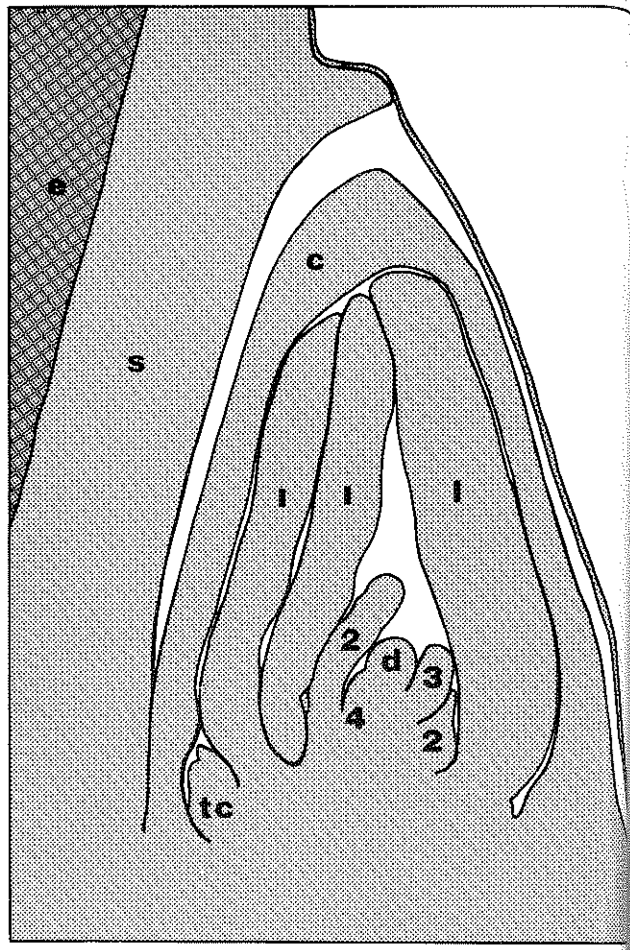


Fig. 4.1b

Fig. 4.1. The structure of the embryo plant of barley is shown in longitudinal section of the grain. This is a very thin slice parallel with the plane of the long axis of the seed which divides it into two similar halves. The scutellum (s) is the structure which absorbs nutrients from the endosperm (e) during germination. The coleoptile (c) encloses four leaves (1-4) the youngest of which (4) is just visible as a primordium on the flank of the apical dome (d). The coleoptile tiller bud (tc) is well developed. The tiller bud is also usually found in the axil of leaf 1, but is generally in a different plane from that of the coleoptile bud.

(Fig. 4.1a is a longitudinal section of the whole grain. The boxed part of the embryo is shown at a higher magnification in Fig. 4.1b.)

4. GERMINATION

In the mature grain an embryo plant is present. Its shoot apex has three to four leaf primordia and a tiller bud is present in the axil of the coleoptile tiller and the axil of leaf 1 (Fig. 4. 1b). Within a few days of being sown in suitable conditions roots start to grow and shortly after that the coleoptile begins to grow (Figs. 4.2 barley, 4.3 wheat). In barley the lemma and the palea adhere to the seed during growth and ripening of the grain, and early growth of the coleoptile takes place beneath the lemma (Fig.4.2). The coleoptile, which is adapted to thrust its way through the soil, ceases growth soon after it reaches the surface. Shortly after this the first true leaf of the seedling plant emerges from a pore at the tip of the coleoptile (Fig. 4.4).

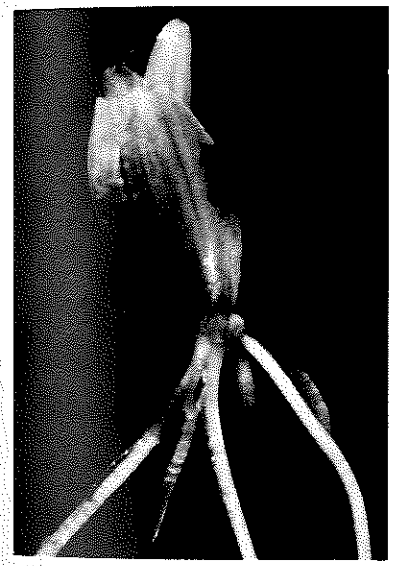


Fig. 4.2.

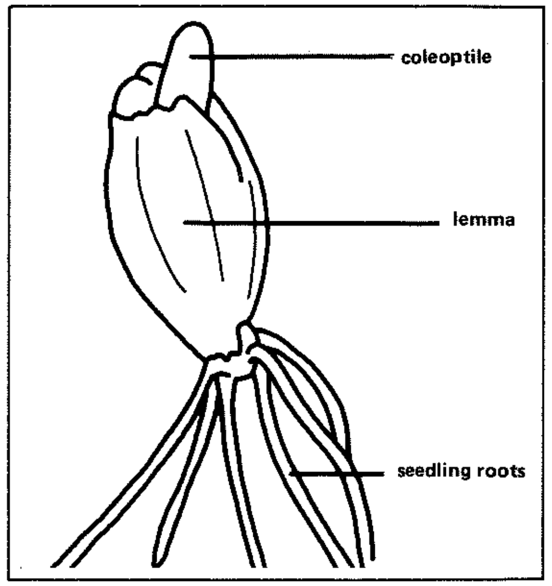


Fig. 4.2. Diagram

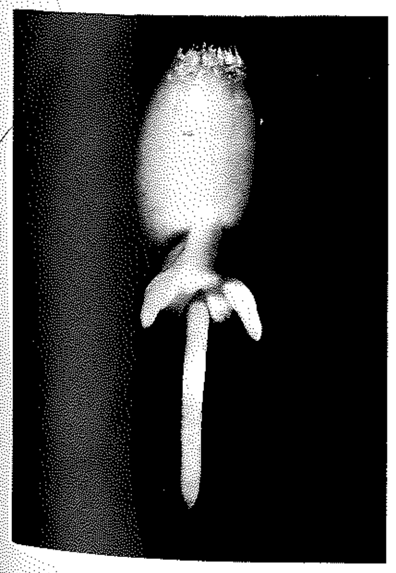


Fig. 4.3.

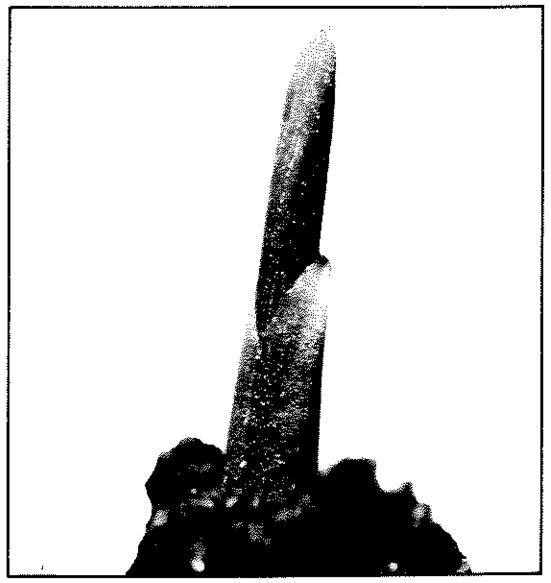


Fig. 4.4.

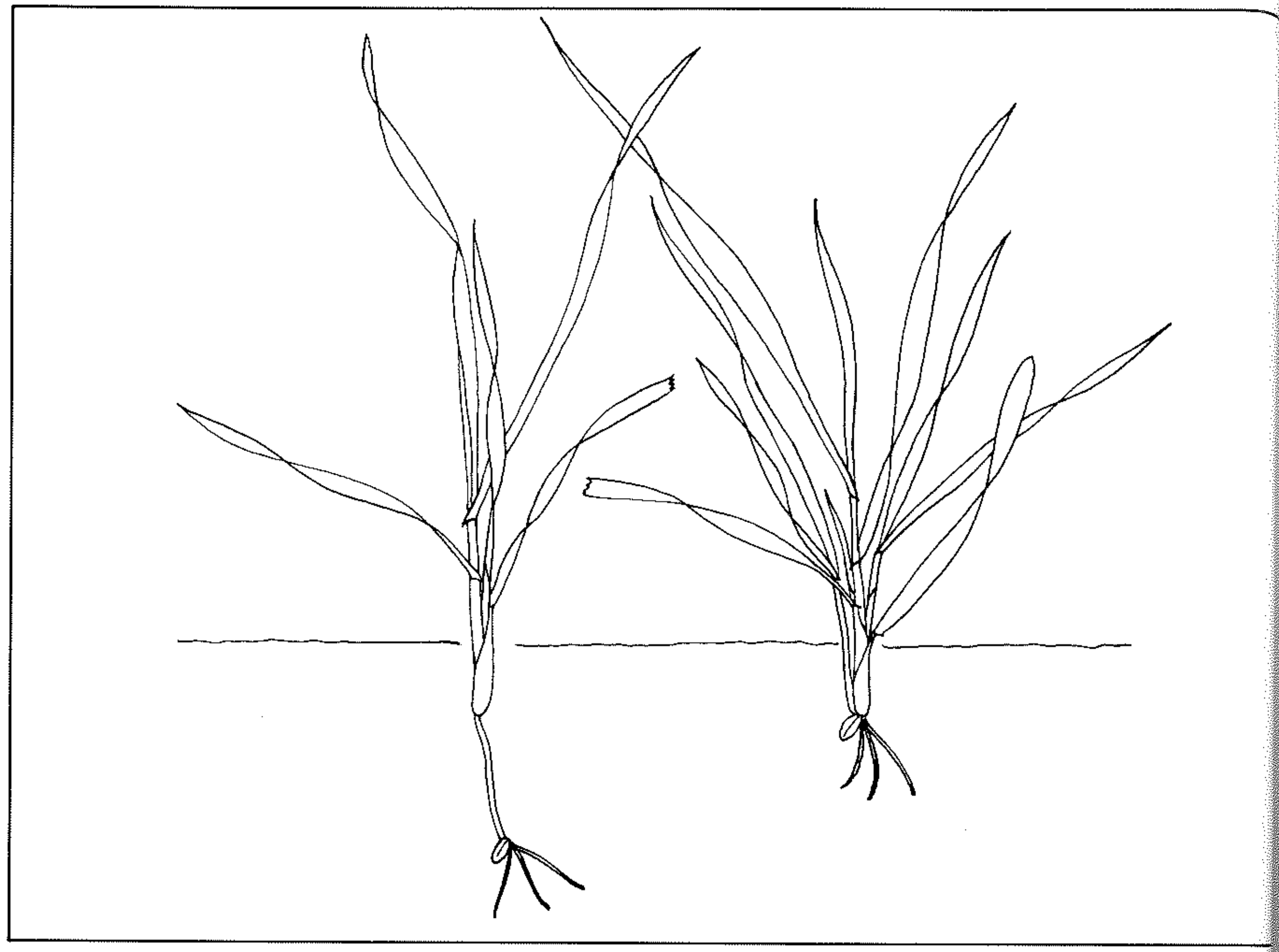


Fig. 4.5.

Fig. 4.5. The left hand plant is from a deeply sown seed and the one on the right from a seed sown at optimal depth. The coleoptile has been removed to show the extent of internode growth. The coleoptile internode of the deeply sown plant has elongated to bring the 'crown' of the plant to the same depth, relative to the soil surface, as the crown of the plant sown less deeply. Note that only one tiller has developed in the deeply sown plant whereas in the other plant there are three leafy tillers.

4. GERMINATION

At this stage in the life cycle, a plant from a deeply sown seed adjusts the position of its shoot apex in the soil. The internode between the coleoptile and the first leaf elongates so that the 'crown' is positioned just below the soil surface. If sown very deeply internode one may also elongate. If young plants from deeply sown seeds are dug up and the soil removed the position of the seed, the coleoptile internode and the crown can be seen and compared with plants from seed sown at optimal depth (2 to 4 cm) (Fig. 4.5).

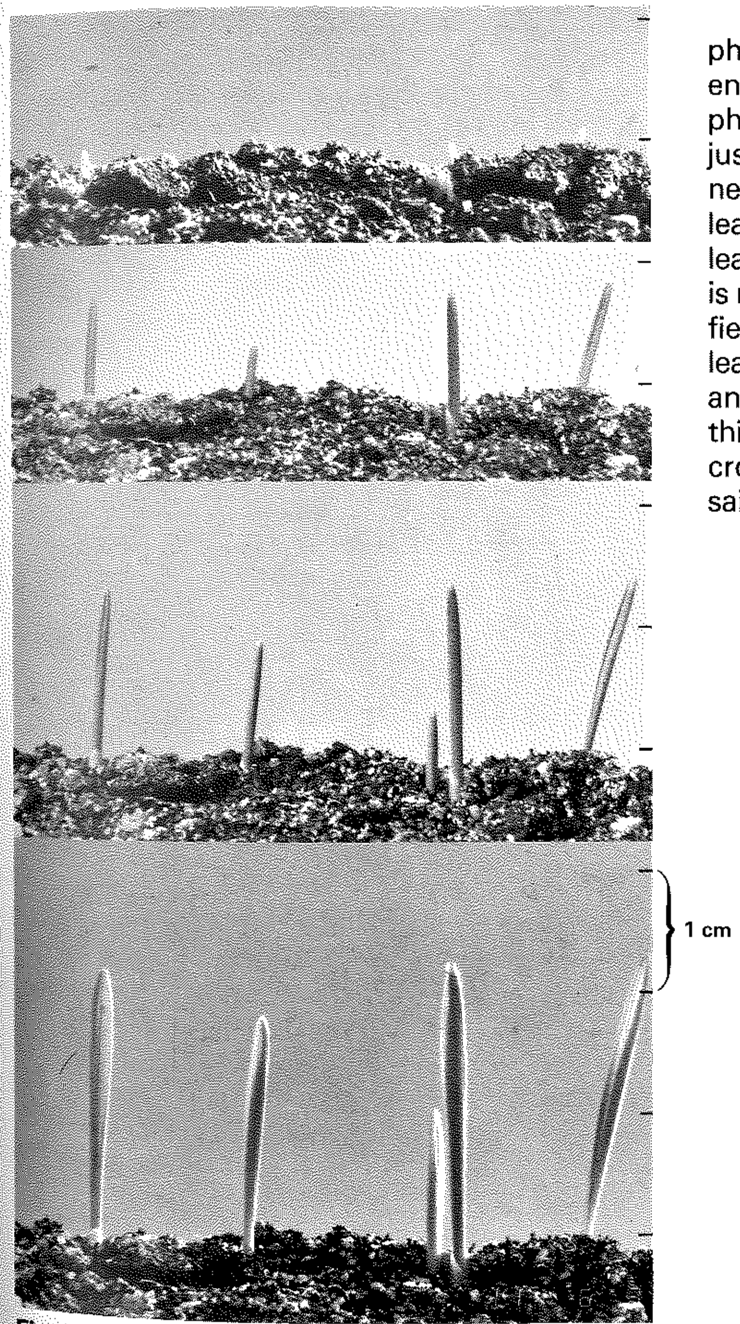


Fig. 4.6.

Fig. 4.6. The sequence of photographs shows the emergence of seedlings. In the first photograph the coleoptiles are just coming through the soil. The next two show the emergence of leaf 1 through the coleoptile. The leaves are still tightly rolled and it is not easy to see the crop in the field. In the final picture the leaves have emerged about 2 cm and are beginning to unfurl. By this stage the rows within the crop can be seen and the crop is said to have 'brairded'.

Fig. 5.1. 0.10mm scale bar

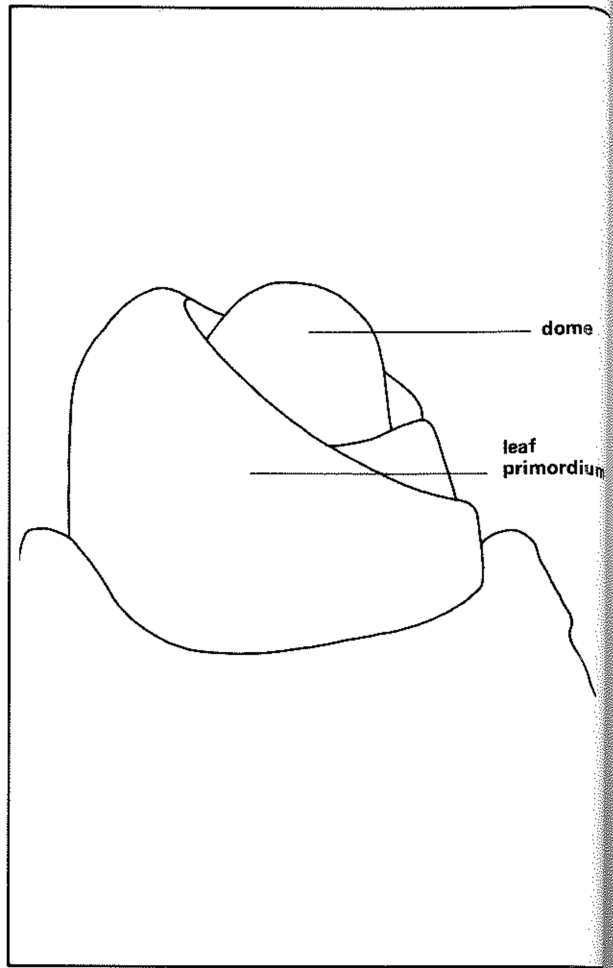


Fig. 5.1. Diagra

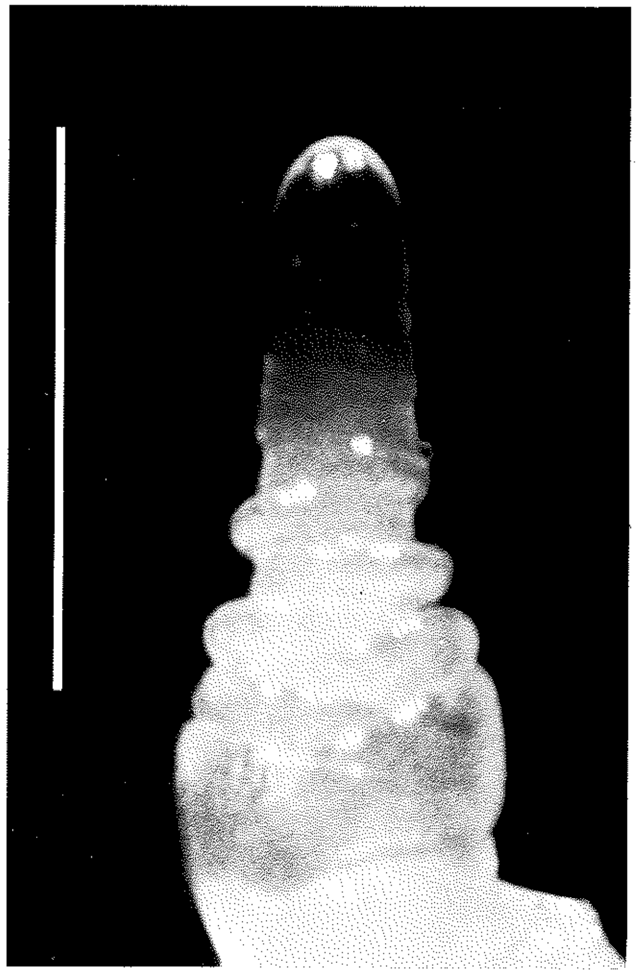


Fig. 5.2. 0.5mm scale bar

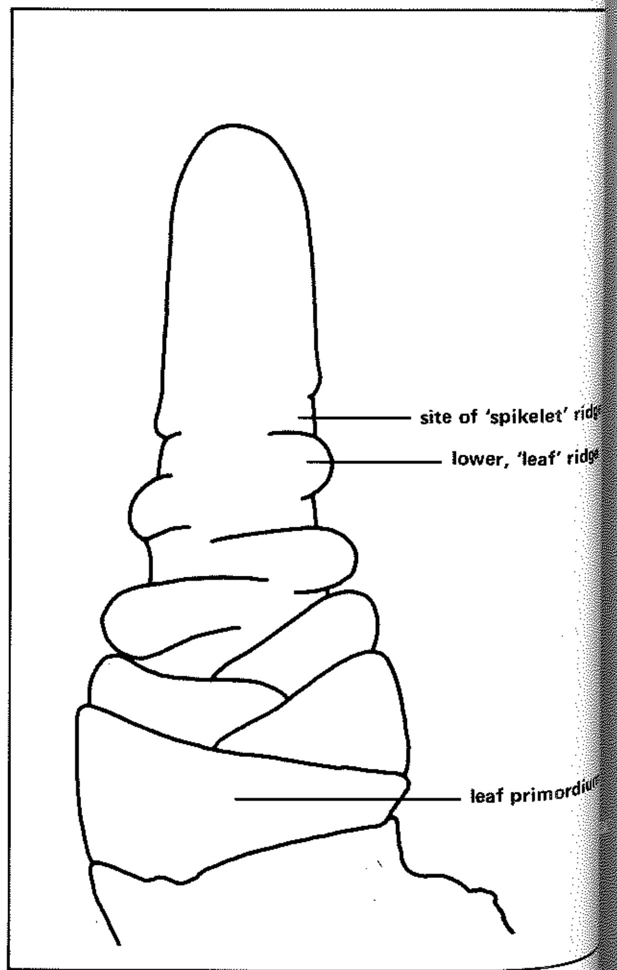


Fig. 5.2. Diagra

5. APICAL DEVELOPMENT
Barley

Vegetative stage

In the seedling plant, when the first leaf is just emerging from the coleoptile, the shoot apex is at the vegetative stage. To expose the shoot apex, dissect off the coleoptile and first leaf, and two or three unemerged leaves. The shoot is very fragile and care and experience are needed to accomplish the dissection successfully.

The apex is about 0.2mm long and conical in shape; a typical example is shown in profile view in Fig. 5.1. It consists of a meristematic dome and two or three leaf primordia. Cell division takes place in this smoothly rounded dome and some of the cells form ridges or primordia on the flanks of the dome. At this stage the primordia are crescent shaped structures enclosing the apex and will grow to form leaves. In the photograph the labelled leaf primordium partially encloses another, seen on the right hand flank. An even smaller leaf primordium is present on the left hand flank hidden beneath the labelled primordium. The dome continues to grow and initiate primordia until all the leaves and spikelets have been produced.

The plant at this stage is a seedling and the apex will remain at the vegetative stage, depending on variety and sowing date, until usually between three and six leaves have emerged on the main shoot. Generally the early sown winter varieties will have the highest number of leaves at a given stage and spring varieties sown in the spring will have the least. This is also true for the stages on the following pages where leaf numbers are given.

The apex shown in profile view in Fig. 5.2 is classified as vegetative but is at a later stage than the one shown above. The dome continues to initiate primordia and because the primordia are produced more quickly than they can grow into leaves, primordia have 'accumulated' on the shoot apex. The apex is more elongated and cylindrical than the one in Figure 5.1.

The primordia at the base of the apex will become leaves but in the upper part the small ridges which are the vestigial leaves do not grow much more relative to the rest of the apex. A spikelet develops in the region immediately above each leaf ridge.

The apex is about 0.5mm long and this stage marks the beginning of ear (floral) initiation.

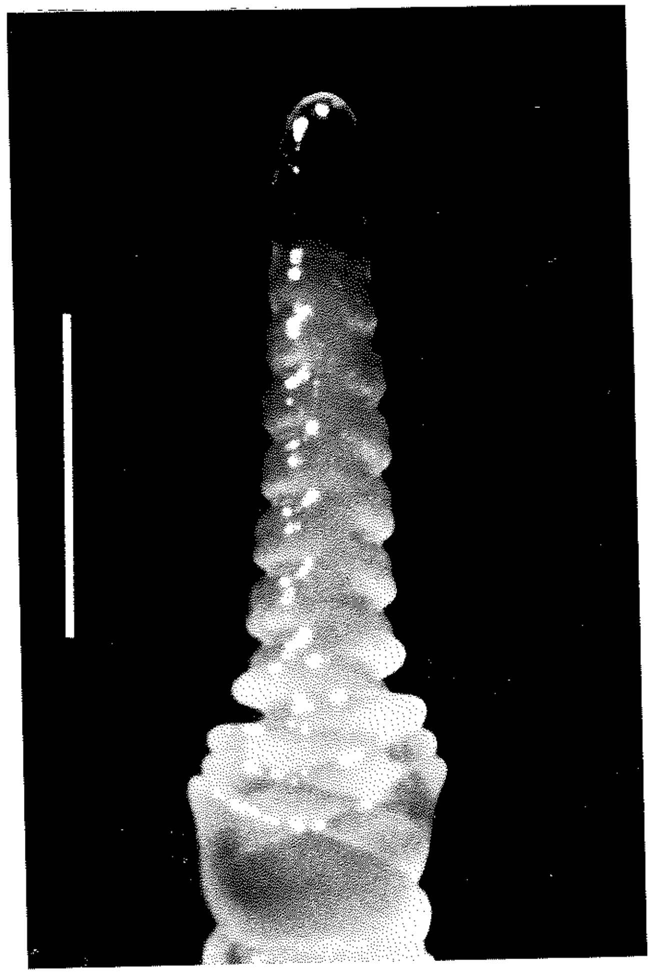


Fig. 5.3. 0.5mm scale bar

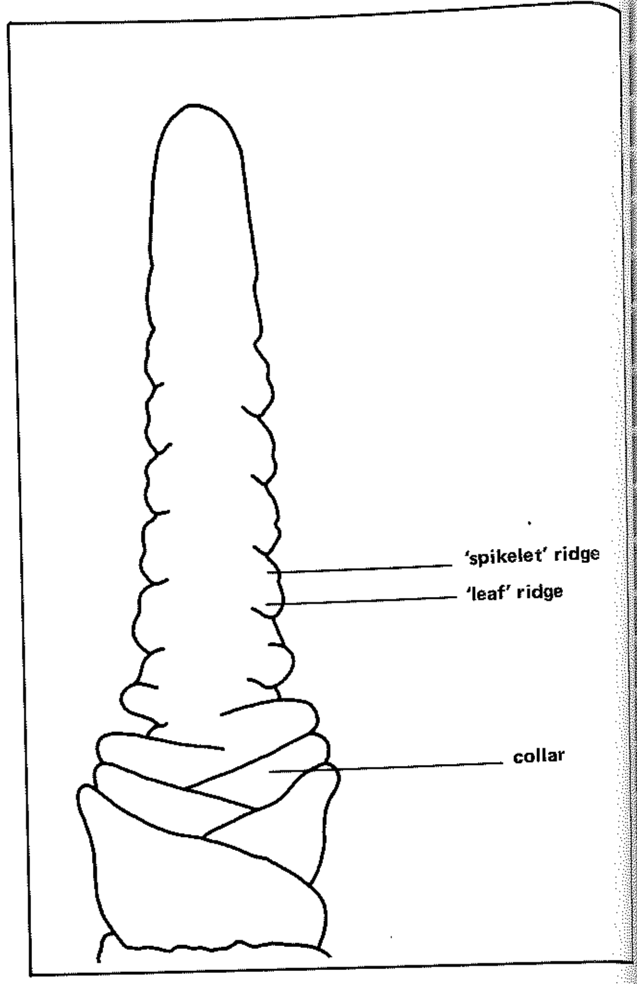


Fig. 5.3. Diagram

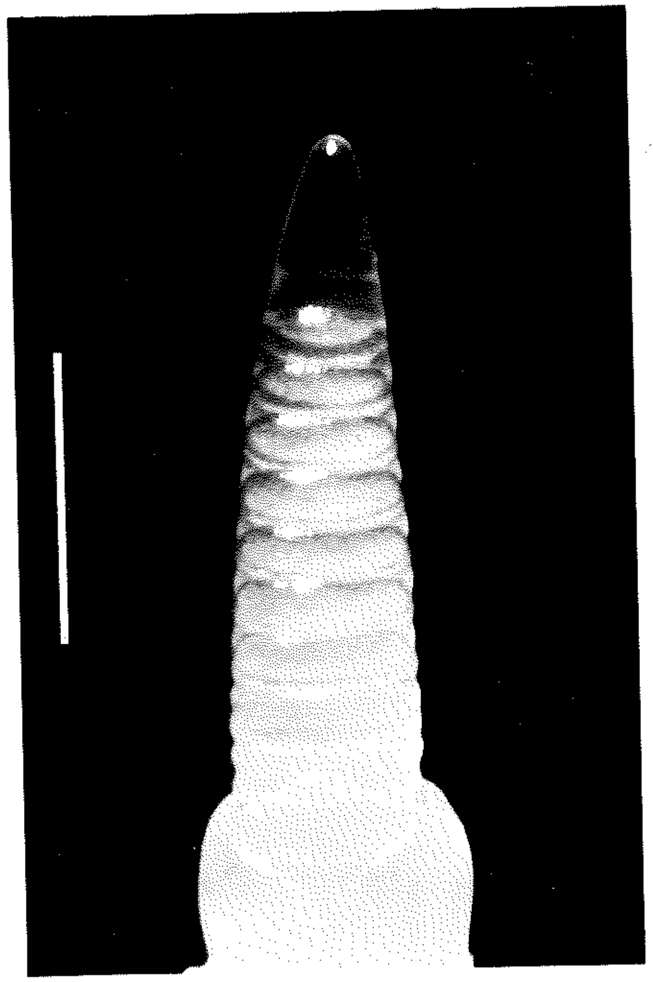


Fig. 5.4. 0.5mm scale bar

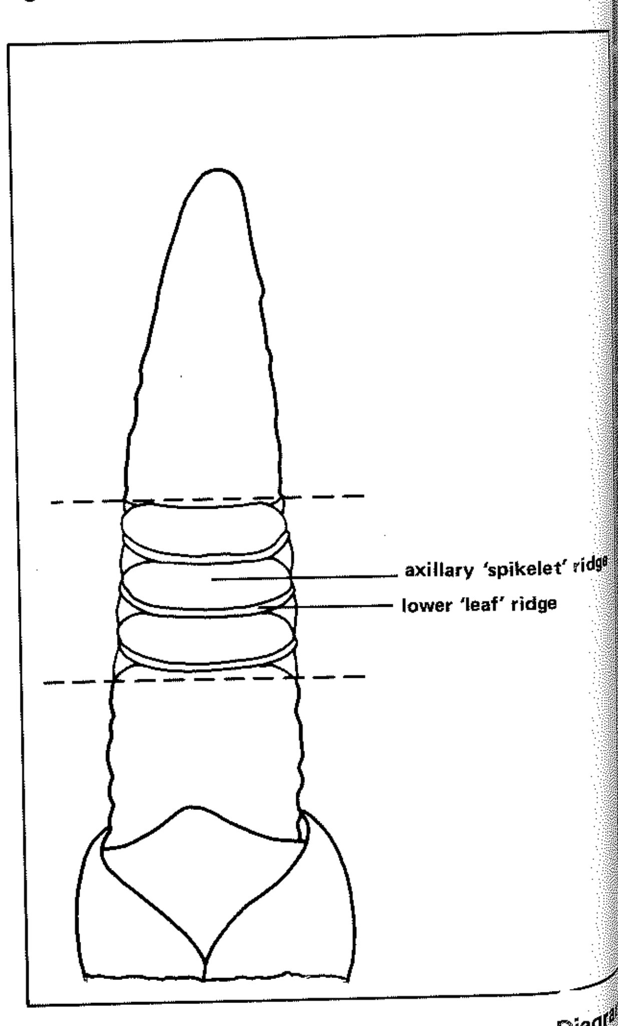


Fig. 5.4. Diagram

5. APICAL DEVELOPMENT
Barley

Double ridge stage

The appearance of double ridges is considered to be an important stage in the plant life cycle. At this stage the spikelet primordia can be seen clearly and this event is often referred to as 'floral initiation', although about half the total number of spikelet primordia have already been formed by this time.

In Figure 5.3 the profile view of an apex at double ridge stage is shown. The apex is about 1mm long and has an elongated cylindrical shape. The stage is so named because a leaf primordium ridge and a spikelet primordium ridge together form a double structure. In the apex illustrated the primordia at the base of the shoot apex are clearly leaflike. The lowermost one would probably have grown to become the flag leaf and the one above it, the collar. The relation between the leaf and spikelet ridge changes with position on the apex and in the upper third the leaf ridge is not easily seen.

In Figure 5.4 the apex has been rotated through 90° about its long axis and the face view is shown. At the base, the margin of the leaf can be seen overlapping the leaflike structure which would have become the collar. The leaf ridge extending around the base of the upper spikelet ridge is visible in the mid-part of the apex. As the apex develops further each spikelet primordium grows and eventually obliterates the leaf ridge.

A plant at this stage will generally have between four and nine leaves emerged on the main shoot, depending on sowing date and variety.

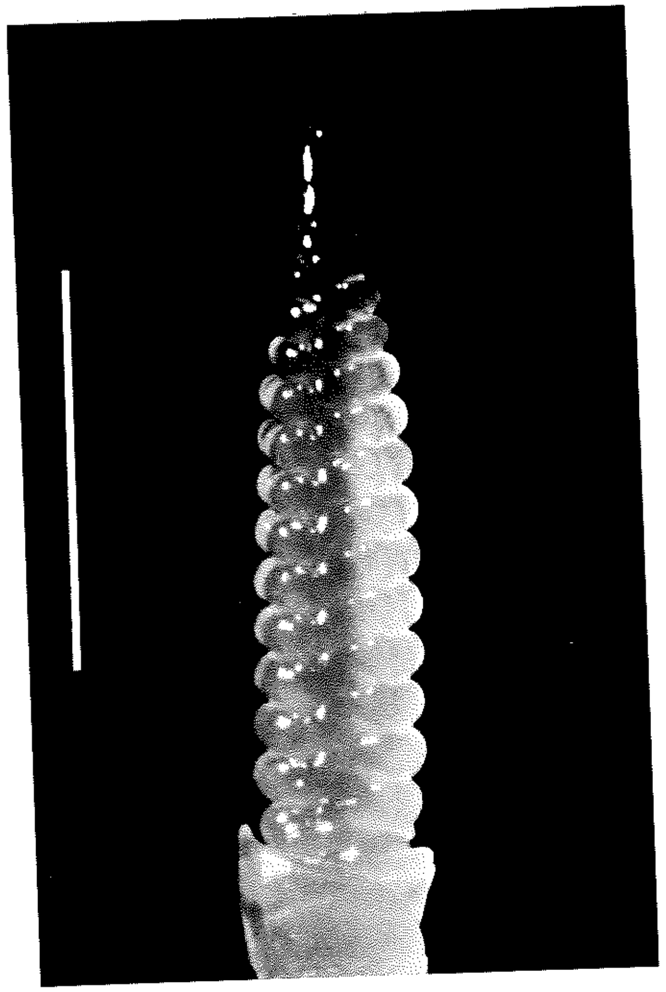


Fig. 5.5. 1mm scale bar

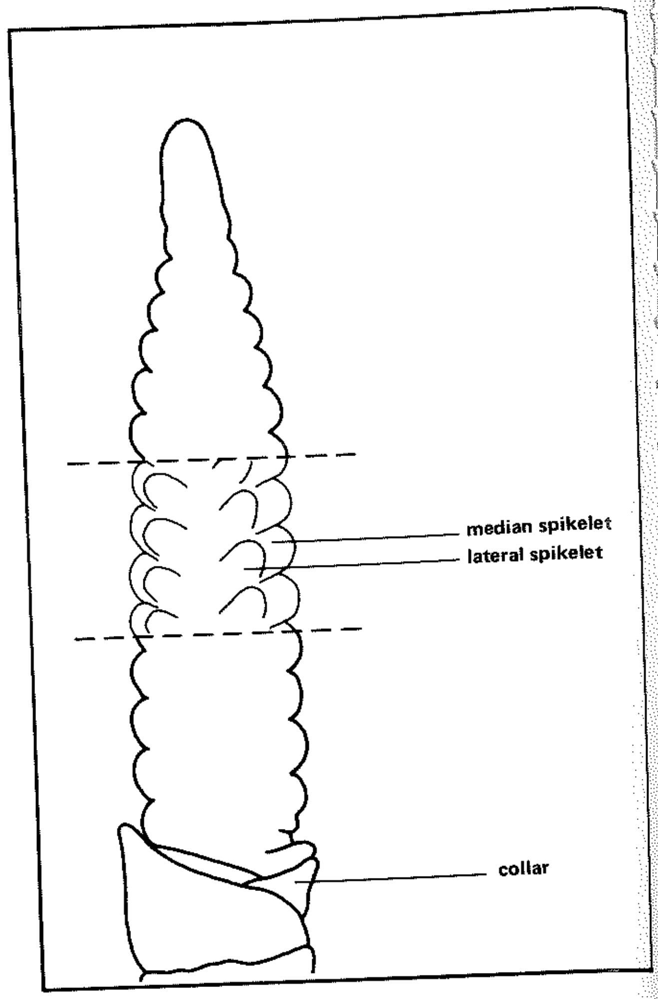


Fig. 5.5. Diagram

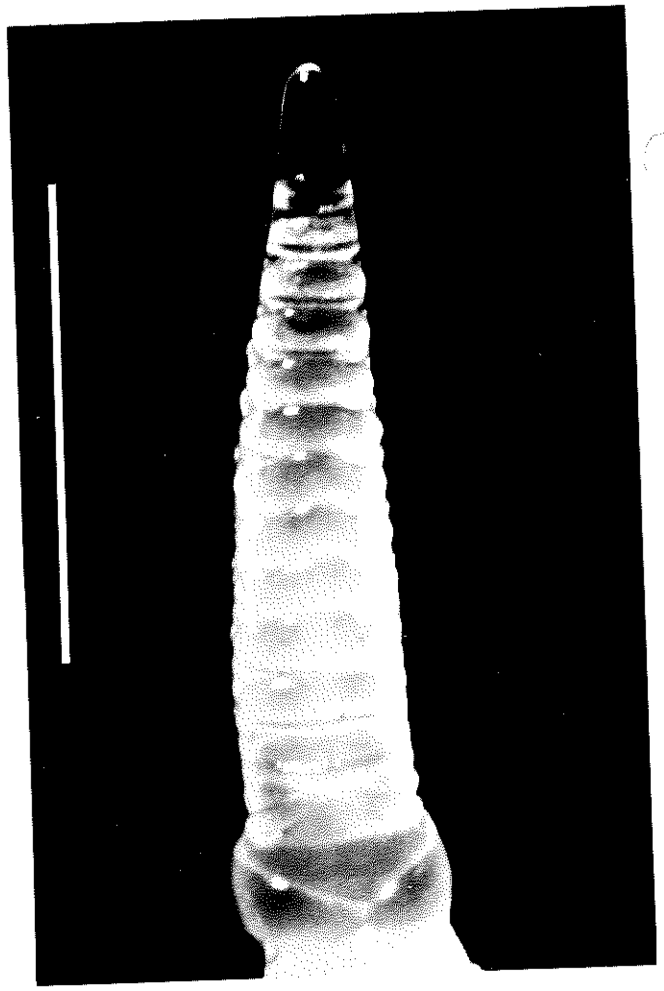


Fig. 5.6. 1mm scale bar

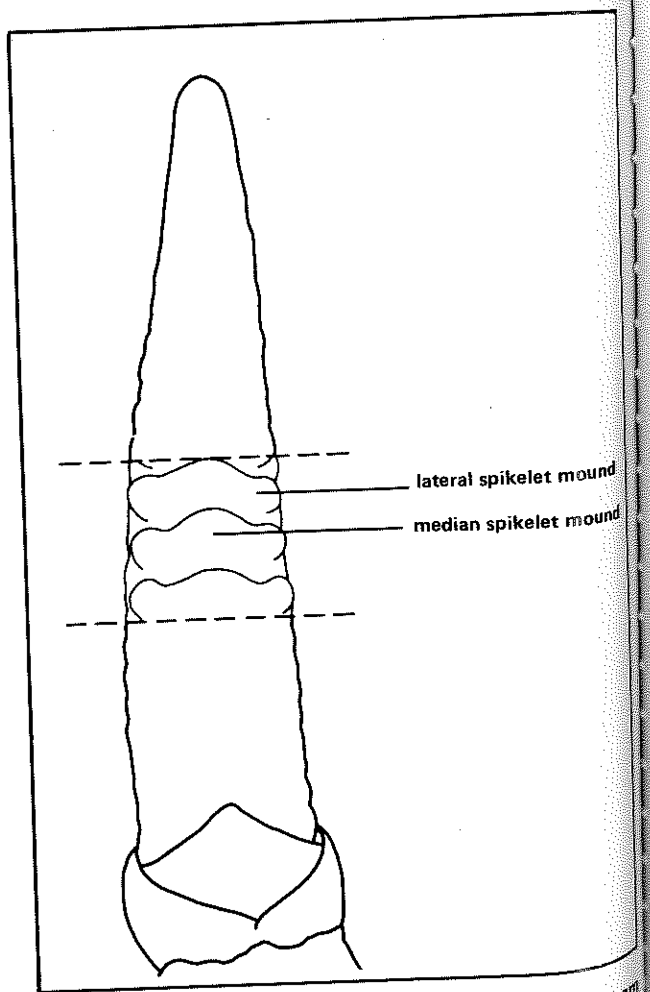


Fig. 5.6. Diagram

5. APICAL DEVELOPMENT
Barley

Triple mound stage

At the triple mound stage the spikelet primordium part of the double ridge has differentiated into three distinct bumps or mounds. The central mound will form the median spikelet while the two mounds flanking it will become the lateral spikelets. In two-row barley varieties these lateral spikelets are sterile but in six-row varieties they develop in the same way as the median spikelet and are fertile.

Figure 5.5 illustrates the profile view of an apex at this stage. In the mid-part of the ear, spikelet primordia are prominent and the lower leaf ridge of the double ridge can no longer be seen. At the base the leaf primordium part of the double ridge can still be distinguished and the form of the developing collar is clearly related to a leaf. Although in the photograph triple mounds are visible it is often easier to identify this stage from the face view.

Figure 5.6 shows the face view of an apex at triple mound. In the mid-part of the apex the sinuous outline of the three primordial structures is apparent. At the base and the tip of the shoot apex the typical double ridge form of the primordia can still be seen, showing that even at this early stage the mid-part is developmentally the most advanced.

An apex at the triple mound stage is about 1.5mm long.

A plant at this stage will generally have between five and nine leaves on the main shoot, depending on sowing date and variety.

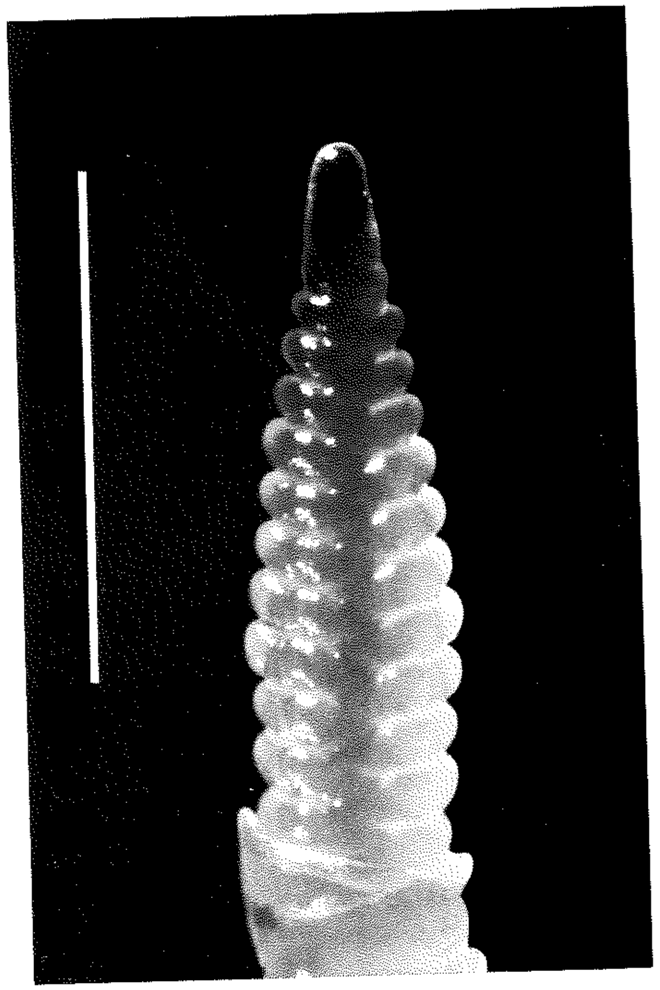


Fig. 5.7. 1mm scale bar

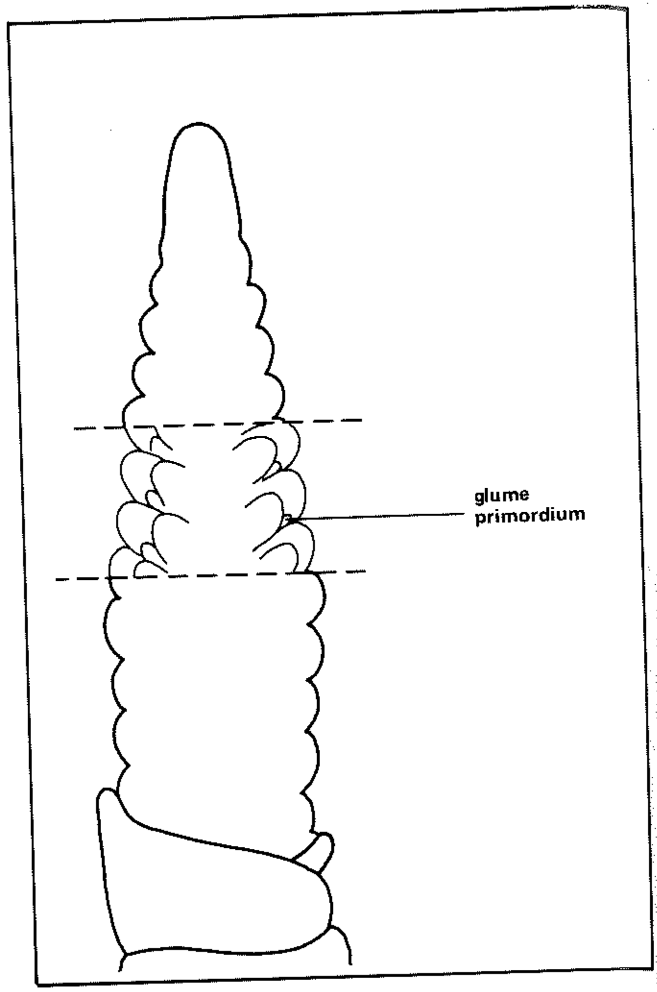


Fig. 5.7. Diagram

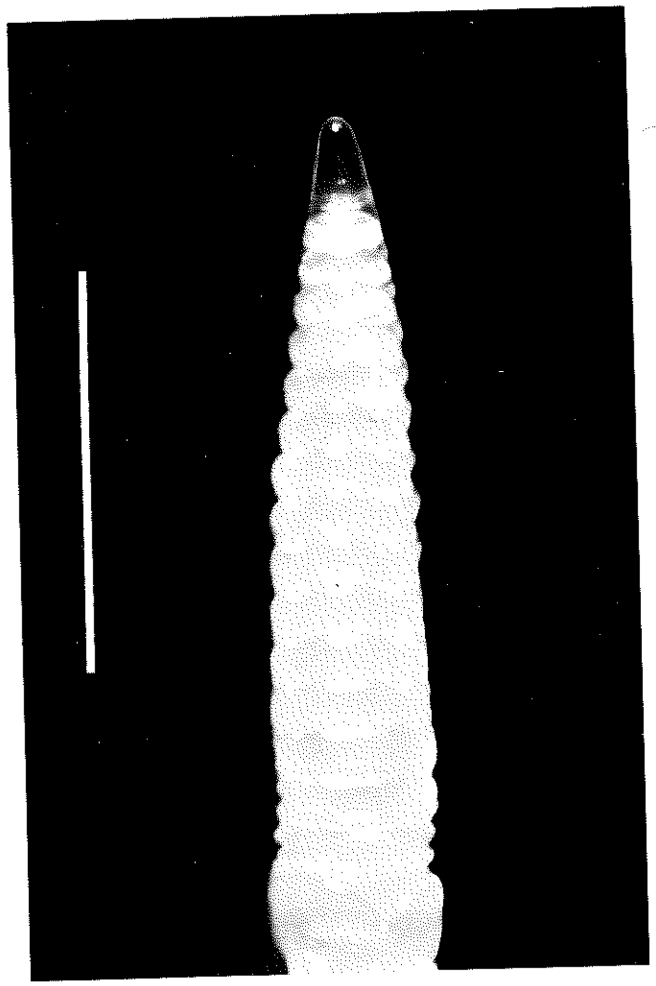


Fig. 5.8. 1mm scale bar

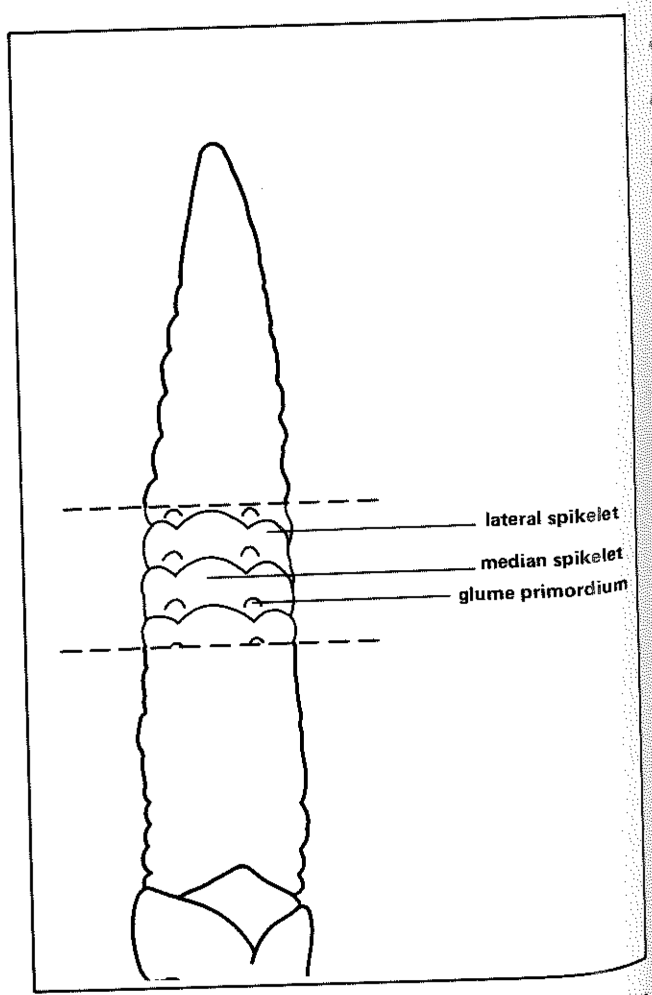


Fig. 5.8. Diagram

5. APICAL DEVELOPMENT
Barley

Glume primordium stage

This and subsequent stages of the barley shoot apex are characterised by the appearance of the various structures of the median spikelet. The first structures to differentiate are the glumes; this stage lasts only for a short time and merges into the next stage (lemma primordia). The glume primordia are small, as are the mature glumes in barley, and they are rather difficult to see.

The profile view of an apex at glume primordium stage is shown in Figure 5.7. Glume primordia, which are little more than small bumps, differentiate first in the mid-part of the apex. They are more easily detected when the apex is examined in face view.

In face view (Fig. 5.8) the two small glume primordia are found on the lower flanks of the median spikelet primordium close to the junction with the lateral spikelet primordia.

A plant at this stage will generally have between five and 10 leaves emerged on the main shoot, depending on sowing date and variety.

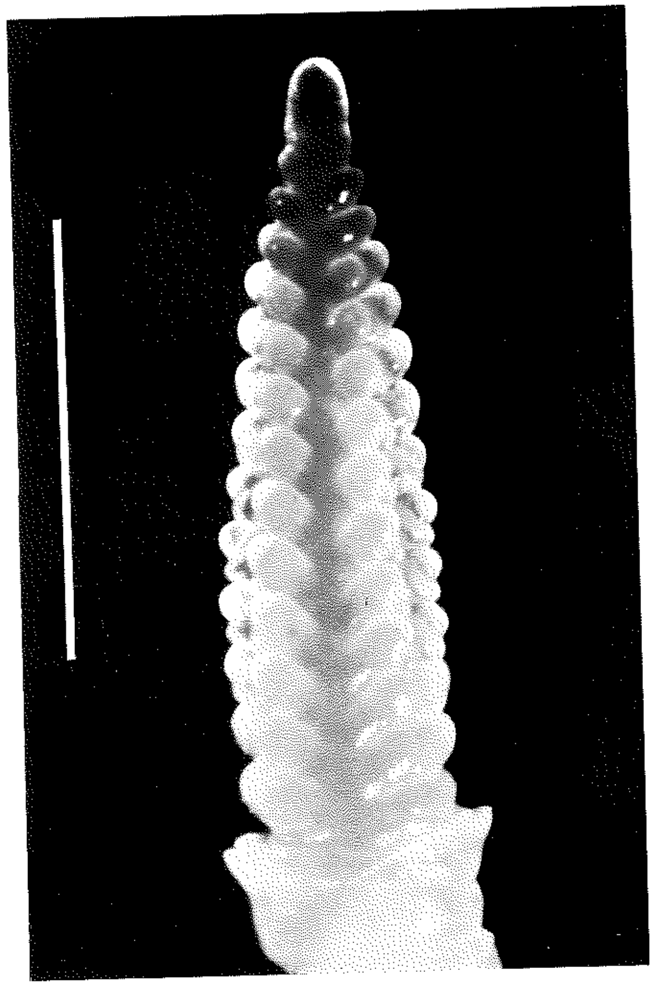


Fig. 5.9. 1mm scale bar

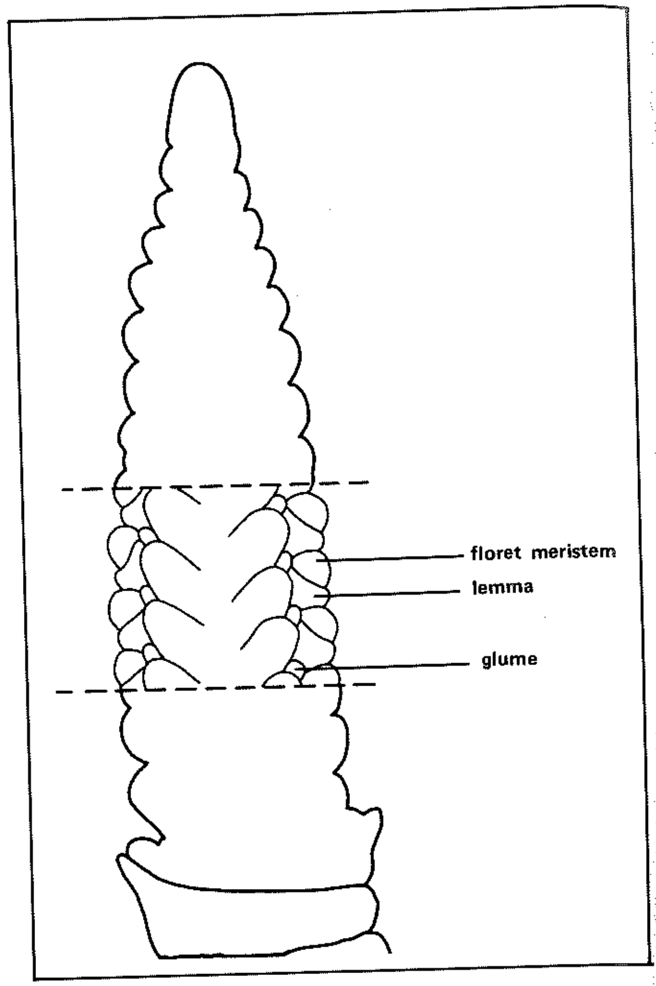


Fig. 5.9. Diagram

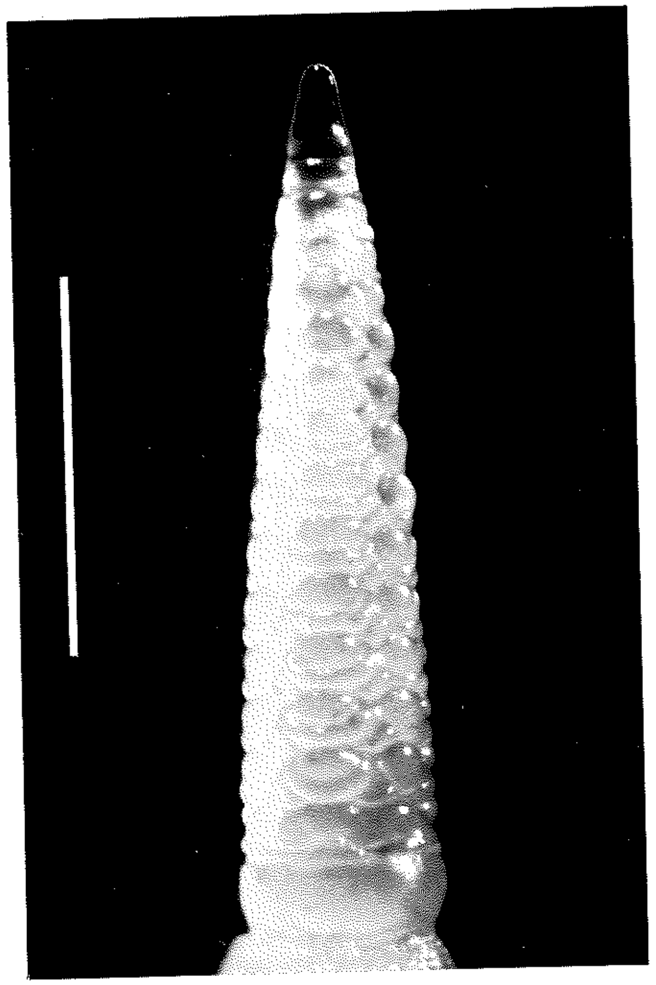


Fig. 5.10. 1mm scale bar

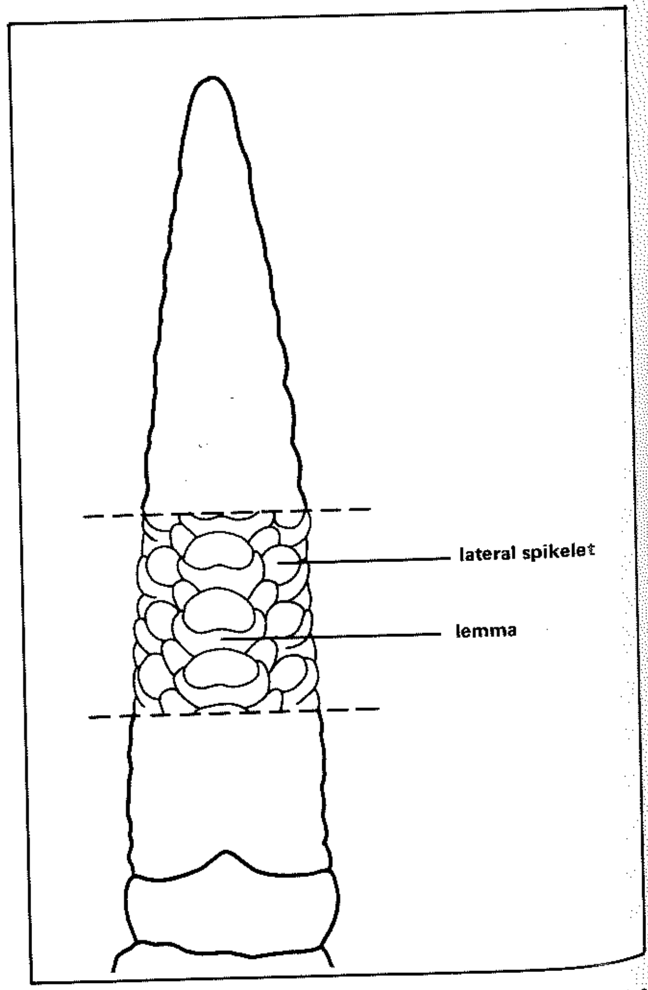


Fig. 5.10. Diagram

5. APICAL DEVELOPMENT
Barley

Lemma primordium stage

At the stage when the lemma primordia appear the median and lateral spikelets are clearly differentiated into separate structures. The lemma is the most prominent structure of the mature spikelet, ensheathing the sexual organs, and the primordium from which it develops is correspondingly large.

The diagram (Fig. 5.9) shows an apex at lemma primordium stage, in profile. In the mid-part of the ear, two ranks of lateral spikelets can be seen, with the median spikelets in profile. The glumes are now easily distinguished and the lemma primordium is visible as a prominent ridge below the floret meristem (which will later initiate the stamens, carpel, etc.). At the tip of the apex, primordia are younger and less well developed and the dome continues to initiate more primordia, the youngest of which can be seen as a bump on the left-hand flank.

In face view (Fig. 5.10) the lemma is seen as a crescent-shaped structure, which extends around behind the spikelet meristem. The glume primordia are situated on the lower right and left flanks of the lemma primordium and the ridges which can be seen on the lateral spikelet primordia are the lemmas of the lateral spikelets.

A plant at this stage will generally have between five and 10 leaves emerged on the main shoot, depending on sowing date and variety.

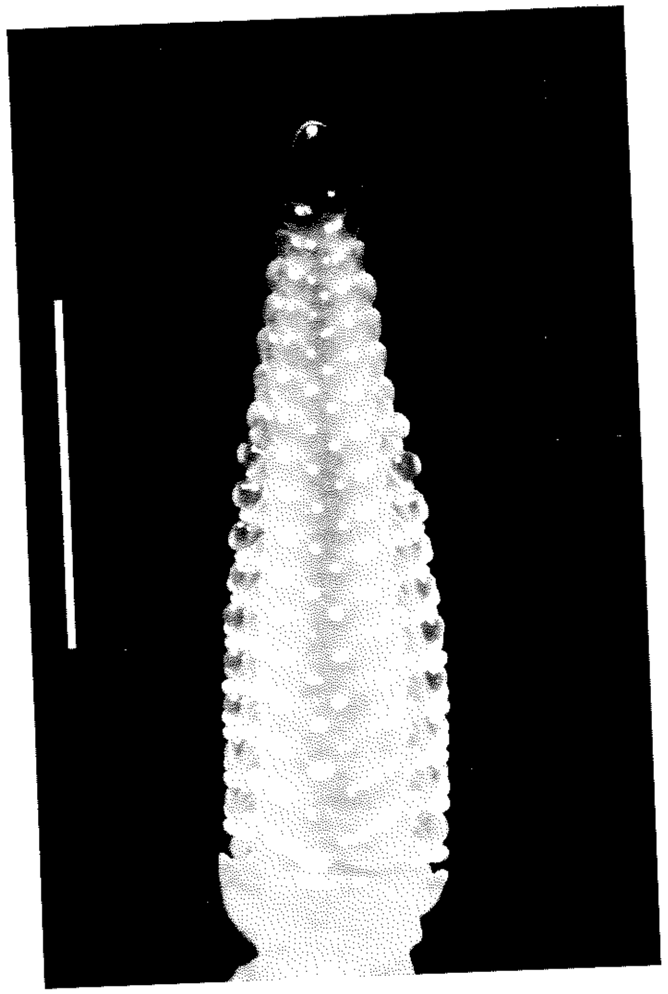


Fig. 5.11. 1mm scale bar

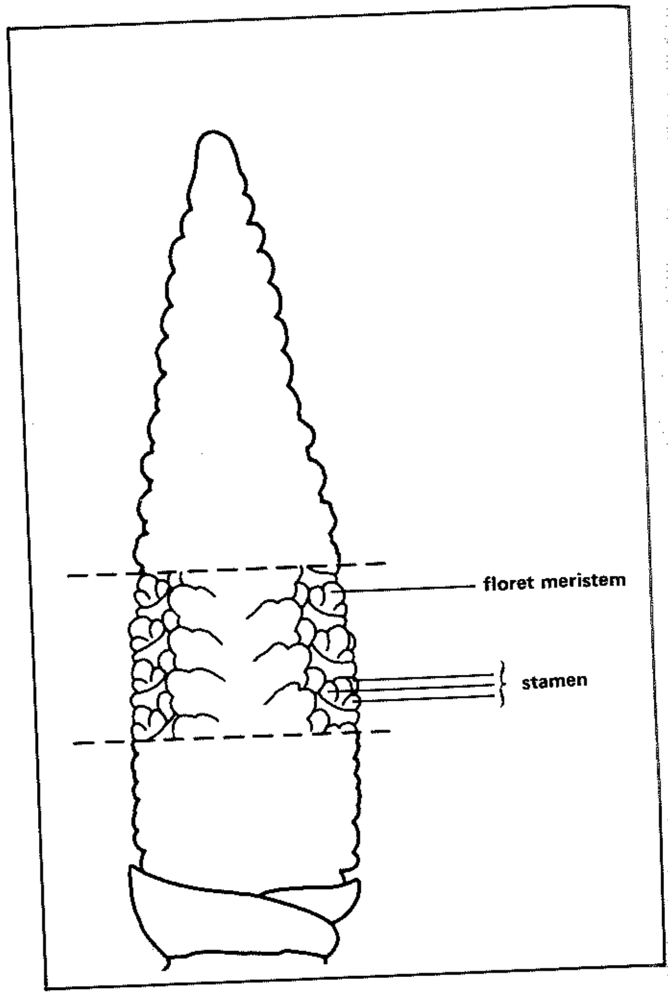


Fig. 5.11. Diagram

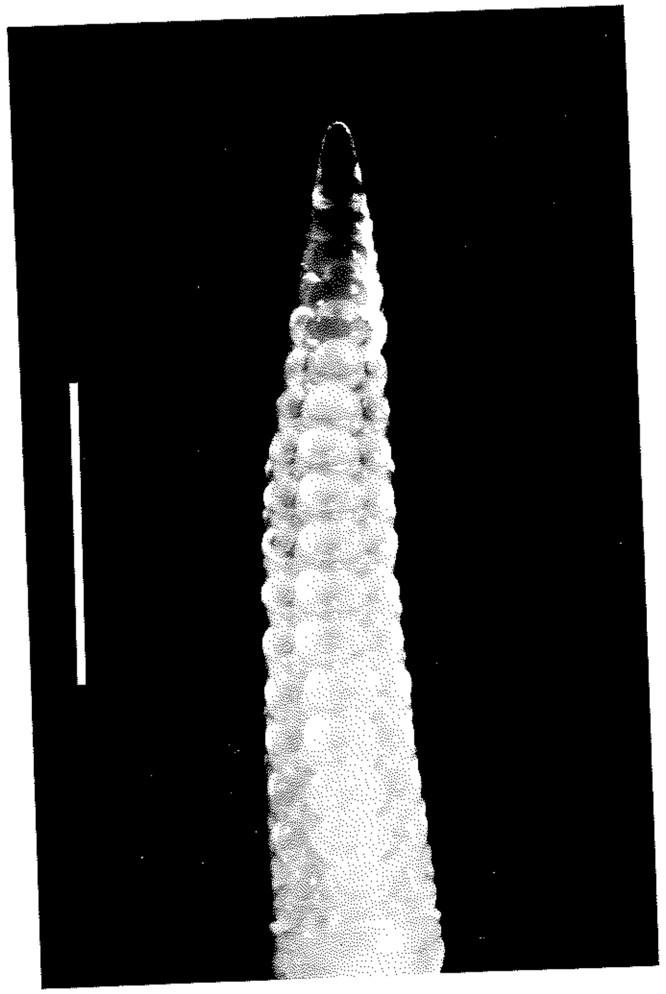


Fig. 5.12. 1mm scale bar

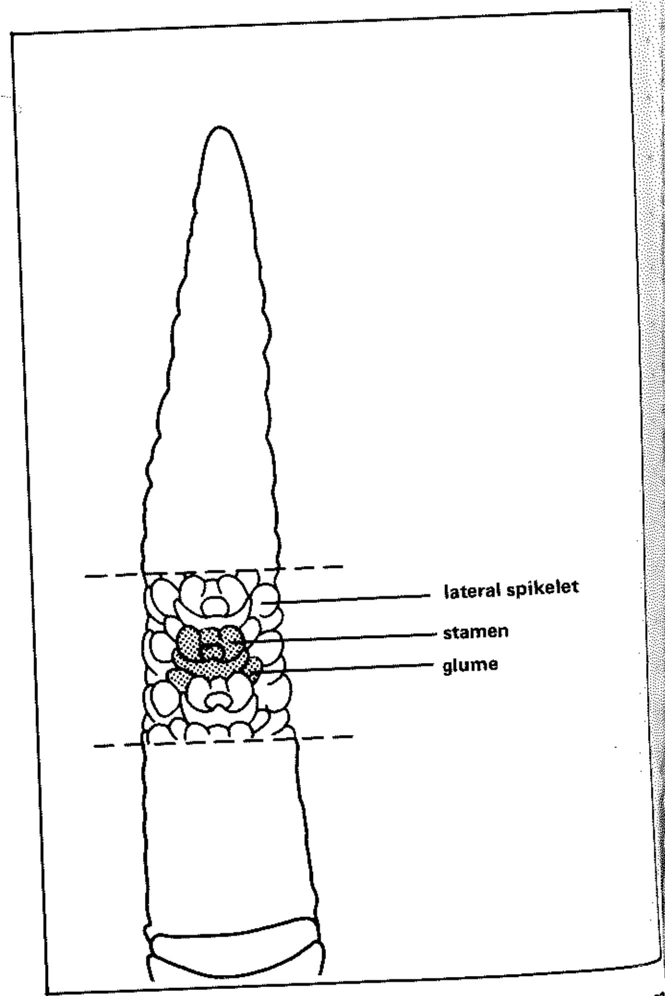


Fig. 5.12. Diagram

5. APICAL DEVELOPMENT
Barley

Stamen primordium stage

The appearance of the stamen primordia indicates that the embryo spikelet is almost complete. Shortly after stamen primordia are formed the carpel primordium begins to form. The primordia of the other floral parts, the lodicule, palea and rachilla also develop about this time but they are hidden by the other structures and cannot easily be seen (see chapter 7).

In the mid-part of the apex shown in profile view in Fig. 5.11 the meristematic dome of the spikelet, encompassed by the crescent-shaped lemma, has differentiated to form stamen primordia.

The position of stamen primordia can be more easily seen in face view. In Fig. 5.12 diagram one median spikelet has been shaded. Three stamen primordia, one in the anterior median position and two posterior lateral stamens can be seen. Soon after this stage the carpel is initiated between the two posterior stamens. Two lodicule primordia form beneath the lemma one on either side of the anterior stamen, and the palea and rachilla develop but are hidden behind the stamens and the carpel.

A plant at this stage will generally have between six and 11 leaves emerged on the main shoot, depending on sowing date and variety.

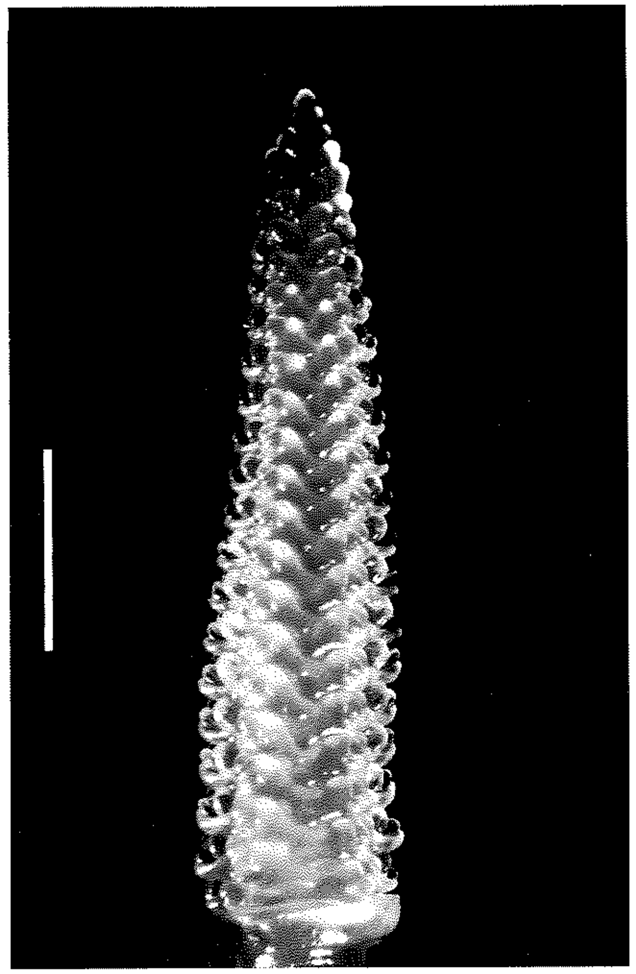


Fig. 5.13. 1mm scale bar

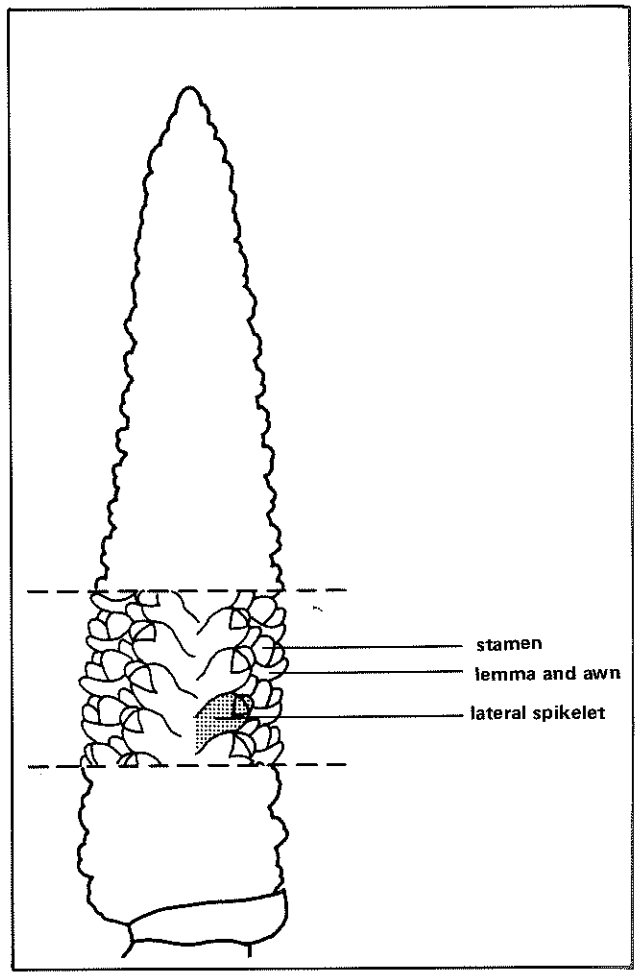


Fig. 5.13. Diagram

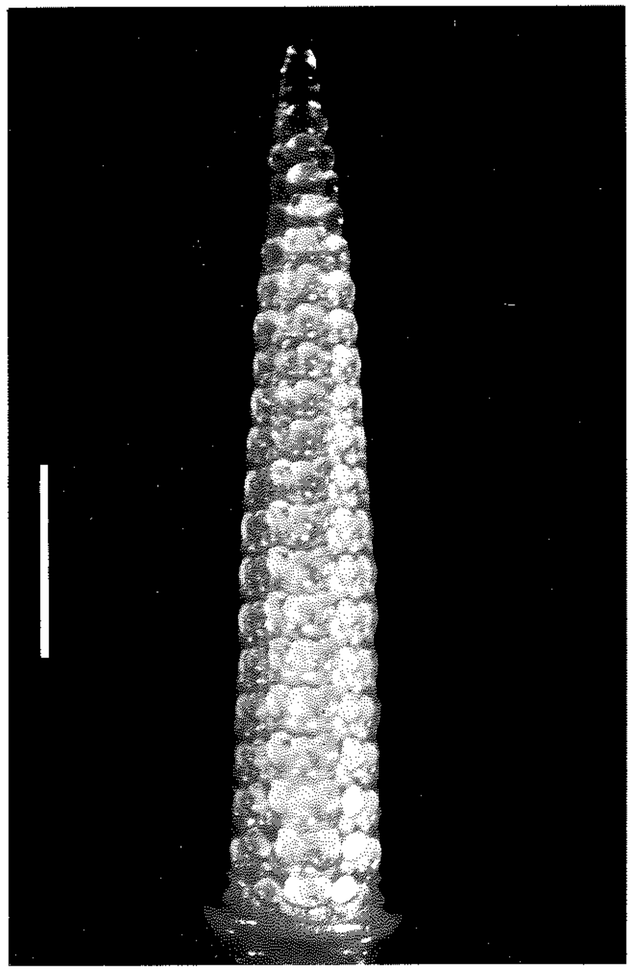


Fig. 5.14. 1mm scale bar

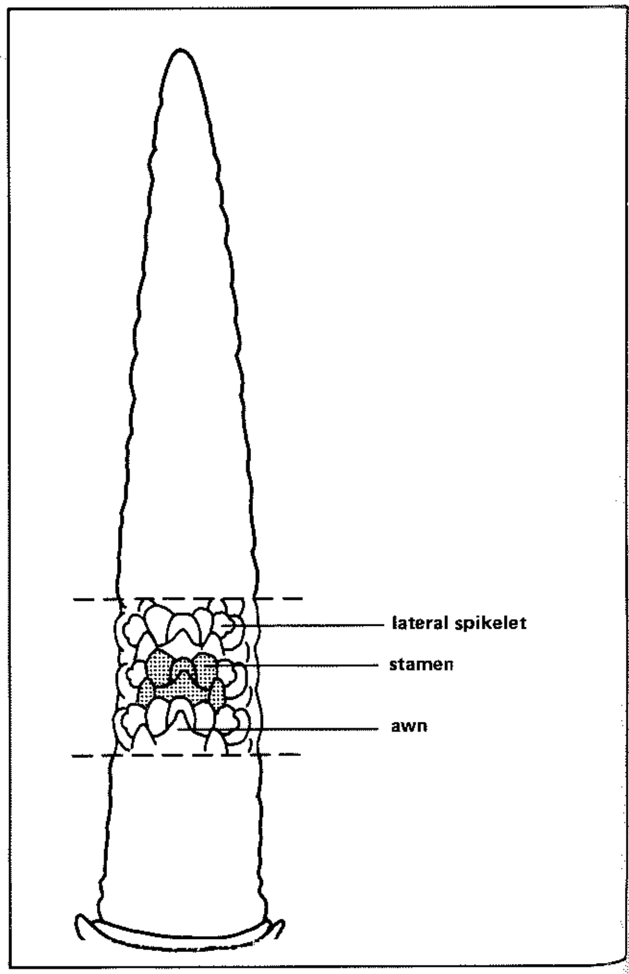


Fig. 5.14. Diagram

5. APICAL DEVELOPMENT
Barley

Awn primordium stage (maximum number of primordia)

At this stage the embryo ear has its full complement of spikelet primordia and the initiation of all the structures within the median spikelet is complete. At the tip of the ear the meristematic dome has ceased activity and is relatively small.

In profile view (Fig. 5.13) the awn primordia look like horns which grow from the tip of the lemma and curve over the stamen primordia. This ear has about 45 spikelet primordia most of which, although they have been formed over a long period, are at about the same stage of differentiation. At the tip of the ear the primordia are less well developed and the last formed ones are no more than ridges on the flanks of the dome. The collar can be seen at the base of the ear where the spikelet primordia are also less advanced than those in the mid-region.

A plant at this stage will generally have between seven and 12 leaves emerged on the main shoot depending on date of sowing and variety.

In the diagram of Fig. 5.14 showing the face view of an apex, a median spikelet has been shaded. The development of the tip of the lemma to produce the awn can be seen. The awns grow rapidly, relative to the rest of the lemma, soon becoming as long as the ear and developing the minute spicules which give the mature awn its unpleasant roughness. The lateral spikelets develop in a similar way, but later than the median spikelets. In Fig. 5.13, a typical two-row barley, the glumes and the lemma of the lateral spikelets can be seen in embryo form and anthers and carpel etc. are produced later but they do not develop fully and so these spikelets are sterile. Figure 5.15 shows, in profile, a six-row barley at this stage. The young awns of the laterals are visible, although they are not as long as the median awns.

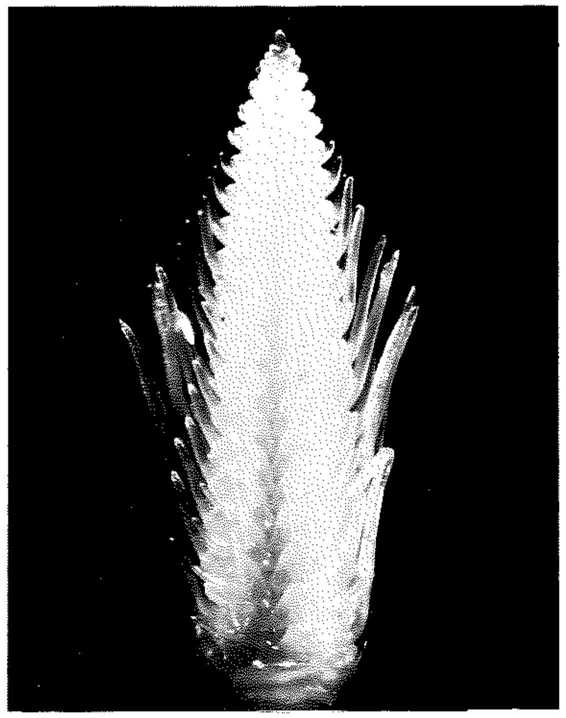


Fig. 5.15.

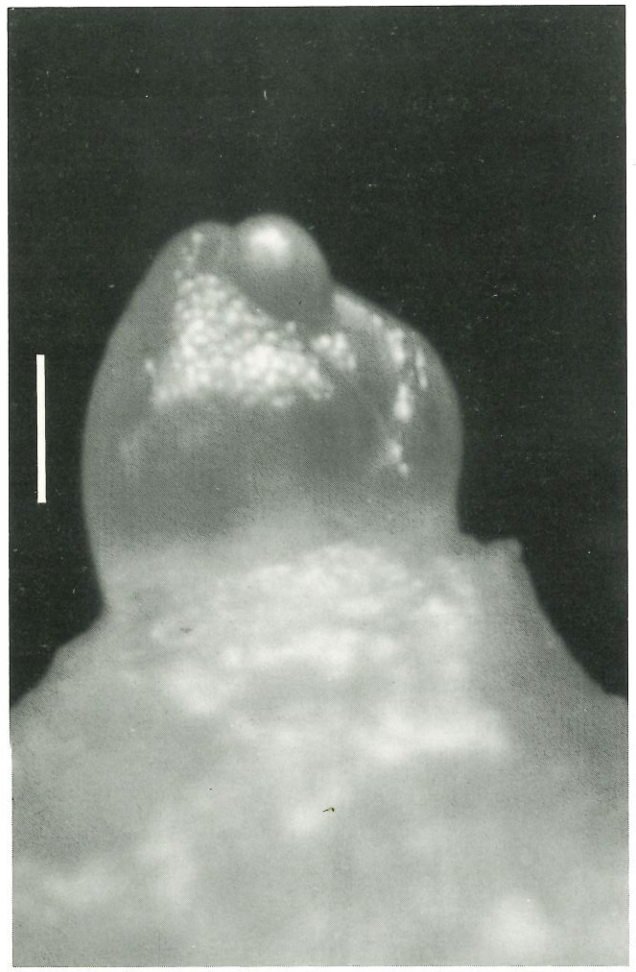


Fig. 5.16. 0.25mm scale bar

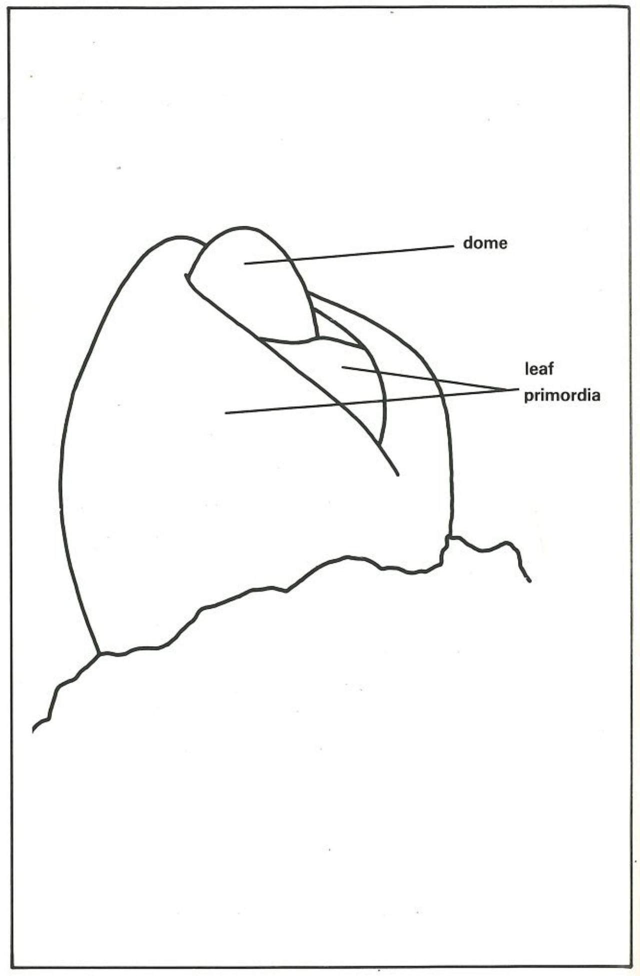


Fig. 5.16 Diagram

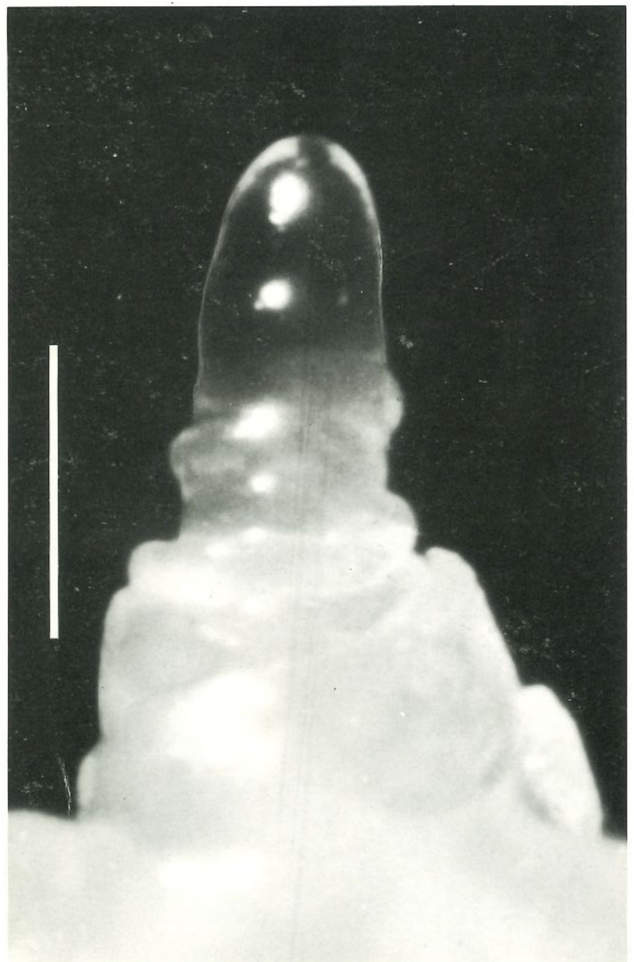


Fig. 5.17. 0.25mm scale bar

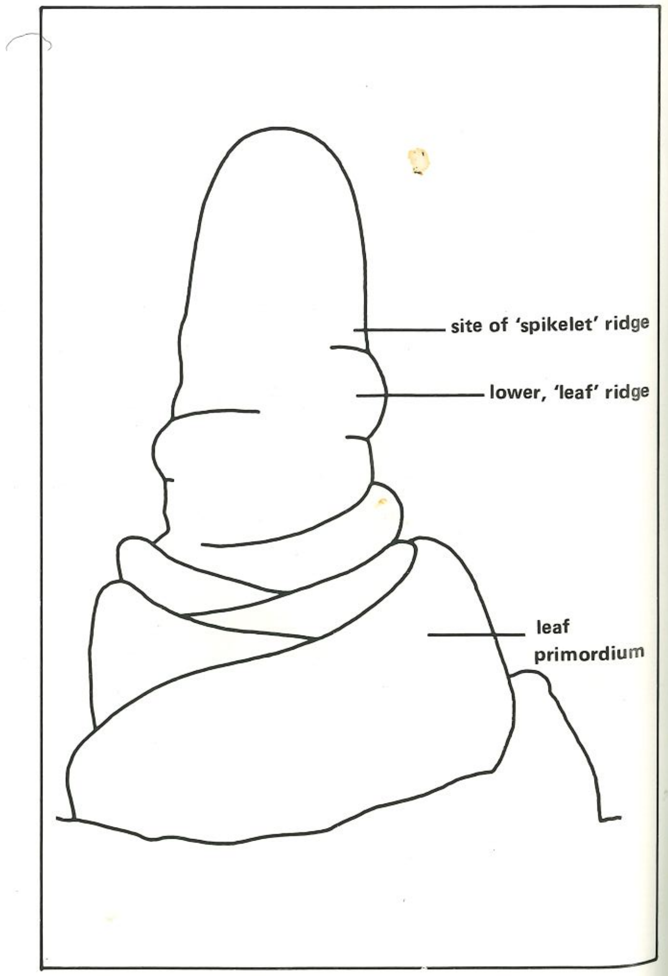


Fig. 5.17. Diagram

5. APICAL DEVELOPMENT
Wheat

Vegetative Stage

A shoot apex dissected from a seedling wheat plant in which the first leaf is just emerging is about 0.2mm long and conical in shape (Fig. 5.16). At the apex of the cone is a smoothly rounded meristematic dome. The crescent-shaped folds of tissue on the flanks of the shoot apex are leaf primordia which grow up within the sheaths of the expanded leaves. During the first part of the life cycle of the wheat plant the dome initiates leaf primordia; later it initiates spikelet primordia.

The wheat plant at this stage is a seedling and the apex will remain at the vegetative stage from germination until between four and eight leaves have emerged on the main shoot depending on sowing date and variety. Generally the early sown winter varieties will have the highest number of leaves at a given stage and spring varieties sown in the spring the lowest. This is also true for the stages on the following pages where numbers of emerged leaves are given.

As the plant grows the form of the apex changes and becomes more cylindrical. The dome initiates primordia more quickly than they grow to form mature leaves and so primordia accumulate on the shoot apex. The elongation of the shoot apex marks the beginning of the floral phase when spikelets are initiated. Fig. 5.17 shows the profile view of a shoot apex at the late vegetative stage. Primordia seen at the base will grow into leaves but the ridges towards the dome are leaf primordia whose development will be arrested at an early stage. These ridges are often poorly defined and difficult to see at this stage. Growth of the tissue between the ridges will give rise to the next stage, double ridges. The apex at this stage is about 0.5mm long.

Vegetative and early floral stages of barley and wheat are similar. Differences only become distinguishable as the spikelets develop. (i.e. the triple mound stage in barley compared with the glume primordium stage in wheat.)

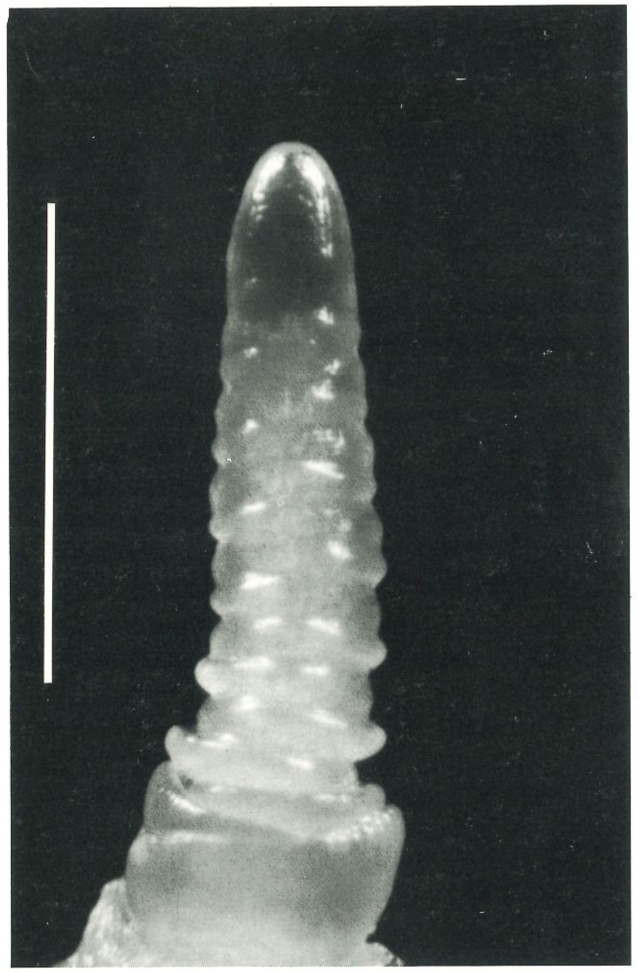


Fig. 5.18. 0.5mm scale bar

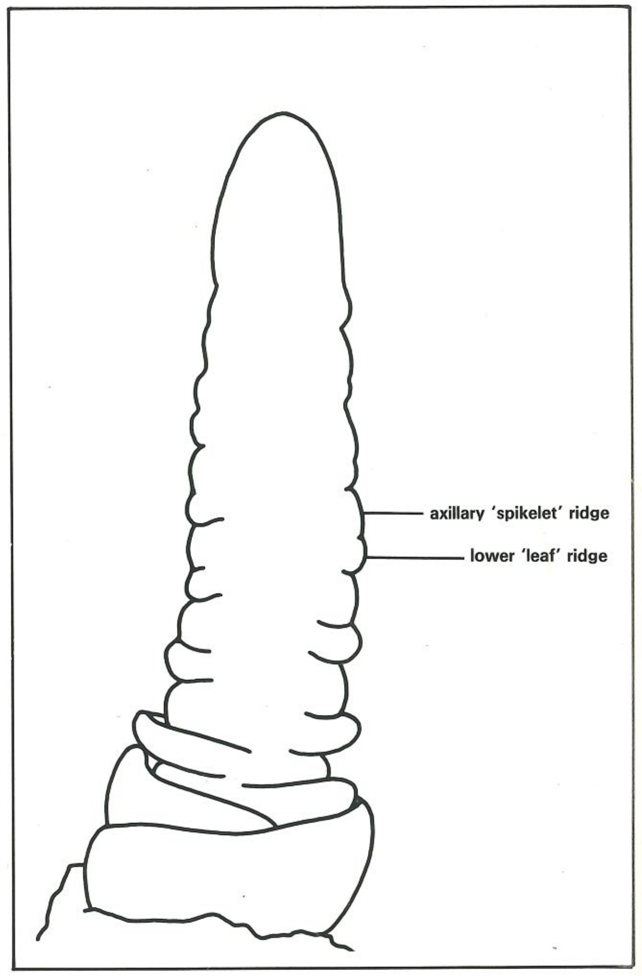


Fig. 5.18. Diagram

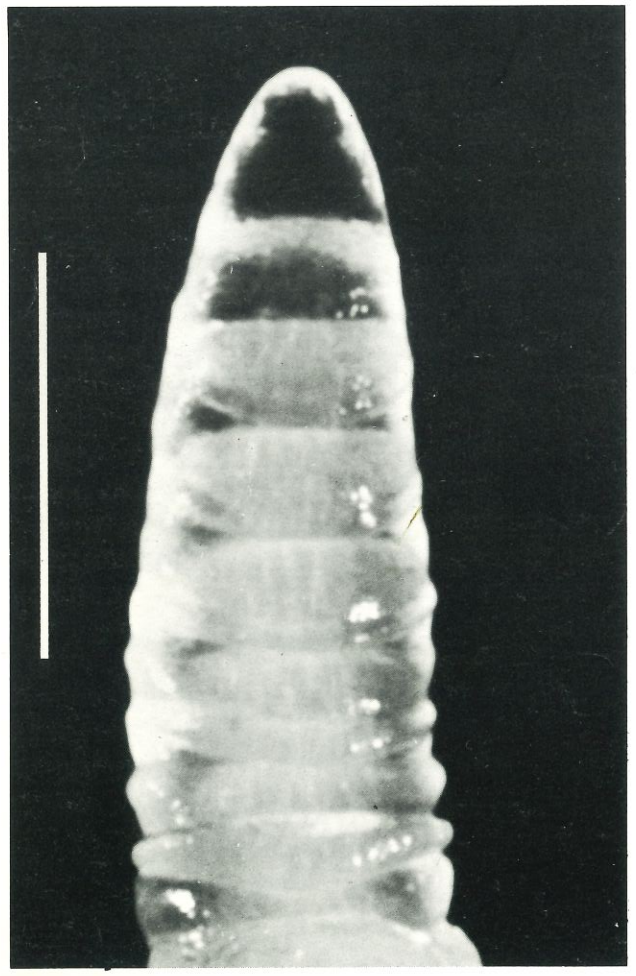


Fig. 5.19. 0.5mm scale bar

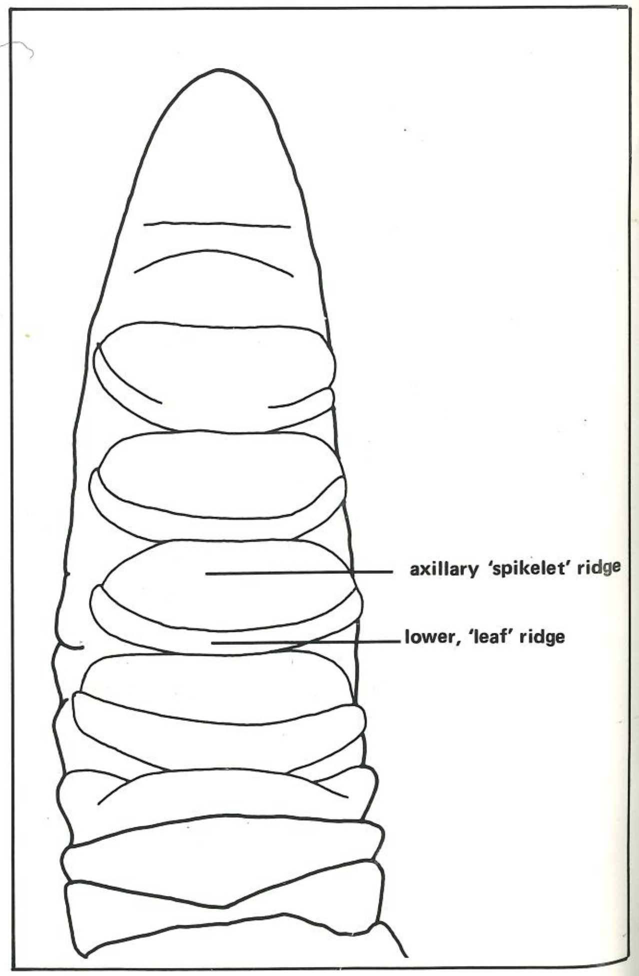


Fig. 5.19. Diagram

5. APICAL DEVELOPMENT
Wheat

Double ridge stage

At this stage the primordia which will differentiate to become spikelets are visible.

In Fig. 5.18 the profile view of an apex at double ridge stage is shown. It is elongated and bears several primordia and in the mid-part the characteristic double ridge form of the primordia can be seen. The lower, less prominent ridge is a leaf primordium and the upper, larger ridge is the primordium which will develop into the spikelet.

In face-view (Fig. 5.19) the primordia can be seen to extend around almost half the circumference of the shoot apex. At the base the leaf-like nature of the lower ridge can be seen, but towards the dome the lower leaf ridge becomes smaller, relative to the spikelet ridge and it is scarcely visible in the two uppermost 'double ridges'.

The double ridge stage lasts for a relatively long time and as the apex progresses towards the next stage, glume primordia, the upper spikelet primordium grows bigger and bulges over the leaf ridge which does not develop further and soon can no longer be seen in the mid-part of the apex.

The shoot apex is about 1.2mm long and almost one half of the primordia which will become spikelets have been initiated.

A plant at this stage will generally have between four and 10 leaves emerged on the main shoot depending on date of sowing and variety.

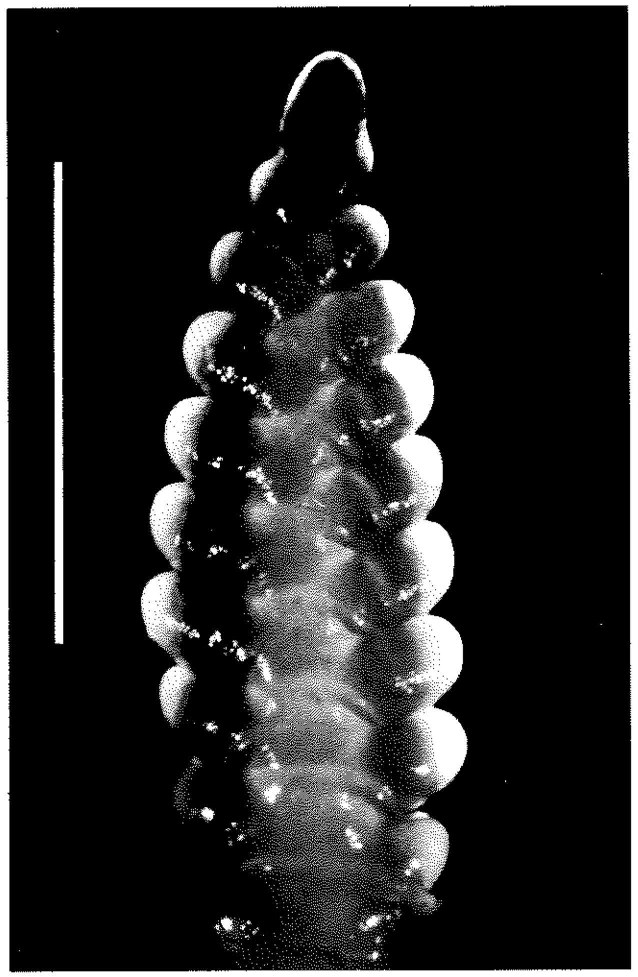


Fig. 5.20. 1mm scale bar

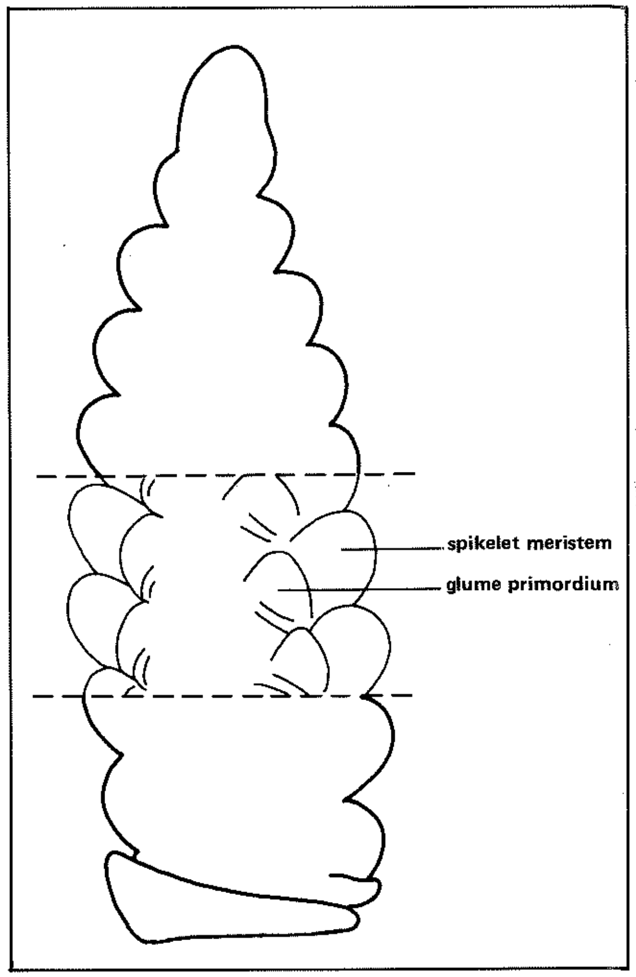


Fig. 5.20. Diagram

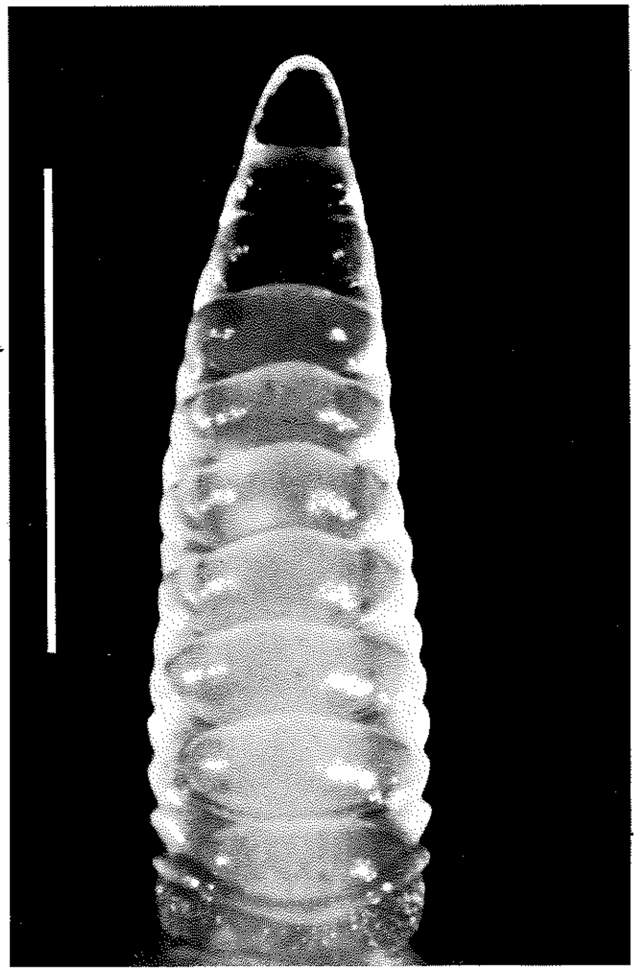


Fig. 5.21. 1mm scale bar

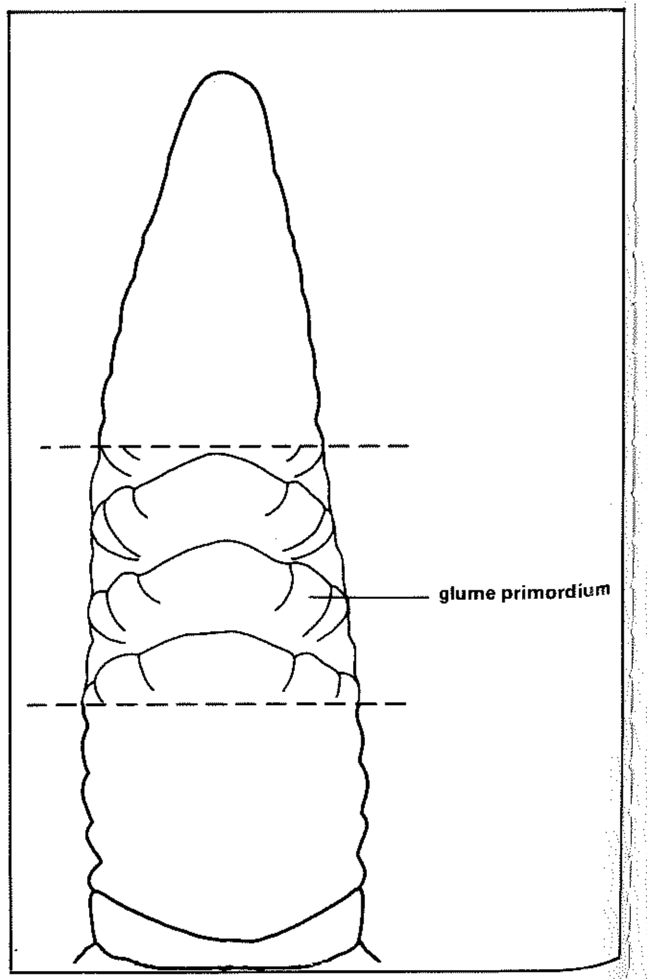


Fig. 5.21. Diagram

5. APICAL DEVELOPMENT
Wheat

Glume primordium stage

A spikelet of wheat contains several florets, enclosed in two large, strong glumes. In barley there is only one floret per spikelet and this difference between the species is evident in the apices at this stage. The shoot apex of wheat is shorter and stouter with fewer spikelets and the glume primordia are much larger and more easily seen than in barley.

The profile view of an apex at glume primordium stage is shown in Fig. 5.20. The apex is spindle shaped and on each of the larger, most advanced spikelets in the mid-part of the apex, one of the two glumes formed on each spikelet can be seen.

In face view (Fig. 5.21) the two glume primordia can be seen as ridges on the left and right flanks of the spikelet meristem. Each of the ridges will eventually extend around the semi circumference of the spikelet and overlap with the opposite glume at the bottom and top of the spikelet primordium.

A plant at this stage will generally have between five and 10 leaves emerged on the main shoot depending on sowing date and variety.

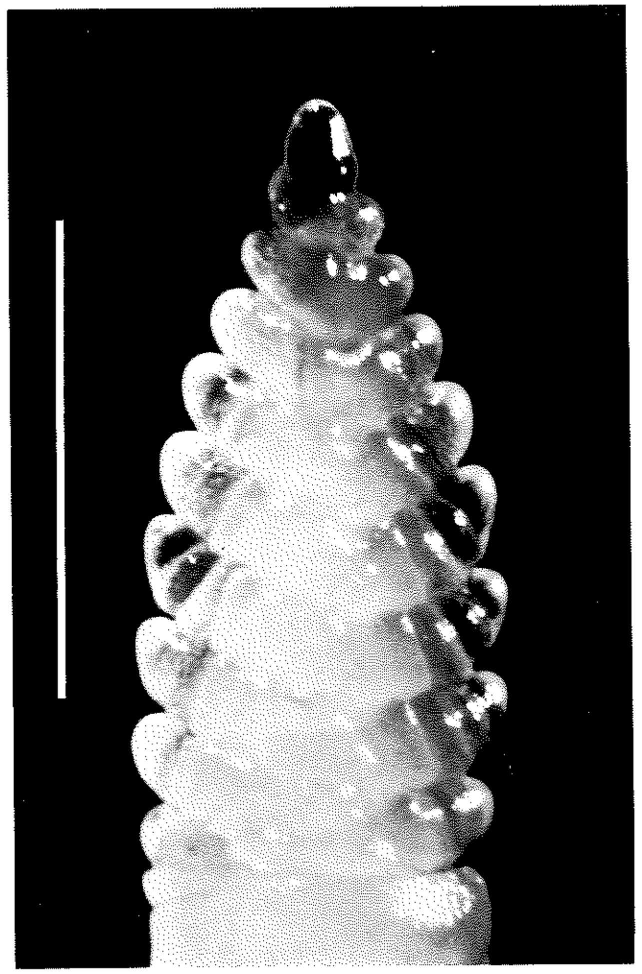


Fig. 5.22. 1mm scale bar

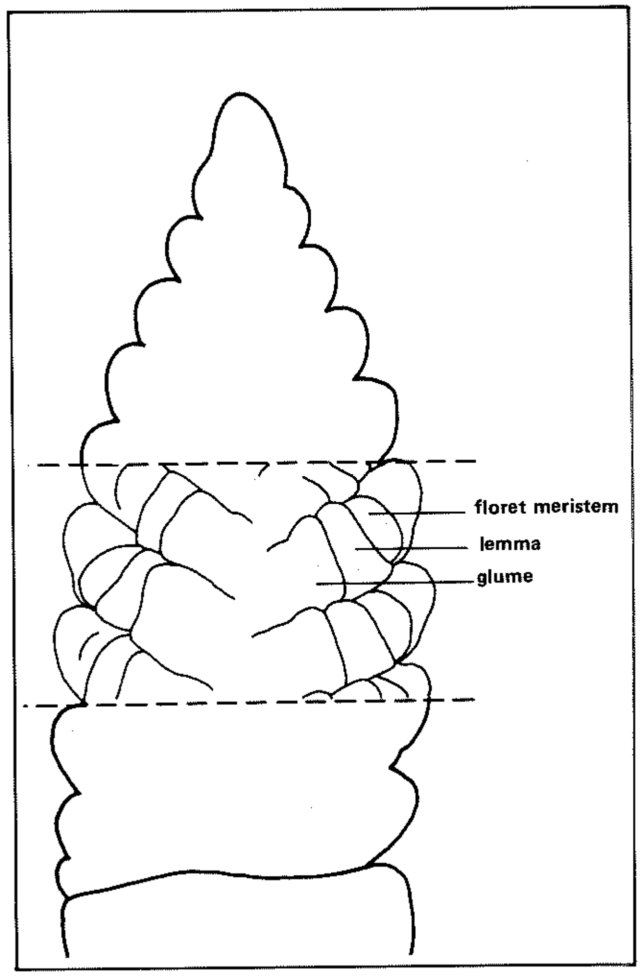


Fig. 5.22. Diagram

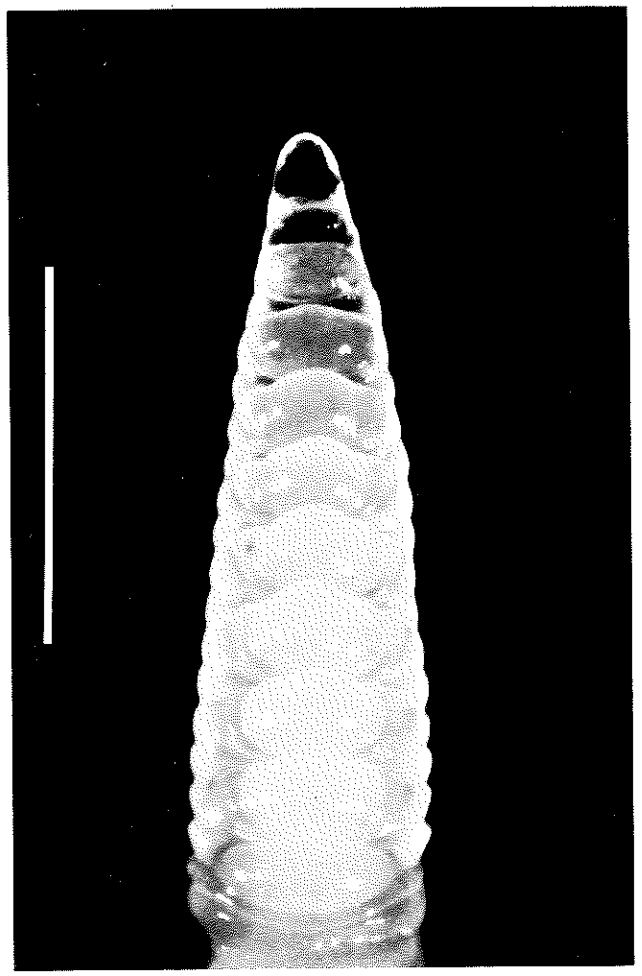


Fig. 5.23. 1mm scale bar

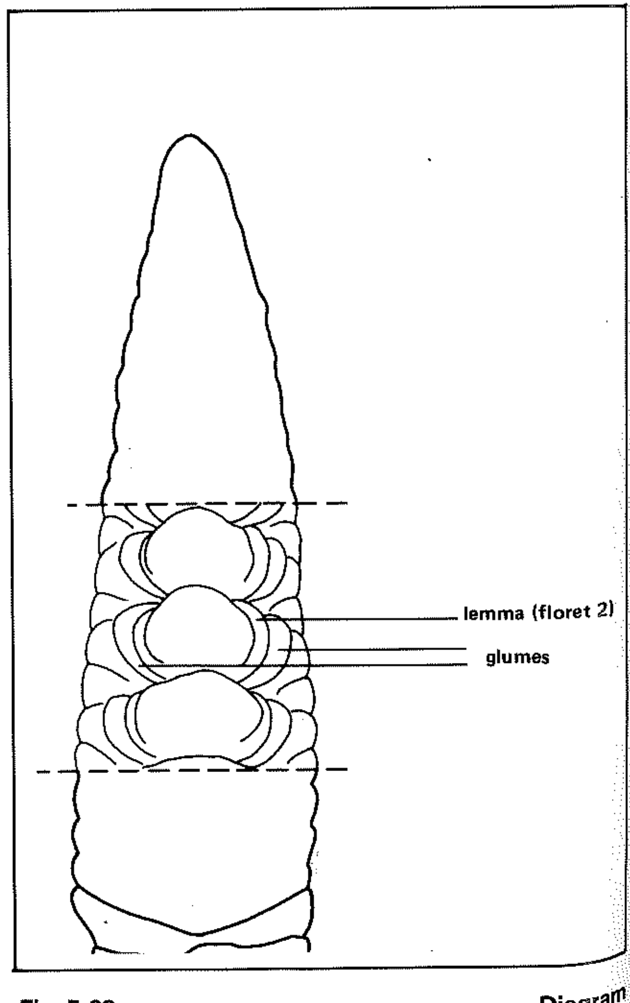


Fig. 5.23. Diagram

5. APICAL DEVELOPMENT
Wheat

Lemma primordium stage

Each spikelet primordium in the embryo ear will initiate eight to 10 floret primordia. After the initiation of glume primordia the florets start to form. The lemma primordia are initiated first and then the axillary meristems differentiate to form the other floral structures. At the same time as the development of the spikelets proceeds the meristematic dome of the shoot apex continues to initiate more spikelet primordia.

The profile view of an apex at this stage (Fig. 5.22) shows that the spikelets in the mid-part of the apex are the most advanced. In this view one of the glumes can be seen on each spikelet and parallel to it is a lemma primordium ridge. The spikelet meristem is actively initiating further floret primordia.

In face view (Fig. 5.23) the ridges of the lower and the upper glumes and the lemmas of florets 1 and 2 can be seen. Florets 1 and 2 arise almost at the same time but floret 1 is slightly larger. In the labelled spikelet, floret 1 is on the left hand side. Floret 3 will initiate above floret 1 and further florets will initiate alternately on the flanks of the spikelet meristem.

A plant at this stage will generally have between five and 11 leaves emerged on the main shoot depending on sowing date and variety.

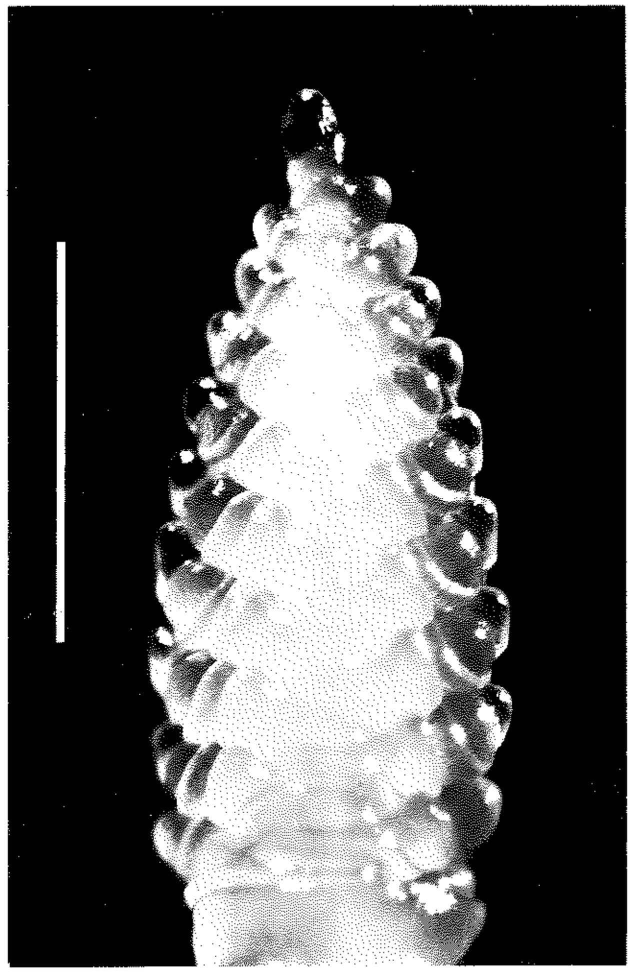


Fig. 5.24. 1mm scale bar

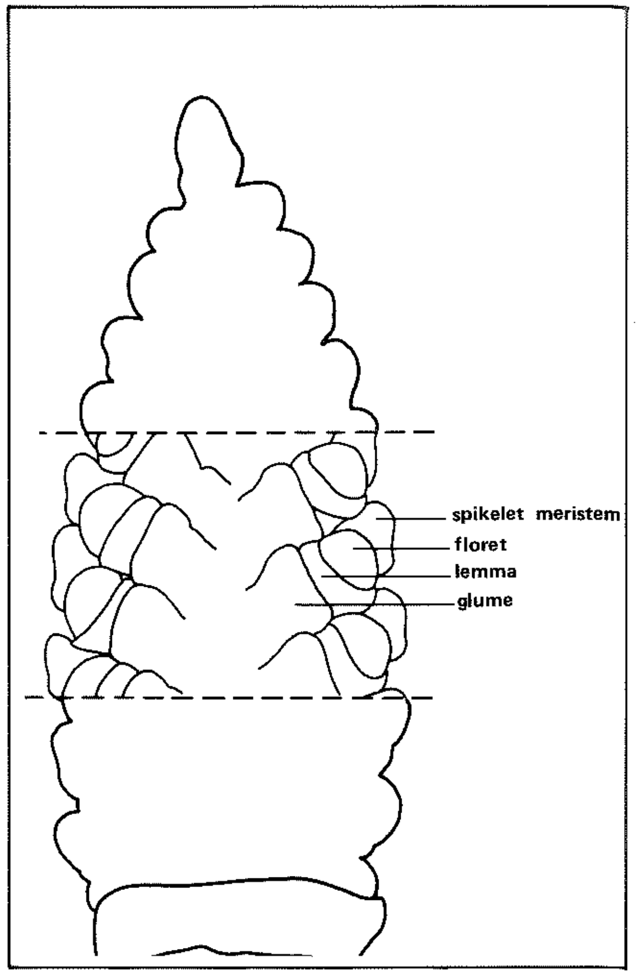


Fig. 5.24. Diagram

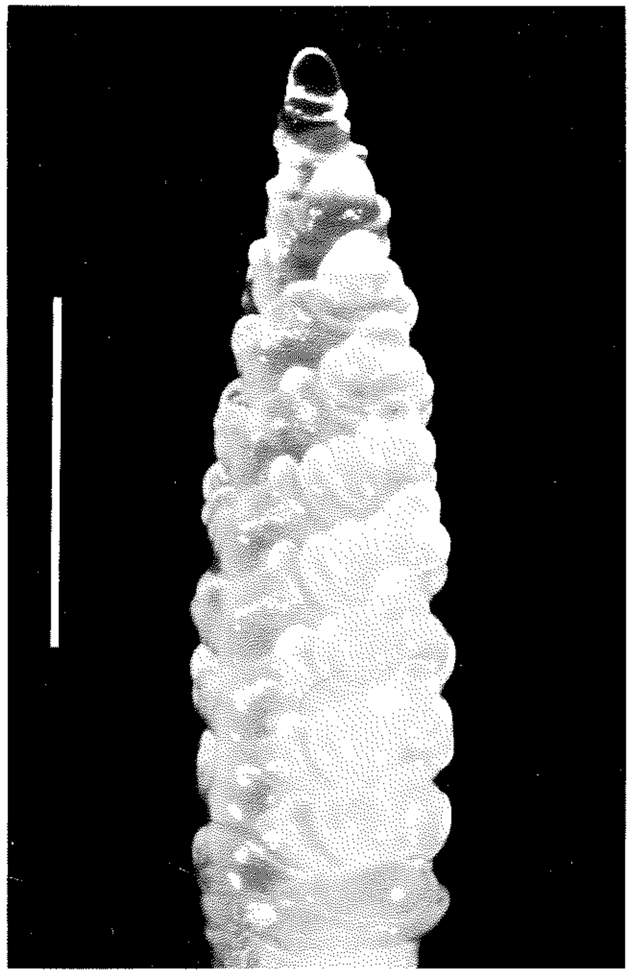


Fig. 5.25. 1mm scale bar

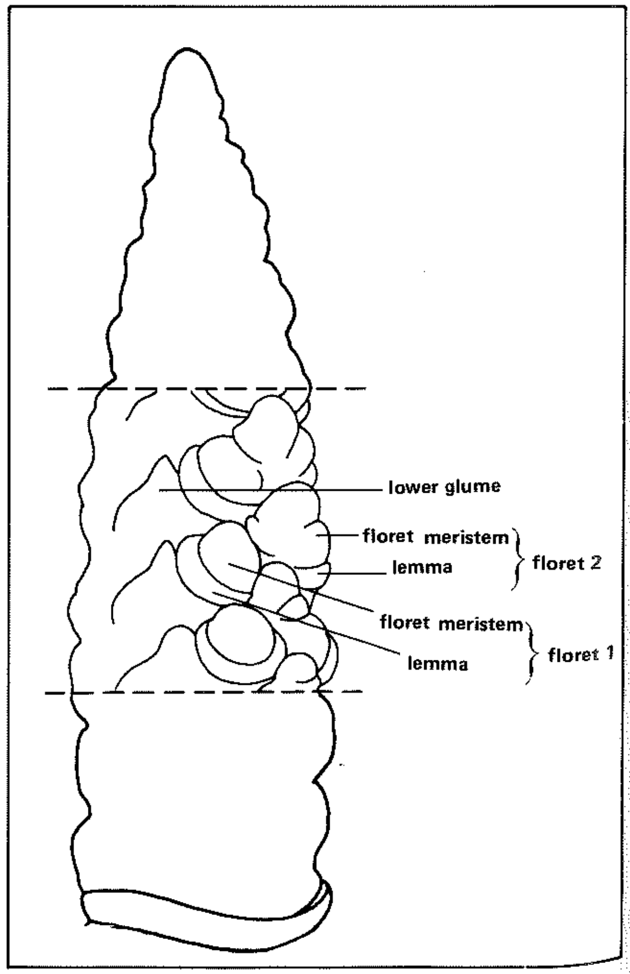


Fig. 5.25. Diagram

5. APICAL DEVELOPMENT
Wheat

Floret primordium stage

At this stage the multi-floret nature of the spikelet is clearly visible. A floret meristem grows in the axil of each lemma. The spikelet meristem continues to initiate further florets.

In face view (Fig. 5.24) only one side of each spikelet is visible. The smoothly rounded ridge of the lemma primordium is subtended by the more angular glume primordium. The region in the axil of the lemma has grown to form a smoothly rounded meristematic dome. This floret meristem will eventually initiate the palea, two lodicules, three stamens and a carpel (see Chapter 7).

In the lower diagram (Fig. 5.25) the shoot apex has been turned a few degrees from the face view to show more clearly the arrangement of the spikelets. On each spikelet the alternate arrangement of the florets can be seen and the smoothly rounded meristematic dome of the floret is prominent. In the annotated spikelet the lemma and floret primordia of florets 1 and 2 are visible and floret 3 is just beginning to form. As these florets differentiate further the spikelet meristem will initiate several more florets.

A plant at this stage will generally have between six and 11 leaves emerged on the main shoot depending on sowing date and variety.

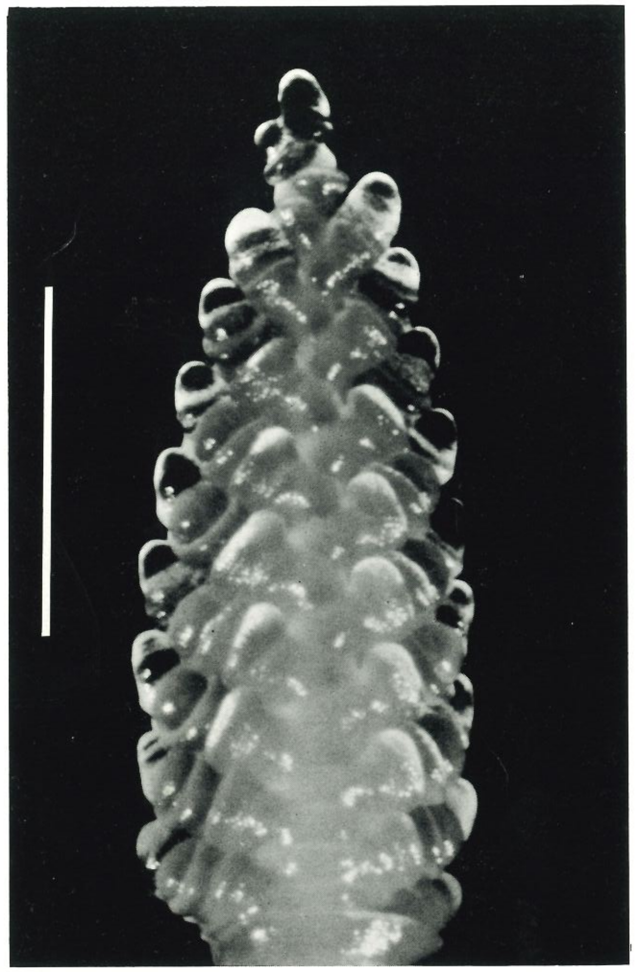


Fig. 5.26. 1mm scale bar

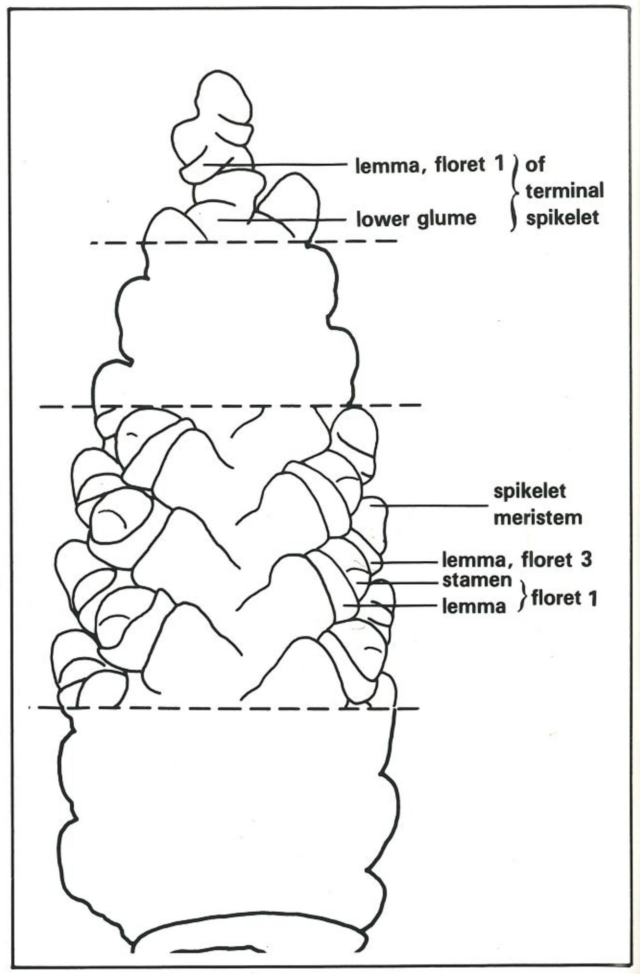


Fig. 5.26. Diagram

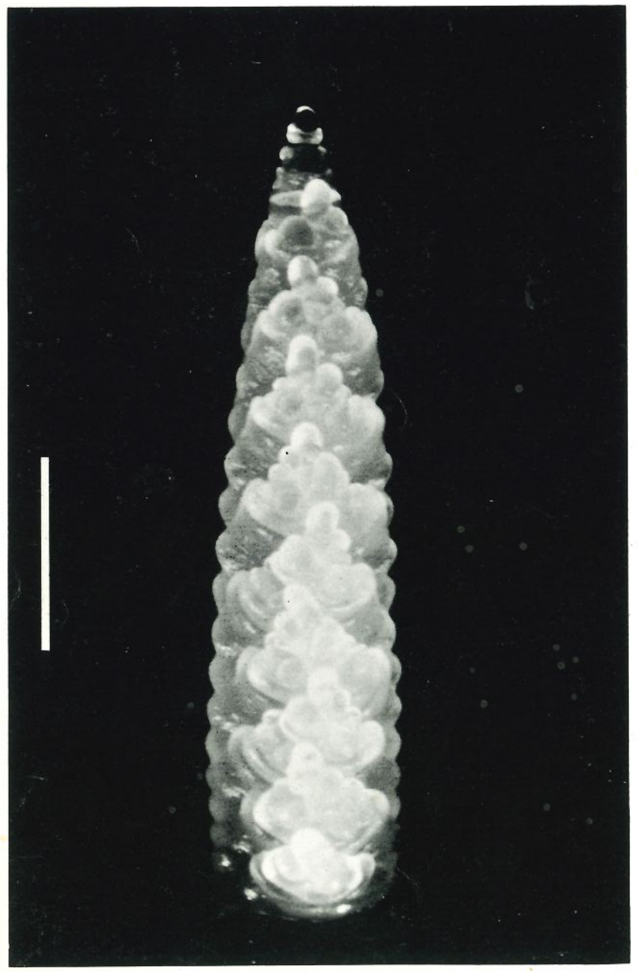


Fig. 5.27. 1mm scale bar

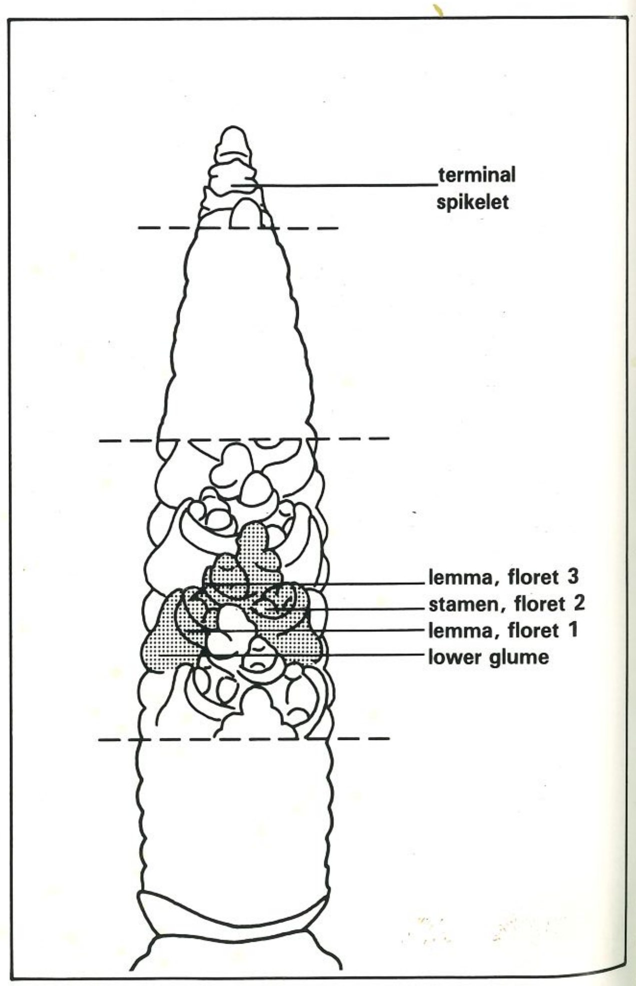


Fig. 5.27. Diagram

5. APICAL DEVELOPMENT
Wheat

Terminal spikelet stage

This stage in the plant's life cycle marks the completion of the spikelet initiation phase and it is equivalent to the maximum number of primordia stage in barley. The embryo ear is almost completely formed; no more spikelets will be initiated and the plant is soon to move into the next phase, in which maturation of floral parts, rapid growth of the ear and stem elongation take place.

At this stage the last few primordia initiated by the dome of the shoot apex do not develop into spikelets but become the glumes and floret primordia of a terminal spikelet. It therefore has its plane of symmetry at right angles to that of the other spikelets. The apex at this stage is about 4mm long.

The plant at this stage will generally have between seven and 12 leaves emerged on the main shoot depending on sowing date and variety.

An apex in profile view at an early stage in the formation of the terminal spikelet is shown in Fig. 5.26. In the mid-part of the shoot apex the stamens are just beginning to differentiate in the lower floret (these spikelets are viewed 'edge on').

An apex at a later stage is shown again in profile view in Fig. 5.28. The terminal spikelet in face view is shaded. The lemma of floret 1, on which the awn is beginning to grow, and the lemma of floret 2 are growing to cover the developing stamens.

The apex shown in Fig. 5.27 is at a slightly later stage than the one shown in Fig.5.26. One spikelet in the mid-part has been shaded and stamen primordia can be seen in the lower three florets. The glumes are growing up around the spikelet and will eventually enfold the florets.

Fig. 5.28.

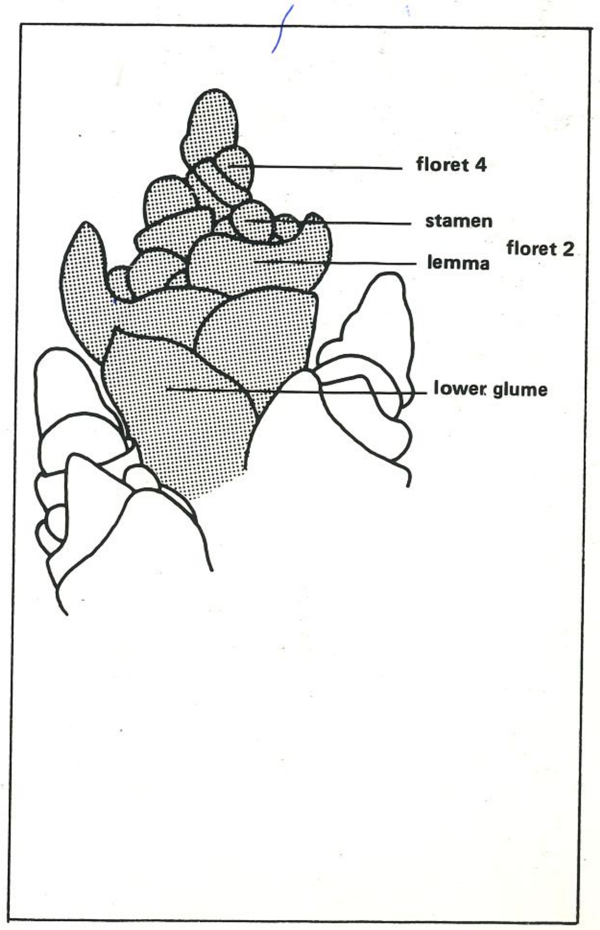


Fig. 5.28. Diagram

At this stage in certain varieties, an additional spikelet develops immediately below some of the spikelets (Fig. 5.29). These are called supernumerary spikelets and they usually remain relatively small and stunted even when mature, although some may set grain.

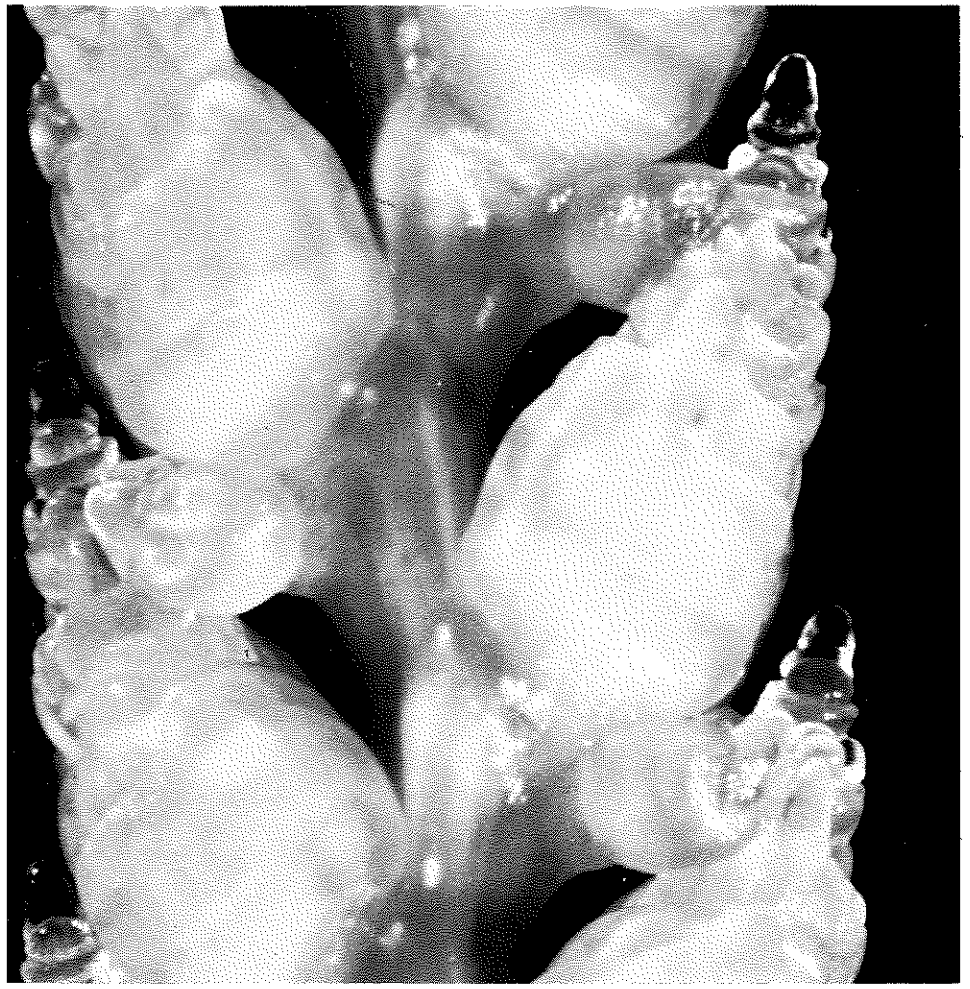


Fig. 5.29.

5. APICAL DEVELOPMENT
Summary

With the attainment of the awn primordium stage (maximum number of primordia) in barley (Fig. 5.31) or the terminal spikelet stage in wheat (Fig. 5.32) a well marked phase of the development of the cereal plant is complete.

By the end of this phase the shoot apex has formed the full complement of leaves and spikelets and the meristematic dome has completed its function. The duration of the phase varies from about 50 days in spring crops to about 200 days in winter crops. During this period the dome initiates between eight and 15 leaves, depending on variety and time of sowing, and then a number of spikelet primordia are initiated. In barley about 40 spikelet primordia are formed, each developing into a median and two lateral spikelets (the latter are sterile in two-row barley), each spikelet with a single floret. In wheat, in which the spikelets are much larger with several florets, about 20 spikelet primordia are initiated. In spring crops (e.g. spring wheat, Fig. 5.30) the spikelet primordia are formed at a fairly constant rate, usually between 1 and 1.5 spikelet primordia per day. In autumn sown crops (e.g. winter barley, Fig. 5.30) initiation of primordia continues through the winter, although it slows down during cold spells. Spikelet primordia are initiated more quickly in barley than in wheat.

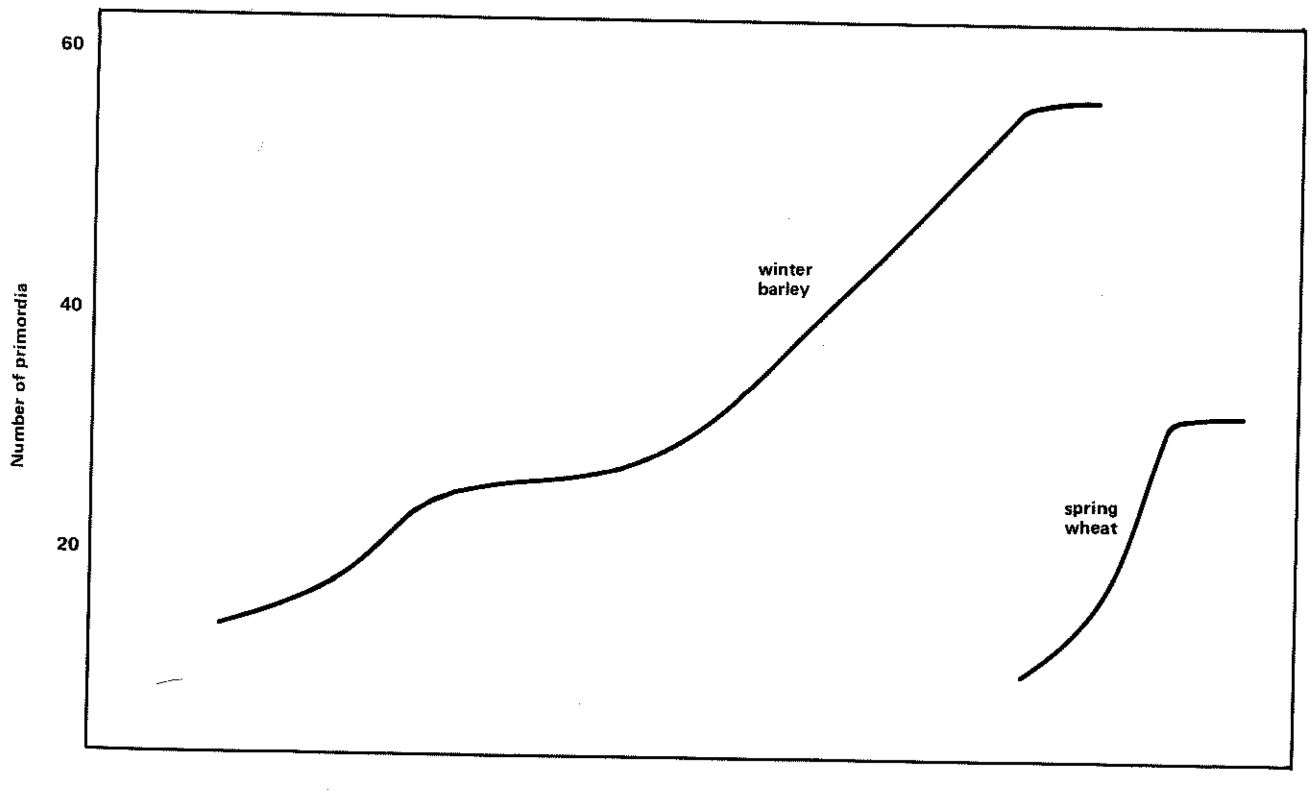


Fig. 5.30.

Fig. 5.31.

BARLEY

Fig. 5.32.

WHEAT

5. APICAL DEVELOPMENT

Summary

An interesting aspect of cereal plant biology is that all fertile florets on an ear flower at almost the same time, within a period of about two or three days and the grains all grow and ripen together. This synchronisation of development is achieved during the ear initiation period. Several days or even weeks may elapse between the initiation of first and last spikelet primordium but the primordia grow and develop at different rates. By the end of the ear initiation phase all those spikelets on the embryo ear which will eventually set grain are more or less at the same size and the same stage of development (Figs. 5.31, 5.32). All the events described so far have occurred while the shoot apex is completely enclosed in the developing leaves and is at or just below soil level. Only towards the end of this phase does the stem start to elongate.

At about the same time as the development of the embryo ear, the initiation and growth of tillers takes place (Chapter 6). The shoot apex of each tiller has the potential to form an ear in the same way as the main shoot. As described in Chapter 6 tillering is usually complete by the end of the ear initiation period. Thus the development of the plant during this early phase in the life cycle of a cereal plant largely determines the **potential** size of two of the yield components, number of ears and number of spikelets.

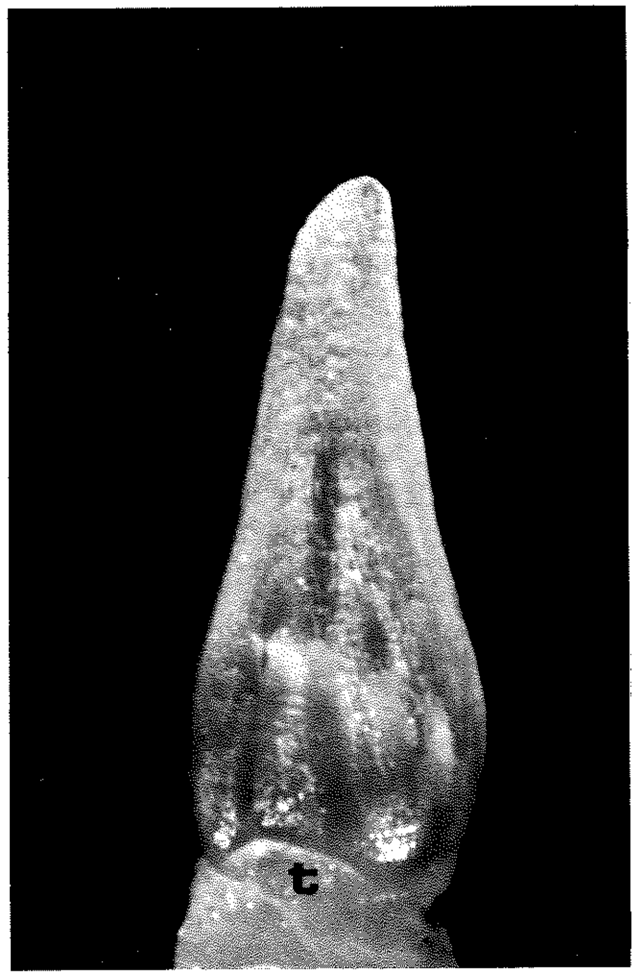


Fig. 6.1.

Fig. 6.2.

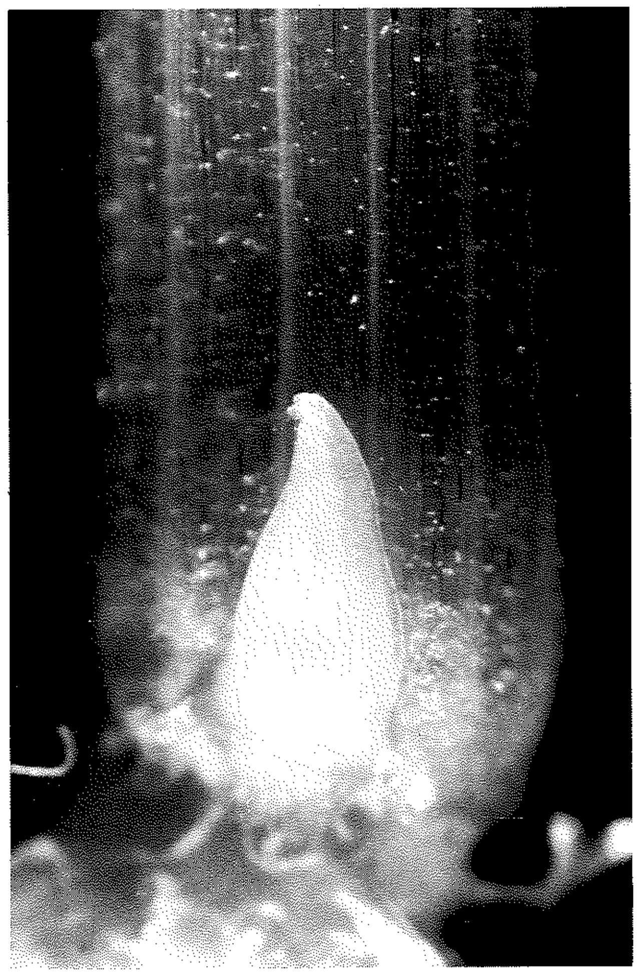


Fig. 6.3.

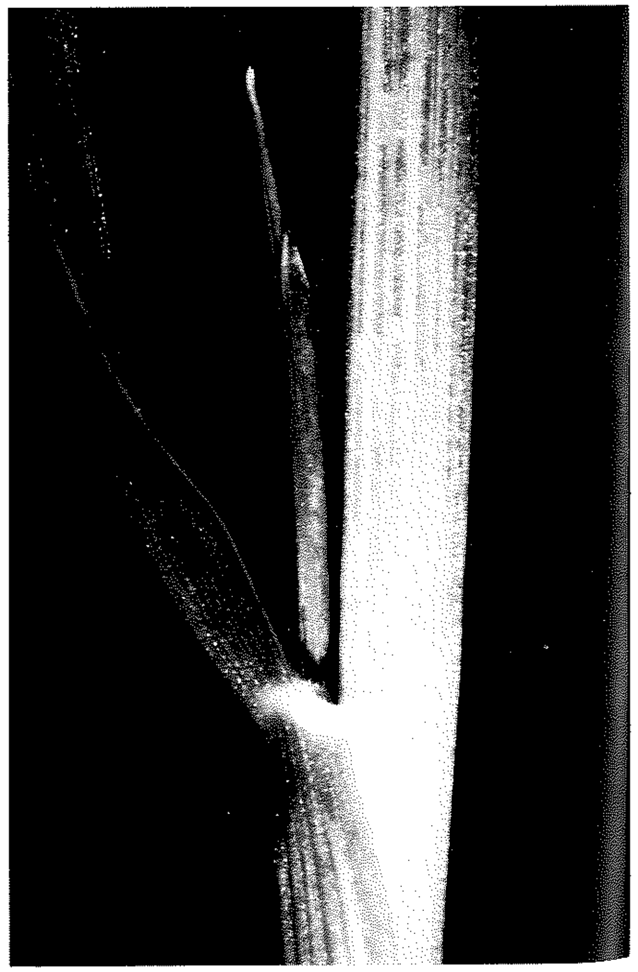


Fig. 6.4.

6. TILLERING
Wheat and Barley

Tiller bud initiation

The first visible stage in the formation of a tiller is the growth of a ridge of meristematic tissue in the axil of a basal leaf. Fig. 6.1 shows the first stage in the development of a tiller in the axil of leaf 2. Leaf 2 has been completely removed, exposing leaf 3. This leaf is about 3mm long, enclosing the shoot apex and is shown with the margins of the leaf towards the observer. A small ridge of meristematic tissue (t) is seen at the junction between leaf 3 and the stem, on the same side as the overlapping margins of the leaf.

Prophyll initiation

As the ridge of meristematic tissue grows, tightly tucked in between leaf sheaths, it becomes dome-shaped and an encircling ridge of tissue is initiated upon its flanks. This ridge grows to form the prophyll which is a sheathing structure, similar to the coleoptile of the main shoot. In Fig. 6.2 the dome is covered and is only visible through the surrounding crescent-shaped margins of the prophyll.

Tiller bud formation

The prophyll grows to enclose the dome and leaf primordia and a flattened triangular-shaped bud is formed (Fig. 6.3). Dissection of a tiller bud at this stage will reveal a shoot apex with leaf primordia and meristematic dome. The dome initiates leaves and then spikelets in exactly the same way as the main shoot.

Tiller leaf emergence

When the tiller bud has grown up within the sheath of the subtending leaf and its tip protrudes above the level of the ligule, the prophyll ceases growth and the first true leaf emerges. Fig. 6.4 shows tiller 1 emerging from the sheath of leaf 1. The prophyll protrudes about 10mm and the first tiller leaf, still tightly rolled, emerges from its tip.

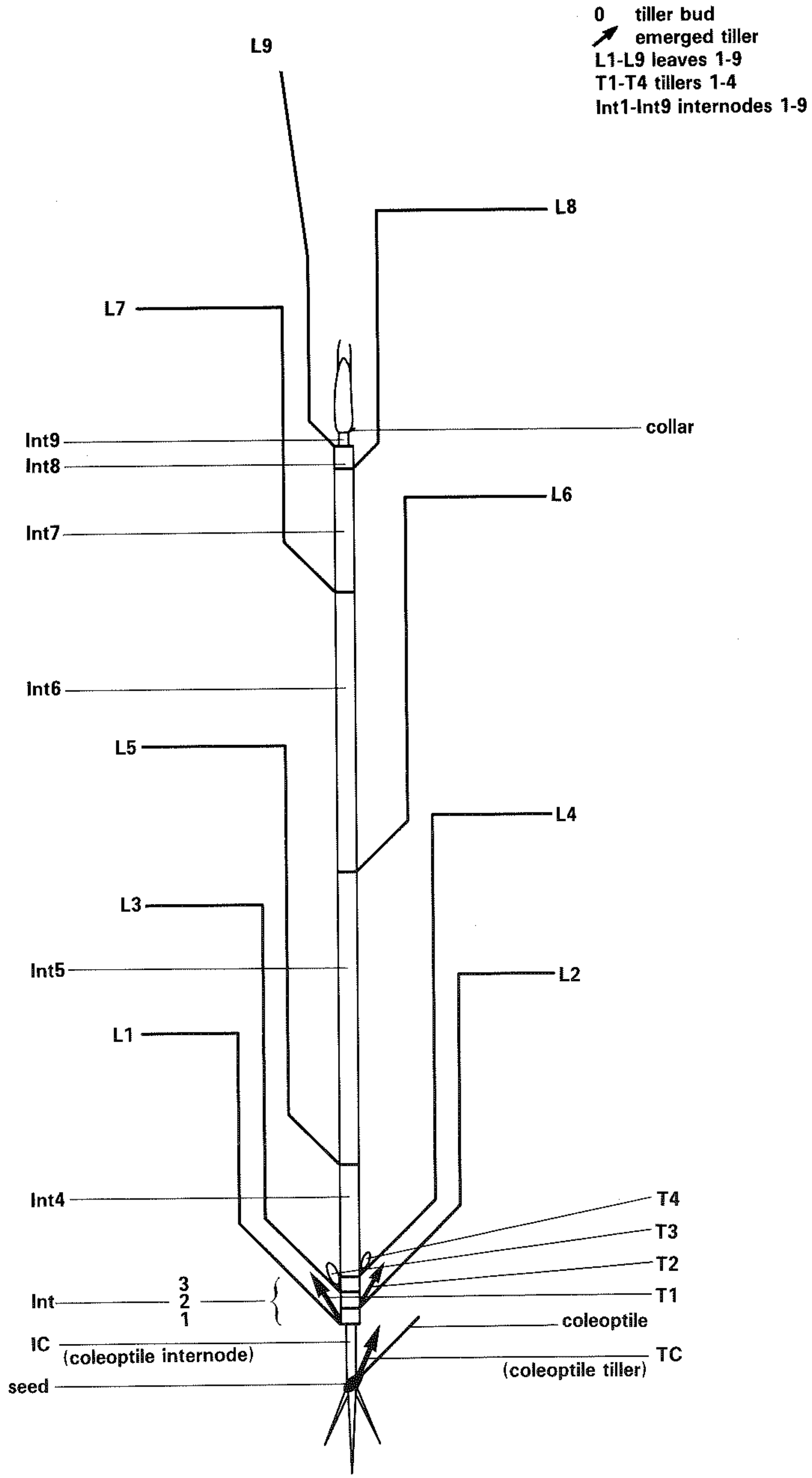


Fig.6.5.

6. TILLERING
Wheat and Barley

There is a characteristic sequence of production and arrangement of tillers in barley and wheat plants. A bud develops in the axil of the coleoptile and each of the lower leaves of the plant. Buds do not form in the axils of leaves which will subtend elongated internodes with the exception of the leaf subtending the lowermost internode and occasionally, the leaf above it. For example, in a spring barley plant with nine leaves (Fig. 6.5) five tiller buds (TC to T4) have formed. In winter cereals the sequence is similar but as there are more leaves produced on the main stem but a similar number of elongated internodes, there may be as many as 10 primary tiller buds produced. Buds are formed on the primary tillers in the same way i.e. in the axil of the prophyll (comparable to the coleoptile of the main stem) and lower leaves of each tiller. These are the secondary tillers. In well grown but sparsely sown crops these may produce tertiary tillers. Certainly the potential for them to do so is there in the form of buds.

Nomenclature

It is usual to designate each tiller by reference to the leaf in the axil of which it occurs (Fig. 6.5). Thus the tiller in the axil of leaf 1 of the main shoot is tiller 1 (T1) and the tiller in the axil of the prophyll of T1 is T1P. It is also convenient to number the internodes by the same system, although in the mature plant, where it is difficult to count leaves, internodes are often numbered with reference to the peduncle, the last internode which carries the ear.

Identification of tillers

The tillering arrangement of leaves on the main shoot can easily be analysed on evenly spaced, young plants. As the plants become older, or if they are clumped in the row, analysis is more difficult. If the seed has been sown deeply (2 cm or more) the internode between the coleoptile and leaf 1 elongates (Fig. 4.5). The coleoptile tiller group when it occurs can then be identified by its separation from the other tiller groups. Tiller 1 is diametrically opposed to the coleoptile tiller, and leaf 1 of the main shoot has a blunt, round tip which helps to identify this leaf. Tiller 2 is again opposed at 180° to tiller 1 and so on. If notes or records are to be made of the tiller status of a plant it is helpful to pull off tiller groups in sequence (TC, T1, T2 etc.) and lay them out on a bench (Fig. 3.2).

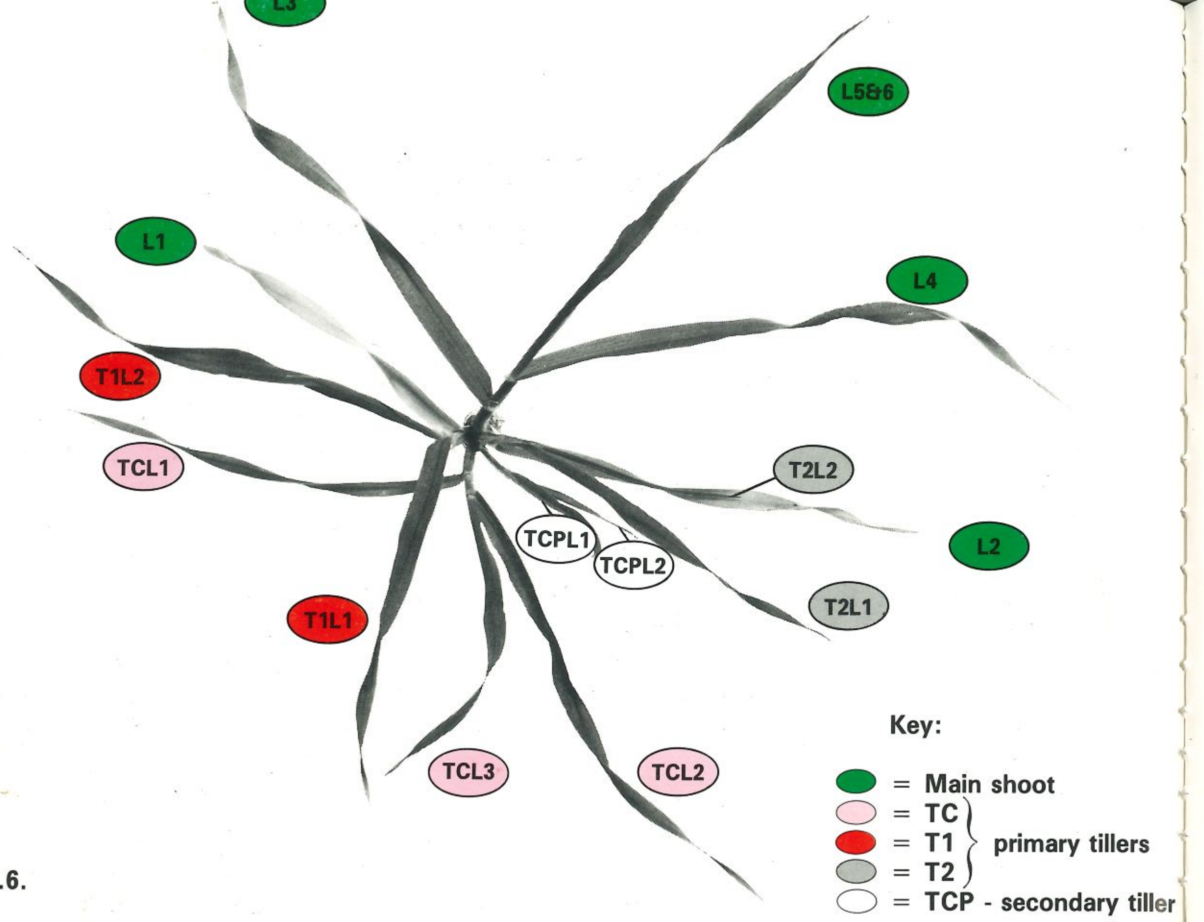


Fig. 6.6.

Diagram of a barley plant with six leaves seen from above. It shows the position of tillers (TC, T1 etc.), leaves on the main shoot (L1, L2 etc.) and on the tillers (TCL1, T1L1 etc.).

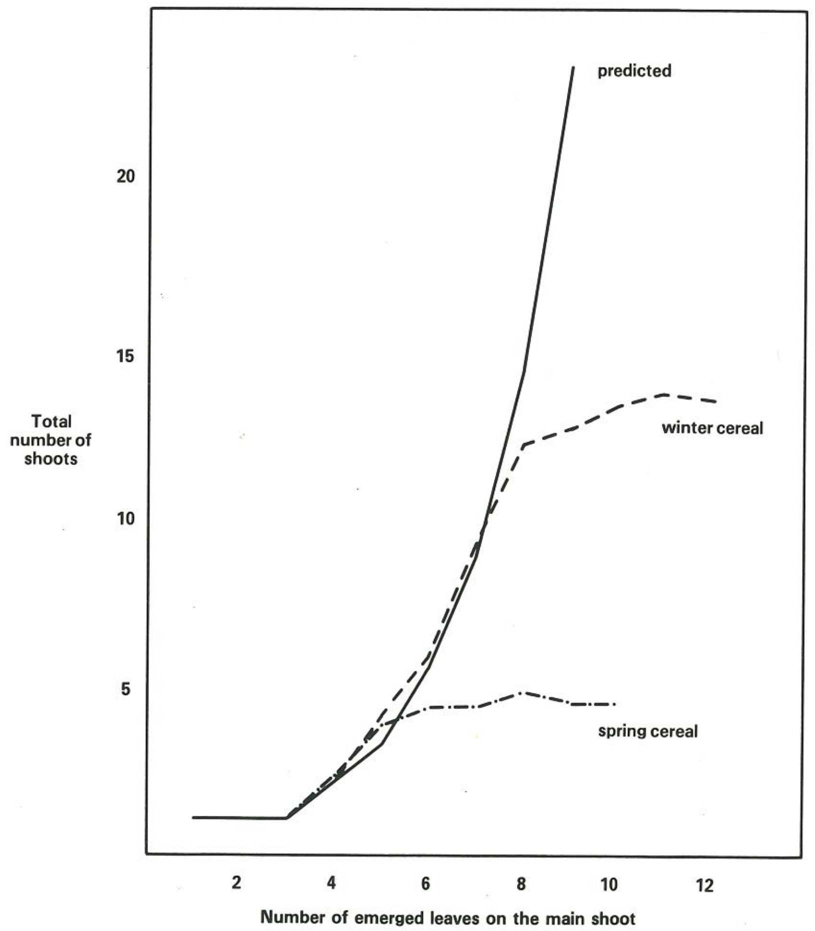


Fig. 6.7

7. SPIKELET AND FLORET DEVELOPMENT
Barley

Following the maximum number of primordia stage further development and growth of the spikelet parts takes place. All the structures formed during the ear initiation phase differentiate fully and by anthesis are ready to fulfil their roles in the fertilisation and grain filling processes.

The young ear at the stages described in this section is enclosed in the sheath of the flag leaf and the sheath of the leaf below the flag leaf; later as the stem elongates and booting stage is apparent, the ear is enclosed only in the flag leaf sheath. It is easy to slit open the leaf sheaths and extract the ear. Any examination should be made on the spikelet in the mid-part of the ear and the stage of development is best described by the appearance of the stamens and carpel. If a measuring eyepiece is available in the stereomicroscope, anther length is a useful additional measurement to describe development.

White anther stage

In each median floret of two-row barley the stamens grow quickly, relative to the lemma which does not enclose them until later. At first the anthers are white and translucent. Fig. 7.1 shows this stage in a spikelet taken from the mid-part of an ear of a two-row barley. This view was obtained by cutting through the rachis just above the attachment of the spikelet and viewing from the back, i.e. from the side of the spikelet normally adjacent to the rachis. The three stamens are prominent, situated in front of the large awn. The anther of each stamen is divided into four lobes. The anthers partially surround the young carpel which is at an early stage of development. The carpel walls are growing around the tissue which will eventually contain the egg cell. At the top of the carpel the two bumps are the beginnings of the styles and stigma. The palea partially encloses the carpel and stamens and the developing rachilla can be seen between the palea and lemma. The median spikelet is flanked by the sterile lateral spikelets.

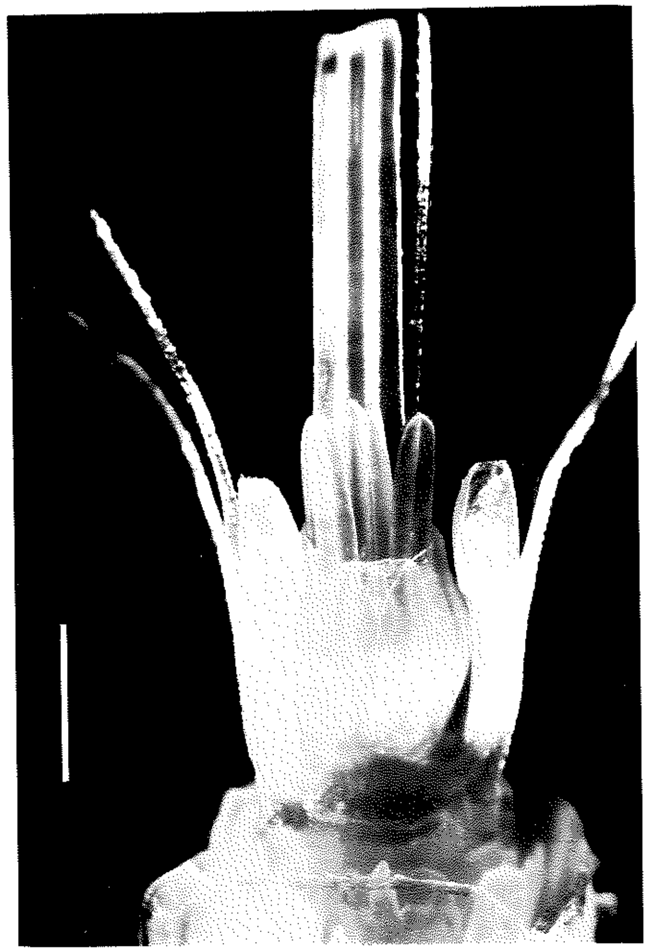


Fig. 7.2. 1mm scale bar

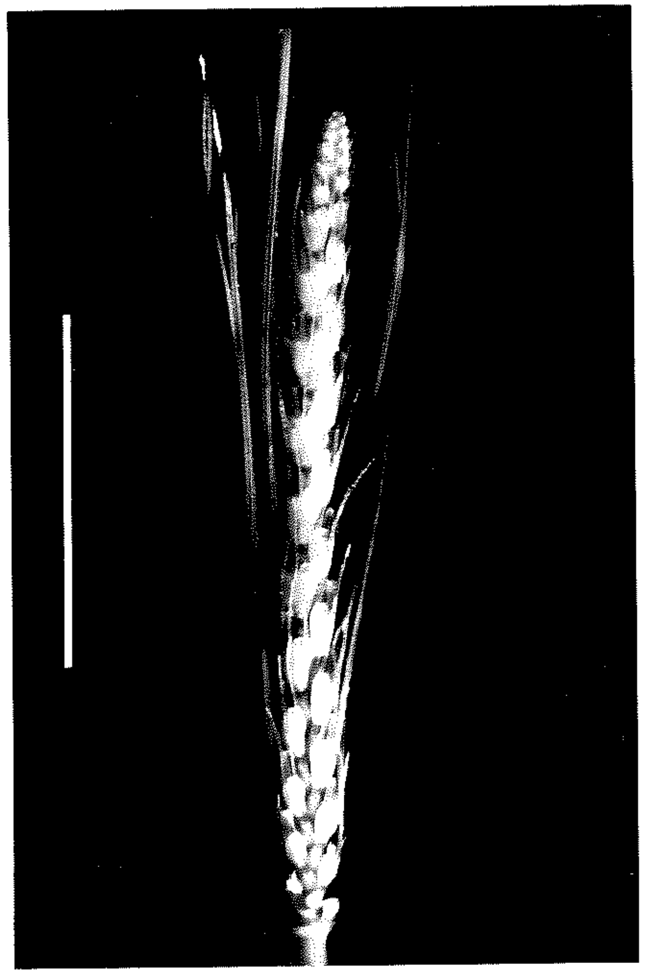


Fig. 7.3. 10mm scale bar

7. SPIKELET AND FLORET DEVELOPMENT
Barley

Green anther stage

When the stamens have grown to about 1mm long they become bright green. At this stage they will protrude beyond the lemma and palea as shown in Fig. 7.2. (This photograph was taken from the same viewpoint as Fig. 7.1.) The carpel is now enclosed by the lemma and palea. If it is dissected out the main features to be seen are two horn-like projections which are the developing styles. Small outgrowths which develop on the style grow into the long filamentous projections which form the stigma lobes (Fig. 7.4).

Meiosis

During the green anther stage, when the ear is about 25mm long (Fig. 7.3) and the anthers are 1.2 to 1.8mm long, depending on variety, meiosis occurs synchronously in the anthers and carpel. Any abnormality in the cellular events which take place during female meiosis may lead to sterility. Abnormalities during male meiosis result in pollen sterility and reduced grain set. The plant is particularly sensitive to water stress at this stage. (More detail about meiosis is given in the glossary. To observe meiosis special staining techniques and a high power microscope are required.)

Yellow anther stage

As the anthers mature and pollen is formed, their colour changes to yellow, often with dark spots. The carpel matures and the feathery stigmas become fully differentiated and ready to unfold and receive pollen. The lemma and palea grow and completely enclose the stamens and carpel. This stage of spikelet development lasts until anthesis and the appearance of the floret is described in the section on anthesis.

Fig.7.4.

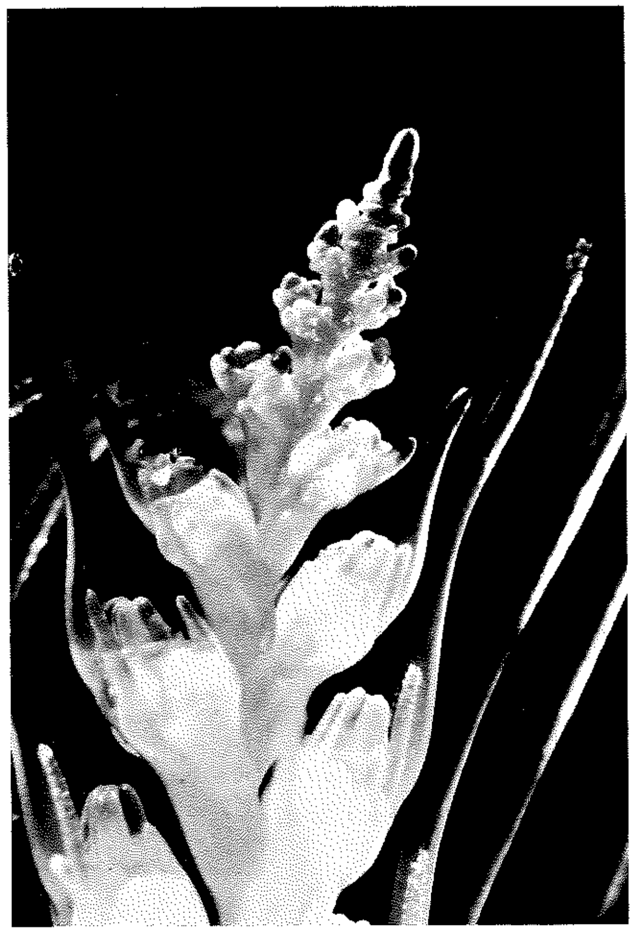


Fig. 7.5.

Fig. 7.6.

Fig. 7.7.

Fig. 7.8.

7. SPIKELET AND FLORET DEVELOPMENT
Barley

Death of spikelets at the tip of the ear

At the awn primordium stage (maximum number of primordia) the meristematic dome ceases to initiate any further primordia but still appears smoothly rounded and translucent (Fig. 7.5). Below the dome the primordia range in maturity from the one most recently formed, which may be at double ridge stage to those in the middle of the ear which have all the floral organs initiated and a prominent awn. For a few days after the awn primordium stage the dome remains apparently normal and the primordia near the tip continue to develop.

After a few days (depending on climatic and other conditions) degeneration at the tip of the ear begins; small regions of collapsed tissue can be seen on the dome which eventually becomes completely dried up (Fig. 7.6). This wasting of tissue progresses from the dome down the ear and a number of developing spikelets die. (Fig.7.7). In a typical ear about 12 of the last-formed, least-developed spikelet primordia are lost during this period. The spikelets adjacent to those which die grow normally and usually set a grain. Death of the tip spikelets is complete before anthesis and at ear emergence the dead tip can be found between the two uppermost developed spikelets (Fig.7.8).

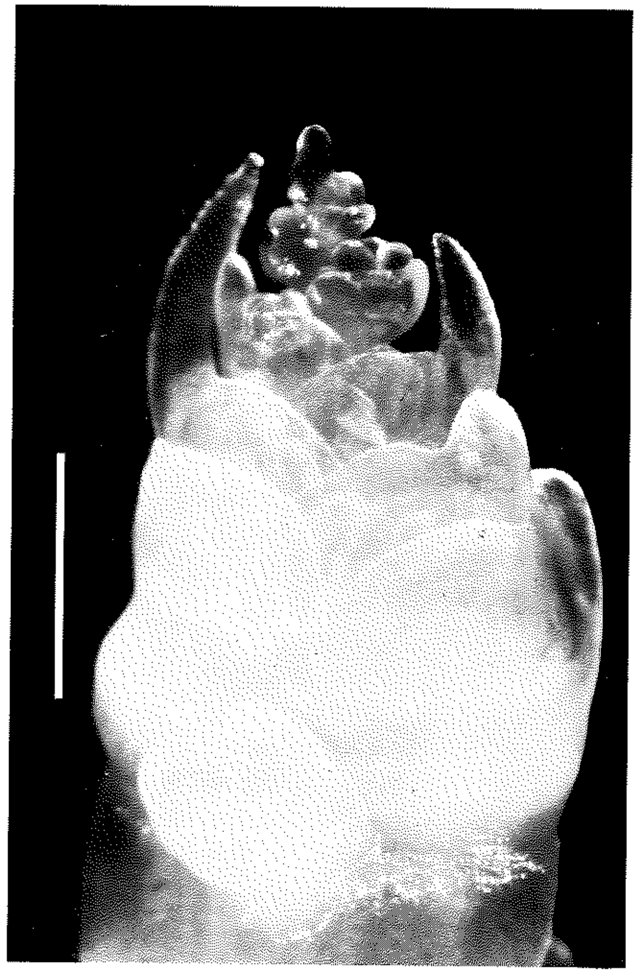


Fig. 7.9 1mm scale bar

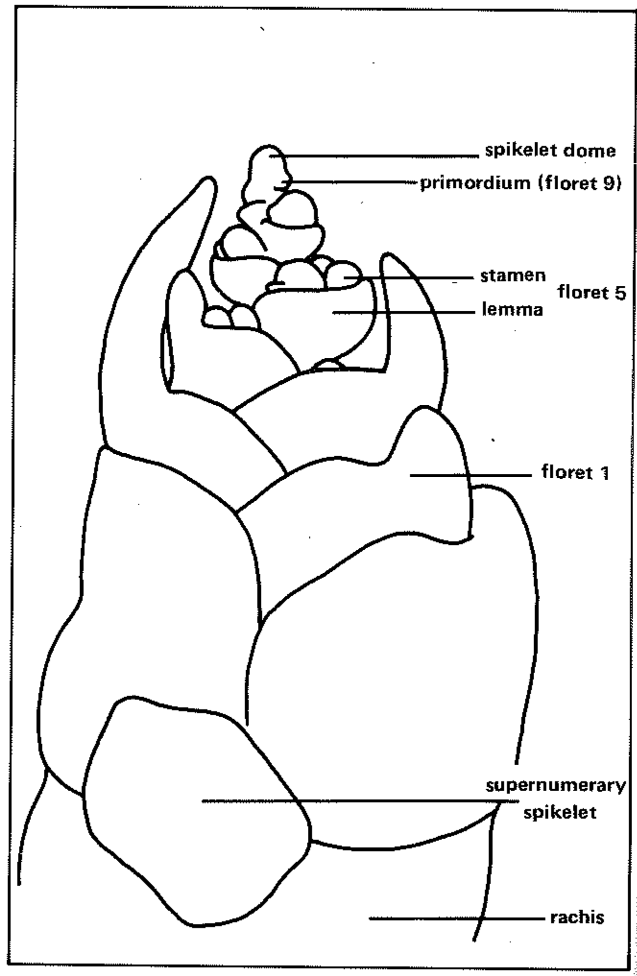


Fig. 7.9 Diagram

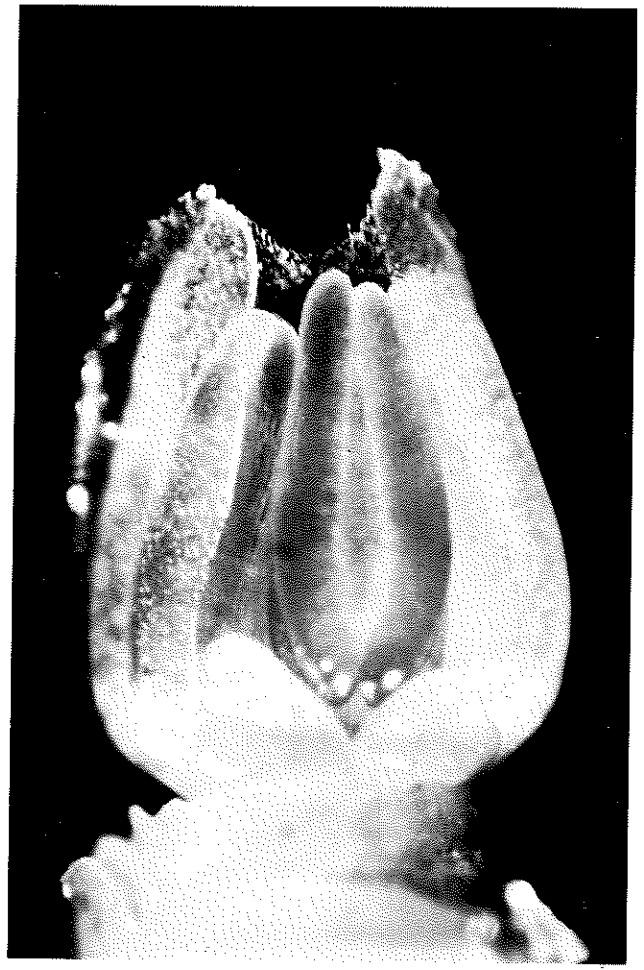


Fig. 7.10

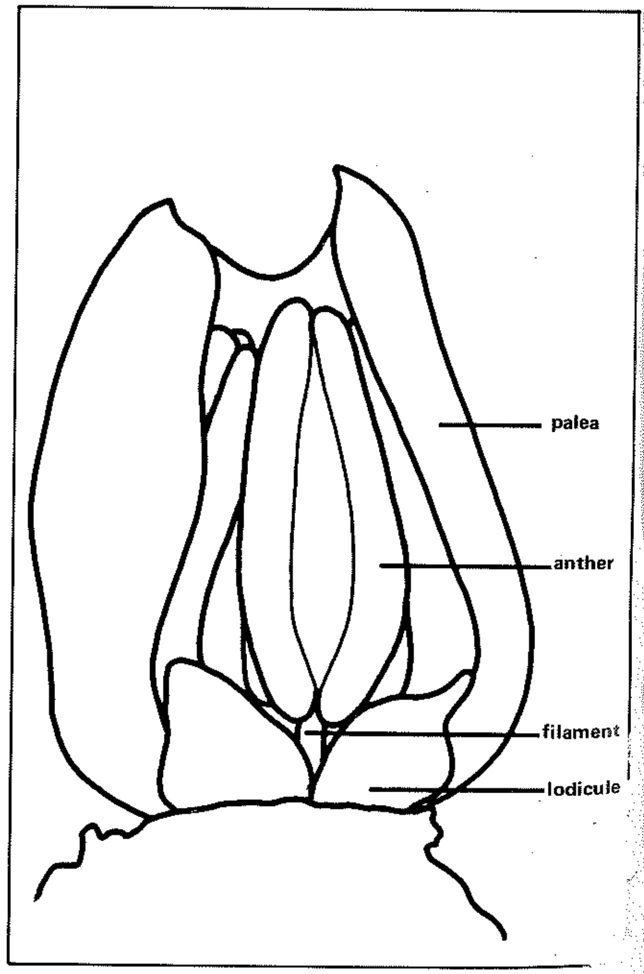


Fig. 7.10 Diagr

7. SPIKELET AND FLORET DEVELOPMENT

Wheat

This phase extends from terminal spikelet stage, when the lower florets in each spikelet have all the floral parts present, until shortly after ear emergence when the stamens and carpel are fully mature and anthesis takes place.

During this phase the rapidly growing ear is enclosed by the last two leaves of the shoot and during the latter part of the phase only by the flag leaf sheath (boot stage). It is easy to split open the leaf sheath and remove the ear. In wheat the glumes are strong and stiff and it is difficult, particularly in the later stages, to dissect out florets.

White anther stage

A complete spikelet at this stage is shown in Fig. 7.9. The meristematic dome has initiated nine floret primordia, the last of which is present only as a bump. The dome probably would not produce any more primordia. The glumes partially enclose the florets, and the lemmas of florets 1 and 2 completely enclose the stamens and other structures. Small awns are present on lemmas 2 and 3. Stamen primordia are visible in the upper florets. There is a small stunted supernumerary spikelet at the base of the spikelet.

The anthers may be examined by removing glume 1 and the lemma of floret 1 (Fig. 7.10). This reveals two lodicules and three stamens. The two lateral stamens are partially enclosed by the membranous wings of the palea. The filaments of the stamens are very short; the anthers are four lobed and are creamy white and translucent. The carpel (hidden behind the anterior stamen in the photograph) at this stage has small horn-like outgrowths which grow to form the styles (Fig. 7.11).

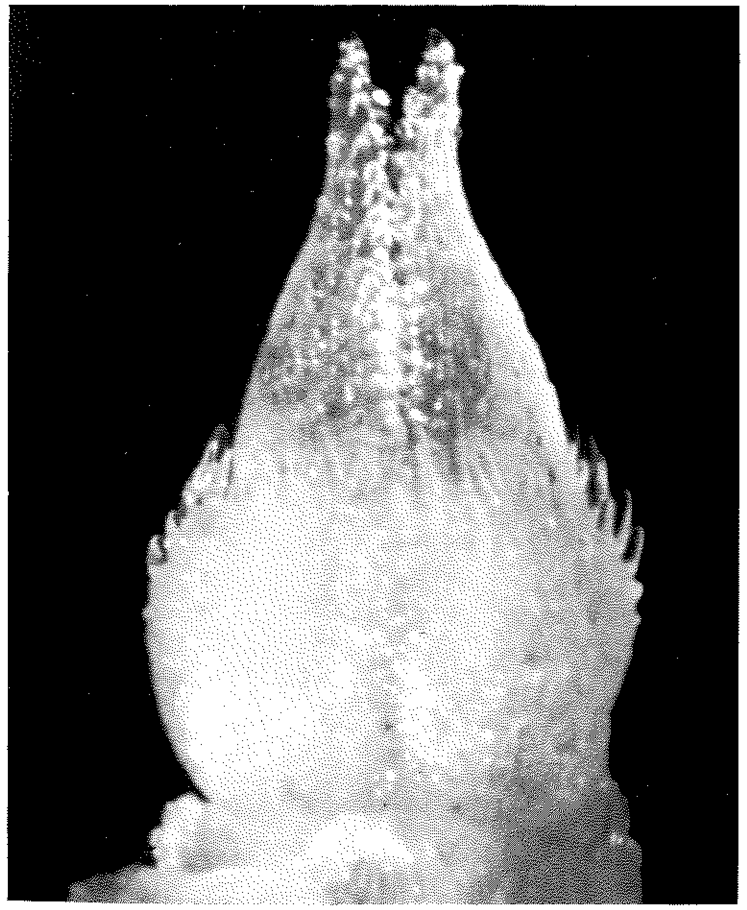


Fig. 7.11.

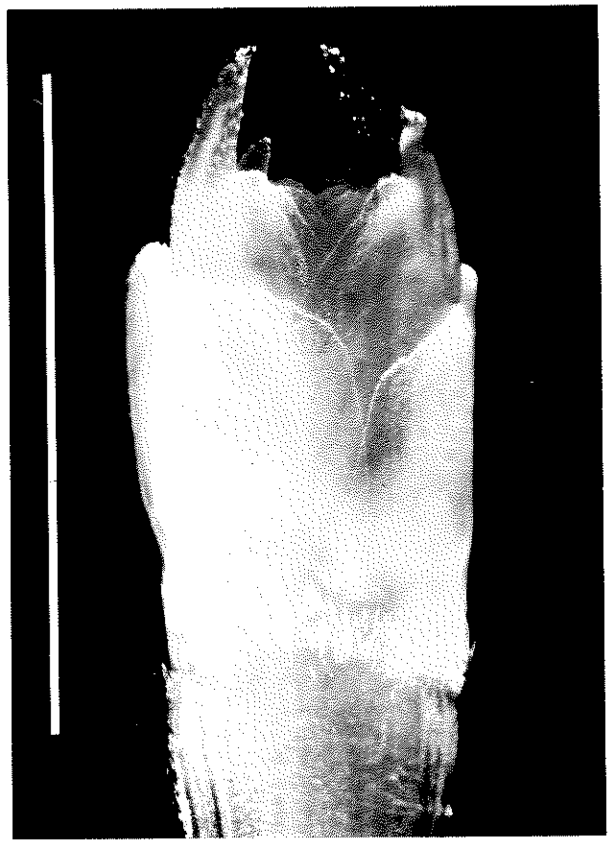


Fig. 7.12. 5mm scale bar

Fig. 7.13.

Fig. 7.15. 5mm scale bar

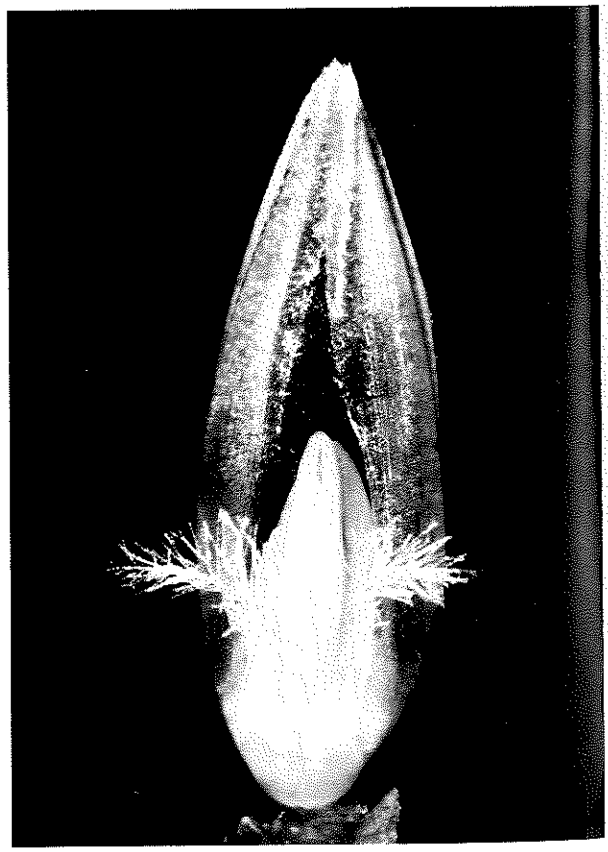
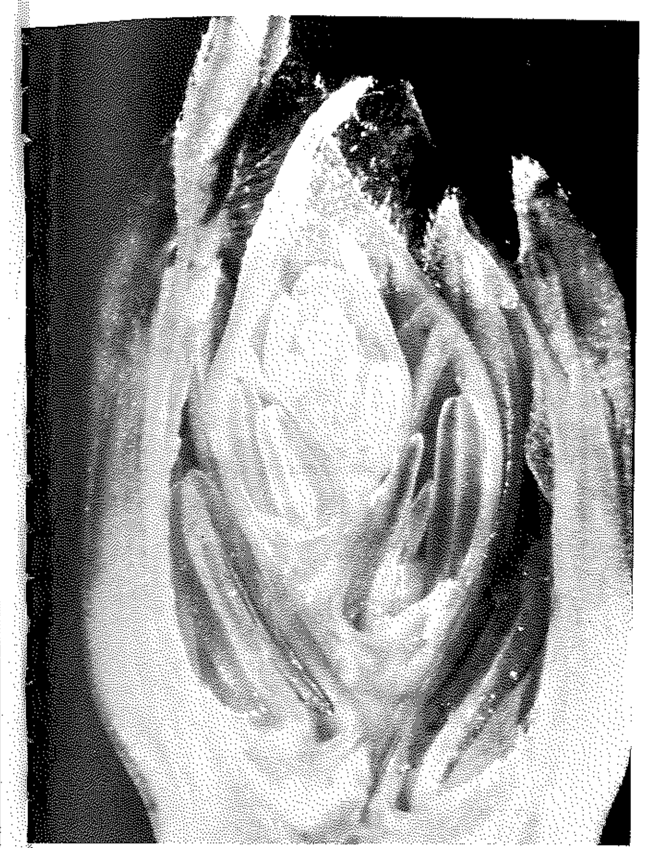
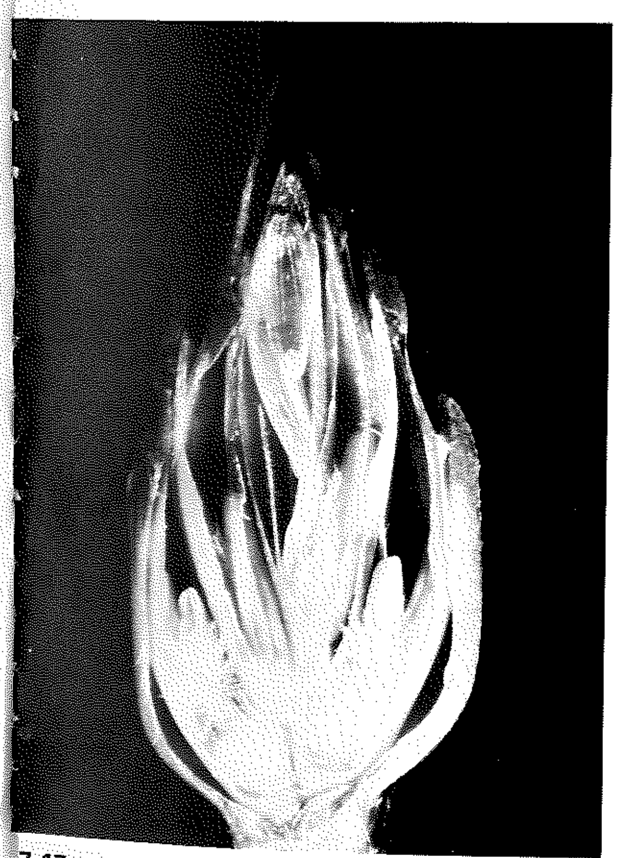


Fig. 7.16

7. SPIKELET AND FLORET DEVELOPMENT
Wheat



7.14.



7.17

Green anther stage

The glumes cover all but the tips of the florets and the lemmas of the older florets almost enclose the dome and the later formed floret primordia (Fig. 7.12). In Fig.7.13 glume 1 and the lemma of floret 1 have been removed to show other floral structures of floret 1. At the base of the floret, two fleshy lodicules are prominent. The wings of the palea fold over to partly enclose the three stamens which have short filaments and bright green anthers about 1mm long. The carpel, not visible in Fig. 7.13, has well developed styles upon which the feathery stigma lobes are differentiating.

The development of the florets within a spikelet may be examined by cutting the entire spikelet through in the plane of the glumes as shown in Fig. 7.14. This spikelet is slightly more mature than the one shown in Fig. 7.12 and the dome is completely enclosed by the floret. The dome can be seen to be apparently healthy but it has ceased to initiate primordia. Nine florets can be counted in the spikelet. The first three have large green anthers.

Meiosis

Meiosis occurs during the green anther stage, when the anthers are about 1mm long. Meiosis in the carpel and the anther takes place at almost the same time (see glossary).

Yellow anther stage

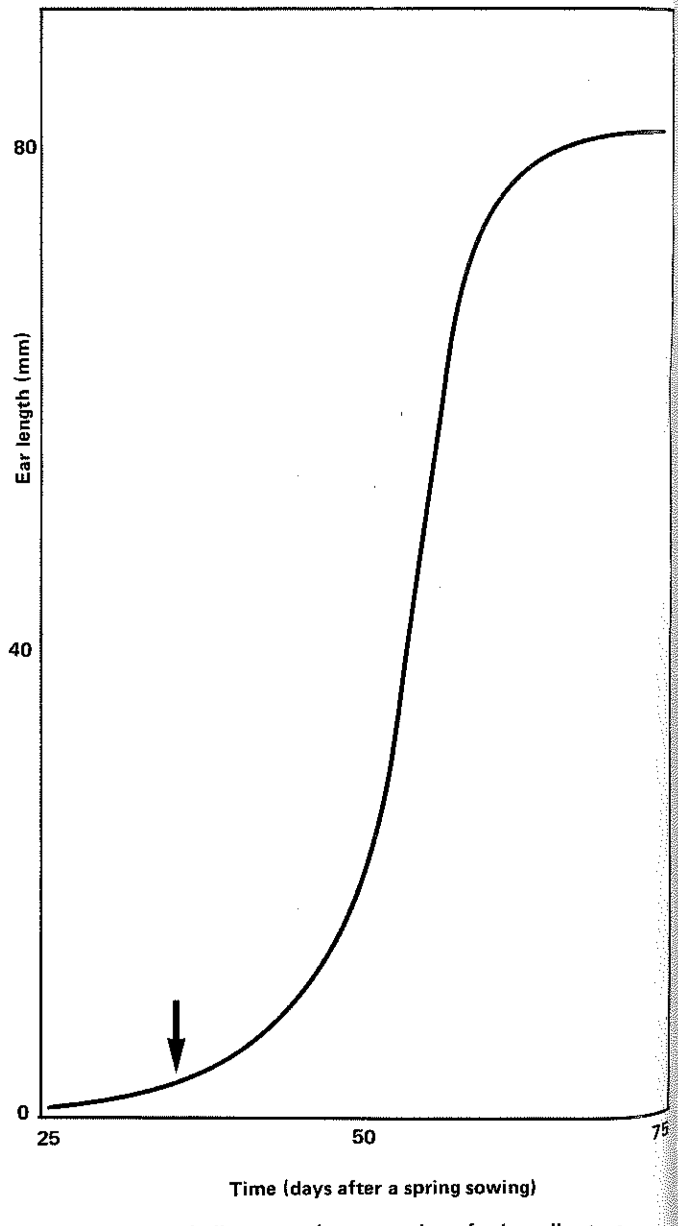
A spikelet at this stage is shown in Fig. 7.15. The glumes are fully formed and the lemmas of the first three florets are visible. The lemma of floret 1 has a short awn point (on the left of the photograph); the awns of floret 2 and 3 are longer. The florets are mature and anthesis is imminent (Fig. 7.16). Fig. 7.17 shows a spikelet sliced through to expose the florets. Floret 1 (left), 2 and 3 are well developed and the act of cutting through the lemma has allowed the stigmas to unfurl. The anthers are bright greenish yellow. Floret 4 has large anthers and a well developed carpel but is less mature than the lower florets. The remaining florets have aborted and at the tip of the rachilla (top centre of the photograph) the dome is completely dead and shrivelled.

7. SPIKELET AND FLORET DEVELOPMENT
Summary

The phase of development described in this chapter extends from awn primordium stage (maximum number of primordia) in barley or from terminal spikelet stage in wheat, until just before anthesis. During this period the florets mature in preparation for the final phase of the life cycle, grain filling and ripening. The embryo ear grows from about 3mm long at the beginning of the phase to 80mm long at anthesis (Fig.7.18) and about 99% of its dry weight at anthesis is accumulated during this phase. At the beginning of the phase the plant normally has produced its full complement of tillers, and the main shoot and each tiller has the potential to produce an ear. Therefore at this point in the life cycle of the plant the potential number of ears and spikelets per ear has been determined.

During the period of spikelet and floret development major changes take place in the growth patterns of the plant. In addition to the increase in the growth rate of the ear, stem growth starts at about the anther primordium stage and occurs concurrently with ear growth.

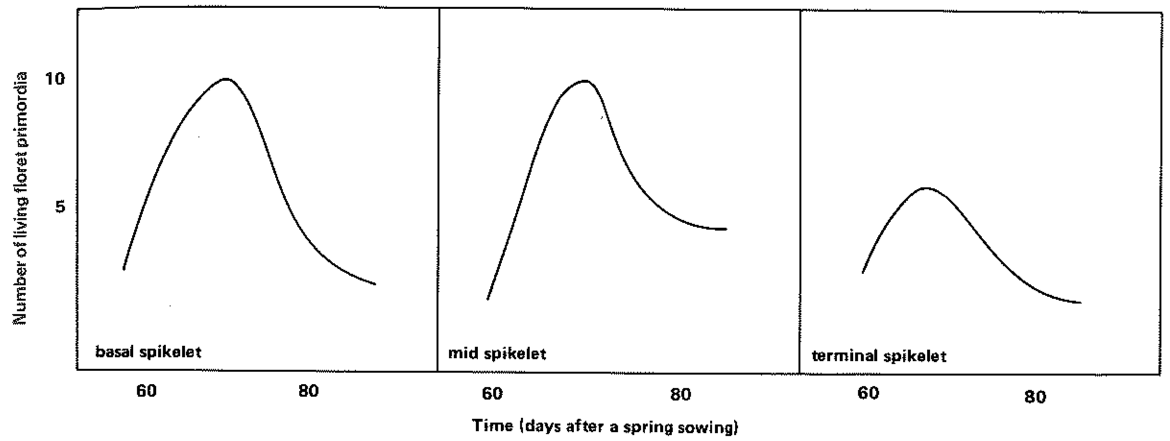
Fig. 7.18.



Arrow indicates maximum number of primordia stage

During this phase some of the developing ears and spikelets die. This may be due to the increase in the growth rate of the ears and stems, leaving insufficient resources (e.g. carbohydrate from photosynthesis or nitrogenous compounds) to support the growth of all potential ears and florets. It is the smallest spikelets or florets with the lowest growth rates which are least able to compete for resources and it is these which die. In barley the smallest spikelets occur at the tip of the ear and in a typical spring barley about 15 of the 40 spikelet primordia die, but depending on conditions the proportion surviving may range from 55 to 80%. In wheat the youngest florets occur at the tip of each spikelet and of the eight to ten floret primordia formed only four to six are potentially fertile (Fig.7.19). In addition, in both barley and wheat, some of the smaller spikelets at the base of the ear may not develop properly.

Fig. 7.19



During this period the husbandry of the crop is directed to maintaining as large a proportion as possible of the potential of the plant. For example, in winter crops the main spring top dressing of nitrogenous fertiliser is often timed to coincide with the beginning of the period of rapid ear and stem growth. Although a proportion of florets die in all cereal plants, stress due to such factors as drought, disease or excessive plant population will exacerbate the loss. Of central importance during this phase of growth and development is the role of certain cells in the anther and the carpel which synchronously undergo meiosis and give rise to pollen in the anthers, and the embryo sac in the carpel. At meiosis the floret appears to be particularly vulnerable to stress; experiments have shown that drought at this stage may lead to impaired development, floret sterility and reduction in grain yield.

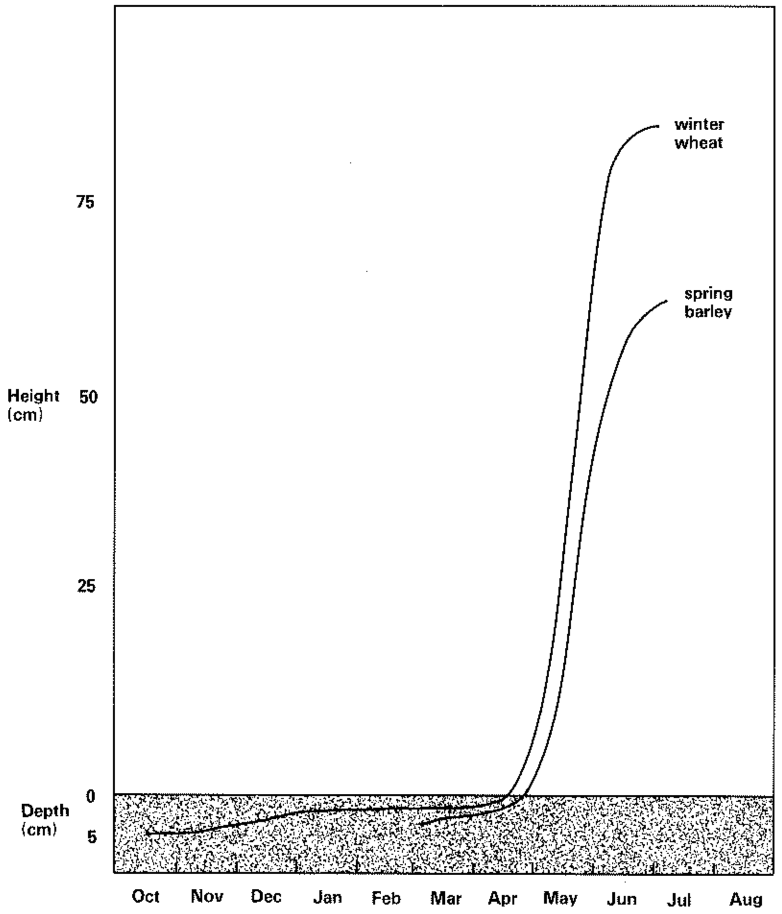


Fig. 8.1

Fig. 8.1. The position of the shoot apex (ear) is shown in winter wheat and spring barley from sowing until after anthesis. In the winter wheat example the seed was sown about 5cm deep and elongation of the coleoptile internode carried the apex up until it was about 2cm deep, where it remained until stem elongation started. In spring barley development is quicker and stem elongation commenced relatively soon after sowing. (Adapted from Hay, 1978).

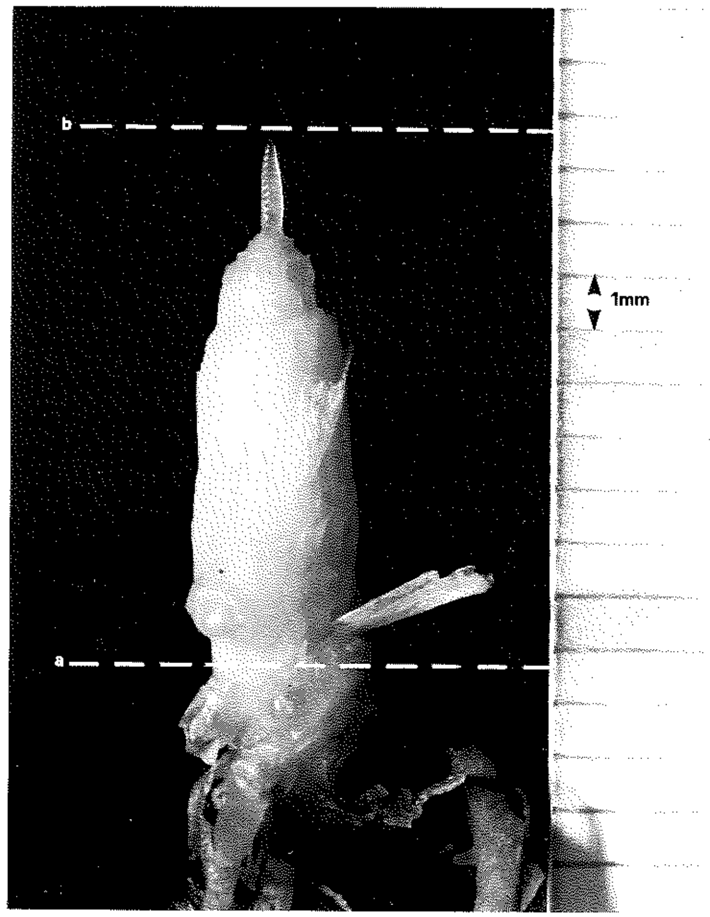


Fig. 8.2

Fig. 8.2 The beginning of stem elongation can be detected by identifying the main shoot and carefully stripping off the leaves, preferably to expose the young ear. The length is measured from the plane of tiller and root insertion (a), to the tip of the young ear (b). The plant shown here is at the stage 'ear at 1 cm'. This is equivalent to the stage used by French agronomists (épi à 1 cm) described by Couvreur et al., 1980. (See chapter 11 p. 85).

8. STEM ELONGATION

In seedlings the shoot apex, which is concealed within the crown, is situated about 2 cm below the soil surface. In plants from deeply sown seeds the position of the crown is adjusted by the elongation of the coleoptile internode (Fig. 4.5). The shoot apex remains below ground until it is florally well developed, when stem elongation begins. Rapid stem growth follows (shooting), which brings the developing ear above the ground, and eventually leads to ear emergence.

Beginning of stem elongation (Ear at 1 cm)

Stem elongation is closely related to the stage of development of the apex and begins when the ear is at lemma primordium stage in barley or floret stage in wheat. It is a significant stage in plant development and can be defined by measurement of the stem and young ear (Fig. 8.2). Rapid stem elongation begins at about the maximum number of primordia stage in barley and at terminal spikelet stage in wheat.

Stem growth is the result of elongation of the internodes (the regions between the nodes Fig. 8.3). An internode may or may not elongate depending on its position on the shoot. In barley and wheat the stem is formed by the elongation, in sequence, of the last 5 or 6 internodes (Fig. 8.4). The lower internodes are compressed into a few millimetres of stem (Fig. 8.3). The number of unelongated internodes depends primarily on sowing date and variety.

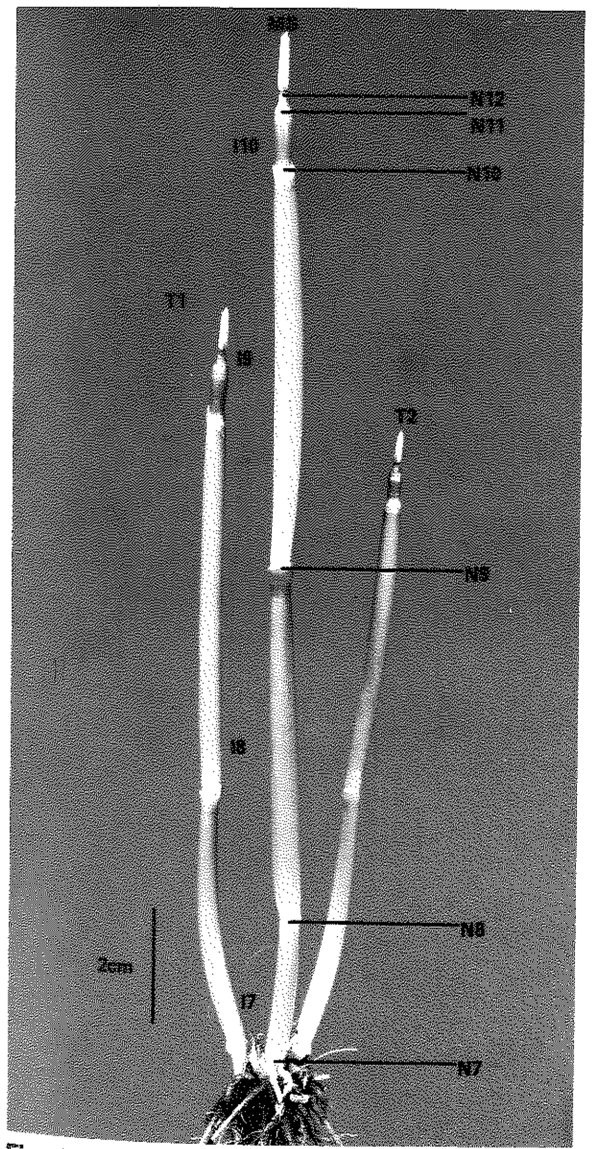
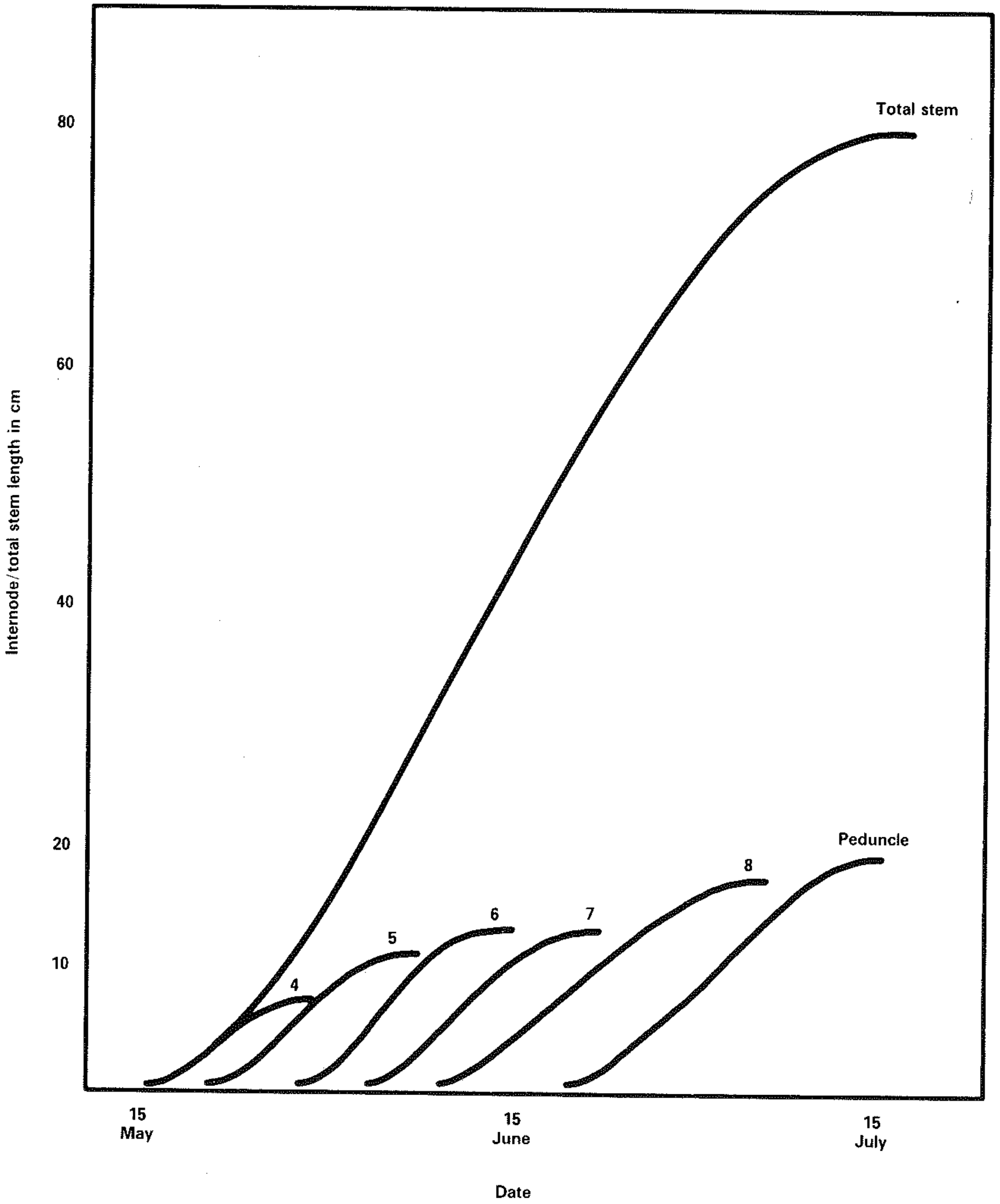


Fig. 8.3.

Detectable nodes

When the stem grows and the internodes elongate the individual nodes become detectable, and this forms a convenient way to define them. A detectable node is arbitrarily defined as one where the internode below it is longer than 2 cm (Fig. 8.3). This diagram shows a wheat plant with all the leaves removed to expose the elongating stem of the main shoot (MS) and tillers 1 and 2 (T1 and T2). The main shoot formed 12 leaves, each attached at a node. The internodes below node 7 (N7) have not elongated and form a short compact piece of stem, concealed by the roots. Internode 7 (I7), I8 and I9 are longer than 2 cm. Therefore nodes 8, 9 and 10 are classified as 'detectable nodes' and the main shoot has THREE DETECTABLE NODES. Internode 10 is beginning to elongate and I11 and I12 (the peduncle) are very small. (An alternative way to identify 'detectable nodes' is to split the main shoot lengthways.)

Fig. 8.4



Stem elongation proceeds in an ordered sequence and is associated with the expansion of the leaves so that when a leaf reaches full size the internode associated with it begins to grow. When this internode is about half its final length the one above it will begin to grow. This sequence continues until the last internode (the peduncle, which carries the ear) is fully elongated and the stem is then at its final length (Fig. 8.4). Usually each successive internode is longer than the preceding one and the peduncle is longest of all.

8. STEM ELONGATION

The node is the region of the stem where the leaf is attached and in the mature stem the prominent 'knot' is the swollen leaf base (Fig. 8.5). The knot plays an important role in the growth habit of the plant. If lodging occurs and the crop is laid flat the stems turn upwards again. This happens at the nodes where, in response to gravity, there are differential growth rates on either side of the knot. The side nearest the ground grows faster than the uppermost side causing the knot to become uneven so turning the stem, and thus the ear, upwards (Fig. 8.6). It may take the combined effort of two or three knots to bring the peduncle and the ear to a vertical position.

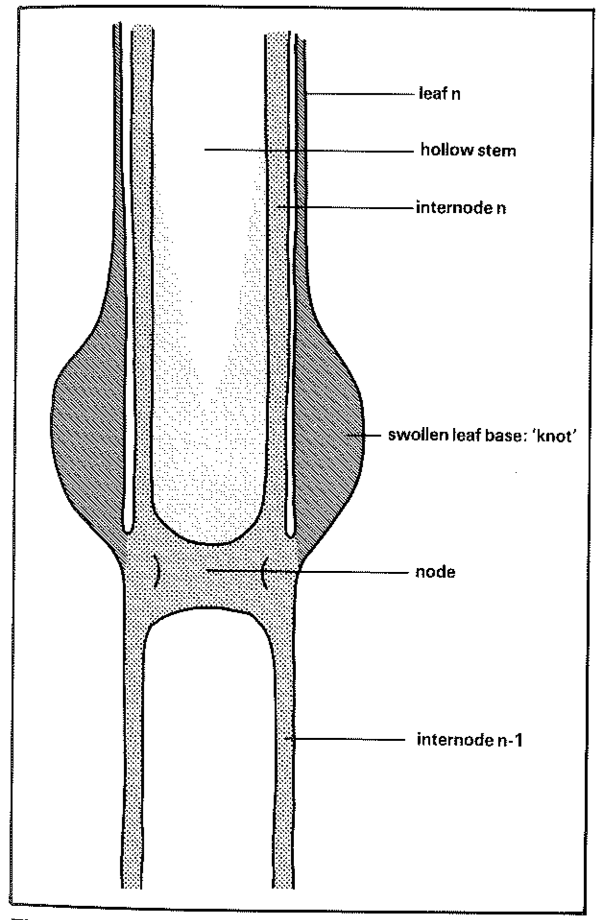


Fig. 8.5.

Fig. 8.5. Longitudinal section of a mature stem showing the position of the node and the knot.

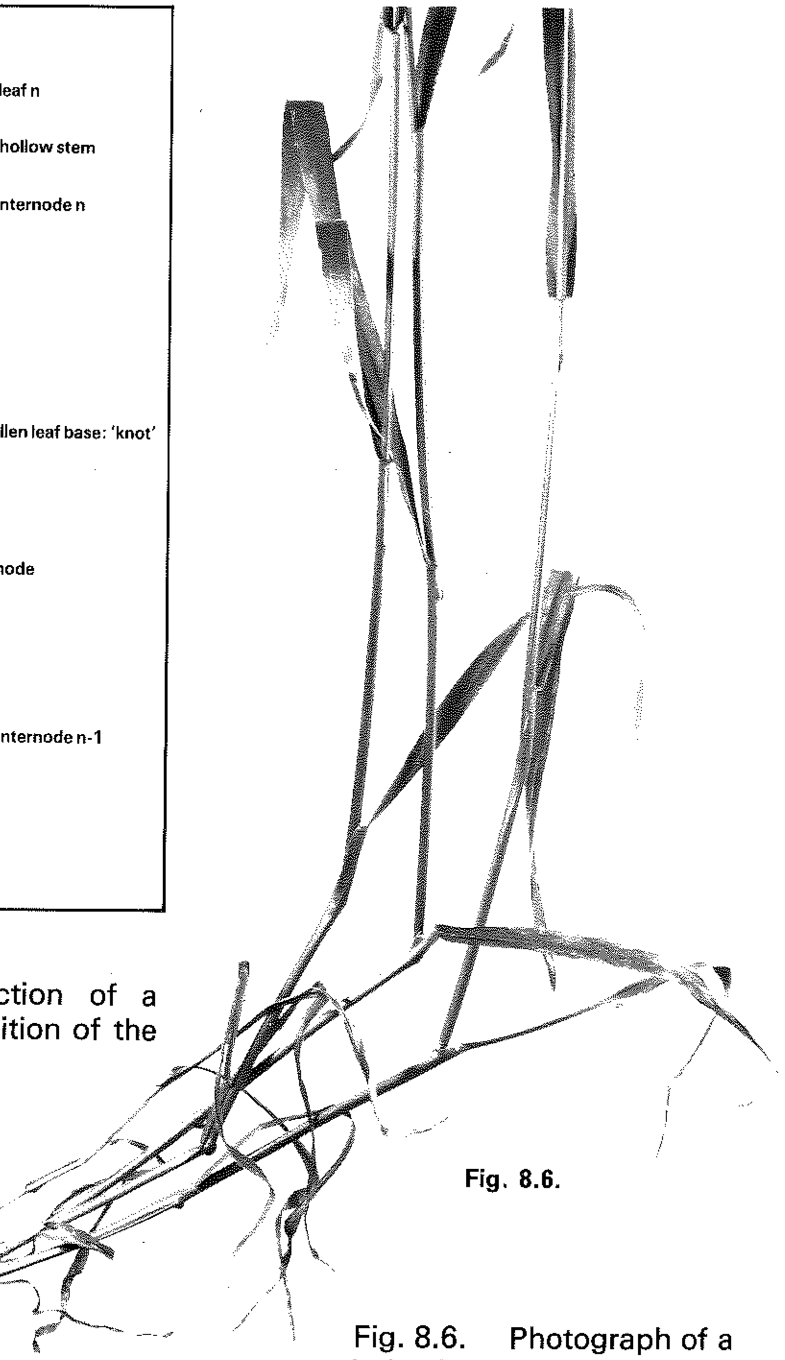


Fig. 8.6.

Fig. 8.6. Photograph of a lodged plant showing the function of the knots in raising the ears to a vertical position.

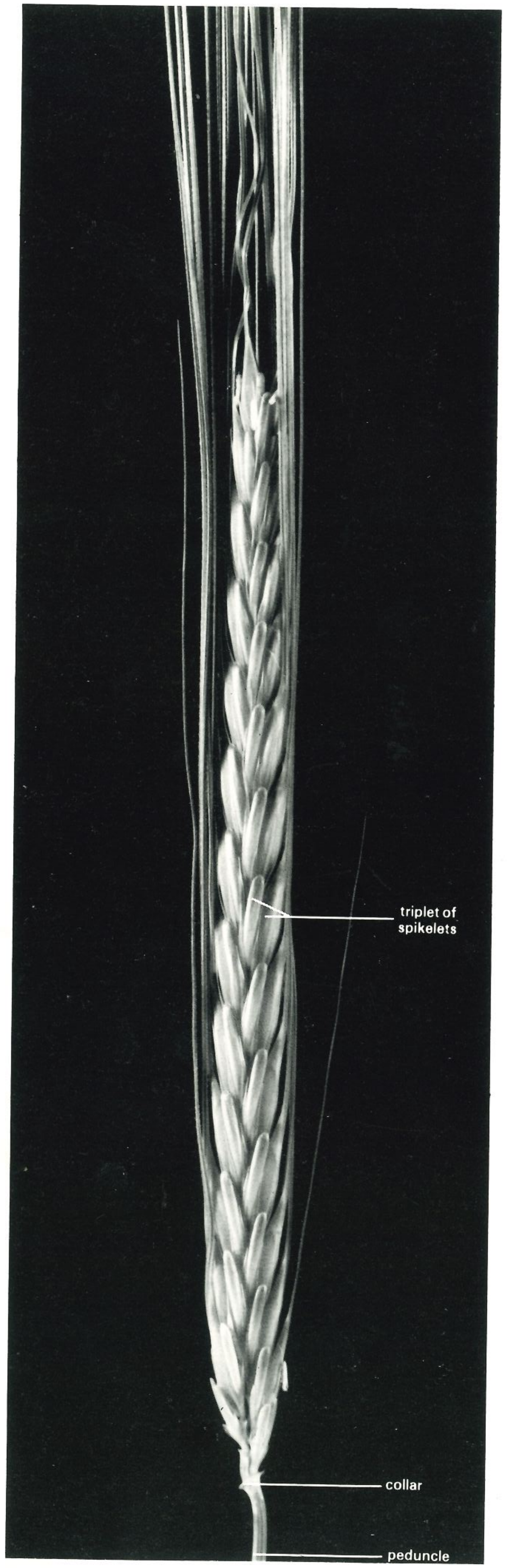


Fig. 9.1

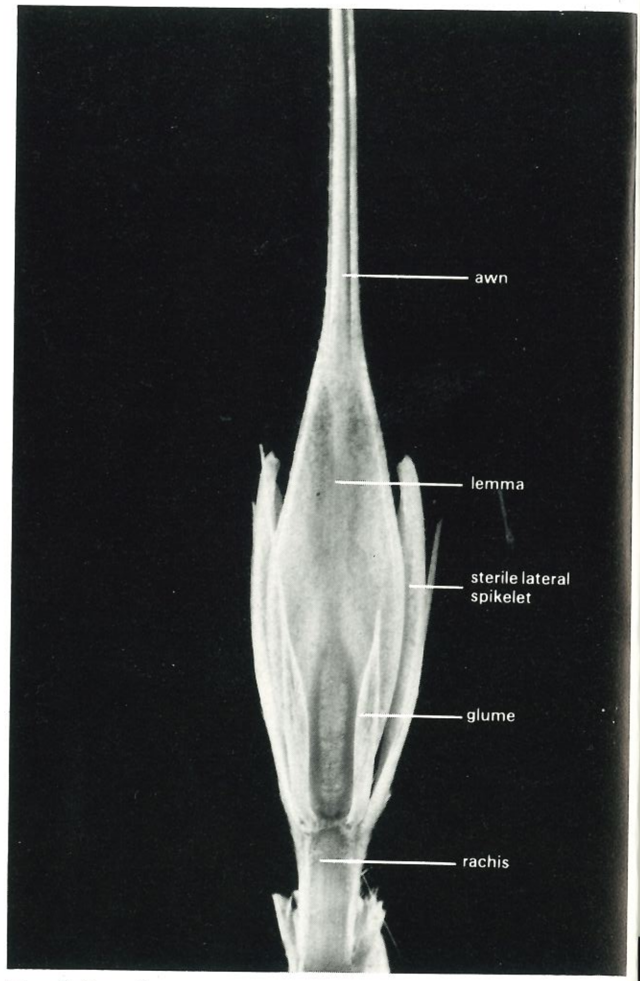


Fig. 9.2

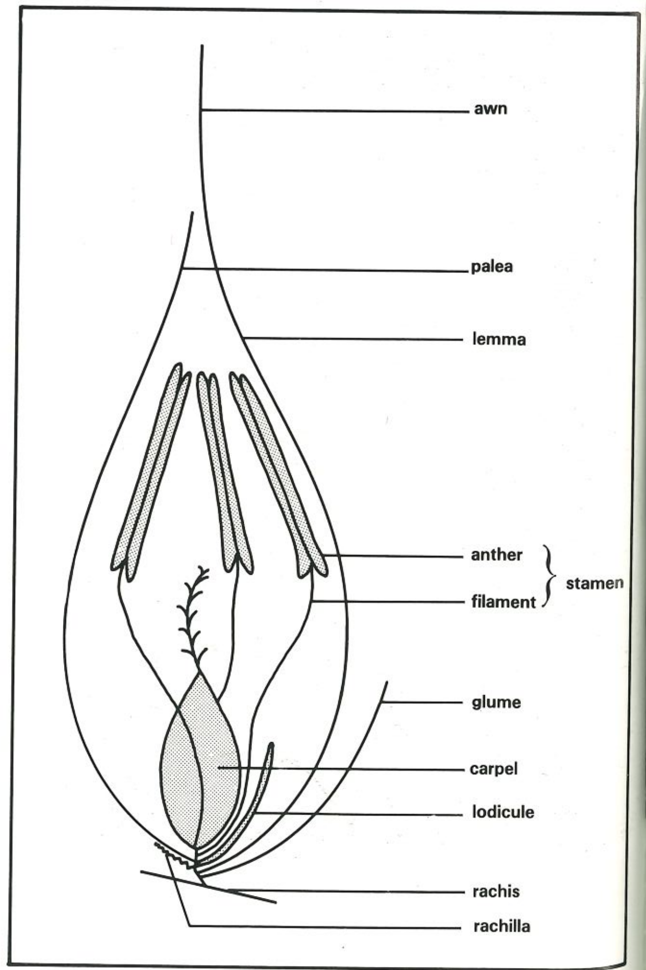


Fig. 9.3

Diagram

9. ANTHESIS

Ear Structure: Barley

The ear of barley has a stem (rachis) made up of nodes and short flattened internodes. The floral structures, spikelets, are borne at the nodes. At the first formed, lowermost node there is a prominent collar, (Fig. 9.1). Usually there are no spikelets at this node and sometimes at the adjacent nodes they are poorly developed and do not bear grain. At all other nodes on the ear there are three spikelets, each with a single floret. In two-row barley types only the median spikelet is fertile; the lateral spikelets are small and bear only rudimentary floral organs. In six-row types all three spikelets at each node are fertile. At the tip of the ear the remains of spikelets which aborted at an early stage of development (p.57) can be seen (Fig.7.8).

Each spikelet is bounded by two small glumes at the base (Fig. 9.2). The lemma (with long awn) and the palea enclose the floral parts — two lodicules, three stamens and a carpel. The lodicules are small fleshy organs which swell and push apart the lemma and palea. The stamens consist of a short filament which elongates at anthesis, and anthers which contain pollen. The carpel has two feathery stigmas.

Fig. 9.3 is a simplified diagram of the median spikelet to show the arrangement of the floral parts. The lateral spikelets are not shown, and only one lodicule and glume have been drawn.

Fig. 9.4 shows a barley spikelet in which anthesis was imminent. The lemma was removed and this disturbance stimulated the floret to begin anthesis.

9.4

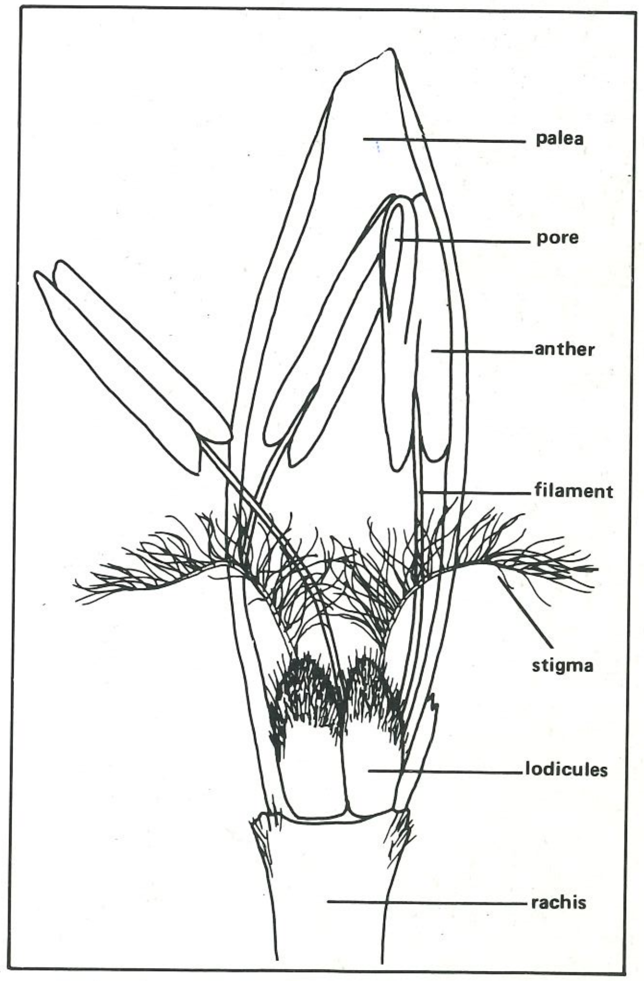


Fig. 9.4

Diagram

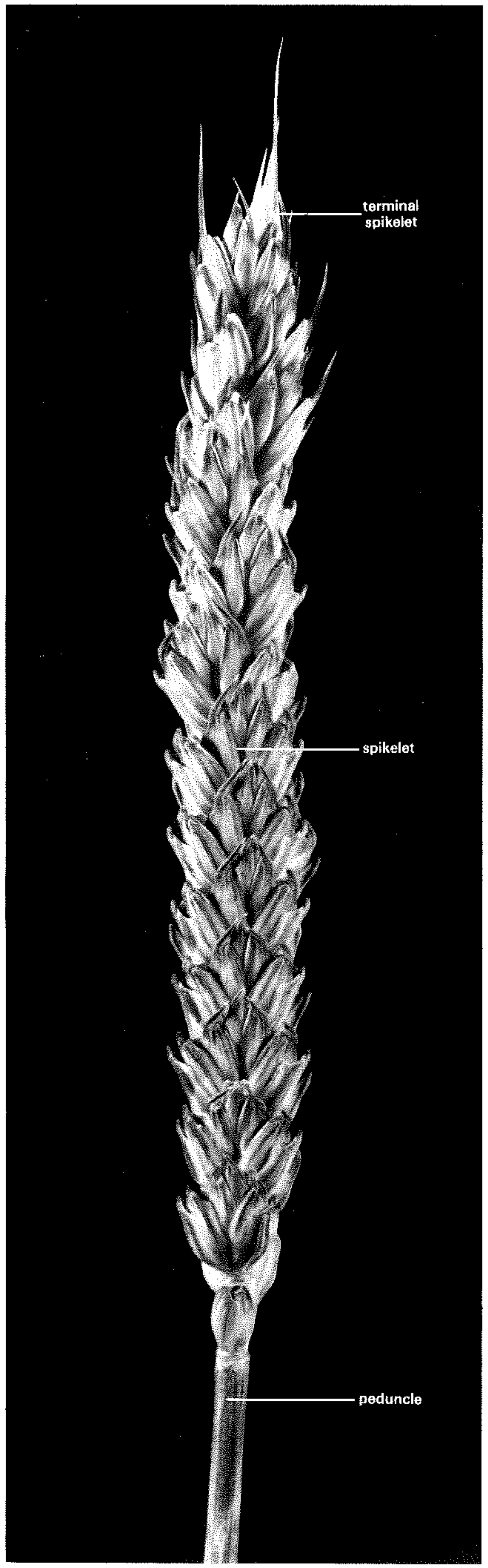


Fig. 9.5

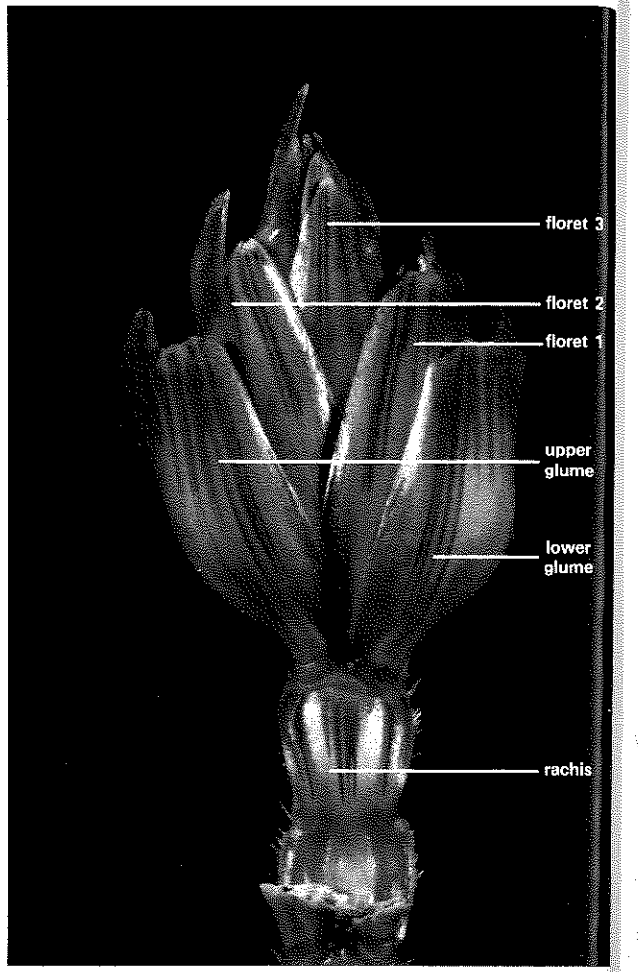


Fig. 9.6

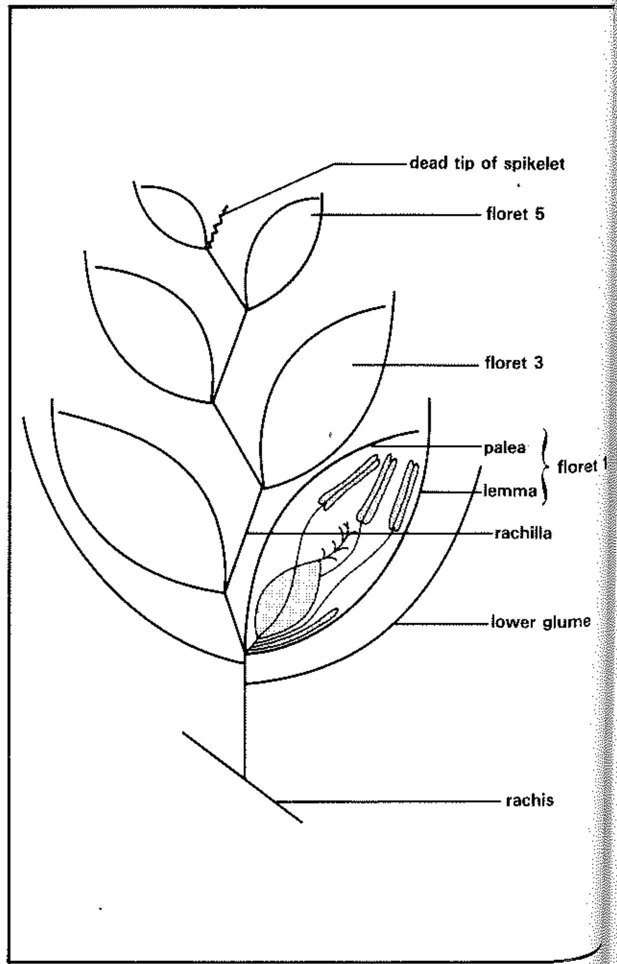


Fig. 9.7

Diagra

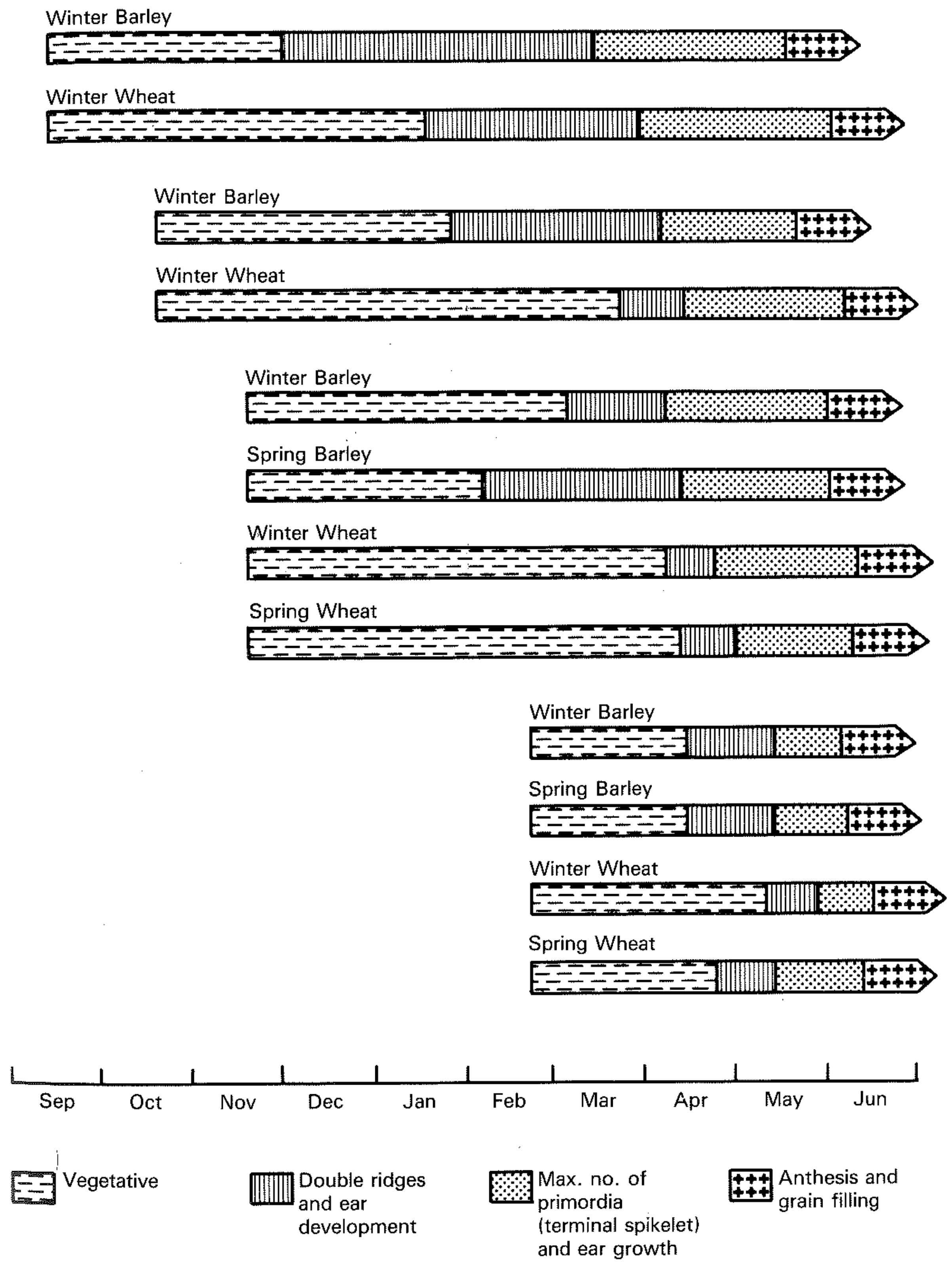


Fig. 11.1.

The effect of sowing date on the development of winter and spring barley and wheat.

Description of plant development

There are numerous published 'scales' of cereal development. These scales or codes are generally a description of a particular development stage, defined by brief descriptions of relevant features, often supplemented by a diagram or photograph. Depending on their intended use (routine agronomy procedures, chemical research, etc.) they are based either on external features, or cryptic characteristics for which some dissection is necessary. The most comprehensive methods for describing plant development are the so-called 'growth stage' scales. These are based largely on the external appearance of the plant and the best known scales of this type are the Feekes (Large, 1954) and Zadoks (Zadoks, Chang & Konzak, 1974; ADAS, 1978) scales.

Other scales seek only to identify a potentially critical stage of development and relate to one part of the growth cycle only. These usually rely on measurements rather than descriptions involving plant morphology or numbers of parts. Examples of this type of description are the length of the longest leaf sheath (Tottman, 1977) or the 'épi à un centimetre' (ear at 1 cm), used by French agronomists (Couvreur et al., 1980).

Many of the scales, in addition to a brief written description, assign a numerical code to each stage. These codes are merely a shorthand way of describing the plant, suitable for quick recording. They are not metrical and should not be used for numerical or statistical analysis. Any record of a stage should include a brief verbal description e.g. '11, first leaf fully emerged' (Zadoks code).

Zadoks growth stages, based on external plant appearance

There are a number of scales based on such characters as the number of leaves or tillers or the maturity of the grain. These characters can be seen with only minimum preparation and do not require a lens or microscope or other equipment. Zadoks scale is the most comprehensive and gives standard descriptions for all phases of the life cycle and incorporates features from other growth stage scales. Only the Zadoks scale is considered here but the caveats which relate to it also apply to other similar scales.

Table 11.1 Main sections of the Zadoks growth stage scale. (Each section is subdivided, e.g. seedling growth from 10 to 19).

0	Germination
1	Seedling growth (number of unfolded leaves on the main shoot)
2	Tillering
3	Stem elongation (number of detectable nodes)
4	Booting
5	Ear emergence
6	Anthesis
7	Milk development
8	Dough development
9	Ripening

The Zadoks stages are based on several different aspects of plant development and each aspect is the basis of a section of the scale (Table 11.1. For a detailed description of the use of the Zadoks scale, see Tottman (1977)). The relevant sections for crop management use, i.e. when most decisions are made with regard to husbandry treatment, are sections 1, 3, 4 and 5. However, if it is important to relate treatment to apex development, how far is external appearance, as measured by Zadoks scale indicative of apex stage?

'Seedling growth', Zadoks Section 1, covers a major part of the pre-anthesis life cycle, for during the phase when leaves are emerging on the main stem the ear is initiated and makes a considerable part of its growth. Leaf number is a good measure of plant development, leaves emerge at regular intervals (in relation to time and temperature) and thus a leaf count divides the life cycle into meaningful increments. However, number of emerged leaves at a particular stage of development is related to total number of leaves but total number of leaves varies with husbandry, particularly with date of sowing (Table 11.2a). Therefore there is not an absolute correspondence between number of emerged leaves and apex stage (Table 11.2b).

Table 11.2a Variation in total number of leaves on the main shoot with date of sowing. sowing.

Sowing date	Total number of leaves Barley	Total number of leaves Wheat
September	16-14	16-12
October	13-12	13-11
November	12-11	11-9
February	9-11	8-11

Table 11.2b Number of emerged leaves at double ridges and maximum number of primordia (barley) or terminal spikelet (wheat) in relation to the total number of leaves produced on the main shoot

	Total number of leaves 16	15	14	13	12	11	10	9	8
Barley									
Number of emerged leaves at:									
Double ridges	8	8	7	7	6	6	5	4/5	
Max. no. of primordia	13	12	11	10/11	10	9	8	7/8	
Wheat									
Number of emerged leaves at:									
Double ridges	11	10	9	8/9	8	7	6	5/6	5
Terminal spikelet	13	12	11	10/11	10	9	8	7/8	7

Use of the tables to estimate occurrence of double ridges and maximum number of primordia (or terminal spikelet):

With reference to the date of sowing of the crop, look up, in Table 11.2a, the total number of leaves normally expected on the main shoot (for example, barley sown in October (see shaded area) will produce a total of 13 or 12 leaves on the main shoot). Refer this to Table 11.2b where the number of emerged leaves at each stage is given. (The example shown (shaded) indicates that when there are seven or six leaves emerged on the main shoot the plant is likely to be at the double ridge stage and when 10 or 11 leaves are emerged, at maximum number of primordia. This could be confirmed by dissection).

Fig. 11.2.

Fig. 11.2 Tagging a plant helps to keep track of the number of emerged leaves on the main shoot — for example marking leaves 3, 6 and 9 facilitates counting. This barley plant has leaf 3 ringed. Any durable tag will do; a ring of plastic coated single core wire is particularly suitable.

In practice the number of leaves on the main shoot can be counted with precision except for the later stages of early sown crops, when death and weather damage means that lower leaves cannot be counted. A system of leaf tagging of a representative sample of plants will overcome this difficulty (Fig. 11.2).

The criteria for Zadoks Section 3 (stem elongation) are reliable indicators of plant development because ear development and stem elongation are closely related. The main difficulty in estimation of plant development by reference to this section is related to the definition of 'detectable node'. (This is dealt with in Chapter 8, p.65). Reference to elongated internodes provides an unambiguous assessment of development. The first category in this section, 30 — pseudostem (leaf sheath) erection, has in practice been found difficult to estimate objectively. The last two stages in this section are not based on number of detectable nodes but on the emergence of the flag leaf (37) and its ligule (39). Stage 37 usually coincides with stage 33 or 34 (i.e. three or four detectable nodes) depending on factors including date of sowing, which affect the number of elongated internodes.

Sections 4 and 5, which are also related to stem elongation or where the ear itself is the criterion of development also accurately reflect ear development.

Of the other sections, 2 (tillering) does not measure development, for the number of tillers depends strongly on the growth conditions and nutrient supply, and plants at the same stage may have different numbers of tillers. For this reason stage descriptions such as 'fully tillered' should be avoided. It is often important for other reasons to know the number of tillers per plant or per unit area, but the information does not provide any estimate of development. Section 9 deals with anthesis, which, in any particular ear, is often complete in two or three days, with the majority of spikelets flowering on the same day. Similarly it is often possible to identify a day upon which most ears come to anthesis. The later stages of grain development occupy three sections. Important stages such as maximum dry weight of the grain are often best estimated by dry matter or water content measurements (see Chapter 10 p.76).

Stages based on measurement

Certain critical stages of plant development are not well defined by growth stage scales and efforts have been made to find more objective methods to describe these stages.

Leaf sheath exceeds 5cm This measurement was proposed by Tottman (1977) to define more precisely for winter wheat 'pseudostem erect' (Zadoks stage 30). It was also found to be a useful indication of the stage of differentiation (late double ridge stage) of the young ear. This stage is defined as occurring when the length of the sheath of the last unfolded leaf exceeds 5cm, measured from ground level to ligule (base of leaf blade). The research to provide this objective assessment was done mostly on crops sown in early to mid-October. With the trend to earlier sowing and with a wider spread of sowing dates, it has been found that the relation between sheath length and apex stage for winter wheat depends on sowing date. For early autumn sowing the double ridge stage is generally not achieved until sheath length is longer than 5cm, whereas in the later sowing double ridges will be present before the sheath is this length.

Ear at 1cm This stage (épi à un cm) was defined by French agronomists (Couvreur et al., 1980). It estimates a similar stage of shoot development to that described in the previous paragraph or the Zadoks 30 stage. It involves a simple dissection, for the plant must be removed from the soil and the main stem examined by bisecting it with a knife (Fig. 11.3) or, as described on page 65 by pulling away the ensheathing leaves. This measurement appears to be a good indicator of apex stage and occurs at the time when the lemmas or florets become visible, that is after the double ridge stage and shortly before the embryo ear has completed spikelet initiation.

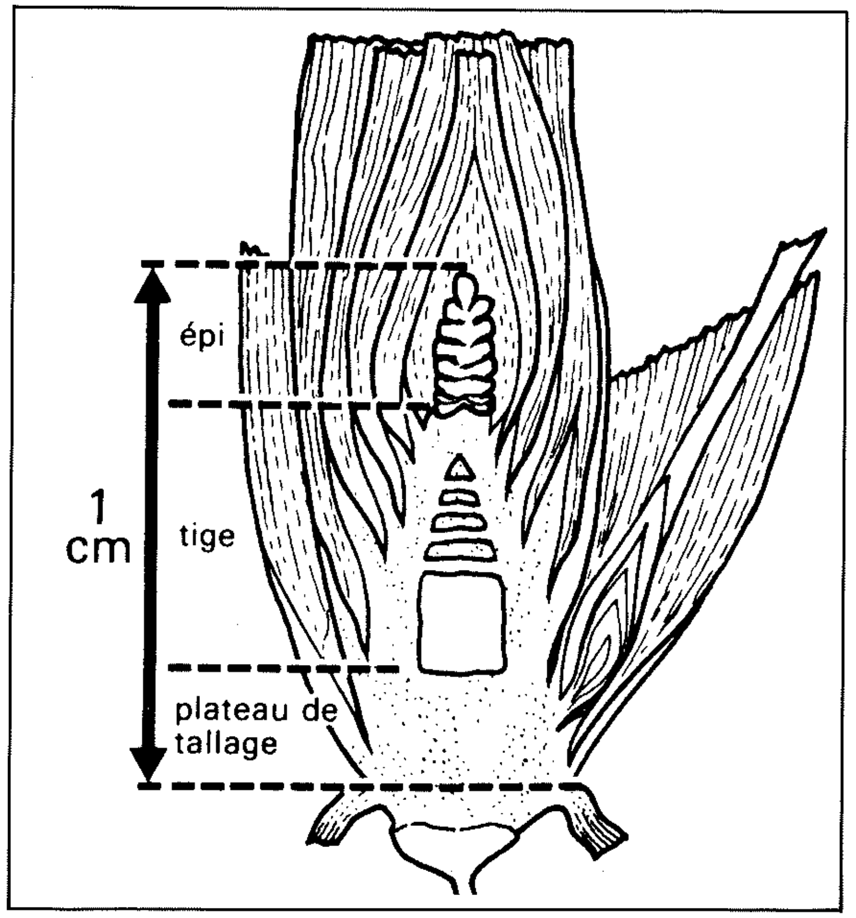


Fig. 11.3.

Fig. 11.3. Diagram from Couvreur et al., (1980) showing the 1cm measurement. Épi (ear), tige (stem), plateau de tallage (plane of tillering).

Assessment of apex stage by dissection

Because the response to some treatments or stresses depends upon the condition of the apex, direct inspection by dissection gives information about the primary site of action of the environmental or chemical factor and does not depend on correlated development of other externally visible organs, which may be affected differently by genotype or environment.

For successful use this method needs greater manual dexterity and botanical knowledge than does the use of growth stage estimation of the 'Zadoks' type. For early stages of development it is necessary to use a stereoscopic dissecting microscope (see Appendix II), but the necessary skill and knowledge can easily be obtained with a little practice. A good way to do this is by regular monitoring of plant development from an early stage, starting soon after plant emergence. This enables the operator to observe the increasing complexity, stage by stage and to interpret the more advanced stages in relation to the successive appearance of each new structure.

Prediction of plant development

The rate at which the cereal plant develops in response to such environmental factors as temperature and daylength is well understood, and the relation between environmental factors and development rate can be expressed in the form of mathematical equations. By combining these equations it is possible to produce a mathematical description or 'model' of the life cycle of the plant and using a computer to do the complex calculations to make a day-by-day simulation of plant development. A number of such models are being developed by various research groups and a model designed specifically for wheat in Britain has been formulated by four AFRC Institutes (Porter et al., 1983). To simulate development the model must be given certain data. From information on the latitude and the date of sowing of the crop the model calculates the daylength for each day. Daily maximum and minimum temperatures enable the computation of accumulated temperature (thermal time). Using this method it is possible to estimate the effect of temperature on plant development. Because varieties differ in their response to temperature and daylength, the model must also be supplied with parameters which describe the response of the particular variety, the development of which is being simulated.

While models of the sort described above are still in a prototype stage and under continuing research, it is possible that they may become important tools in crop management. They might operate as follows. Initially the model would be supplied with basic data about variety, date of sowing, latitude of the farm and with temperature data based on averages for the site for, say, the previous 10 years. As the season progresses the maximum and minimum temperatures read at the site or nearby meteorological station are entered into the computer. Then, at any time, the computer can estimate the stage of development. Further, it can predict on the basis of long term average weather for the site the time at which some critical stage for a particular management operation will occur.

It is open to question whether and how this computer technology will be applied to crop management. It may be centralised and operated by a large organisation such as ADAS. However, a typical computer program to simulate development can be run on a desk-top computer and it will become feasible for individual farmers or consultants to consider using this.

Used together with crop monitoring based on growth stage or dissection techniques, computer simulation of crop development may have considerable potential as a management tool.

Summary

1. For many research purposes, i.e. the testing of new chemicals or new varieties, it is preferable to use direct observation of apex stage rather than 'growth stage'. Such observations may be related to other correlated characters for recommendation purposes.
2. For certain purposes ear at 1cm or leaf sheath length (adjusted for date of sowing and other factors) can give objective estimates of development.
3. Zadoks Section 1 provides a reliable method of measuring progress through the early part of the life-cycle. If used to estimate apex stage it must be adjusted for such factors as date of sowing and variety.
4. Zadoks Section 2 cannot be used to assess development.
5. Stem elongation measured by Zadoks Section 3 gives a reliable estimate of pre-anthesis development. (Zadoks stage 30 is not reliable, see 2. above).

Critical stages

It is not the purpose of this guide to identify critical stages of development in relation to specific chemical or other treatments. Such information should be sought from the manufacturer's recommendations or from the publications giving technical advice from organisations such as ADAS, as it becomes available. However, it is appropriate to single out certain key development stages the identification of which have general applicability for efficient crop management and recording. Systematic recording of these stages can be valuable for organising husbandry treatments or predicting the effect of stress.

Plant emergence (p.15)
Double ridges (p.19 and p.33)
Maximum number of primordia (barley, p.29) or
Terminal spikelet (wheat, p.41) or
Ear at 1cm (p.65 and p.85)
Anthesis (Chapter 9).
Maximum grain dry weight (p.79)
Maturity

12. GLOSSARY

Anther	The terminal part of a stamen, producing pollen, in pollen sacs.
Anthesis	Flowering
Apical meristem	Shoot apex, Growing point. Zone of cell division at tip of the stem, having it origins in a group of cells. The growing point consists of actively dividing cells. Behind the meristem division continues and differentiation begins, becoming greater towards the mature tissues. In addition to providing for growth in length of the main axis, the apical meristem is the site of origin of primordia of leaves, flowers and buds.
Awn (Figs. 12.1, 12.2)	A stiff bristle-like projection from the tip or back of the lemma or glumes in cereals and grasses. The lemma awn in barley is usually very long and rough, the glume awns are small and weak. Most British wheats have only small awns or awn points on the lemmas. The PBI spring wheat, Highbury has long stiff awns on all florets.
Carpel	The ovule-bearing structure which forms the female part of the flower. A carpel consists of three parts: the ovary, a swollen basal portion containing the ovule, styles, which are filamentous prolongations of the tip of the ovary, and the stigmas, the specialised filaments on which pollen lodges and germinates.
Coleoptile	Protective sheath surrounding the shoot in cereal and grass seedlings.
Collar (Fig. 12.1)	Structure at the base of the ear which marks the transition from stem to rachis; a rudimentary leaf.
Cross pollination	Out pollination. The conveyance of pollen from an anther of one flower to the stigma of another, either on the same or on a different plant. It leads to cross fertilisation.
Crown	A very short stem with leaves and nodal roots.
Dome	Zone of cells at the tip of the apical meristem (shoot apex) which, by cell division, forms the sites for production of leaf and spikelet primordia.
Endosperm	Nutritive tissue nourishing the embryo; formed in the embryo sac by division of the endosperm nucleus after fertilisation.
Filament	Stalk of a stamen.
Flag leaf	Uppermost leaf on the stem.
Floret (Figs. 12.1, 12.2)	Flower with lemma and palea, of cereals and grasses.
Glume (Figs. 12.1, 12.2)	A chaffy or membranous bract at the base of a cereal or grass spikelet.
Internode	The length of stem between two successive nodes.
Lemma (Figs. 12.1, 12.2)	The lower of two membranous bracts enclosing the flower in cereals and grasses.
Ligule	A membranous outgrowth at the junction of the leaf blade and leaf sheath in many grasses and cereals.
Lodicules	Two small scale-like structures below the ovary which, at flowering, swell up, forcing open the enclosing bracts, exposing the stamens and carpels.

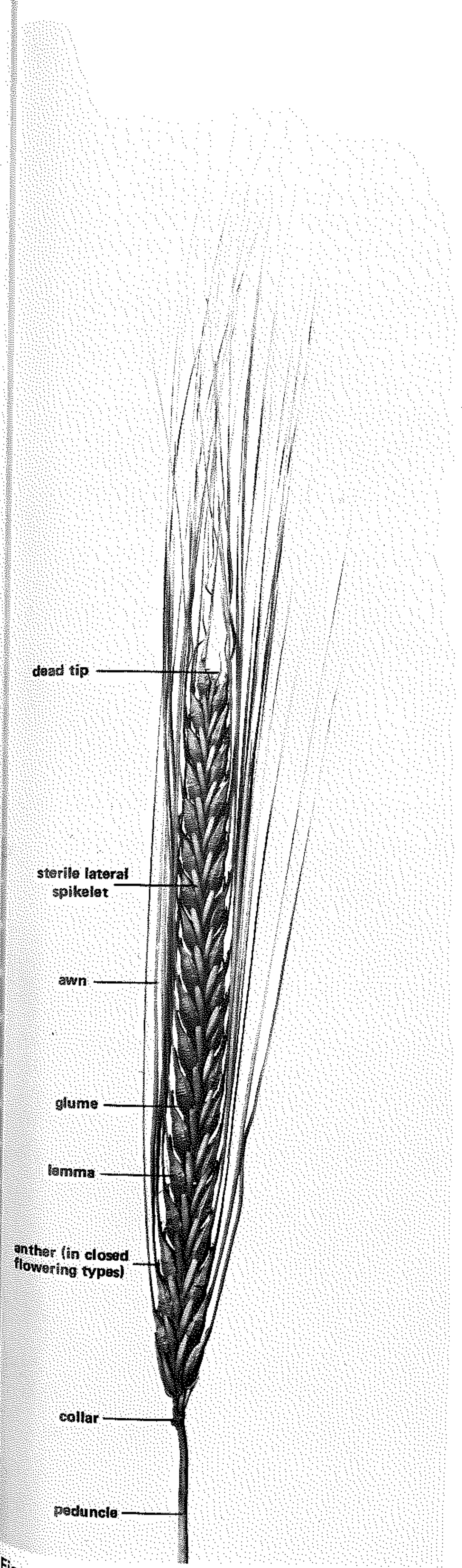


Fig. 12.1.

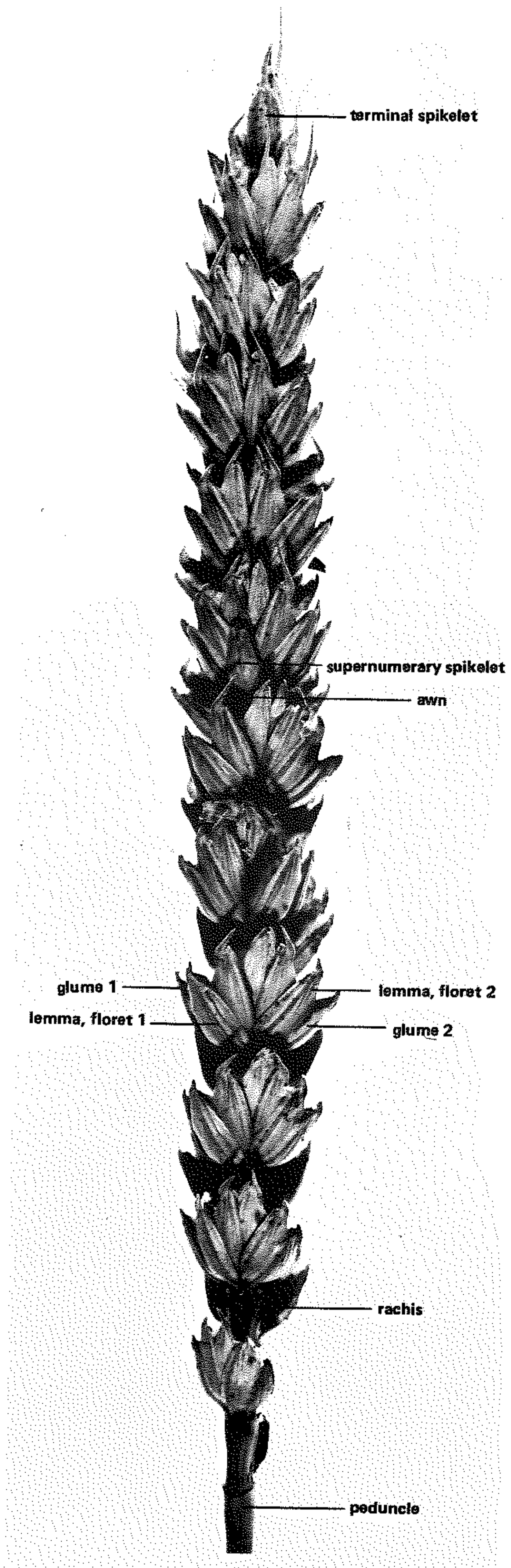


Fig. 12.2

Meiosis	A type of nuclear and cell division in which the chromosome number is reduced from diploid to haploid (i.e. the number of chromosomes is reduced to half - a reduction division). Meiosis occurs at some time in the life cycle of all sexually reproducing organisms, because gametes must be haploid to compensate for the chromosome doubling at fertilisation. This reduction is one of the bases of genetic segregation. To observe meiosis special staining techniques and a high powered microscope are required.
Meristem (see also Apical meristem)	Plant tissue capable of undergoing cell division, so giving rise to new cells and tissues. In cereals and grasses the principal meristems are the apical meristem and meristems from which stem and leaf growth arise.
Node	The place where a leaf is attached to a stem. On the elongated stem the lower part of the leaf associated with the node becomes swollen. This is sometimes called a 'joint' or 'knot'.
Palea	The upper of two membranous bracts enclosing the flower in cereals and grasses.
Primordium	The earliest recognisable initial of an organ or structure in development.
Prophyll	First 'leaf' of a tiller; a sheathing structure resembling the coleoptile.
Rachilla	The axis in the centre of a spikelet of a cereal or grass.
Rachis (Figs. 12.1, 12.2)	Main axis or stalk of the ear.
Scutellum	A flattened portion of the embryo of a cereal or grass — probably the cotyledon; it is pressed against the endosperm and serves as an absorptive organ.
Shoot apex	See Apical meristem.
Spikelet (Figs. 12.1, 12.2)	One of the units of which the inflorescence is made in cereals and grasses, consisting of several florets on a thin axis (rachilla), at the base of which are two bracts (glumes) marking the limit of the spikelet.
Stamen	One of the male reproductive organs of a flower, consisting of a stalk or filament and anther containing pollen.
Stigma	Terminal expansion of the style, surface of the carpel which receives pollen.
Style	The portion of the carpel between the ovary and stigma. It is elongated and thread-like.
Tiller	Side shoot arising at ground level.

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