THE PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT

I. SEEDLING GROWTH AND THE PATTERN OF GROWTH AT THE SHOOT APEX

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Summary

Seedling growth of wheat in a constant environment is studied over a period of 21 days. Dry weights of leaves, leaf sheaths, stem, and roots are given for 11 occasions. The pattern of dry weight change is also presented in terms of the changing ratios of plant parts.

Growth rates of leaf primordia are determined in terms of volume change based on the technique of serial reconstruction.

For an 11-day shoot apex, a detailed account is given of cell-size distribution along the leaf primordia and within the apex itself. It is estimated that, prior to the onset of cell enlargement, the mean cell-generation times for the young leaf primordia range from 12 hr to 3 days.

An integrated picture of the early growth of the primary shoot is attempted, mainly in terms of the concept of relative growth rate. The rates for leaves and roots are particularly high while seed reserves are available. There is a progressive change in dominance from leaf growth to stem growth. Early growth of each leaf primordium is exponential, but the exponent decreases with leaf number in a rather discontinuous manner. Following the exponential phase, the rates rise to maxima and then fall asymptotically to zero.

It is suggested that intra-plant competition for energy substrates may play an important role in determining the pattern of development of the primary shoot of wheat.

I. INTRODUCTION

Precise quantitative information on both structural and functional attributes of plant growth is required if we are to have an understanding of the internal factors and mechanisms which integrate the parts of a plant into the whole organism. This was clearly recognized in ontogenetic studies of wheat and Sudan grass by Ballard and Petrie (1936) and Petrie (1937), of oats by Williams (1936, 1938, 1948), of tobacco by Petrie, Watson, and Ward (1939), Watson and Petrie (1940), and Petrie and Arthur (1943), of flax by Tiver (1942), and of linseed by Tiver and Williams (1943). More recently, studies on similar lines have been made for barley and rye by Williams and Shapter (1955) and for the tomato plant by Gates (1955*a*, 1955*b*, 1957). Common features of all these studies are adequate sampling on from five to ten occasions during growth, the separation of the plants at least into their major parts, and the analysis of growth in terms of dry weight change. To greater or lesser extents, too, these studies have included chemical work sufficient to build up a picture of the intake and distribution of certain essential elements, particularly nitrogen and phosphorus.

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The extraction of general principles relevant to the physiology of growth from complex sets of data such as the above is not easy, and has been attended by only partial success when attempted by Watson and Petrie (1940) and by Williams (1955). Perhaps the most significant positive contribution has been their emphasis upon competitive demand within the plants for metabolites and nutrients alike. Differences in growth pattern induced by differential nutrition and other treatments were seen as a consequence of such competition, for the growth of a given organ was found to be stimulated, relative to other organs, if it was nearer the source of a deficient nutrient or metabolite. Bald (1946) considered the principle of intra-plant competition to be adequate for the interpretation of differences in growth form, maturity, and yield between varieties and strains of the potato plant. It is also significant that zoologists have been thinking along similar lines, for Spiegelman (1945) developed this theme on quite a broad basis, and gave it mathematical form. His examples were drawn mainly from coelenterate hydroids, which possess some characteristics in common with plants. Thus they are normally anchored to their substratum, and they possess apical dominance which is rather similar to that in plants.

It is now accepted that the early development of successive organs is quite as significant for our understanding of plant growth as is the later and more obvious unfolding of these organs. Nevertheless, our knowledge of the quantitative changes during early growth is very limited, and much might be gained by measuring rates of growth of vegetative organs from the time of their initiation through to maturity and senescence. This is the main purpose of the present study, and the wheat seedling was chosen as the test object because a great deal is already known about this plant, and because further information about it is likely to be relevant to other cereals and to many gramineous pasture plants. It was necessary to restrict the work initially to the quantitative description of growth in one controlled environment. Dry weight changes in the first four leaves, the stems, and the roots were determined from the time that these parts could be separated with reasonable precision. For all smaller structures, the technique of serial reconstruction was adopted, and growth determined as volume change with time.

It was Wilhelm His who drew attention to the importance of measurement for the understanding of morphogenetic processes, and it is to him that we owe the procedure of serial reconstruction for the understanding of embryonic structure and development. In one place His (1888) says:

"The ways of determining the forms and volumes of germs and embryos are somewhat longer and more tiresome than the simple inspection of stained sections; but the general scientific methods of measuring, of weighing, or of determining volumes cannot be neglected in embryological work, if it is to have a solid foundation of facts, for morphologists have not the privilege of walking in easier or more direct paths than workers in other branches of natural science."

While serial reconstruction has been used over and over again for the description of form changes in embryos and embryonic organs in animals and plants, there seem to be no recent examples of its use in any precise quantitative sense. The present paper attempts this task for the shoot apex of the wheat plant.

II. EXPERIMENTAL PROCEDURE

(a) Plant Culture, Sampling, and Dissection

A spring wheat (*Triticum aestivum* L., cv. Nabawa) was grown in a constant environment of which the temperature was 20°C and the light intensity was approximately 950 f.c. at plant level. The grain was set to germinate in petri dishes and, after 24 hr, was sown in 10-oz cans filled with vermiculite. During the course of the experiment the pots were flushed through daily or more often with Hoagland No. 2 nutrient solution.

As they matured, leaves 1 and 2 tended to develop chlorotic areas near their tips. Later experience suggests that the use of half-strength instead of full-strength nutrient would have eliminated this condition. The plants also suffered a mild water stress for a short time on day 20.

The replication was five throughout, but the number of plants per can varied with the age to which they were grown. In the first experiment there were 12 grains or seedlings per replicate for days 0, 1, and 6; 10 plants per replicate for days 8 and 11; 8 per replicate for days 13 and 15; and 6 for days 18 and 21. In the second experiment there were 12 grains or seedlings per replicate for days 0, 1, 2, 3, 4, and 8.

As plant dissections had to be extended over a considerable period on each sampling occasion, the replicates were always drawn in the same order from blocks of cans which had been sown at 75-min intervals. In this way it was possible to ensure that the age at time of dissection of each seedling was within 35 min of the day specified.

At day 1, dissection was limited to the separation of the embryo (without scutellum) and the rest of the grain. The coleoptile and the roots were first separated on day 2, leaves 1, 2, 3, and 4 were first separated on days 3, 6, 8, and 15 respectively, and leaf sheaths 1, 2, and 3 on days 8, 11, and 18 respectively. The roots were cut at their points of emergence from the coleorhiza, but their dry weights were later adjusted to include an estimate of the weight of the stumps within the coleorhiza. Leaves were separated at their bases or at the ligule as soon as this was present. The stem fraction was the least satisfactory in that all organs too small to be dissected off were included with it. Some adjustments were made (see Table 1), and it should be noted that tillers contribute appreciably to stem dry weight after day 15.

All parts were dried at 80°C in an oven with forced draught.

(b) Volume Integration

Plants additional to those used for dissection and dry weight determinations were sampled for the serial reconstruction studies. The whole embryo at day 1, or that part of the primary shoot which contained the apex and the younger leaf primordia, was fixed in formalin-acetic-alcohol. Acid fuchsin was added to the fixative to facilitate dissection prior to embedding in wax. For each of 11 sampling occasions, transverse serial sections of four axes, and longitudinal sections of one axis were cut at 10 μ and stained in iron alum haematoxylin and erythrosin. Volume estimation of irregular solids can be made from equally spaced sectional areas, preferably taken along the major axis of the solid, and this is the principle underlying serial reconstruction. The areas of about 15 sections were determined for the larger primordia, but all sections were usually determined for small structures. Areas were determined from photographic enlargements, like those illustrated in Plate 2, by superimposing a centimetre grid (on glass), and counting squares and tenths of squares. Even with such irregular shapes, it was found that duplicate determinations with different grid positions agreed very closely. Volumes were determined by a graphical procedure which is illustrated in Figure 1 for an 11-day



Fig. 1.—Diagram illustrating the graphical procedure used for determining the volumes of leaf primordia and internodal tissues of the shoot apex. For full explanation see text. GP, growing point; T, tunica; C, corpus; L4, L5, etc., successive leaf primordia. Diagram based on an 11-day apex, 1.32 mm long.

seedling axis. Outline drawings of some of the sections used for leaves 4 and 5 are shown to the right of the diagram, and others for the apex and leaves 6 and 7 are to the left, together with their section numbers. It was necessary to set vertical limits to the stem tissue associated with successive primordia, so the upper limit was defined by that section in which the primordium appeared half united with the axis (e.g. sections 11, 27, and 33 of Fig. 1). The stem areas at these points were taken as those of the first complete stem sections immediately above. Another problem was to provide an objective definition of the inner limit of the leaf primordium. The work of Barnard (1955) is relevant here, for he has shown that leaf primordia in wheat arise by the periclinal division of cells of the tunica, the corpus contributing nothing to their development. The histological pattern of the vegetative apex in an 8-day seedling is shown in Plate 3. In longitudinal section, the two-layered tunica is clearly distinguishable from the corpus, and the thickness of the tunica was found to be remarkably constant throughout the period of the experiment. This fact was used in defining areas appropriate to the tunica, T, and the corpus, C, in Figure 1, and the same convention was extended to the partitioning of the stem into portions deriving from the tunica and corpus respectively.

The partial areas of the central diagram of Figure 1 are directly proportional to the volumes of the structures they represent, and the total volume has in effect been divided into major units made up of a primordial leaf lamina (the ligule and leaf sheath arise at a later stage), and two stem portions. Together these are equivalent to the *growth units* of Sunderland and Brown (1956). However, for studies of the growth rates of leaf primordia, it is desirable to include all tissues derived from the tunica and not to restrict measurements to that part of the primordium which projects from the stem. At least in the present case, such restriction would have introduced large positive errors into estimations of relative growth rate in very young primordia. In what follows, a leaf primordium is defined as the lamina plus the outer or tunica-derived part of the associated stem tissue. The growth rates of the corpus-derived tissues, or pith, also become more meaningful as a result of this procedure.

The present method of serial reconstruction would be suspect if it could be shown that there had been appreciable differential shrinkage or distortion of the parts measured. It seems inevitable that there should be some shrinkage during fixation, but obvious distortion of cell walls was not found (see Plate 2), except in more mature tissues than those actually measured. Compression and distortion during cutting and mounting were thought to be more likely sources of error and were examined accordingly. For several ages of material, measurements made first on the face of the wax block and then on the mounted section indicated an area reduction of $18 \cdot 7 \pm 1 \cdot 6$ per cent. Although this reduction is rather large, its relative constancy indicates that relative rates of volume change would be little affected by it.

Only one axis for each of the 11 occasions was examined in the detailed manner of Figure 1; for the other three axes, the volumes of all but the smallest primordial laminae were estimated from the regressions of Figure 2. Stem and apical volumes were determined directly for each axis. In the regressions, actual volume (direct method) is expressed as a function of the product of total length (132 sections or 1.32 mm for L4 in Fig. 1) and the sum of A_1 and A_2 , where A_1 is the basal area (by difference of the stem areas) and A_2 is the cross-sectional area half way up the free part of the lamina. Equation (1) refers to L1 and L2 alone, and equation (2) refers to L3-L9 inclusive. Although the separate equations were used in what follows, there is a good case for pooling all the values to give the following equation:

$$Y = -0.3066 + 0.8646X + 0.0407X^2,$$

where Y is the logarithm of the actual volume V, and X is the logarithm of V' as defined in Figure 2.

(c) Cell Size

The determination of cell-size distribution along the lengths of the primordia and the pith was attempted for one 11-day axis only. Appropriate sections were projected, and all nuclei or recognizable fragments of nuclei were counted. Since the mean length of the nuclei, as seen in longitudinal section, was 9 μ and the thickness of the sections 10 μ it follows that there would be 10 whole nuclei per section for every 19 counts by this method. Knowing the volume of the whole section, it was possible to compute the mean cell size for that section.



Fig. 2.—Regressions used for determining the volume V of a leaf primordium from its length and two sectional areas. Equation (1) for L1 and L2; equation (2) for L3-L9 inclusive. See text for further explanation.

III. PRESENTATION OF DATA

(a) Dry Weight Change

The dry weights for the main categories of plant parts, are presented in Table 1 and Figure 3. For the latter the values are plotted additively, so that the upper curve describes the growth of the whole organism, including the grain. The coleoptile has been regarded as a leaf sheath, and the coleorhiza included with the stem. The dry weights of individual leaves and leaf sheaths, and of the coleoptile are presented in Tables 2 and 3 and in Figure 4. This figure also shows the dry weight changes of the grain and the roots to the same scale. The justification for uniting the data for the two experiments will be found in the parallel sets of values for day 4 (see Tables 1, 2, and 3); similar sets for day 8 showed equally good agreement. There is, however, an initial difference of 4 mg in mean grain weight for the two experiments, and this is reflected in the pairs of values for rest of grain (Fig. 4) for days 1, 4, and 8. The lower values in each case refer to the first and longer experiment, the upper values refer to the second experiment, which was done to fill in the detail for the first 4 days of growth.

From Figure 3, two distinct phases of growth are apparent. In the first, dry weight increase in the young seedling is dependent on grain reserves, and in the second the seedling is self supporting. There is, however, some overlap of these

Expt.	Day	Leaves	Leaf Sheaths	Stem	Roots	Total without Grain	Rest of Grain	Whole Plant
2	0							55.78
2	1	0.06*	0.15*	0.38*	0.18*	0.77	$54 \cdot 29$	55.06
2	2	$0 \cdot 21^{+}$	0.38	0.51^{+}	0.72	$1 \cdot 82$	$52 \cdot 21$	54.03
2	3	0.75†	1.16	0.66^{+}	$2 \cdot 58$	$5 \cdot 15$	48.36	$53 \cdot 51$
2	4	$2 \cdot 15^{+}$	$2 \cdot 16^{+}$	0.69^{+}	$5 \cdot 24$	$10 \cdot 24$	$42 \cdot 12$	$52 \cdot 36$
1	4	$(2 \cdot 36^{\dagger})$	$(2 \cdot 17^{+})$	$(0 \cdot 64^{+})$	$(5 \cdot 51)$	(10.68)	(39.66)	(50.34)
1	6	8.76†	3.58^{+}	0.73†	$10 \cdot 09$	$23 \cdot 16$	$26 \cdot 09$	$49 \cdot 25$
1	8	$21 \cdot 57$	5.30†	1.07^{+}	$12 \cdot 84$	40.78	$13 \cdot 15$	$53 \cdot 93$
1	11	40.34^{+}	$8 \cdot 99$	1.77†	$13 \cdot 90$	$65 \cdot 00$	$5 \cdot 29$	$70 \cdot 29$
1	13	$53 \cdot 01^{+}$	$11 \cdot 95^{+}$	$3 \cdot 12^{+}$	$15 \cdot 61$	83 · 69	$6 \cdot 12$	89.81
1	15	$73 \cdot 70$	17.68^{+}	5.68^{+}	$19 \cdot 56$	$116 \cdot 62$	$4 \cdot 93$	$121 \cdot 55$
1	18	$106 \cdot 01$	$22 \cdot 28$	$27 \cdot 73$	30.68	186.70	4.74	$191 \cdot 44$
1	21	$123 \cdot 84$	$30 \cdot 41$	$53 \cdot 29$	$42 \cdot 55$	$250 \cdot 09$	$4 \cdot 83$	$254 \cdot 92$

 Table 1

 Dry weights (mg per plant) of whole plant and principal parts

*Estimated from total embryo weight and volumes of parts (see text and Fig. 4). In addition, a constant correction of 0.21 mg. was made to the roots and deducted from the stem fraction from day 2 onwards, this being the estimated weight of root stumps within the coleorhiza.

[†]Corrected to include (for leaves and leaf sheaths) or exclude (for stems) the estimated dry weights of parts too small to be dissected, but of known volume. Values in parenthesis in Tables 1, 2, and 3 establish the link between the two experiments.

phases. Thus the weight of the whole organism begins to increase after day 6, suggesting that gain from photosynthesis had begun to exceed respiratory losses. On the other hand, weight losses from the grain continue until some time between day 8 and day 11. What is not obvious from Figure 3 is that the relative growth rate, R, of the seedling is much higher in the first than in the second phase of growth. By plotting the same data on a logarithmic scale, this is shown quite clearly (see Fig. 5, second curve from top). The mean values of R for days 1–4 and 8–18 are 0.862 and 0.151 g/g/day respectively. The transition from the higher to the lower rate takes about 4 days (day 4–day 8). The still lower rate for days 18–21 (0.099 g/g/day) can perhaps be attributed to the period of water stress suffered on day 20 (see Section II(a)).

An R value of 0.151 for a self-supporting grass seedling suggests that growing the test plants in continuous light of rather low intensity was not detrimental to growth. Mitchell (1956) obtained maximal R values of about 0.16^* for a number of grasses grown at about the same temperature but with only 12 hr of light of a much higher intensity (2700 f.c.). The highest values of R obtained by Ballard and Petrie (1936) for wheat, and by Williams (1936) for oats grown in a glass-house, were 0.08



Fig. 3.—Dry weights of principal plant parts plotted additively for early seedling growth in wheat.

and 0.14 respectively. Their day temperatures were reasonably comparable, but night temperatures were low.

Root growth was highly correlated with the two phases of growth. The growth of the five (or six) primary roots was dependent mainly on grain reserves, and dry weight increase of the root system almost ceased between days 8 and 11 (Fig. 4). Growth in the second phase was by adventitious roots and by fine branching of the primary roots.

* These were for shoots only. The shoot value for the present experiment was 0.17.

The growth of the coleoptile and of the first leaf blade seem to have depended mainly on grain reserves. However, the first leaf emerged from the coleoptile $3\frac{1}{2}$ days after sowing, and would soon contribute to dry matter production.

Expt.	Day	Leaf 1	Leaf 2	Leaf 3	Leaf 4
2	3	0.72			
2	4	$2 \cdot 08$			
1	4	$(2 \cdot 30)$			-
1	6	$8 \cdot 29$	0.45		
1	8	$17 \cdot 62$	$3 \cdot 84$	0.11	
1	11	$20 \cdot 92$	$17 \cdot 80$	$1 \cdot 59$	
1	13	20.05	$24 \cdot 82$	$8 \cdot 04$	
1	15	$20 \cdot 83$	$29 \cdot 16$	$23 \cdot 07$	0.64
1	18	$21 \cdot 68$	$30 \cdot 17$	$46 \cdot 49$	7.67
1	21	$20 \cdot 90$	$29 \cdot 98$	$49 \cdot 52$	$23 \cdot 44$

TABLE 2 DRY WEIGHTS (MG PER PLANT) OF INDIVIDUAL LEAVES

As has already been shown, the comparison of growth rates in time is greatly helped by examining the data on a logarithmic scale. This also holds for the comparison of the rates of growth of different organs at the same time (see Fig. 5).

Expt.	Day	Coleoptile	Leaf Sheath 1	Leaf Sheath 2	Leaf Sheath 3
2	2	0.38			
2	3	$1 \cdot 16$			
2	4	$2 \cdot 13$			
1	4	$(2 \cdot 13)$			
1	6	$3 \cdot 35$		·	
1	8	$3 \cdot 69$	$1 \cdot 58$		
1	11	$3 \cdot 49$	$4 \cdot 99$	0.51	
1	13	$3 \cdot 53$	$4 \cdot 90$	$3 \cdot 49$	·
1	15	$3 \cdot 44$	$5 \cdot 67$	8.07	
1	18	$2 \cdot 82$	$6 \cdot 25$	$9 \cdot 89$	$3 \cdot 31$
1	21	$2 \cdot 73$	$5 \cdot 98$	10.78	$10 \cdot 92$

Table 3 dry weights (mg per plant) of the coleoptile and of individual leaf sheaths

Unfortunately, the only separation that could be made at day 1 was for embryo and rest of grain. However, it is possible to estimate the dry weights from the volumes of the main parts. The assumption was made that, at this early stage, dry weights are proportional to the volumes occupied by the various parts. Figure 6 was built up by serial reconstruction as in Figure 1, but for the whole embryonic axis, so that areas within the diagram were proportional to volume. The volumes of the parts are listed beside the diagram, and their dry weights were estimated from these and the weight of the whole embryo (0.77 mg). The resulting values are included in Table 1 and their logarithms in Figure 5. Further corrections, also based on the volume studies, are incorporated in Table 1 and Figure 5. Tables 2 and 3 report only the weights of parts actually dissected.



Fig. 4.—Dry weights of individual leaves and leaf sheaths, and of roots and grain for early seedling growth in wheat. E, times of emergence of successive leaves.

Differences in the slopes of the curves for coleoptile, leaves, stem, and roots (Fig. 5) imply quite marked differences in their relative growth rates during the first phase of growth. Numerical values of R for days 1–3 were as follows:

coleoptile	$1 \cdot 03$	stem	$0 \cdot 28$
leaves	$1 \cdot 22$	\mathbf{roots}	$1 \cdot 32$

Root growth was fastest at first but soon fell to a very low rate (R = 0.08 for days 8–11). Coleoptile growth also fell very quickly and ceased at day 6. By contrast, the relative growth rate of the leaves fell more slowly and settled down to a steady rate (R = 0.138 for days 11–18). In so doing, the leaves became much

the largest part of the plant. The true leaf sheaths could not be effectively separated before day 8 and, as might be expected, their rate of growth closely parallels that of the leaves. The part called stem here might perhaps have been called "rest of plant", for its relative growth rate for days 1–3 was probably dominated by that of the



Fig. 5.—Dry weights (logarithmic scale) of principal plant parts and of total plant for early seedling growth in wheat.

coleorhiza, and after day 15 it was increased by the inclusion of tillers. The rather high rate for the mid period (R = 0.313 for days 11–15) can reasonably be attributed to the stem itself.

(b) Derived Data

Many papers on plant growth and nutrition have presented ratios of the dry weights of the shoots to roots as a means of defining the effects of treatment on

structural change. A better picture is obtained when such ratios are referred to the total plant weight, for the plant can be divided into any required number of parts, and the ratios plotted additively to give a unified picture. This has been done for the present experiments in Figure 7. It should be noted, however, that the parts have here been separated on a strictly morphological basis, so that the leaf weight ratio is based on all leaf laminae, irrespective of whether they were exposed to the light or not.

The leaf weight ratio increased from the small value of 0.08 (day 1) to a maximum of 0.63 (day 13). The subsequent fall in this ratio would have been less



Fig. 6.—Volume distribution in embryo (without scutellum) after soaking the grain for 24 hr.

pronounced if tiller leaves had been included for days 18 and 21. The leaf-sheath ratio (including coleoptile) was rather constant throughout the experiment. The root weight ratio rose rapidly from 0.24 (day 1) to 0.50 (day 3) and then fell more slowly to 0.17 (day 15). The high initial value of 0.49 for the stem weight ratio is a reflection of the fact that the stem fraction was then made up of the transition zone, the coleorhiza, and the epiblast (Fig. 6). These grew rather slowly at first, so the stem weight ratio fell to only 0.03 by day 6. The sudden increase after day 15 was due to the growth of tillers.

The distribution indices of Figure 8 provide a descriptive explanation of the changes with time in the weight ratios of Figure 7. Distribution indices are obtained by expressing the increments in dry weight of leaves, roots, etc. for each interval as percentages of the total dry weight increment for that interval. Where, as in this

case, such indices are available for a succession of harvest intervals, they give quantitative expression to the changing growth pattern (Williams and Shapter 1955).

Figure 8 shows that, for the first few days, more than 50 per cent. of the dry matter from the grain was used for root growth, and only about 15 per cent. for leaf



Fig. 7.—Dry weight ratios of principal plant parts plotted additively for wheat seedlings.

growth. However, by the time that grain reserves were exhausted (days 8–11) the indices were more than reversed, for the roots were then getting only 4 per cent., and the leaves 78 per cent. of the dry matter increase. Thereafter the root index increased and the leaf index decreased fairly slowly.



Fig. 8.—Indices of distribution of dry matter between the principal plant parts of wheat seedlings.

(c) Volume Change

The primary data for volume changes at the shoot apex are presented descriptively in Figures 9 and 10. For each of the 11 occasions, a volume-distribution diagram is shown complete, but on a small scale, at the right; at the left is shown the detail in the region of the apex. The diagrams were compounded from mean lengths and areas for the four replicates at each occasion. In interpreting them, it should be borne in mind that they present spatial arrangement in a rather schematic way. At the same time they do provide a useful bridge to the still more abstract treatment of Figure 11.



Fig. 9.—Volume distributions within shoot apices of the ages shown. *GP*, growing point; 1,2,3, successive internodes; *L2*, *L4*, leaf primordia.

Three leaf primordia are preformed in the grain (see day 1) and new primordia appeared at intervals of rather more than 2 days under the conditions of the experiment. The ninth, and last leaf primordium was already present on day 15, and the apex began to elongate prior to spike formation. The change from vegetative to



Fig. 10.—Volume distributions within shoot apices of the ages shown. *GP*, growing point; 4,5,6, successive internodes; *L4*, *L6*, leaf primordia; *SP*, spike primordium.

reproductive development gains expression in a number of ways, all of which imply a shift in dominance from foliar to cauline structures. The growth rates of the earlier leaf primordia are very high indeed (Fig. 9), the highest being a fourfold increase in leaf one (L1) from day 1 to day 2. Even L3 doubled its size over the same period. For the interval day 18-day 21, however, the fastest rate is for L6





(Fig. 10), and this reduces to a 75 per cent. increase per day. Leaves L8 and L9 increased little more than 20 per cent. per day over the same period.

That there is a progressive increase in apical growth as such is clear from Figures 9 and 10, for the apical dome grows further and further away from the site of initiation of the most recent leaf primordium. However, it is not easy to get a completely satisfying measure of this change. The line drawings at the foot of Plate 3 also demonstrate the change, and show that the cauline part of the apex changes from a rather flat cone to an acute one, and that the apical dome grows further and further away from the apex of this cone. This suggests that the height of the dome above a given stem sectional area (e.g. $100 \text{ mm}^2 \times 10^{-3}$) might be a suitable index of this aspect of apical growth.

Figures 9 and 10 show also that there is a progressive change with leaf position in volume distribution along the length of the primordium. This is best seen in the larger primordia of similar length (e.g. L1 at day 2, L3 at day 8, and L4 at day 13), where the distal portions become more and more acute.

Up to day 6, only one, or barely one, leaf primordium has failed to overtop its apex; there were two such primordia on days 8 and 11; and three from day 13 onwards. This is an expression of the fact that there are longer intervals between the emergence of successive leaves than between the formation of successive primordia (see also Fig. 11), and that the height of the apex is itself increasing. Sharman (1947) and Cooper (1951) have shown that leaf primordia can accumulate in large numbers under the apices of some grasses, and it seems that even in wheat—which Sharman classifies as having a short type of apex—there is a tendency to accumulate leaf primordia in this way.

The actual volumes of the leaf primordia are presented in Table 4 and those for the associated corpus tissue are in Table 5. The former also appear on a logarithmic scale in the lower part of Figure 11. This figure attempts to integrate the information on volume change in the leaf primordia with the dry weight changes in the first four leaf blades of the primary shoot. Both dry weight and volume determinations were available for leaf 3 on day 8 and these values link the two sets of data. This link is admittedly rather tenuous, so it is reassuring to find the high degree of continuity shown by the data for leaves 1, 2, and 4. The value given for L5, day 21, is an estimated volume based on basal area and length; this also fits well into the general picture. The dry weight scale of Figure 11 has been extended down to give an idea of the total range of size (about five logarithmic cycles) traversed by the leaf from its first appearance as a recognizable primordium to full maturity.

Conversion of individual mean volumes to dry weights would involve the unwarranted assumption that the density of these meristematic tissues remained unchanged with time and between successive primordia. The data for leaf 3, day 8, imply a density of 0.31 mg dry matter per mm³, a value which is very much higher than that from the data of Brown and Broadbent (1950) for pea root tips (0.075 for the zone 0.4-2.4 mm from the tip). The higher value is too high to the extent of the shrinkage and compression suffered in preparation for volume estimation, but the difference is far too great to be explained on this basis. The mean cell size was very much smaller in the wheat apex (see below) than in the pea root tips, though the way that this could affect the issue is obscure.

It might be thought that the composite nature of the information presented in Figure 11 could invalidate any general conclusions which one might seek to draw from it. In the first place, the volumes represent the *whole* of the leaf primordia including the tunica-derived tissue at their junction with the stem. This tissue could *not* be included when the primordia were first dissected for dry weight determination (e.g. leaf 3, day 8, in Plate 1 and in Fig. 11). However, the volume of the tunicaderived tissue was then a small fraction of the whole—only $1 \cdot 4$ per cent. in the case of leaf 3. Secondly, the ligule had not differentiated at the first dissection, and examination of many axes suggested that the whole of the portion removed would have developed into leaf blade and made little or no contribution to leaf sheath.

	10	10 1110 (11		0		,			
Day	Ll	L2	L3	L4	L5	L6	L7	L8	L9
1 2 3 4 6 8 11 13 15 18 21	110 450	10·4 22·7 74 176	$ \begin{array}{r} 1 \cdot 5 \\ 3 \cdot 0 \\ 6 \cdot 7 \\ 11 \cdot 0 \\ 40 \\ 354 \end{array} $	$ \begin{array}{c} 0 \cdot 9 \\ 1 \cdot 3 \\ 4 \cdot 9 \\ 21 \cdot 3 \\ 89 \\ 610 \end{array} $	$ \begin{array}{c} 0.8 \\ 4.3 \\ 12.8 \\ 34.6 \\ 62 \\ 276 \end{array} $	$ \begin{array}{r} 1 \cdot 1 \\ 2 \cdot 9 \\ 7 \cdot 8 \\ 12 \cdot 6 \\ 36 \cdot 7 \\ 195 \end{array} $	$1 \cdot 0$ $2 \cdot 1$ $3 \cdot 2$ $9 \cdot 7$ 38	0.9 1.4 2.8 5.5	$\begin{array}{c} 0 \cdot 7 \\ 1 \cdot 3 \\ 2 \cdot 2 \end{array}$
		1	1	1	1	1		•	•

VOLUMES	$(MM^3 \times 10^{-3})$	OF	LEAF	PRIMORDIA	(LAMINA + TUNICA)

For these reasons the dry weights of Figure 11 are for leaf blades only. However, the inclusion of leaf sheaths would have made only triffing differences to the time trends of Figure 11. Lastly, there is the implicit assumption that tissue density is

Day	Ll	L2	L3	L4	L5	L6	L7	L8	L9
1	5.6	1.5	0.3						
2	$6 \cdot 6$	1.8	$0 \cdot 3$						
3		$3 \cdot 5$	0.7	$0\cdot 2$					
4		$5 \cdot 8$	1.5	$0\cdot 2$					
6			4.6	1.0	$0\cdot 2$				
8		4 	$14 \cdot 3$	4.0	$0 \cdot 9$	$0 \cdot 3$			
11	1			8.9	$2 \cdot 5$	$0 \cdot 8$	$0 \cdot 3$		
13				$21 \cdot 8$	$5 \cdot 9$	$1 \cdot 9$	0.8	$0\cdot 4$	
15					$9 \cdot 3$	$3 \cdot 0$	$1 \cdot 2$	0.6	0.3
18					$25 \cdot 8$	$7 \cdot 1$	$2 \cdot 5$	1.1	0.6
21						$28 \cdot 3$	7.7	$2 \cdot 7$	1.4

			Г	ABLE 5				
TOT TIMES (xxx ³ ∨ 10−3)	OF CORPUS	TISSUE	ASSOCIATED	WITH	SUCCESSIVE	LEAF	PRIMORDI

constant throughout the early development of the leaf primordia. Even this would not have serious consequences for the argument unless changes in tissue density were large and discontinuous. A little consideration will show that two- or even threefold changes in density, provided they were continuous, would have little effect on the pattern of dry weight change implied by Figure 11. The dry weight values of Figure 11 were established with precision and were therefore joined by continuous curves. Straight lines were fitted to the volume data for such time intervals as seemed justified by inspection. Leaves 1 and 2, and leaves 6–9 presented no difficulty here; terminal values for leaves 3 and 5 seemed to demand discontinuous change with time; and leaf 4 came in for rather special treatment because the dry weight extrapolation was deemed to be more reliable than the volume for day 13.

					T					
	Harvest Interval (days)									
	1-2	2–3	3-4	4-6	6–8	8–11	11–13	13–15	15–18	18-21
Ll	1.39		1.06	0.69	0.38	0.06	-0.02	0.02	0.01	-0.01
L2	0.78	$1 \cdot 14$	0.88		$1 \cdot 07$	0.51	0.17	0.08	0.01	0.00
L3	0.685	0.79	0.51	0.65	1.08	0.90	0.81	0.53	0.23	0.02
L4			0.405	0.67	0.74	0.48	0.93		0.82	0.38
L5			-	-	0 · 85 ∫	0.36	0.50	0.30	0.48	
L6					-	0.32	0 • 49 >	0.24	0.35	0.51
L7						-	0.40	$ 0\cdot 21\rangle$	0.36	0.41
L8							-	0.20	0.23	$0\cdot 24$
L9								-	0.21	
S.E.	0.086	0.054	0.136	0.021	0.061	0.017	0.072	0.039	0.030	0.080
Linear										
regression†	***	*	**	n.s.	**	***	***	*	***	**
Non-linear										
regression†	*		n.s.		**	*	**	n.s.	*	n.s.

TABLE 6

RELATIVE GROWTH RATES FOR LEAVES (G/G/DAY) AND FOR LEAF PRIMORDIA (IN ITALICS, CM³/CM³/DAY) Bracketed values within harvest intervals do not differ significantly. For statistical treatment of the volume data see p. 419

 \dagger Signifiant effects with probabilities less than 0.05, 0.01, and 0.001 are indicated by *, **, and *** respectively.

Table 6 summarizes the data of Figure 11 as relative growth rates, first for the leaf primordia (volume basis) and then for the early leaf blades (dry weight basis). The latter show the expected rapid falls from high values at the times of emergence to zero at days 11, 15, and 18 for leaves 1, 2, and 3 respectively. Unfortunately the time trends prior to emergence are not well established, being based on only four apices per occasion. In spite of this, it is possible to make rather precise comparisons of the relative growth rates for successive primordia within each harvest interval. This is because we are here concerned with relative volume changes between primordia within apices. The standard errors of Table 6 thus apply only within their respective time intervals, and beneath them are indicated the significances of the linear and non-linear regression coefficients of relative growth rate on leaf number. Detailed comment on these significances is scarcely necessary, but they support the general conclusions that follow. Up to interval 13–15 days the youngest

two or three primordia present at the time grow at similar rates, but the next oldest leaf primordium grows faster. After day 15, the younger primordia separate into two growth-rate groups, leaves 8 and 9 growing little more than half as fast as leaves 6 and 7. It may be significant that the spike primordium is initiated early in this same period, and that unpublished evidence suggests that a minimum of seven foliage leaves are formed on the primary shoot of this variety of wheat. It is even possible that the eighth and ninth primordia would have become foliar ridges of the lower part of the ear.

In the light of all the evidence of Figure 11, it also appears that successive leaves attain their maximum relative growth rates during the few days prior to their emergence from within the previous leaf. A further point is that there appears to be a discontinuity at about day 8 in the relative growth rates of the primordia. Thus the rates for leaves 3 and 4 and the beginning of leaf 5 are similar and average 0.66, whereas those for leaves 5 (later stage), 6, and 7 are also similar to one another and average 0.38. The exhaustion of seed reserves soon after day 8 (see Fig. 4) provides the most obvious explanation for the general reduction in relative rates of growth.

(d) Cell-size Distribution within an Apex

These data for an 11-day-old vegetative apex are presented in Figure 12. The mean cell volumes are plotted as a function of height above the base of the fourth primordium; the apex is the same as that used to illustrate the procedure for volume integration (Fig. 1) and the data are subject to the same errors due to shrinkage and compression as are the volume data already presented. The values for successive primordia overlap so completely that they are treated separately within Figure 12. To a limited extent the curves are repeated as broken lines to assist the reader to compare those for adjacent primordia or, in one case, the base of primordium 4 with corpus and tunica values.

Table 7 shows that the average cell volumes for the primordia present at day 11 are remarkably similar (ranging from $2 \cdot 22$ to $2 \cdot 55$ units for lamina plus tunica). The cells of the associated corpus tissue are larger but are also similar among themselves. Within the apical dome, however, the relative sizes of tunica and corpus cells becomes reversed, those nearest the tip being $3 \cdot 0$ units for the tunica, but only $2 \cdot 4$ units for the corpus (Fig. 12). The primordium of leaf 5 is the youngest to show a definite trend in cell size from base to tip, with a minimum of about $2 \cdot 15$ units near the base of the free part of the lamina. In the primordium of leaf 4, the region of minimal cell size is much more extensive, the actual minimum (about $2 \cdot 25$ units) being a third of the way up. A few cells near the tip of this primordium are quite large and may have entered the phase of cell enlargement. This primordium is just entering its phase of most rapid relative growth (Fig. 11).

The cell generations, n, of Table 7 are mean values based on the assumption that all cells had been dividing in all parts of the apex. The results must therefore be accepted with caution. The values for L7 indicate that about eight generations for the tunica, and six for the corpus, take place in the apex before a leaf primordium is recognizable. Since L4 was at this stage on day 3 it follows that it took seven more



Fig. 12.—Mean cell-size distribution within an 11-day apex as a function of distance from the base of the fourth internode (see diagram of Fig. 1). The distributions for L4-L7, and for the tunica and corpus are shown separately, together with the limits of the appropriate internodes (shaded alternately).

generations and 8 days to acquire its cell number at day 11, which gives a mean generation time of 27 hr. If, as seems likely, the mean cell volumes were about the same for all leaf primordia prior to the onset of cell enlargement, the volume data of Table 4 indicate that the mean generation times ranged from about 12 hr for L1 to as much as 3 days for L8 and L9. The discrepancy of two generations between the values for tunica and corpus would seem to be explainable in terms of the geometry of the apex.

IV. DISCUSSION

The procedure of serial reconstruction has so far been used mainly for the description of form changes in embryos and embryonic parts of plants. Good examples

THE APEX, LEAF PRI	MORDIA, AN	ND ASSOCIA	TED CORPU	S TISSUE	AT DAY 11	
Attribute and Unit	Part*	Apex	L7	L6	L5	L4
Volume (mm ³ \times 10 ⁻³)	$\mathbf{L} + \mathbf{T}$ C	$\begin{array}{c} 0\cdot 92 \\ 0\cdot 26 \end{array}$	$\begin{array}{c} 0\cdot 85\\ 0\cdot 36\end{array}$	$2 \cdot 75$ $0 \cdot 80$	$13 \cdot 7 \\ 3 \cdot 0$	$\begin{array}{c}100\cdot 5\\9\cdot 7\end{array}$
Number of cells	L+T C	318 94	383 98	$\begin{array}{c} 1195\\ 195\end{array}$	5372 741	39,707 2,407
Average cell volume ($\mu^3 \times 10^3$)	L+T C	$2 \cdot 89$ $2 \cdot 77$	$2 \cdot 22 \\ 3 \cdot 67$	$2 \cdot 30 \\ 4 \cdot 10$	$2 \cdot 55 \\ 4 \cdot 05$	$2 \cdot 53 \\ 4 \cdot 05$
Cell generations (n) , where cell No. $= 2^n$	L+T C	8·3 6·6	8 · 6 6 · 6	$\begin{array}{c}10\cdot 3\\7\cdot 6\end{array}$	$12 \cdot 4$ $9 \cdot 5$	$\begin{array}{c} 15 \cdot 3 \\ 11 \cdot 2 \end{array}$

TABLE 7 SUMMARY OF VOLUMES, NUMBERS OF CELLS, MEAN CELL VOLUMES, AND CELL GENERATIONS FOR THE APEX, LEAF PRIMORDIA, AND ASSOCIATED CORPUS TISSUE AT DAY 11

*L+T = lamina plus tunica; tunica only, for the apex. C = corpus or tissue derived from the corpus.

were provided by Avery (1930), McCall (1934), and Boyd and Avery (1936) for the developmental anatomy and morphology of wheat, oats, and maize embryos and seedlings. Avery (1933a, 1933b) presented similar studies of early development in the seedling and leaf primordia of tobacco. Randolph (1936) and Merry (1941) described the developmental morphology of the caryopsis and embryo of maize and barley respectively. More recently Jacobs and Morrow (1957) made use of serial reconstruction for the study of xylem development in the shoot apex of *Coleus*. Perhaps the most complete account of the developmental anatomy of the shoot of any plant, however, has been that of Sharman (1942) for maize. This work also attempted to relate the sequence of events in the development of the vascular system to the probable movement of food and water during growth. For the apical region of the shoot of *Lupinus albus*, Sunderland and Brown (1956) have devised new dissection techniques for the determination of the volumes and numbers of cells in young primordia and internodes. Protein contents and respiration rates within the same apical system have since been presented by Sunderland, Heyes, and Brown (1957) and Sunderland (1960) has studied the contribution of cell division and expansion to the growth of leaves of *Lupinus albus* and *Helianthus annuus*.

The details of foliar histogenesis are now well understood for the Gramineae. Minor differences in the accounts of Rösler (1928) for wheat, Kliem (1937) for oats, and Sharman (1945) for *Agropyron* are discussed by Barnard (1955), and it is clear that foliage leaves arise as the result of periclinal divisions, usually restricted to the hypodermis and dermatogen just below the apex. These divisions spread laterally and soon give rise to a collar of tissue surrounding the axis (see Plate 3). By contrast the origin of the vegetative bud is by periclinal divisions of subhypodermal cells, the cells of the more superficial layers only dividing anticlinally. This difference of origin may be correlated with the nature of the leaf as an organ of limited growth, and of the bud as one of unlimited growth reduplicating the whole apex. To distinguish the superficial and deep-seated tissues in the present work, the terms "tunica" and "corpus" have been used (Fig. 1) for convenience rather than for theoretical reasons. However, as defined, they express the fact that the leaf primordia of wheat are the product of the two outer cell layers alone.

It is appropriate now to attempt an integrated picture of the early growth of the primary shoot of the wheat plant. Quite the best index of growth for this purpose is the relative growth rate, R, and this is adopted in the diagrams of Figures 13 and 14. These portray the relative rates of dry weight change in the main parts (including roots) and in successive individual leaves respectively. These rates are in fact based on the slopes of the appropriate curves of Figures 5 and 11.

Attention has been drawn to the probable influence of seed reserves on growth rates. The relative growth rates for leaves, R_L , and for roots, R_R , are exceptionally high prior to day 5, and even that for the stem, R_s , is a great deal higher than during the next five days. Another striking feature of Figure 13 is the contrast between the time trends for R_L and R_S such that R_S changes from being well below R_L to values which are greater than those for R_L . This reversal might be thought to be due to the inclusion of small tillers with the stems after day 15, but it has since been confirmed in an experiment in which the tillers were weighed separately. The reversal is an expression of the change in dominance from leaf growth to stem growth. With this goes the progressive increase in the rate of growth of the apex (see p. 416 and Figs. 9 and 10) and a general decrease in the R values for successive leaf primordia (Fig. 14). Even the corpus tissue associated with L1-L4 at first grows slowly or not at all (Table 5) at times when the primordia themselves are growing very fast (Table 4). By contrast, the lower diagrams of Figure 10 show for the end of the experiment that the apex, and with it the corpus tissue, was then growing faster than primordia 8 and 9. These trends reach their conclusion, as far as the primary shoot is concerned, at the double-ridge stage of inflorescence initiation, when further development of the lower ridge is suppressed, while the upper ridge develops as a spikelet. There is clearly a need to subject the developing inflorescence to the same quantitative description before attempting to carry this analysis further.

The pattern of development revealed by the R values for the leaves (Fig. 14) is a complex one, and interpretation of it is necessarily tentative. The most regular feature is that R for each of the early leaves rises to a maximum just prior to

emergence and then falls asymptotically to zero. Unpublished evidence indicates that $R_{L5}-R_{L7}$ would also follow such a course, and that the maxima themselves would fall on a curve which was asymptotic to an R value between 0.5 and 0.6. The individual curves for post-maximal growth are those to be expected for organs



Fig. 13.—Relative growth rates for leaves, stem, and roots as a function of time.

passing through the phases of maturation and senescence. Since final leaf size increases with leaf number, R must be maintained at high values for a longer time with each successive leaf, the more so that its maximum is less rather than greater with each successive leaf. This is clearly true within the limits of the data.



Fig. 14.—Relative growth rates for successive leaves of the primary shoot of wheat as a function of time. The arrows mark the times of emergence of the first four leaves.

Perhaps the most novel feature of the pattern of development revealed by Figure 14 is the variety of trend for R prior to leaf emergence. It is commonly supposed that the growth of an organ is exponential, or nearly so, for some time, and that it then falls away from exponentiality as the processes of maturation set in

Here, however, the leaf primordium tends to show an early phase of exponential growth followed by a substantial *increase* in the exponent to what may well prove to be a second, though briefer, phase of exponential growth. Plate 1 demonstrates, for the third leaf primordium, the visible consequences of this increase in the exponent, for the relative growth rate is clearly greater for the second 2-day period (cf. Fig. 11). If, characteristically, there are two distinct phases of exponential growth for leaf primordia, it is reasonable to suppose that the first phase for L1, and parts of those for L2 and L3 took place during embryo development.

An obvious basis for two distinct phases of exponential growth would exist if it could be shown that the cell division and cell expansion phases were fairly distinct for the leaf primordia of wheat. The evidence, as far as it goes, suggests that the onset of cell expansion may coincide with the increase in R, but it does not explain why the rate does increase. It has yet to be shown whether cell division continues for wheat in the manner shown by Sunderland (1960) for lupin and sunflower leaves. It is possible that the onset of cell expansion is conditioned by the timing of endogenous auxin production or by interactions with other growth regulators. However, there seems little direct evidence on this point. For the leaves of Solidago sempervirens L., Goodwin (1937b) showed that, with the cessation of cell division and the onset of cell enlargement, there was a sudden change in the length-breadth growth relations, and he suggests a correlation with the presence of large amounts of auxin demonstrated earlier (Goodwin 1937a). Another possibility is that effective vascular connection seems to be made at this time, for the first protophloem elements of the median vascular strand were then first seen to have been differentiated. By way of example, Plate 2 shows transverse sections of an 11-day seedling for which vascular differentiation was well advanced in L3 (just prior to emergence), but had scarcely begun in L4 (at beginning of rapid growth phase). The median strand has single protophloem and protoxylem elements, and two other strands have single protophloem elements only. According to Jacobs (1956), auxin is also implicated in xylem differentiation, and there is a clear case for a detailed study of the timing of effective vascular connection with the sources of substrate for growth. Prior to the establishment of such connections, all such substrate must get to the young primordia by active transport across a region of small, undifferentiated, and more or less isodiametric cells. Such conditions are consistent with the low rates observed for early primordium development.

Before leaving this question of exponential growth in leaf primordia, it is worth comparing the present results with those for *Lupinus albus* reported by Sunderland and Brown (1956). Table 4 and Figure 3 of their paper show that the volumes of successive primordia and their cell numbers increase exponentially with plastochron age. Accepting a plastochron interval of 2 days, this volume increase is equivalent to an R value of 0.32, which is somewhat less than that for L7 for the wheat seedling, though covering a similar range of absolute size (Fig. 11). As with L7, however, there would still be plenty of time for a later increase in Rshould such be characteristic for the later development of leaf primordia in general. A difference for *Lupinus* is that mean cell volume increases appreciably during what appears to be the early exponential phase of volume increase. The more recent study by Sunderland (1960) includes volume change in the fifth primordium of lupin and

in the second primordium of sunflower. In both cases there is an indication that R increases with time, but the fresh weight data which follow do not support this trend.

Another phenomenon which appears also to be correlated with the onset of the higher rate of primordial growth is a rather sudden increase in the stainability of the cytoplasm of the cells, particularly in the lower part of the primordium. This is exemplified in the lower figure of Plate 2, where L4 is stained more heavily than either L3 or L5. Only in the apex is the staining as heavy as in L4. The increase in stainability is likely to be due to an increase in ribonucleic acid and to imply an increase in the potential for protein synthesis. Bünning (1952, 1956) appears to be speaking of the same general phenomenon when he refers to an increased density of cytoplasm and an increase in the size of the nucleoli as characteristic of cells of high embryonality. He cites the outgrowth of leaf primordia as one among many examples of organ and tissue production which are conditioned by such increases in embryonality. According to Bünning, cells of high embryonality suppress the embryonality of neighbouring cells. This inhibiting effect is believed to be active for some distance within the tissues, and to be responsible for many processes of differentiation. The inhibiting effect is thought to be due to competition for specific substances rather than to the production of inhibitors.

Although Bünning was thinking of the initiation of leaf primordia rather than of their later development, it may be that the concept of intra-plant competition for specific substances applies with even greater force to the latter. Thus, it will be noted that each primordium enters its phase of maximal potential for growth just before emergence, and that from then on its growth shows a measure of independence from events elsewhere in the plant. Before this phase of maximal potential, and in spite of constant conditions for growth, the growth rates of the primordia seem to be determined by such events as the exhaustion of seed reserves and, later, the onset of inflorescence development. Initially the level of supply of energy substrate from seed reserves seems to have been sufficient to supply not only the heavy demand of L1 but also to maintain a higher rate in L2 than in L3 or L4. With the exhaustion of these reserves soon after day 8, the rate dropped to a lower level (L5–L7) presumably determined by products of photosynthesis in L1 and L2. Concerning the still lower rates for L8 and L9, one can only draw attention to the correlative rise in stem growth and the onset of spike development at about day 15.

This quantitative description of the growth of the primary shoot of the wheat plant shows that there is abundant scope for the operation of intra-plant competition for metabolites and nutrients. That assimilates appear to be the most likely substances competed for may simply follow from the fact that all mineral nutrients were maintained in adequate supply. In his studies of the influence of light and temperature on lateral bud development in ryegrass, however, Mitchell (1953a, 1953b) concluded that these factors operated mainly through their effects on the general level of energy substrate in the plant. Competition for the products of photosynthesis seems also to be a likely explanation for many of the compensatory phenomena discussed by Jacobs and Bullwinkel (1953) for *Coleus*. Still more recently, Milthorpe (1959) suggested that the rate of cell division in the terminal meristem of cucumber was influenced mainly by the supply of assimilate. Events in the expanding bud were thought to be dominated first by competition for carbohydrate but later by competition for mineral substrates.

It will be evident that competition for substrate of any kind will be conditioned by the nearness of the competitive sinks to the source or sources of that substrate, by the efficiency of the transport systems involved, and by many other considerations.

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EXPLANATION OF PLATES 1-3

Plate 1

Early stages of growth of the third leaf primordium in wheat. The seedlings were harvested 4, 6, and 8 days after sowing. $\times 42$.

Plate 2

- Fig. 1.—Transverse section of an 11-day wheat seedling. The inner leaf is L4 section 87, of the same apex depicted in Figure 1. Most of L3 is also visible and is in an advanced state of vascular differentiation. $\times 165$.
- Fig. 2.—Tranverse section of the same seedling (section 39, Fig. 1). At the centre is the growing point (heavily stained), L5 (lightly stained), and then L4 (heavily stained). L3 is cut at the level of the ligule. $\times 165$.

Plate 3

- Fig. 1.—Longitudinal section of an 8-day wheat seedling, showing the two-layered tunica of the growing point. The overtopping leaf is L4; the smaller leaves may be identified from the appropriate diagram of Plate 3, Figure 2. $\times 178$.
- Fig. 2.—Outline drawings of similar longitudinal sections for selected times throughout the experiment. $\times 52$.



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THE PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT. I

1 0.2 0.4 DAY 2 DAY 11 DAY 4 DAY B DAY 15 DAY 21 2

THE PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT. I