THE PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT

III.* GROWTH OF THE PRIMARY SHOOT AND INFLORESCENCE

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Summary

The growth of the primary shoot of wheat and particularly of its inflorescence is described for plants grown in a controlled long-day environment.

The technique of serial reconstruction is used to build up a comprehensive picture of volume growth for successive leaf primordia, the inflorescence, the spikelet, and the parts of the basal floret of a representative spikelet. This picture is linked with dry weight data for late developmental stages of all these structures. The whole is integrated in terms of relative rates of change of the parts.

Length growth studies of the spike, the spikelet, and the floret parts reveal a number of correlative changes which would repay fuller investigation.

Attention is drawn to the contrast between growth curves for stamens and for the carpel. That for the carpel is complex, and is most readily interpreted on the hypothesis that the gynaecium is composed of several foliar structures fused together.

Volume growth for the stamens and carpels of the first five florets of a median spikelet is described in detail.

I. Introduction

In the first paper of this series, the seedling growth of wheat was studied in detail over a period of 21 days (Williams 1960). In particular this gave a precise quantitative description of the growth of the leaf primordia of the primary shoot. Williams and Rijven (1965) have since extended this description to the changes in DNA, RNA, proteins, and cell wall materials in the fourth leaf of wheat from an early stage to full maturity. In both papers, extensive use was made of the relative growth rate, or relative rate of change, $R = \mathrm{d}\log X/\mathrm{d}t$, for the description and explanation of growth phenomena (Williams 1964).

Williams (1960) also made some preliminary observations on the change from vegetative to reproductive development. This transition gained expression in a number of ways, all of which implied a progressive change in dominance from leaf growth to stem growth. There is clearly a need to carry these observations further by extending the description of the whole shoot to later stages of its development. This, then, is the primary objective of the present paper, which describes the later development of the primary shoot including the ear, the spikelet, and the floral

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parts up to the stage of anthesis. As in the first paper (Williams 1960), growth is described in terms of dry weight change and of volume change based on serial reconstruction. Some of the more general results of this work have been presented elsewhere (Williams 1964, 1966).

II. Experimental Procedure

(*a*) *Plant Culture, Sampling, and Dissection*

A spring wheat (*Triticum aestivum* L. cv. Nabawa) was grown in a controlled environment of which the "day" temperature (from 8.30 a.m. to 4.30 p.m.) was 20°C and the "night" temperature was 15°C. The plants received natural light during the "day" and incandescent lighting of 25–30 f.c. at plant level during the "night". These long-day conditions ensured early flower initiation and rapid development of the ear.

Grains within the weight range 55–65 mg were set to soak on June 6, 1959 (day 0), and those with seminal roots just emerged were sown next day, 6 per pot, in 144 pots of perlite. Hoagland No. 2 nutrient solution, but with the ammonium dihydrogen phosphate at half the usual strength, was used throughout the experiment, and the pots were flushed with water at intervals.

The pots were arranged in six blocks within two controlled-environment cabinets. Successive harvest classes were made by progressive thinning, and there were six replicates of four plants per harvest class. Some harvest classes were used for dissection and dry weight determinations, and others for volume determinations of meristematic organs close to the shoot apex. For the later stages of ear development it was possible to get weight and volume estimates from the same plants. Progressive thinning was resorted to because space was at a premium; its main defect was that root systems could not be recovered.

Dry weight samples were taken every fourth day from day 4 to day 40 inclusive, and on days 46, 50, and 55. Dry weights for young ears were also obtained for days 42 and 44. Samples for volume determinations were taken every fourth day to day 20, then every second day to day 46, and on days 50 and 55. The occasions for which specific organs were measured for volume or weight will be apparent from the tables and text-figures. As far as practicable estimates of both volume and weight at a common harvest were obtained so as to provide a link between these two sets of data. These common harvests were always early in the cell expansion phase for the organ in question.

For the early harvests, roots were trimmed off at their points of emergence from the coleorhiza as in earlier experiments (Williams 1960), but the scutellum was left attached as part of the "stem" fraction. The remnants of grain and root were discarded. Leaves were separated at their bases and into leaf and sheath at the ligule as soon as this was present. Tillers were kept separate from day 12 onward, and detailed dissection and study was confined to the main shoot. The inflorescence was dissected just below the lowest foliar ridge. Spikelets, florets, and floret parts were separated at their bases. All dissected parts were dried at 80°C in an oven with forced draught.

One difficulty arose from the fact that the number of leaves on the main shoot was not always seven. About one in four had eight leaves, and in these cases inflorescence development was delayed. This difference was not easily detectable until day 32. However, length measurements made on 30 plants at day 50 showed that the lengths of leaves 6 and 7 were not affected by the presence or absence of leaf 8. All dry weights for inflorescences and their parts are from plants having only seven leaves on the main shoot, the replicate numbers being made up from spare plants.

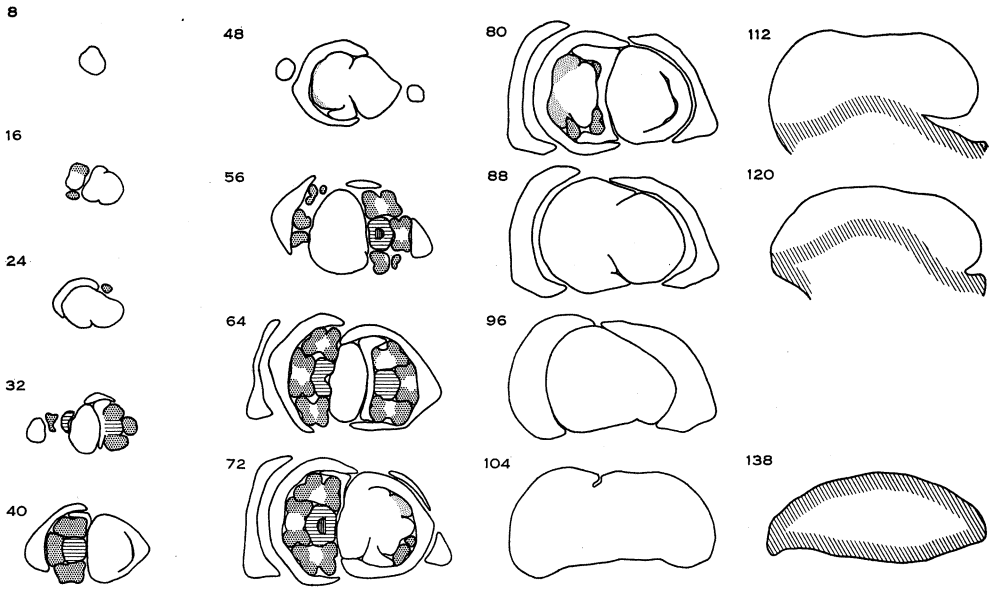

Fig. 1.—Outline drawings of every eighth transverse section through the median spikelet of a 36-day axis. Sectional areas of these and the intermediate sections were used to build up the volume–distribution diagram of Figure 2. Detailed descriptions of the sections are not called for, but sections 16, 32, 40, 56, and 72 pass through the carpels (through the ovule when present) of florets 5, 4, 3, 2, and 1 respectively. The empty glumes are shown free in section 96, and the last three sections illustrate the union of the spikelet with the rachis. Anther loculi are stippled, and carpellary tissue is horizontally hatched.

(*b*) *Length Measurements*

Length measurements of the spike and floral parts were compiled from several sources. Direct measurements of spike length were made from day 36 to anthesis. Measurements of all other parts on days 50 and 55 were made under a dissecting microscope with eyepiece micrometer. The photographic records (e.g. Plates 2–4) were used for spike lengths from day 20 to day 38, and for spikelet lengths from day 24 to day 34. Spikelet lengths were taken to the centre of the rachis. All other lengths are based on the serial transverse sections prepared for the volume-integration studies. For most organs, the number of 10 μ sections from tip to point of half junction with the axis was counted and expressed in mm. Anthers were counted from end to end.

(c) *Volume Integration*

The procedures adopted for the volume-integration studies of shoot apices and early-stage ears were much as described by Williams (1960) for earlier stages. The material was fixed in formalin–acetic–alcohol. For each of the sampling occasions, transverse serial sections of at least two axes were cut at 10 μ and stained with iron alum, haematoxylin, and erythrosin. For some supplementary studies the tannic acid schedule of Sharman (1943) was used. This was much superior, for it readily stains the cell walls of young plant tissues and enables the detection of protophloem elements at the onset of vascular differentiation. Longitudinal sections were seldom needed.

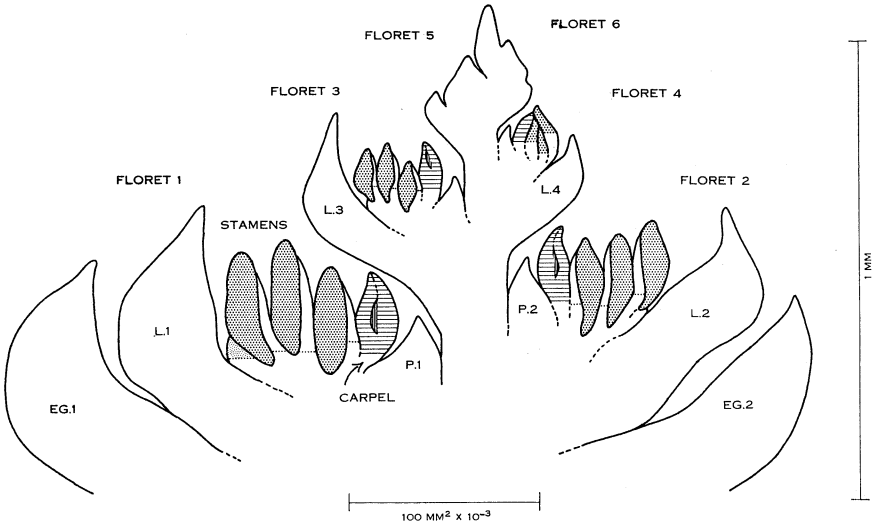

Fig. 2.—Volume distribution diagram for a median spikelet from a 36-day primary shoot (12 days after the appearance of double ridges). Anthers are stippled, carpels horizontally hatched, and ovules vertically hatched. Volumes are proportional to areas within this figure, and in Figures 3 and 4.

The essentials for volume integration are illustrated in Figures 1 and 2 which refer to a median spikelet of a 36-day axis. A photograph of an ear at this stage of development is presented in Plate 1. The outline drawings of Figure 1 illustrate the range of size and shape of the areas required to be determined at such a stage. In practice all areas were determined directly from images on the ground-glass screen of a projection microscope. The Reichert Lanameter* is especially convenient for this work, but other forms of projection equipment could be used. Areas were determined using calibrated, transparent grids. For the smaller structures, every section was measured, but for larger structures a minimum of eight, but usually about 12, equally spaced sections were measured. The volume–distribution diagram of Figure 2 was built up in the same manner as that for the vegetative shoot apex (Fig. 1 of Williams 1960). However, the problem of defining objective limits for

* Now marketed as the Visopan.

the organs of the inflorescence was more difficult than that for the leaf primordia. Thus it was not possible to include the volume of stem tissue which, on theoretical grounds, could be associated with very early growth of an organ (cf. the procedure for leaf primordia). The lower limits for stamens and the carpel (ovary plus style later) were defined by their points of half junction with each other. For lemmas and paleas the volumes include estimates of the "buttress" tissue which supports them. There is no need to define the finer points of the procedures, for workers will inevitably differ on the criteria they use. However, they were selected with care and applied as objectively as possible.

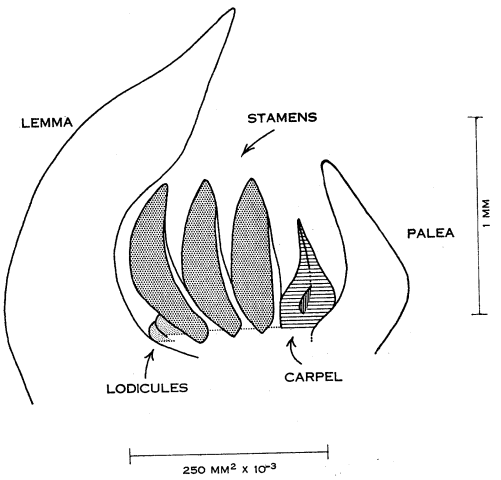

Fig. 3.—Volume distribution diagram for a basal floret and subtending lemma of a median spikelet from a 42-day primary shoot (18 days after the appearance of double ridges).

The volume–distribution diagrams of Figures 3 and 4 are for basal florets of 42- and 50-day plants respectively. It is clear that the problem of defining the limits of organs is very much less at these late stages. Although lodicules are shown in these diagrams, no attempt was made to study their rates of growth.

The very regular form of the stamen, and to a lesser extent that of the carpel, suggested the desirability of developing regression equations for the rapid estimation of volumes of these organs from simple parameters. For stamens, the following equation applies where anther lengths range from 0·1 to 2·5 mm:

$$Y = -0{\cdot}3563+1{\cdot}2096X-0{\cdot}0455X^2+0{\cdot}0013X^3, \quad (1)$$

where Y is the logarithm of 10 V, V being 10^3 times the actual volume in mm^3; and X is the logarithm of 10 V', where V' is the product of anther length and median trans-sectional area in the same units. The parallel regression for volumes of carpels ranging in length (from the base to the tip or to the junction of the styles when the ovary was distinct) from 0·05 to 1 mm is:

$$Y = 0{\cdot}1900+0{\cdot}4690X+0{\cdot}3066X^2-0{\cdot}0485X^3. \quad (2)$$

In this case V' is the product of carpel length and transectional carpel area at the centre of the ovule.

These regressions are reported in detail, mainly as a guide to procedure. They are based only on one cultivar grown under a single set of conditions.

(*d*) *Data Correction using a Volume–Time Relation*

The time-consuming nature of these volume-integration studies made it quite impractical to do more than two axes for each harvesting occasion. Twenty-four axes were harvested and, since these were quite variable in size, they were selected down to six median-sized axes using an appropriate length criterion. These

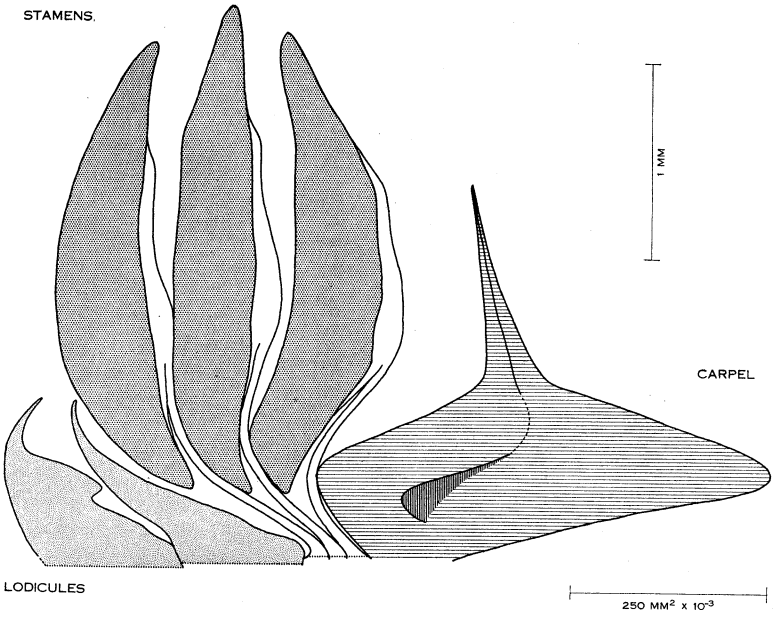

Fig. 4.—Volume distribution diagram for a basal floret, without palea, from a 50-day primary shoot (5 days before anthesis).

six were embedded and two taken at random for sectioning. This gave satisfactory results for leaf and early ear development, but not for the later development of the floral parts, where residual variation was still considerable. However, it was noted for the interval, day 30–day 46, when these parts were differentiating and growing, that the volume growth of the whole spikelet was exponential. In Figure 5 spikelet volume is plotted against time and is fitted with the linear regression shown within the figure. From the regression, the age equivalents of the individual spikelets were determined, as shown, and these ages substituted for chronological age when plotting the volumes of specific parts. The efficiency of the procedure is well demonstrated in Figure 12, in which departures from trend are extremely small.

III. Results

(a) *Dry Weight and Volume Change in the Primary Shoot*

The dry weights of the primary shoot and its parts are given in Table 1. Inflorescence weights are for plants having only seven leaves on the primary shoot, and the last four values for the whole shoot are composite ones on this same basis. Leaves and leaf sheaths grew exponentially for half the period of the experiment. The relative rates of growth then decreased markedly. However, it is usual for cereal leaves to stop growing altogether at about this time (Williams 1964). The present remarkable increases right up to anthesis (day 55) could be attributed to

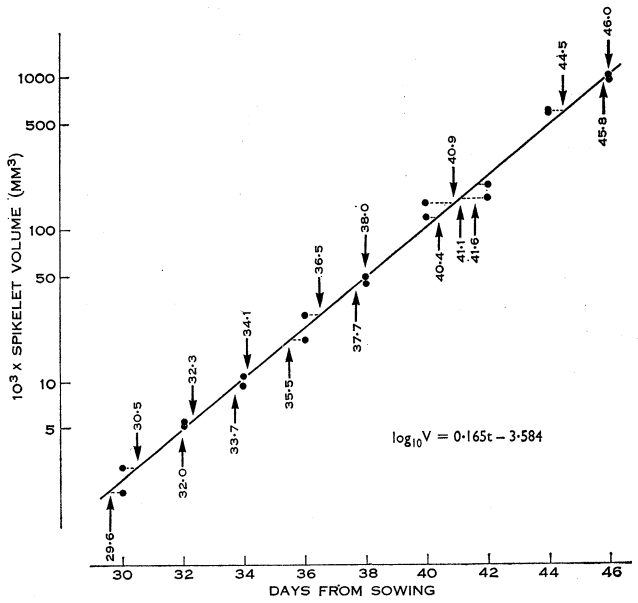

Fig. 5.—Regression of spikelet volume (logarithmic scale) on time. The age equivalent of each spikelet is given to the nearest tenth of a day. See text for further explanation.

the continuous supply of all plant nutrients and to the fact that progressive thinning of the plants minimized shading. The stem did not grow until after day 16, but then grew rapidly. Inflorescence weight was first recorded on day 32 and then increased four- to fivefold per 4-day interval until about day 50.

A fuller understanding of the pattern of shoot growth can be had from growth curves of individual leaves. These have been described for the first 21 days (Williams 1960, Fig. 11), and are now extended to anthesis in the long-day plants of the present experiment (Fig. 6). The two sets of data, both on logarithmic scales, overlap considerably (day 8–day 21), and are consistent in all essential features. In the current study, leaves 8 and 9 were not studied further, being recognized as foliar ridges of the inflorescence. The erratic course of early growth for leaf 5, correlated with the exhaustion of seed reserves, is again evident.

The volume and dry weight data are linked rather arbitrarily through common values for leaves 4, 5, and 6. In the early experiment, a similar common value

TABLE 1

DRY WEIGHTS (MG) OF THE PRIMARY SHOOT AND ITS PRINCIPAL PARTS

Day	Leaves	Leaf Sheaths	Stem	Inflorescence	Primary Shoot
4	—	—	—	—	4·2
8	9·3	3·1	2·9	—	15·3
12	23·1	6·6	2·6	—	32·3
16	38	10·7	2·3	—	51
20	64	15·4	3·2	—	83
24	107	30	6·1	—	143
28	160	52	13	—	225
32	216	73	25	0·2	314
36	274	106	63	0·9	444
40	347	159	129	4·6	640
46	399	241	220	34	894
55	455	312	637	203	1607

for leaf 3 yielded an apparent density of 0·31 mg dry matter per mm³. Densities for leaves 4, 5, and 6 of the present experiment were 0·23, 0·18, and 0·19 respectively.

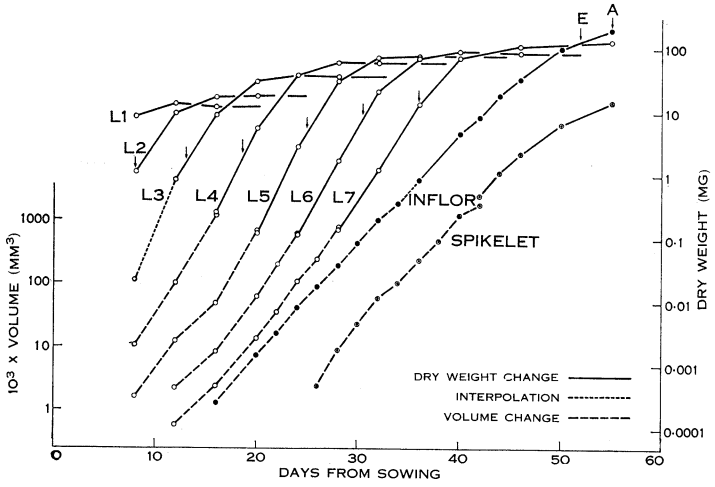

Fig. 6.—Dry weight and volume changes for successive leaves, the whole inflorescence, and a median spikelet plotted on logarithmic scales. The arrows mark the times of emergence of successive leaves, *E* and *A* those of ear emergence and anthesis respectively.

The reasons for this rather wide range of values is not obvious, but the continuity of the data for all the organs of Figure 6 is reassuring, and seems to justify the uniting of the weight and volume data.

The data are remarkable for the very long period over which inflorescence growth was almost strictly exponential, though perhaps with a slightly higher exponent at first. Growth of the median spikelet was also exponential for a considerable period, but with a much higher initial rate.

The best way to integrate all this information is to express it in terms of the concept of relative growth rate, $d\log x/dt$, or the slopes of curves such as those of Figure 6. The diagram of Figure 7 is such a synthesis and is based on both the experiments (cf. Williams 1960, Fig. 14). Although all the major features of the diagram have this sound basis in experiment, it will be evident that much detailed interpretation has gone

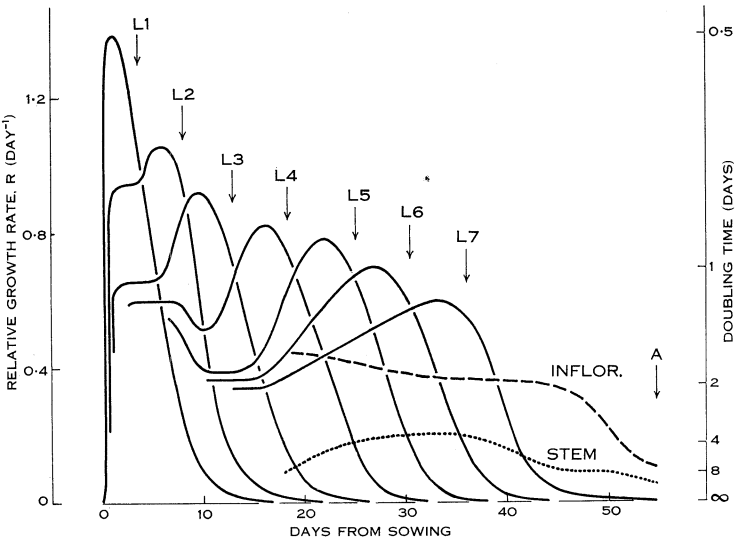

Fig. 7.—Relative growth rates for seven leaves (*L*1–*L*7), the stem, and the inflorescence of the primary shoot of wheat. The arrows indicate the times of emergence of the successive leaves, and *A* that of anthesis. The scale at the right indicates doubling times, or mean cell generation times for early stages of organ growth.

into its construction. It portrays the pattern of growth for seven foliage leaves, the stem and the inflorescence of the primary shoot of wheat grown under long days. The features of this diagram have been described fairly fully elsewhere (Williams 1964), but they form an essential background to a description of inflorescence growth, and to the transition from vegetative to reproductive development. A major early influence is that of seed reserves which are thought to dominate rates and trends during the first 10 days. The long period of exponential growth for the inflorescence is well shown, and has a doubling time of about 2 days.

(*b*) *The Inflorescence*

(i) *Length Growth*

Length growth data for the spike, spikelet, and floral parts are plotted on logarithmic scales in Figures 8–11. These need to be examined along with the

photographic record of Plates 2–4. In the commentary which follows, growth rate means relative length growth, or the slopes of the lines in Figures 8–11.

The growth rate of the spike (Fig. 8) decreased slightly at day 24, and this change was correlated with the onset of active spikelet growth (Plate 2, Fig. 3). Spikelet growth was checked in turn at day 30 perhaps with the onset of floret growth (Plate 3, Fig. 1). From day 36 onward, however, internode growth resulted in a sharp increase in the growth rate of the spike (Plate 3, Figs. 7 and 8) and this was correlated with a further reduction in the rate of spikelet growth (rachilla and spikelet growth

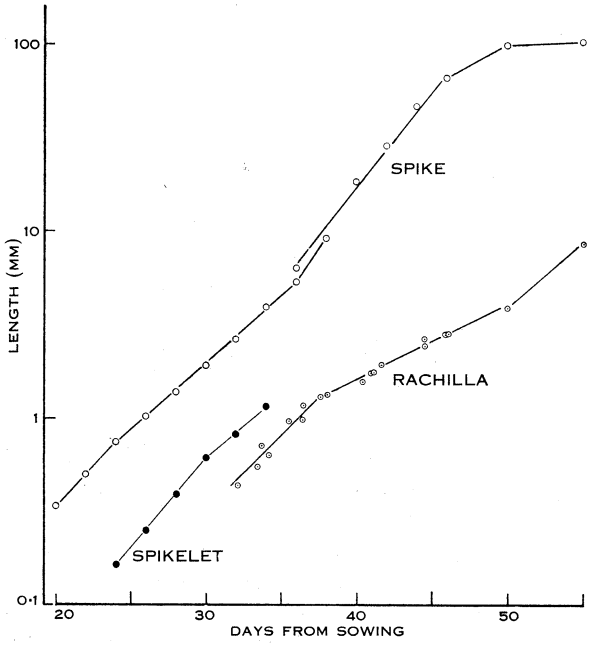

Fig. 8.—Length growth of the spike, spikelet, and rachilla on a logarithmic scale.

are essentially the same). The growth rate of the spike was fairly constant until day 46 and ceased by day 50. There was then a sharp increase in the rate of rachilla growth, due also to internode extension.

The data for rachilla growth are repeated in Figure 9 along with those for the length growth of the empty glumes and the lemma. These foliar organs all grew at a high rate similar to that of extension growth in the spike. They did not show an early phase of slow growth such as was found for the foliage leaf by Williams and Rijven (1965). After day 46 the growth rates of the glumes and lemma fell away and ceased much as did that of the spike as a whole. It will be noted that the rachilla was at first longer than the lemma of the basal floret, but became very much shorter by day 50. Associated with this change is the fact that the florets

are at first naked on the rachilla but become progressively covered by the growing lemmas and glumes. In Plate 4, Figure 2 (day 42), the tip of the rachilla is only just visible above the lemmas. Later it is completely covered.

Figure 10 records the length growth of the palea, anthers and carpel (ovary plus styles for later stages). The palea does exhibit a period of slower growth until approximately day 38, and is then shorter than the anthers. Eventually it becomes

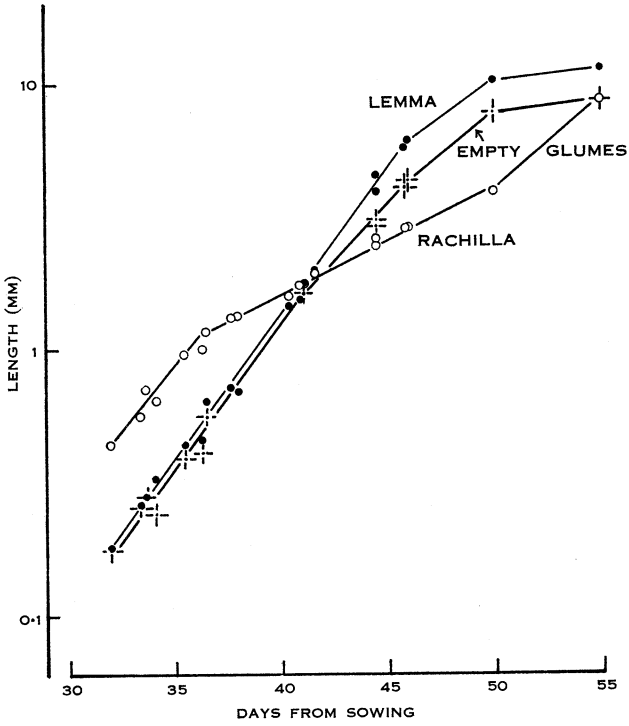

Fig. 9.—Length growth of the rachilla, empty glumes, and lemma (basal floret) on a logarithmic scale.

almost as long as the lemma. Anther and carpel growth fell away fairly continuously with time, but there was a suggestion of a negative relation between style and ovary growth for the interval, day 38–day 41 (Fig. 11).

(ii) *Growth in Volume and Dry Weight*

Volume changes in the parts of the basal floret of a median spikelet are presented for the interval, day 32–day 46, and are linked with dry weight values for days 50 and 55, in Figure 12. The age equivalents of Figure 5 were used in setting up the volume data of this figure, and free-hand curves were readily drawn for each organ. Those for the lemma and palea are very similar to those for length growth (Figs. 9 and 10). The curve for the palea has the sigmoid form characteristic of the foliage leaf (Fig. 6).

There is a striking contrast between the curves for the stamens and carpel. The reasons for this difference will be apparent from the three-dimensional drawings of Plate 5. These extend over the interval, day 32–day 41, and reveal changes in form which are not readily appreciated by direct dissection of these structures. Earlier stages of development can be seen in the upper florets of Plate 1. Form change in the stamen shows a steady evolution which is entirely compatible with its simple growth curve. For the carpel, on the other hand, every few days brings

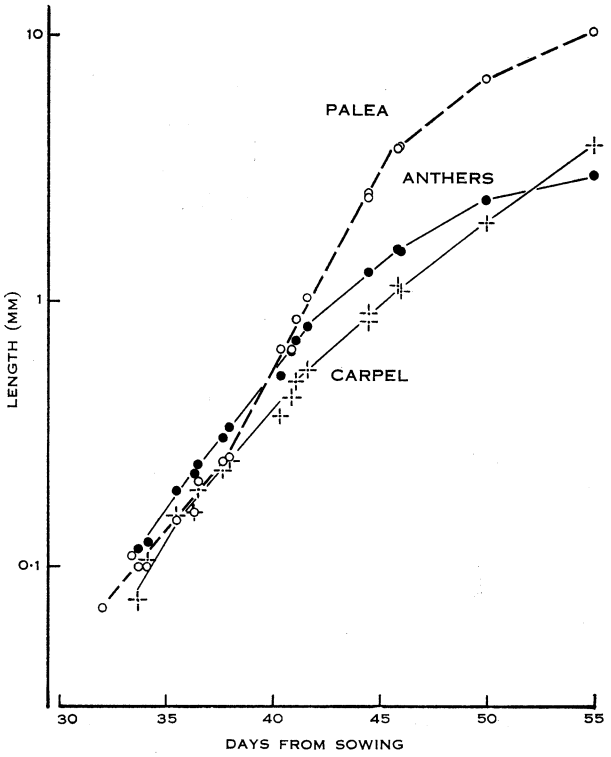

Fig. 10.—Length growth of the palea, anthers, and carpel (including style) on a logarithmic scale.

a qualitatively different change in form, and its growth curve is strikingly discontinuous. This is in keeping with the view (Barnard 1957) that the gynaecium could be composed of as many as four foliar structures fused together. The first (and anterior) member grew rapidly between days 32 and 34 (Fig. 12; Plate 5) and so close to the apex that the latter was no longer identifiable. On day 34 an apex was again prominent, and there was a sudden fall in the growth rate of the gynaecium as a whole. Concerning this fall Williams (1966) suggested that it may have been correlated with the abortion of the floret apex, the negligible growth of a posterior member of the carpel and the establishment of a new apex axillary to the anterior

member. On this interpretation the two lateral members of the carpel, which produce the styles, are the first foliar members of the new axis. Two stages in their development appear in Plate 5 (for days 36·3 and 40·9). Their growth clearly dominates that of the whole gynaecium, and the growth curve has the sigmoid form characteristic of foliar organs (Fig. 12, interval 36–50). Plate 5 also shows how the ovule becomes invaginated by differential growth of the surrounding tissue. The growth curve for the ovule is parallel to that for the stamens, and both are consistent with their cauline origin.

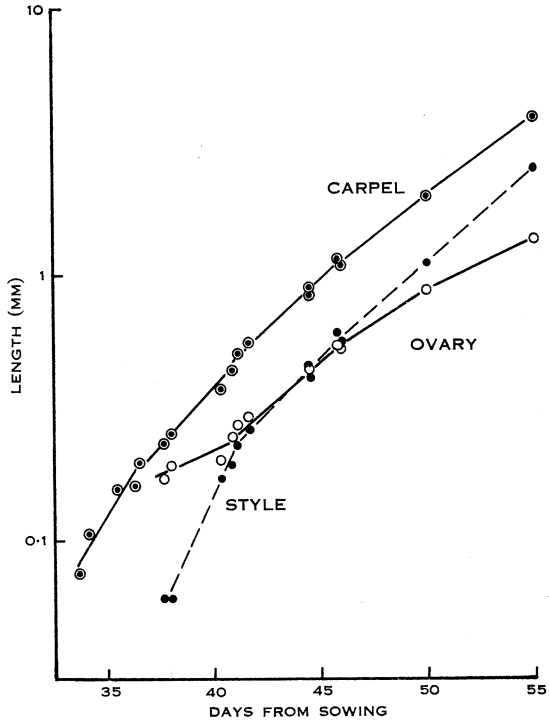

Fig. 11.—Length growth of the carpel, the style, and the ovary on a logarithmic scale.

Figure 13 assembles the relative growth rate data for the spikelet and the parts of the basal floret. After an initial high value, which could be due in part to difficulties of demarcation, R for the spikelet was remarkably constant for about 15 days, with a doubling time of 2 days. That this rate was lower than those for the basal floret parts at this time can only mean that the empty glumes, the rachilla, and the upper florets together had a growth rate which was still lower. Figure 13 also stresses the two main phases in carpel growth, and brings out the contrast with the growth rates of the stamens and ovule.

(iii) *Stamen and Carpel Growth in Successive Florets*

Use of regressions (1) and (2) of the experimental section made it possible to determine volume changes for the stamens and carpels of the first five florets

of a median spikelet (Fig. 14). Once again, stamen growth could be described by simple curves concave to the axis of time, but carpel growth tended to be discontinuous at about day 36 and convex with time thereafter (florets 1–3 only). A feature

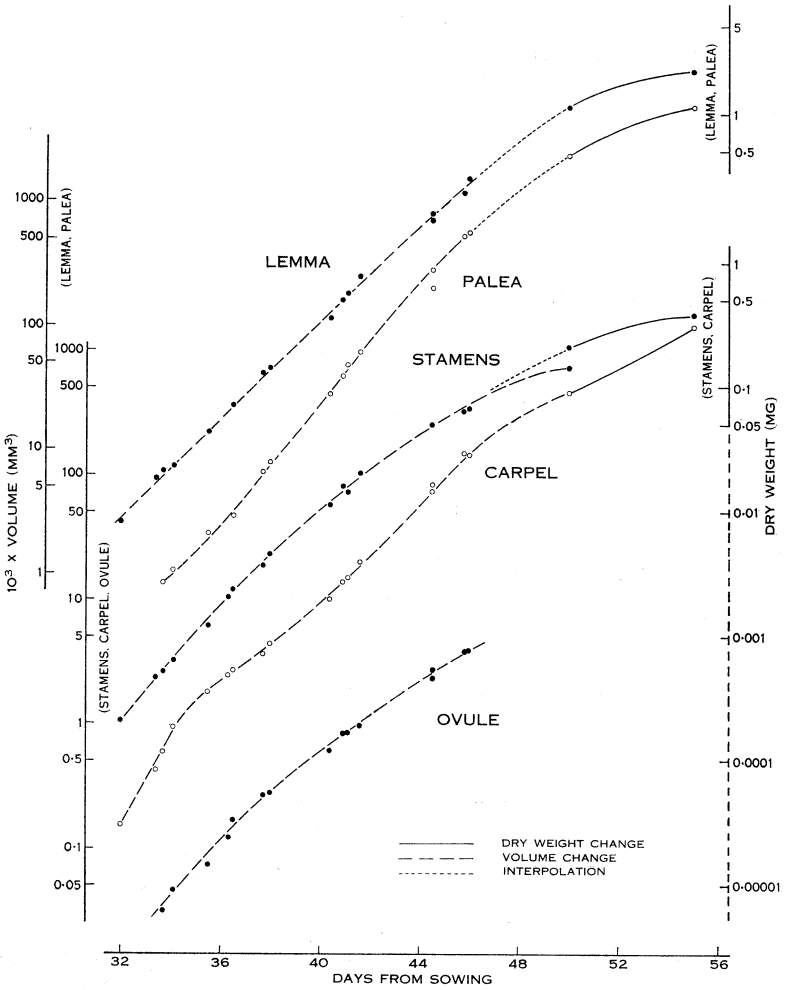

Fig. 12.—Volume and dry weight changes in parts of the basal floret of a median spikelet on logarithmic scales. The stamen volume for day 50 is thought to be low because of excessive shrinkage during processing.

of both sets of data is that departures of the individual values from trend increase with increasing floret number. It is also quite unlikely that florets 4 and 5 could have produced mature anthers or carpels. Even with floret 3 there are slight divergences of trend which could lead to a failure of maturation. Spikelets in this position usually set two or three grains of wheat.

(iv) *Volume Data within a 36-day Spikelet*

The volume data of Table 2 refer to a 36-day inflorescence carrying 16 spikelets. Serial sections had been cut at right angles to the axes of spikelets on one side of

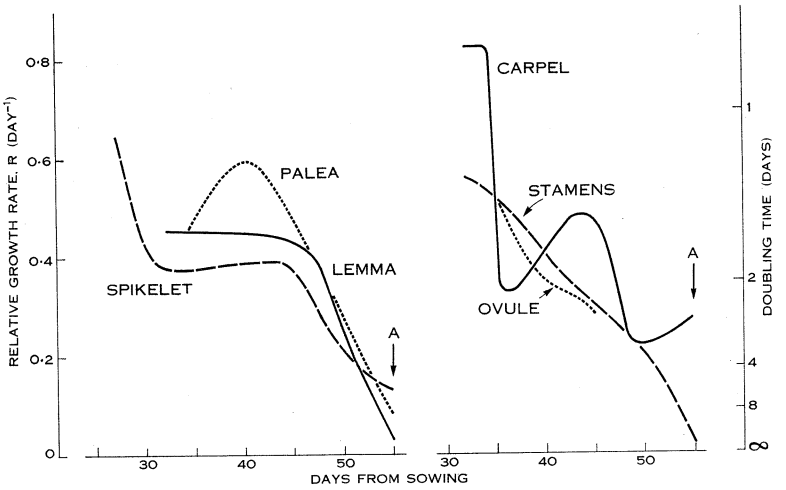

Fig. 13.—Relative growth rates for a median spikelet and parts of its basal floret. *A*. time of anthesis.

the ear, and volume determinations were made for floral parts of the basal florets of six of these. Floral development in the second spikelet was so retarded that volume

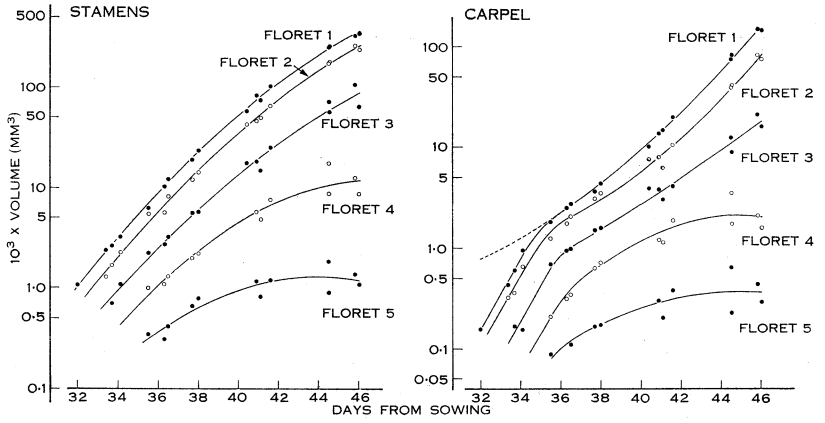

Fig. 14.—Volume changes in the stamens and carpels of the first five florets of a median spikelet over the interval day 32–day 46.

determinations were not attempted for the floral parts. The data show that the median spikelets were developmentally far ahead of those towards the base and tip of the ear.

IV. Discussion

In his account of the development of the inflorescence in Gramineae Williams (1966) took as his starting point the histogenetic analysis of the inflorescence into structures of foliar and cauline origins, as proposed by Barnard (1955, 1957). Barnard concluded that foliage leaves, foliar ridges subtending inflorescence branches and spikelets, glumes, lemmas, paleas, lodicules, carpels, and ovular integuments all arose in the foliar manner, but that tiller buds, inflorescence branches, spikelets, florets, stamens, and ovules arose in the cauline manner. Much earlier, Sharman (1945) drew attention to the distinction between leaf and bud initiation in the Gramineae, and asserted that its significance lay in the fact that the former was of superficial origin, whereas the latter incorporated deeper tissues. However, from

Table 2

Volumes of spikelets, stamens,* carpels,* and ovules* within an ear, 36 days after sowing

Spikelet No. (from base)	$10^3 \times$ Volume (mm^3)			
	Spikelets	Stamens	Carpels	Ovules
14	148·2	3·68	0·908	0·051
12	197·1	6·25	1·618	0·078
10	233·0	7·83	1·965	0·086
8	253·0	10·24	2·350	0·124
6	228·1	7·37	2·132	0·106
4	169·5	5·65	1·635	0·079
2	88·3			

* For floret 1 only.

their studies of inflorescence initiation in *Lolium temulentum*, Knox and Evans (1966) were less impressed with the contribution of subhypodermal cells to the growth of the spikelet primordia. They found that the initial swelling was due mainly to the marked increases in the sizes of the nuclei and the cells of the hypodermis. This does not necessarily conflict with Barnard's claim that tiller buds and spikelets both had their first periclinal divisions in the subhypodermis, and therefore at depth.

The question remains as to whether the distinction between cauline and foliar structures has meaning for subsequent development. Williams (1966) contrasts the growth pattern of the foliage leaf with that of the inflorescence in wheat, but the pre-emergence peak in R for the foliage leaf is not necessarily exhibited by the foliar organs of the inflorescence. It is present for the palea, but not for the lemma (Fig. 13). The late peak in R for the carpel could be so interpreted, but this is still a very open question. Then, too, R curves for the spikelet, stamens and ovule do not closely resemble that for the inflorescence as a whole. They agree only in that they

fall with time, with or without periods of constant rate. However, the main purpose of the present study was to provide a precise quantitative description of the system. It is perhaps premature to expect to find satisfying interpretative principles for such a complex biological system.

Nicholls and May (1963) described length growth in the barley inflorescence and found an early phase dominated by the addition of new foliar primordia, and a second phase of growth due to internode extension. They also noted that, for a limited range of conditions, the appearance of stamen initials coincided with the cessation of primordium formation on the main axis. From these observations they suggest that the number of spikelets per inflorescence is determined by the balance between rates of primordium formation and spikelet development. The present data for wheat suggests that the pattern is much the same as it is for barley, for primordium formation on the main axis ceases and stamens appear between day 28 and day 30 (Plates 2 and 3). However, rapid internode extension seems to start later in wheat.

Single (1964) found large effects of nitrogen nutrition on spikelet number for the primary shoot of wheat, but claims that the number was determined before the time of appearance of double ridges. Single also shows that the number of fertile grains per spikelet can be varied over a considerable period after spikelet number has been determined. He invokes internal starvation for nutrients as a potent factor here, and suggests that it operates even under the most favourable field conditions. This gains support from the data of Figure 14 above, which suggests failure within florets 4 and 5 in plants receiving abundant mineral nutrients. Internal starvation for carbohydrates could also be responsible for such failures. There is clearly a need for further work on the determination of spikelet number and of the number of fertile grains per spikelet.

In a second paper on the barley apex, Nicholls and May (1964) describe the processes of cell division and cell elongation in the rachis of the inflorescence. They also estimated the concentration of gibberellin-like substances in inflorescences at three stages of development, noting that the highest concentration was correlated with the initiation of cell division in the pith region, the first appearance of stamen initials, and the onset of internode elongation. Many more observations, preferably on specific organs, will be needed before these correlations can be elucidated with confidence.

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Explanation of Plates 1–5

Plate 1

Young inflorescence of wheat, 14 days after the double-ridge stage of floral induction and 19 days before anthesis (36-day plant).

Plate 2

Figs. 1 and 6.—16-day apex in which *L*6 is 0·4 mm long, *L*7 is visible, and the apex is elongating prior to ear formation.

Fig. 2.—22-day apex, with double ridges.

Figs. 3 and 8.—24-day apex with spikelet primordia.

Figs. 4 and 9.—26-day apex with empty glume ridges on more advanced spikelets.

Figs. 5 and 10.—28-day apex with flower primordia in the axils of the first and second lemmas of the more advanced spikelets.

Fig. 7.—20-day apex, before the appearance of double ridges.

Plate 3

Figs. 1 and 2.—30-day inflorescence with stamens just appearing on the most advanced florets, and the fifth lemma on advanced spikelets.

Figs. 3 and 4.—32-day inflorescence with many florets showing stamens and the carpel.

Figs. 5 and 6.—34-day inflorescence with the seventh lemma on advanced spikelets, and internodes beginning to elongate.

Figs. 7 and 8.—36-day inflorescences with glumes and lemmas beginning to cover the naked florets, and internodes elongating rapidly.

Plate 4

Fig. 1.—38-day inflorescence.

Fig. 2.—42-day spikelet with the florets almost completely covered by the glumes and lower paleas.

Fig. 3.—46-day spikelet with rapidly growing awns.

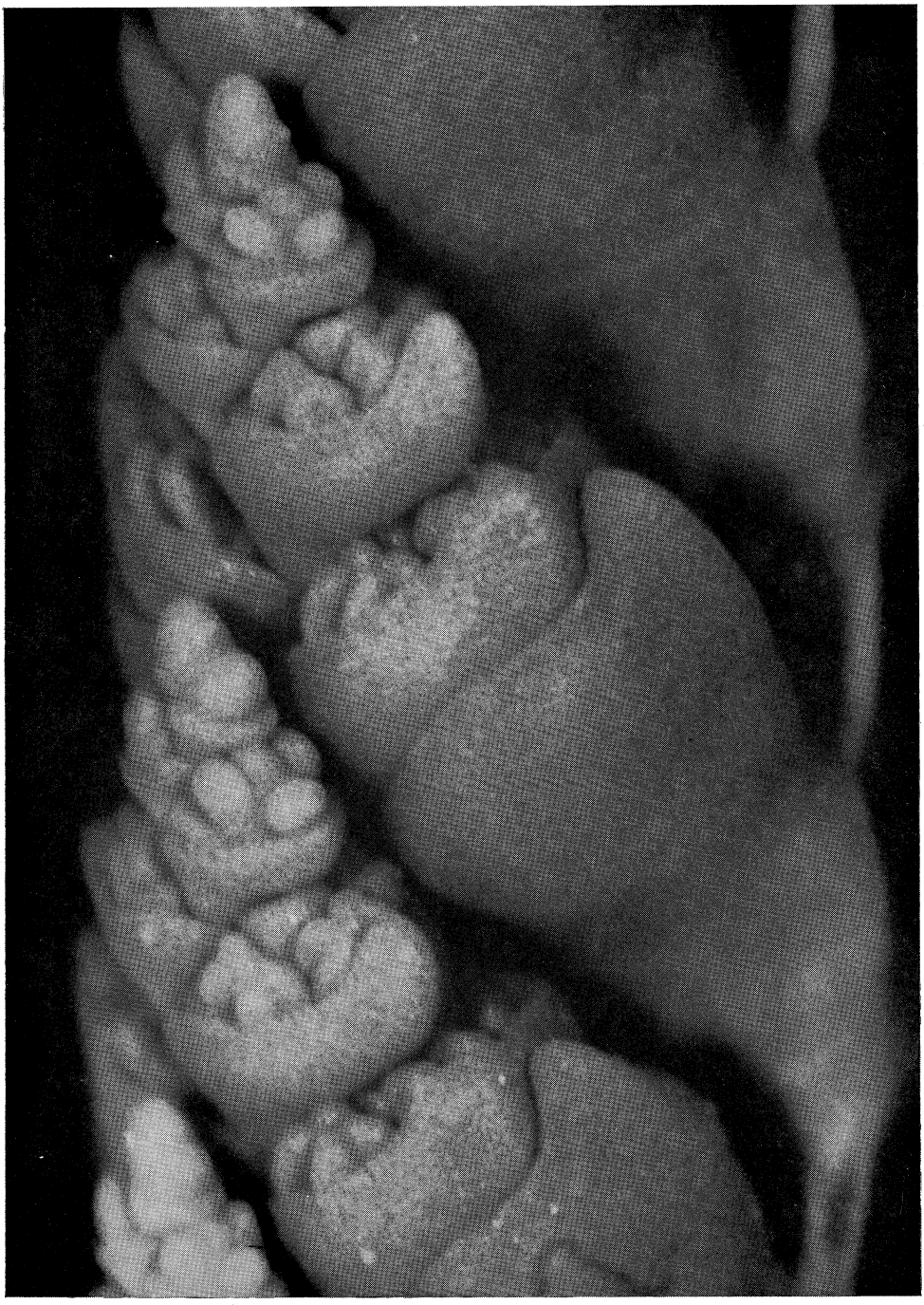
Fig. 4.—50-day spikelet with glumes and paleas fully grown.

Fig. 5.—55-day spikelet on day of anthesis, glumes and lemmas spreading.

Plate 5

Three-dimensional reconstructions of the carpel and stamens for five stages of development. Ages are to the nearest tenth of a day from germination (see text). The contour lines are 10 μ apart and delimit sections of that thickness.

PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT. III



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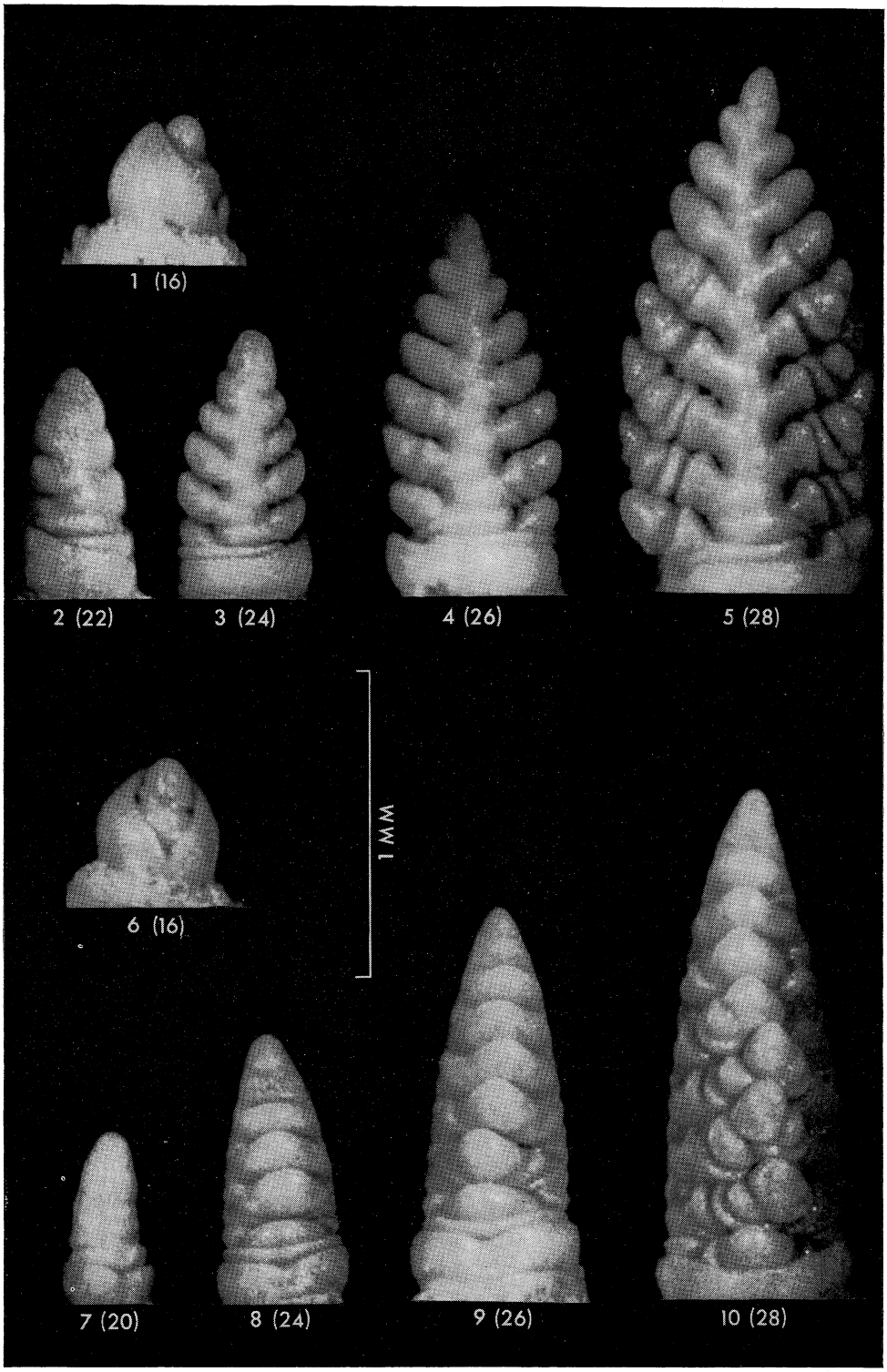

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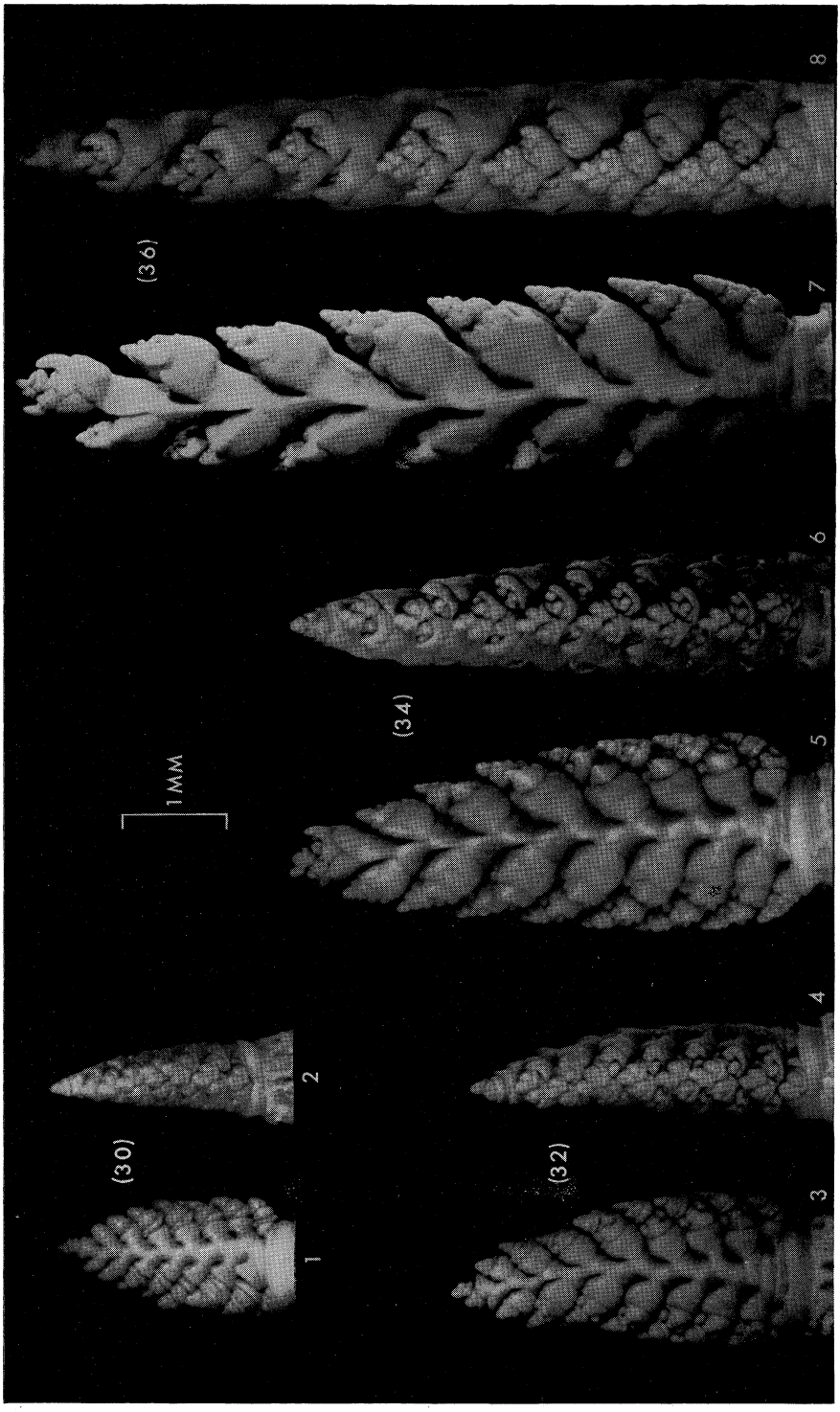

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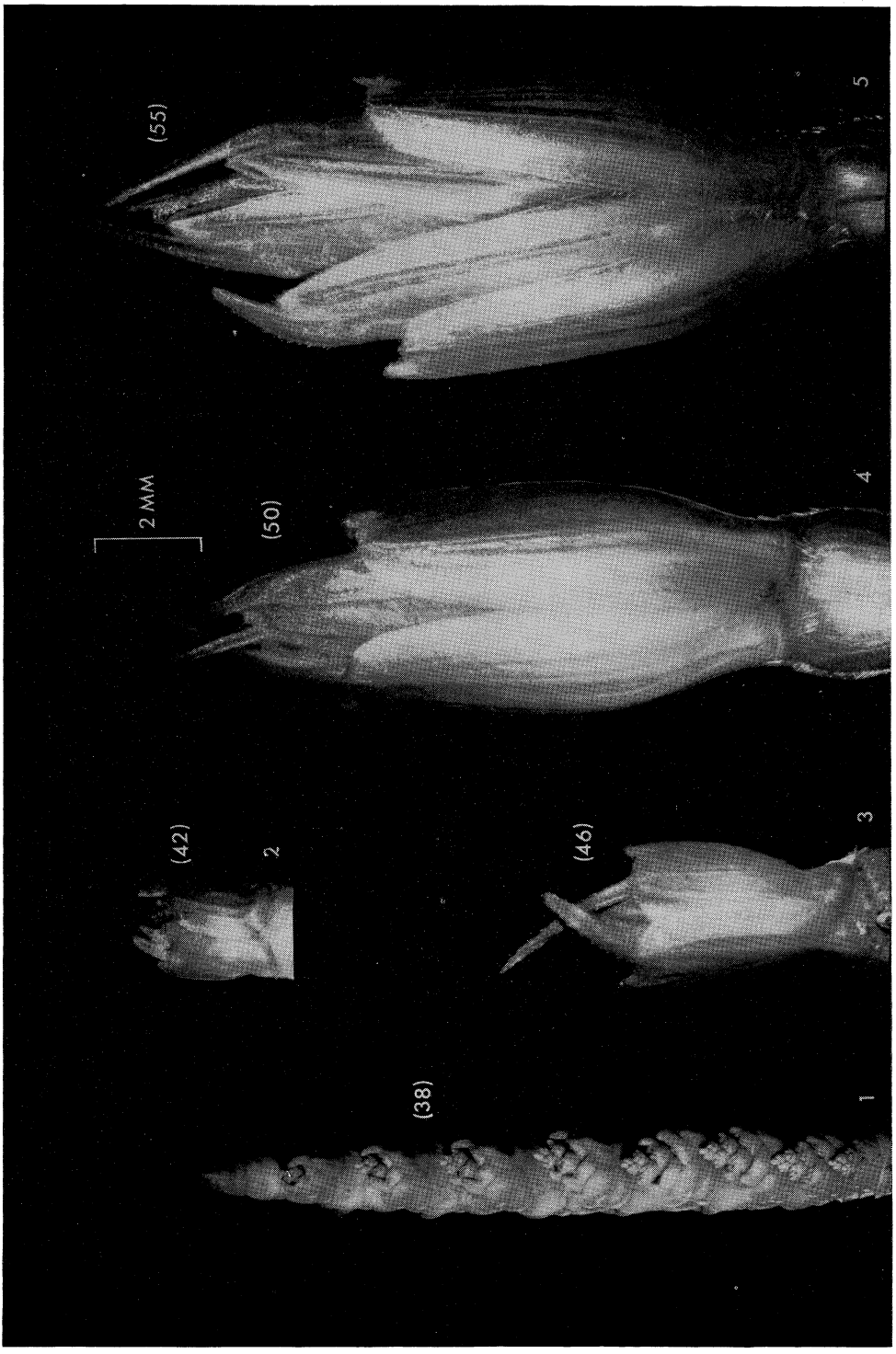

PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT. III