# THE DEVELOPMENT OF THE BARLEY SPIKE [1]

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## INTRODUCTION

A study of the morphological development of the barley spike has practical significance for the agronomist and should be of interest to the botanist. From a study of the morphological development of the barley spike the agronomist can determine the critical period at which spike development may be affected by the environment. Differences in the rate of differentiation and growth in early spike development give a suggestion of the reasons for variation in the mature spike. Finally, the manner of the adjustment of the spike to environmental changes is indicated. To the botanist the development of the barley spike furnishes an example of the sequence of differentiation in a grass stem.

Publications dealing with the development of the barley stem from germination to pollination are few. Two publications that deal with the development of the barley spike from the earliest stages to complete differentiation should be mentioned. Schuster[2] published a description and a set of drawings illustrating several steps in spike and spikelet development. More recently Noguchi[3] has given a brief description of the spike and spikelet development and has illustrated some of the phases of development by drawings. He also gives data showing the length and breadth of the spike of 6-row and 2-row barley at different stages from 10 to 200 days old.

The illustrations accompanying the above-mentioned publications are line drawings and hence present more or less diagrammatically what is shown in this article by photographs. In addition, several stages of development are shown in this article that are not included by the above-mentioned authors.

## MATERIALS AND METHODS

Both 2-row and 6-row barley were used in this study and the photomicrographs that best showed the successive steps in spike and spikelet development were chosen without regard to type. This was justified since both types follow the same sequence of development, the only exception being that the side spikelets of the 2-row barley do not develop as rapidly or as completely as the central spikelets.

The plants were grown in pots in the greenhouse, and when they were 20 days old daylight was supplemented with electric light from 500-watt bulbs placed about 3½ feet above the bench on alternate nights. These conditions of growth produced normal plants except that the electric light hastened the development of the spike.

[1] Received for publication Apr. 15, 1935; issued December 1935.
[2] Schuster, J. Über die Morphologie der Grasblute. Flora [Jena] 100: 213–266, illus, 1910.
[3] Noguchi, Y. Studien über die Entwicklung der Infloreszenzen und der Bluten bei Getreidepflanzen. Jour. Col. Agr., Imp. Univ. Tokyo 10: 247–303, illus. 1929.

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At intervals of a few days, plants were pulled, taken to the laboratory, and the growing points dissected from the stem under the low power of a binocular microscope. Especially ground dissecting needles were used. The growing point was easily exposed and removed for photographing by carefully cutting and removing the leaves enclosing it.

Photomicrographs were taken with an upright camera, adjusted to fit over one side of the binocular microscope. It was necessary to construct a special light-tight collar to connect the microscope and camera. The eyepiece was left in the microscope when exposures were made.

Light for photographing was obtained from a microscope lamp fitted with a 200-watt bulb. A Florence flask filled with water containing sufficient copper sulphate to produce a light blue-green color was used as a condenser. This set-up gave a light of sufficient intensity to produce a good negative on commercial orthochromatic film with about 10 seconds' exposure.

At first great difficulty was experienced in making photographs because of the very rapid drying of the growing points. Later, the growing points when dissected were placed on moist blotting paper in a small preparation dish and stored in a Petri dish lined with wet paper towels. Material handled in this way could be kept for 24 hours without any apparent deterioration. It was also found that specimens stored in the moist chamber for a period of time did not dry out as rapidly as those that had just been dissected.

Two methods of mounting the growing points for photographing were used. In one the specimen was mounted on moist blotting paper over black paper placed in the bottom of a preparation dish. The preparation dish was covered with a watch glass for the preliminary manipulations and focusing and then the watch glass was removed for the final focusing. The other method was to place a drop of petroleum jelly on a glass slide, mount the specimen in the jelly, and then place the slide over a black velvet background. Both methods of mounting were satisfactory except that in using the latter method more speed was necessary to complete the photographing before the specimen dried.

Growing points of barley are very difficult to photograph because they are colorless and nearly transparent. They were photographed against a black background with the light so placed that the high lights and shadows brought out the detail. In some cases in order to provide contrast, a stain composed of a mixture of 90-percent alcohol, a small amount of glycerin and basic fuchsin was applied to the specimen with a camel's-hair brush. The alcohol quickly evaporated, leaving the glycerin and stain in the folds of the various structures. Since the red stain photographed black the details of the structures were clearly outlined.

## DESCRIPTION OF SPIKE DEVELOPMENT

In the resting stage of the barley grain the stem of the embryo is composed of only a few structures. These are the coleoptile and first leaf, which are the largest of the structures, the second and third leaf initials, the growing point, and a tiller bud in the axil of the coleoptile. The coleoptile and first leaf have been dissected from the embryo of the barley seed in plate 1, *A*, to show the second and third leaf

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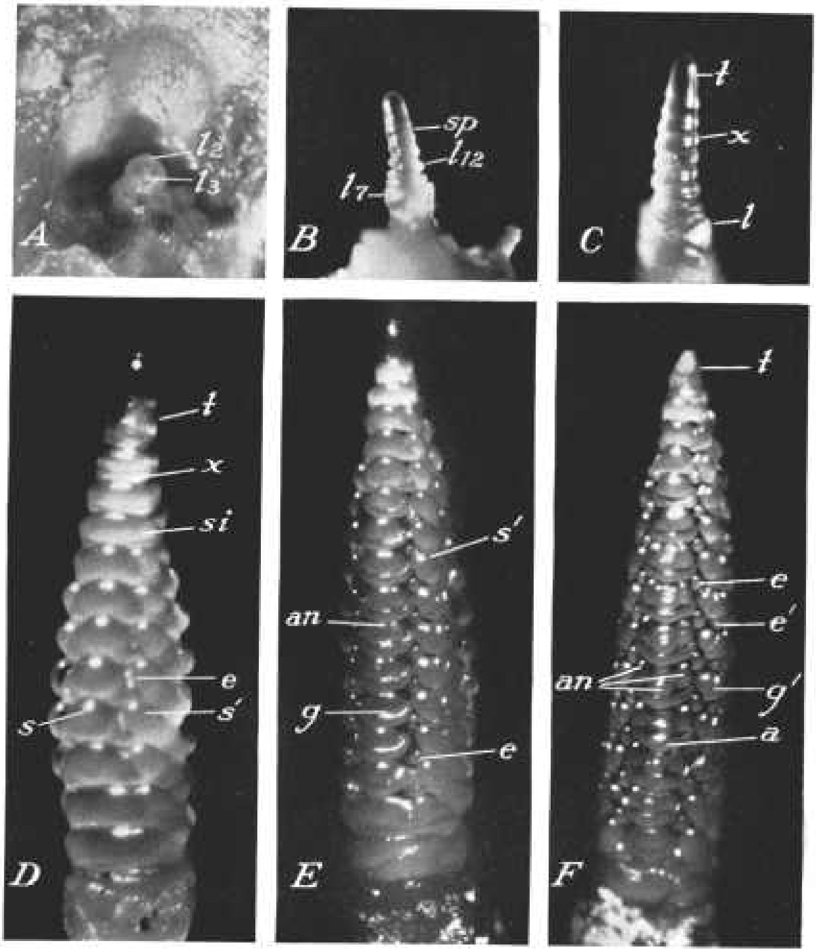



*A*, A part of the embryo of a kernel of barley with the coleoptile and first leaf removed: $l_2$, Second leaf; $l_3$, third leaf. × 21.

*B*, Growing point of a barley stem in the 3-leaf stage: $l_7$, Seventb-leaf initial; $l_{12}$, twelfth-leaf initial; *sp.*, spike primordium. × 17.

*C*, Growing point of a 6-row barley stem in tbe 4-leaf stage, showing double ridges marking the beginning of spike differentiation: *l*, Leaf initial; *x*, double ridge; *t*, tip of spike. × 25.

*D*, Young spike of 6-row barley from a stem in the 5-leaf stage, showing the beginning of spikelet formation: *s*, Central spikelet; *s'*, side spikelet; *e*, empty glume; *si*, spikelet initial; *x*, lower of a double ridge; *t*, tip of spike. × 40.

*E*, Spike of a 6-row barley stem in the 5-leaf stage when the lemma and anthers begin to form. Stain has been used to make clear tbe position of the spike struetures: *e*, Empty glume; *g*, lemma; *an*, antbers; *s'*, side spikelet. × 25.

*F*, A spike of 2-row barley from a stem in tbe 6-leaf stage showing a more advaneed stage of glume, anther, and awn development. Stain has heen used to mark out the structures: *a*, Awn; *an*, anthers; *g'*, lemma of a side spikelet; *e'*, and *e*, empty glume initials of the side and eentral spikelets respectively; *t*, tip of spike partially dried. × 25.

initials. The growing point, which is hemispherical, is partly enclosed by the third leaf initial. By carefully removing the second and third leaves the primordium of the fourth leaf can be seen as a transverse ridge of the growing point.

By the time the second leaf is well grown nearly all of the leaves and leaf initials that the main stem will have can be found. The leaves range in size from those fully grown to leaf primordia just distinguishable as ridges at the base of the growing point. At this stage of stem development the growing point has just begun to elongate in preparation for spike differentiation. Up to this time the growing point has been short and hemispherical.

The growing point of a stem in the three-leaf stage is shown in plate 1, *B*. The leaves that enclosed this growing point ranged in size from the fully grown first and second leaves with the third leaf about 2 inches long down to the sixth leaf that was just large enough to enclose the growing point. The seventh-leaf initial is the basal one (pl. 1, *B*, $l_7$), while the last prominent ridge (pl. 1, *B*, $l_{12}$) is probably the last leaf that the stem would have produced. Above the twelfth-leaf initial is the part of the growing point from which the spike is differentiated.

The first indication of spike differentiation is the appearance of double ridges (pl. 1, *C*, *x*) instead of single ridges as was noted previously. At first the ridges are nearly equal in size, but the upper ridge of each pair grows more rapidly and from it the spikelets are formed. The lower ridge of the pair probably becomes the internode of the rachis, for apparently all of the spikelet structures arise from the upper of the pair of ridges.

Spikelet differentiation is first indicated by the appearance of two slight depressions in the transverse meristematic ridge. The very earliest stages of spikelet differentiation can be noted in the two spikelet initials at the base of the spike (pl. 1, *D*). Growth occurs in both sides and between the two furrows in preparation for the differentiation of the spikelet parts. Soon two little papillae, or empty glume initials, appear on opposite sides of each spikelet (pl. 1, *D*, *e*), but they appear first on the central spikelets.

Several stages of spikelet development are shown on the same spike (pl. 1, *D*). In the center portion of the spike the spikelet initials are quite prominent. The two transverse ridges at the base of the spike and some of the ridges at the top of the spike show only the first evidences of spikelet differentiation. The very tip of the spike is smooth and shows little evidence of the formation of ridges, while in plate 1, *D*, *x*, the lower of a pair of ridges can be seen.

The lemma is the first structure of the spikelet to differentiate (pl. 1, *E*, *g*). It appears as a distinct ridge across the spikelet initial and forms first upon the central spikelets in the central portion of the spike. Differentiation of the palea occurs somewhat later than that of the lemma, but since it is hidden by the other spikelet parts its development cannot be followed in gross dissections.

Soon three little papillae appear upon the meristem above the lemma (pl. 1, *E*, *an*, and *F*, *an*). These little papillae are the primordia of the anthers. The pistil is formed from that portion of the meristem located between the anthers, but it does not differentiate till considerably later than the anthers. The ovary differentiates first, followed by the styles and last, the stigma, but no features of the differentiation of the pistil can be seen in gross dissections.

A side view of a young spike of barley is presented in plate 2, *A*, for the purpose of showing an early stage in the development of the rachis. In the early stages the internodes of the rachis are very short, but as the spike matures the internodes elongate. The degree of elongation determines spike density, a character used in the classification of barley varieties.

The awn begins its development as an outgrowth from the lemma (pl. 1, *F*, *a*). The awns and anthers grow quite rapidly and together with the empty glumes are soon the most conspicuous of the spikelet structures (pl. 2, *B* and *C*). The awn grows much more rapidly than the lemma and palea, which remain short with the anthers extending above them. About the time the last internode of the stem begins to elongate the glumes begin their growth and finally enclose the anthers and pistil. It should also be mentioned that in barbed varieties of barley the barbs can be seen on the awn at an early stage.

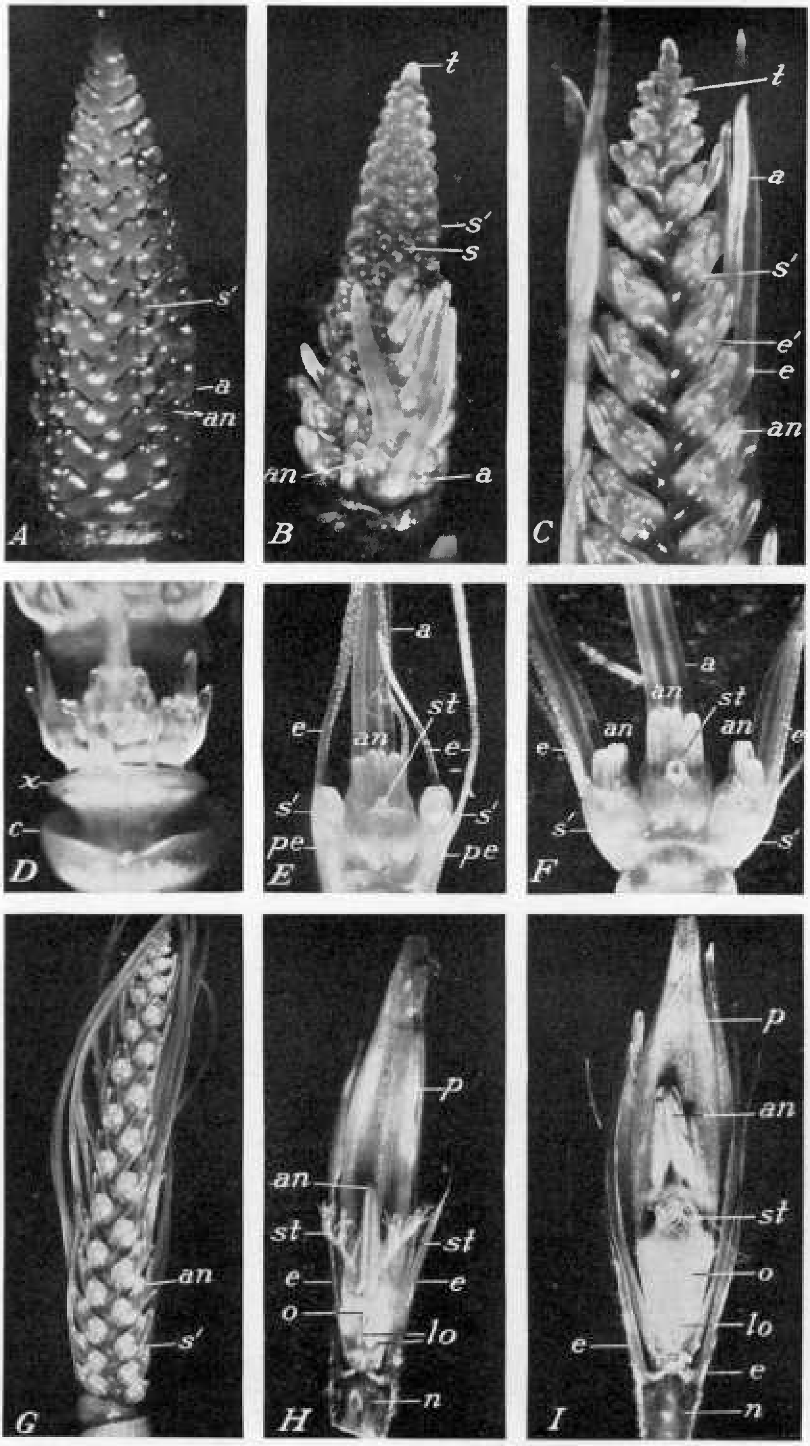
While the spike of barley shown in plate 2, *B*, was chosen principally to show the early development of the awn, it also shows the differentiation of a 6-row barley at the 6-leaf stage. A difference in development at the base and tip of the spike should be noted as well as the relative stages of differentiation in the side and central spikelets.

The relative size and degree of development of the tip of the spike and the spikelets a little lower on the spike should be noted (pl. 2, *C*, *t*). The very tip of the spike is at this stage a bit of undifferentiated meristem, and the spikelets at the uppermost 7 or 8 nodes of the rachis, as contrasted with the spikelets below, are much retarded in development. As has been pointed out, in the early stages of development the tip of the spike remains undifferentiated and smooth in outline. As the spike approaches maturity spikelet differentiation proceeds apically, but the last-formed spikelets never complete development, always remaining infertile and rudimentary. Rudimentary spikelets at the tip of the spike can be seen on any mature barley spike.

At the base of the spike is a structure called the collar (pl. 2, *D*, *c*). This structure is a distinct ridge of tissue circling the stem at the first node of the spike. A similar but less prominent ridge of tissue is found at the first node above the collar (pl. 2, *D*, *x*). So far as has been determined in these studies, the collar and the ridge at the node above are formed by two leaf initials that are just beginning to differentiate but are not far enough along to continue their develop-

EXPLANATORY LEGEND FOR PLATE 2

*A*, Spike of a 2-row barley stem in the 6-leaf stage, showing the rachis and a side view of anthers, awns, and side spikelets. Stain has been used to mark out structures: *an*, Anthers; *a*, awn; *s′*, side spikelet. × 30.
*B*, A 6-row barley spike from a stem in the 6-leaf stage, illustrating awn development and the comparative development of side and central spikelets: *a*, Awn; *an*, anthers; *s*, central spikelet; *s′*, side spikelet; *t*, tip of spike. × 25.
*C*, Part of a barley spike from the stem of a 2-row barley in the 5-leaf stage, showing the differentiation of the tip of the spike: *an*, Anthers; *e*, empty glume; *e′*, empty glume of side spikelet; *s′*, side spikelet; *a*, awn; *t*, tip of spike. × 25.
*D*, Part of a spike from a stem in the 6-leaf stage, showing the collar at the base of the spike: *c*, Collar; *x*, second node of the rachis. × 30.
*E*, Spikelet of a 2-row barley: *pe*, Pedicel; *s′*, side spikelet; *st*, style; *e*, empty glumes; *an*, anthers; *a*, awn. × 15.
*F*, Spikelet of a 6-row barley: *s′*, Side spikelet; *e*, empty glume; *st*, style; *an*, anthers; *a*, awn. × 15.
*G*, Spike of a 2-row barley: *s′*, Side spikelet; *an*, anther. × 8.
*H*, Spikelet before pollination: *r*, Rachis; *lo*, lodicules; *o*, ovary; *e*, empty glumes; *st*, stigma; *an*, anther; *p*, palea. × 5.
*I*, Spikelet after pollination: legend as for *H*.




FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.

ment as leaves at the time spikelet differentiation begins. They are arrested in their development and form the structures mentioned. While spikelets develop at the collar, they are late and usually rudimentary and sterile.

A spike of a 2-row barley well advanced in its development is shown in plate 2, *G*. The awns on the central spikelets are well developed but not fully grown and the anthers protrude well beyond the glumes. The side spikelets are small, without awns on the lemma, and rudimentary anthers extend slightly beyond the glumes. Much in evidence are the empty glumes upon which the barbs can be seen. Barbs can also be seen on the awns.

A spikelet of a 2-row barley (pl. 2, *E*) and a spikelet of a 6-row barley (pl. 2, *F*) are shown for comparison. Both spikelets were taken from stems in about the same stage of development. The last internode of the stem, the one to which the spike is attached, had just begun to elongate. The anthers and stigmas in the spikelets of the 6-row and in the central spikelet of the 2-row barley extend above the flowering glumes. However, just before the head emerges from the boot, the lemma and palea which up to this time have grown slowly begin to grow rapidly and soon enclose the anthers and stigmas. The anthers in the side spikelets of the 2-row barley have been enclosed by the flowering glumes. The side spikelets of the 2-row barley are much smaller than the central spikelet, are without awns on the lemmas, and are pedicellate. The side spikelets of the 6-row barley are nearly as large as the central spikelet, have awns on the lemmas, and are sessile. The side spikelets of the 6-row barley are fertile, while those of the 2-row barley are sterile. The stigmas in neither have branched (pl. 2, *E*, *F*, *st*).

Mature flowers before pollination and after pollination are shown in plate 2, H, and plate 2, I, respectively. The lemmas have been cut away to show the flower parts. Only one anther can be seen (pl. 2, *H*). The other two anthers are hidden in the folds of the palea. Before pollination the anther is not dehisced, the stigmas are erect, branched, and feathery, the lodicules swollen and turgid, and the ovary small. After pollination the anthers are dehisced, the stigmas are collapsed, the lodicules are shrunken, and the ovary has increased in size. The fertilized ovary after a period of growth and differentiation becomes the barley kernel.

Aside from the pistil and palea mentioned previously, two other spikelet structures, the rachilla and the lodicules, have not been followed in their differentiation and development in this study. They are so located that their differentiation and development cannot be shown.

## DISCUSSION

That period in the morphological development of a head-bearing barley stem extending from germination to pollination can be divided into two phases. These phases can be determined approximately by examining the stem and more accurately by examining the growing point. In the first phase of development, the internodes of the stem do not elongate, leaves grow, leaf initials are the only structures differentiated from the growing point, and the growing point above the base remains smooth in outline but increases in length. The changes in the stem and the growing point which mark the transition from the first to the second stage are shown by the beginning of internode elongation in the stem and the appearance of double ridges on the growing point. In the second phase of development, the internodes of the stem elongate, the spikelets and spikelet structures differentiate, increase in size, and complete their development in preparation for pollination.

It is interesting to note how the phases of stem development of a barley plant parallel each other not only in those stems that produce heads but in all stems even down to the tiller buds. When stems producing heads pass into the second phase, i. e., jointing and spike differentiation, it is not long before all stems on the plant follow in rapid succession. An examination of a plant in head shows even the growing point of the tiller buds to be in the process of spikelet differentiation.

Very early differences in the time of differentiation and rate of spikelet development are maintained and are reflected in the mature spike. Referring to plate 1, *D*, *E*, and *F*, the early differences will be noted. The spikelets in the middle of the spike are in advance of the basal spikelets and the basal spikelets are in advance of the tip, which is the last portion of the spike to differentiate. The central spikelets are more advanced in development than the side spikelets in both the 2-row and 6-row types. All of these differences are reflected in the mature spike. The best developed and heaviest kernels are in the middle portion of the spike, the basal kernels next, and the tip kernels are the lightest of all. The kernels in the central spikelets of the 6-row barley are heavier than those in the side spikelets. While the spikelets progressively develop at the tip of the spike, the spikelets remain rudimentary and do not bear kernels. Thus those spikelets that have an initial advantage in differentiation maintain this advantage throughout spike development.

Since the number of spikelets at the joints of the rachis is fixed, response to the environment during early differentiation takes place principally at the tip of the spike. The barley spike is an indeterminate inflorescence and does not terminate in a single spikelet as in wheat. Within limits a certain amount of response to growth conditions is made at the tip of the barley spike in the number of fertile spikelets. Some response can be made at the base of the spike, but the capacity for responding at this point is much more limited.

Although the lemma differentiates before the awn, the awn grows more rapidly. It is not until well along in the development of the spikelet that the lemma and palea become long enough to enclose the anthers and other flower parts. A possible explanation for this behavior is suggested by Kennedy [4], who states that in the spikelet the awn corresponds to the leaf blade and that part of the glume below the insertion of the awn may be regarded as corresponding to the sheath of the leaf. He also states that of the three parts of the leaf the sheath develops last by intercalary growth which pushes up the blade. If the leaf parts and the spikelet parts are homologous as stated, then the slow growth of the lemma is in accord with development of the leaf sheath.

Up to the time that the anthers begin to differentiate, so far as the

[4] KENNEDY, P. B. THE STRUCTURES OF THE CARYOPSIS OF GRASSES WITH REFERENCE TO THEIR MORPHOLOGY AND CLASSIFICATION. U. S. Dept. Agr., Div. Agrostology Bul. 19, 44 pp., illus. 1899.

varieties used were concerned, no difference could be noted between a spike of a 2-row and a spike of a 6-row barley. As development continues the discrepancy in the development of the central and side spikelets of the 2-row barley becomes more apparent. The side spikelets develop very slowly, remain rudimentary without awns and infertile. On the other hand, while the side spikelets of the 6-row barley are always slower in development than the central spikelets, they finally attain nearly the same size, have awns, and are fertile.

## SUMMARY

A study was made of the morphological development of the spike of a 2-row and a 6-row barley by dissecting the growing points from the stems. Photomicrographs of the various stages are shown.

Stem development from germination to pollination can be divided into two phases in each of which the growth response of the stem and growing point are different. In the first phase the internodes of the stem remain short, the growing point produces only leaf initials, and the undifferentiated portion of the growing point elongates. The beginning of the second phase is marked by the elongation of the internodes of the stem and the appearance of double ridges on the growing point. In the second phase the internodes of the stem elongate and the spike and its parts differentiate and develop.

The order of differentiation of the various parts of the spike as far as could be seen in this study are: Spikelet initials, empty glumes, lemma, palea, anthers, awn, and pistil.

Early differences in the time and rate of differentiation of the spikelets in the different parts of the spike are maintained and account for some of the variation in size among the spikelets of the mature spike.

The barley spike is an indeterminate inflorescence, and with the number of spikelets at each joint of the rachis limited, some response to the environment can be made in the number of fertile spikelets at the tip of the spike.