STUDIES ON THE GROWTH OF THE BARLEY APEX

II. ON THE INITIATION OF INTERNODE ELONGATION IN THE INFLORESCENCE*

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Summary

The processes of cell division and cell elongation were examined in the pith of the rachis of the barley inflorescence from the time double ridges first appeared until shortly before ear emergence for plants grown under continuous illumination.

Estimates of the concentration of gibberellin-like substances in inflorescences were also made at three stages of development for barley plants grown under both continuous illumination and 8-hr light periods. The highest concentration of gibberellin-like substances coincided with the initiation of cell division in the pith region, while at the same time stamen initials first appeared and internode elongation in the inflorescence began. In the light of these findings tentative suggestions are made about the role of gibberellins in the growth of long-day plants.

I. INTRODUCTION

Two distinct phases of growth have been shown to exist in the rachis of the barley inflorescence (Nicholls and May 1963): in the first, primordium formation occurs in acropetal succession and there is little change in mean interprimordial distance; in the second, no new primordia are formed and the increase in length of the apex is due to an increase in length of the internodes of the rachis. The change-over from the first to the second growth phase is marked by the appearance of stamen initials on the most advanced floral primordium.

The initiation of internode elongation in *Hyoscyamus niger* and *Samolus parviflorus* which can be induced by applying either certain photoperiodic regimes or gibberellic acid (GA_3) is correlated with an increased mitotic activity of the subapical meristem (Sachs, Bretz, and Lang 1959*a*, 1959*b*). The initiation of internode elongation has also been correlated with peaks in activity of gibberellin-like substances extracted from induced long-day and cold-requiring dicotyledonous rosette plants (Harada and Nitsch 1959; Lang 1960; Reinhard and Lang 1961). These observations point to the possibility that gibberellins are somehow involved in the initiation of internode elongation, a notion that has been extended to caulescent plants by observations of interactions between GA_3, certain growth retardants, and mitotic activity of the subapical meristem (Sachs *et al.* 1960).

* The results presented in this paper were included in the thesis presented by one of us (P.B.N.) for the degree of Ph.D. in the University of Adelaide.

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In this work experiments were planned to examine the processes of cell division and cell elongation in the pith region of the rachis of spring barley inflorescences in relation to the two phases of growth previously recognized. Furthermore, estimates of the concentrations of gibberellin-like substances extractable from apices were made on plants grown in different environmental conditions, and harvested at several critical stages of growth including the stage when the increase in interprimordial distance began.

II. Materials and Methods

Barley plants (*Hordeum distichon* L. cv. Prior) were grown under similar conditions in the same controlled-environment cabinet to those described previously (Nicholls and May 1963). Humidity control was not maintained during growth of plants used for extracting gibberellin-like substances but no significant differences in rates of growth and development of apices were observed between these plants and those grown in high humidity conditions. The inflorescences used in the extraction experiments were taken from plants grown under either continuous fluorescent light (24-hr light period) or 8 hr fluorescent light and 16 hr darkness (8-hr light period).

(*a*) *Measurements of Cell Number and Segment Length*

Plant material for these determinations came from plants given 24-hr light periods. It is to be noted that this barley variety is a quantitative long-day plant, and accordingly the assumption is made in Section IV that the same pattern of morphological development occurs in 8-hr light periods. Inflorescences were fixed in formalin–acetic acid–ethanol (90 : 5 : 5 by volume) for 24 hr and then stored in 70% ethanol. Dehydration was achieved using the t-butanol procedure of Johansen (1950) and embedding was in paraffin wax (m.p. 52°C). It was found useful to thread a piece of wire through the subtending stem internodes in the plane of the spikelets as an aid to orientation for sectioning. Sections of 10 μ thickness were stained with iron-mordanted celestine blue (Gray and Pickle 1956) and mounted in canada balsam.

The measure here designated "segment length" is defined as the distance, in the direction of the longitudinal axis of the shoot, between comparable points of consecutive spikelets on the same side of the shoot axis, and thus comprises two nodes and two internodes (Plate 1, Fig. 1). The common points chosen were the axil of the primordium, whose position on the shoot (numbers begin from the base) is used to designate the segment, and the axil of the primordium immediately below it (Plate 1, Figs. 1 and 2).

The measure here designated "cell number" is defined as the number of cells in a single column along the shoot axis within the pith region of the segment. Values are recorded for segments and are means from four consecutive serial sections comprising a median longitudinal piece of tissue 40 μ thick.

(*b*) *Determinations of Gibberellin-like Substances*

Inflorescences were harvested at the following stages of development : the first appearance of double ridges, the first appearance of stamen initials, and at the first

appearance of anther lobes (when awn elongation also begins). During harvesting, material was quick-frozen in a glass-stoppered flask immersed in dry ice, and at the completion of the harvest this material was lyophilized. Subsequently the dried material was stored at −23°C.

For assay, a selected number of inflorescences (about 200 at early stages, down to 60 at later stages of development) was weighed and then extracted with ethyl acetate (2·5 ml) for 2 hr at 23°C. This procedure was repeated first for 3 hr and then 17 hr, and finally the residue was rinsed twice with 0·5-ml portions of ethyl acetate. Extracts and washings were combined, evaporated to dryness over a water-bath at 30°C, and the residue taken up in water (2·5 ml) overnight at room temperature. 10- and 100-fold serial dilutions were made from a portion (0·25 ml) of this solution and, from each dilution, three subsamples (0·7 ml) were taken for the estimation.

A bioassay method, based on the gibberellic acid-induced release of reducing sugars from barley endosperm (Paleg 1960, 1961), and described by Nicholls and Paleg (1963), was used. The assay which can detect 30 pg gibberellic acid per millilitre was essential for this study since only small amounts of tissue (2–72 mg dry weight) were available. One unit of activity is here defined as the quantity of gibberellin-like substances giving the same response as 1·0 pg of gibberellic acid and one unit of specific activity as one unit of activity per 1 μg dry weight of plant material.

(c) *Terminology*

Many terms used here were defined in detail in our earlier paper (Nicholls and May 1963). In brief the most common ones are: primordium number—the total number of lateral appendages on the main axis whether mature or just initiated; vegetative phase—the period bounded by germination at one end and the appearance of double ridges at the other; spikelet phase—bounded by the appearance of double ridges and the appearance of stamen initials; elongating phase—bounded by the appearance of stamen initials and the cessation of peduncle elongation.

III. Results

(a) *Cell Number and Segment Length*

The sample of inflorescences used for cell number and segment length measurements came from a larger population on which accurate determinations of mean apex length and mean inflorescence status were made (Nicholls and May 1963, Fig. 2). The stage of inflorescence development was found to be closely related to apex length under the specified environmental conditions. Use has been made here of this finding to adjust, to a common mean rate of growth, the rates of growth of individual inflorescences in the samples employed in determinations of cell number and segment length. The adjustment was considered desirable as some inflorescences of a particular chronological age were developmentally similar to the population mean at a younger or older chronological age. The procedure adopted has been, therefore, to present measurements of cell number and segment length in terms of apex length rather than time. However, since this sample of inflorescences came from the larger population referred to above, the data presented in terms of apex

length can be restated in terms of chronological age of the population mean. This involves substituting for apex length (L_A) the following relationship to time after sowing in days (T):

$$\log L_A = 0{\cdot}1013T + 1{\cdot}754.$$

This relationship is only applicable under the specified environmental conditions for the period from double-ridge formation (day 11) to flag leaf emergence (day 21), the period within which measurements of cell number and segment length were made; outside this period the relationship is non-linear.

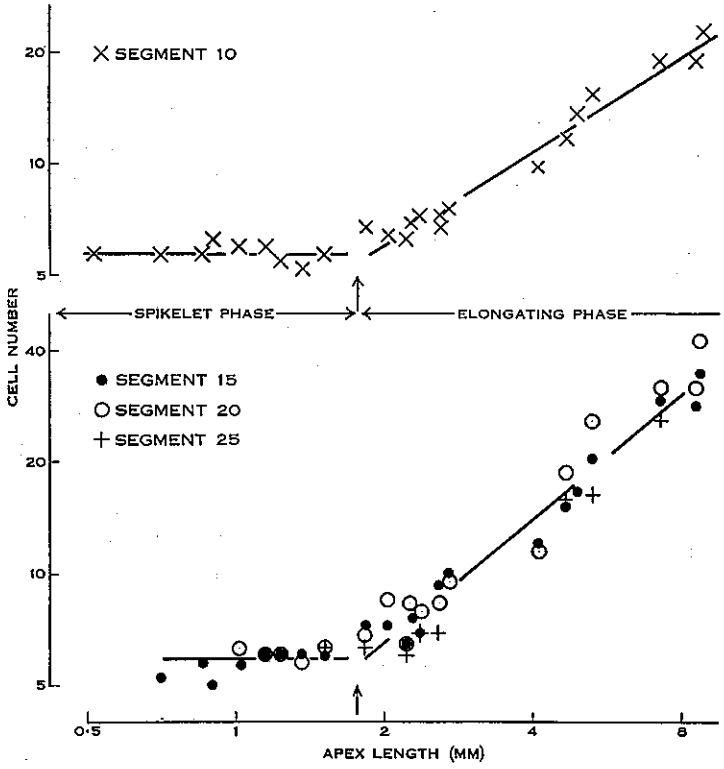

Fig. 1.—Changes in cell number (see text for definition) with apex length in four segments along the shoot axis. The change from the spikelet to the elongating phase of growth is marked by the appearance of stamen initials.

It follows from the foregoing discussion that transforming measurements of cell number and segment length to logarithms and examining these against transformed values for apex length will give a similar picture to an examination against time—time not for individual inflorescences, but for the population mean.

Values for cell number per segment are plotted against apex length, both on logarithmic scales, in Figure 1. It is evident that during the spikelet phase, while new primordia are being formed on the apex, cell number per segment remains relatively constant. Following the appearance of stamen initials, an increase in cell

number occurs and this is related to the increase in apex length as the regression equations in Table 1 show. There was no significant difference between the equations for segments 15, 20, and 25, although overall the slope shows a progressive trend upwards. Thus, cell division begins at the appearance of stamen initials when, it has previously been noted, the mean interprimordial distance begins to increase (Nicholls and May 1963).

Segment lengths are also related to apex length, over the range of apex lengths examined (Fig. 2). The relationship depends, however, on segment position and stage of development as illustrated by the equations in Table 1. During the spikelet phase, the increase in segment length that occurs is difficult to reconcile with the constant mean interprimordial distance observed previously (Nicholls and May

TABLE 1

REGRESSION EQUATIONS AND THE TRANSFORMED EQUATIONS, EXPRESSED IN THE EXPONENTIAL FORM, FOR DATA IN FIGURES 1 AND 2

Segment No.	Regression Equations for Cell Number (Y_c) and Segment Length (Y_s) on Apex Lengths (L_A)	Transformed Regression Equations for Cell Number (Y_c) and Segment Length (Y_s) on Age (T)
10*	$\log Y_c = 0{\cdot}842 \log L_A - 1{\cdot}989$	$Y_c = e^{0{\cdot}197T-1{\cdot}18}$
15*	$\log Y_c = 0{\cdot}983 \log L_A - 2{\cdot}413$	$Y_c = e^{0{\cdot}230T-1{\cdot}59}$
20*	$\log Y_c = 1{\cdot}162 \log L_A - 3{\cdot}005$	$Y_c = e^{0{\cdot}274T-2{\cdot}45}$
25*	$\log Y_c = 1{\cdot}198 \log L_A - 3{\cdot}222$	$Y_c = e^{0{\cdot}280T-2{\cdot}59}$
10†	$\log Y_s = 0{\cdot}129 \log L_A + 1{\cdot}782$	$Y_s = e^{0{\cdot}0302T+4{\cdot}63}$
15†	$\log Y_s = 0{\cdot}667 \log L_A + 0{\cdot}070$	$Y_s = e^{0{\cdot}156T+2{\cdot}86}$
20†	$\log Y_s = 0{\cdot}858 \log L_A - 0{\cdot}582$	$Y_s = e^{0{\cdot}200T+2{\cdot}13}$
10*	$\log Y_s = 0{\cdot}811 \log L_A - 0{\cdot}462$	$Y_s = e^{0{\cdot}190T+2{\cdot}32}$
15*	$\log Y_s = 1{\cdot}039 \log L_A - 1{\cdot}158$	$Y_s = e^{0{\cdot}243T+1{\cdot}53}$
20*	$\log Y_s = 1{\cdot}185 \log L_A - 1{\cdot}650$	$Y_s = e^{0{\cdot}277T+0{\cdot}987}$
25*	$\log Y_s = 1{\cdot}141 \log L_A - 1{\cdot}613$	$Y_s = e^{0{\cdot}266T+0{\cdot}895}$

* Elongating phase. † Spikelet phase.

1963). However, until cell number begins to increase (stamen initials) there is a range of segment lengths on the apex (Fig. 2), with the longest at the proximal end (segment 10), and the shortest at the distal end (segment 25). Furthermore, as the inflorescences increase in length, and approach the stage of stamen initials, the regression lines converge, and it may be that the rates of increase in segment lengths, and the rates of primordium formation, are so related as to give an apparently constant *mean* interprimordial distance. It is also noteworthy that previously (Nicholls and May 1963) no allowance was made for the length of the apical dome above the youngest visible primordium (a diminishing error with increasing numbers of primordia on the inflorescence). Despite these uncertainties the mean interprimordial distance at the stage of stamen initials (apex length 1·625 mm) calculated previously is close to that calculated from mean segment length at the same stage of development (both close to 80 μ).

The individual cell lengths of several columns of cells in the pith region of segment 15 were measured from a series of microphotographs, representatives of which are presented in Plate 1, Figure 1. The results (Table 2) show that mean cell length is at a maximum at the end of the spikelet phase and immediately after stamen initials become visible. The changing distribution of cells within several

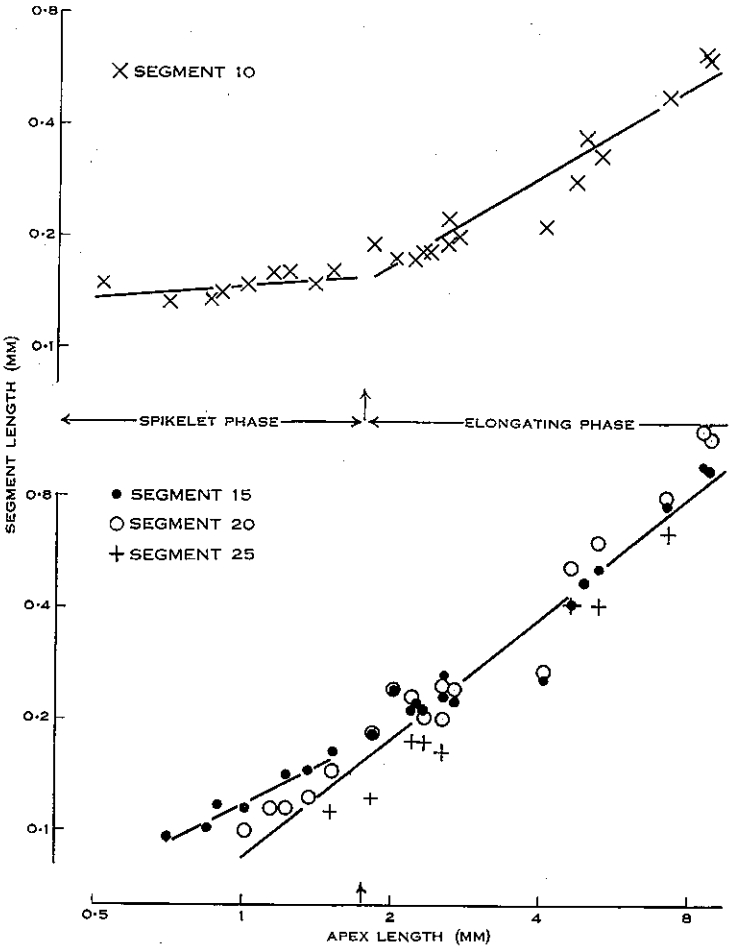

Fig. 2.—Changes in segment length (see text for definition) with apex length in four segments along the shoot axis. The change from the spikelet to the elongating phase of growth is marked by the appearance of stamen initials.

length classes is illustrated in Figure 3. In younger apices the distribution is unimodal but after stamen initials become visible (apex length 2·06 mm) the distribution becomes bimodal. The trimodal distribution observed in the apex of length 5·30 mm was found to be associated with a lower internode having twice as many cells as the upper; the lower cells were half the length of the upper ones. This observation is consistent with the notion that cells in the pith region of rapidly elongating

internodes undergo division synchronously. If cells are undergoing synchronous division then the frequency of observation of cells in the mitotic state would depend largely on the doubling times for cell number. These can be calculated as follows: the regression equations in Table 1 contain the term log L_A which, as noted above, can be expressed in terms of days from sowing (T); substitution and rearrangement give data in the exponential form from which the number of days (t) necessary to give a doubling in cell number (Y_c) is easily obtained. The calculated doubling times range from about 2·5 days (segment 25) to about 3·5 days (segment 10). Times of this duration would indicate that observations of mitosis would be rather rare if synchronous cell division was in fact occurring. No such observation was made in the 150 internodes examined in the elongating phase, whereas in the spikelet phase cells in various stages of mitosis were observed in the terminal meristem of almost all apices.

TABLE 2

MEAN CELL LENGTH OF PITH CELLS IN SEGMENT 15 FROM APICES OF VARYING AGE

Apex Age (days)	Apex Length (mm)	Mean Cell Length (μ)	Stage of Development
11	0·90	27·8	Advanced double ridge
13	1·24	27·4	Lateral spikelet visible
14	1·53	28·1	Lemma initial visible
15	2·06	37·6	Stamen initials visible
16	2·26	31·3	Stamen initials visible
19	4·65	29·6	Awns elongating
20	5·30	24·4	Awns elongating

In brief the situation appears to be that a bimodal distribution reflects the larger differentiating cells of the nodes, and the smaller dividing cells of the internodes. A trimodal distribution results from dividing cells of one internode only of a segment being fixed soon after a phase of cell division has been completed.

(*b*) *Gibberellin-like Substances*

Standard solutions of GA_3 were kept in a refrigerator for no longer than 2 weeks, during which time only single subsamples of the collection of apices could be assayed. Duplicate subsamples were assayed, therefore, against different standard solutions. The dosage response curves of the two standard solutions used in this work are shown in Figure 4. These curves are significantly different, and therefore the gibberellin-like activities in those subsamples assayed at the same time as a dosage response curve were calculated from the appropriate single curve rather than the mean. Nevertheless, this procedure gave good agreement between the activities of subsamples assayed on different occasions.

The specific activities of gibberellin-like substances detected in apices at three different stages of growth are recorded in Table 3. In both day-length treatments the specific activity was appreciably higher at the stage designated stamen

initials than at the double-ridge stage. Furthermore the specific activity was higher, at both stages, in a 24-hr light period than in an 8-hr light period. At the third stage of development (anther lobes appearing, awns elongating) activities lower

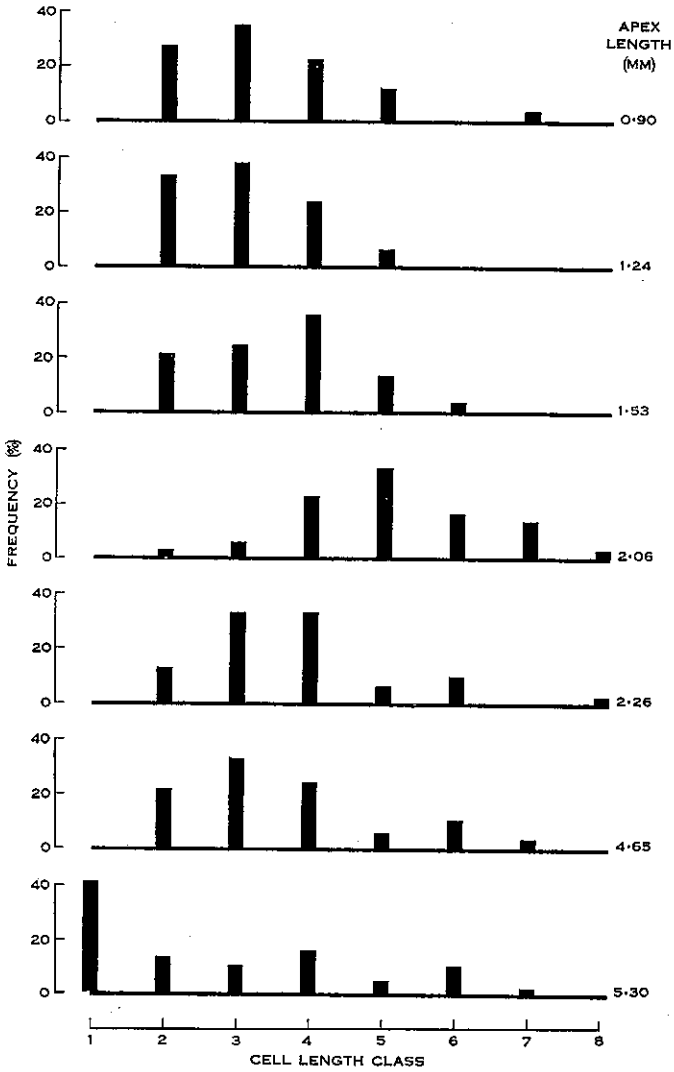

Fig. 3.—Frequency histograms showing the distribution of cell lengths (uncorrected for shrinkage) in pith cells of segment 15 taken from apices of increasing age. The cell lengths (μ) corresponding to the cell length classes 1–8 are, respectively, <16, 16–20, 21–25, 26–30, 31–35, 36–40, 41–45, >45.

than those observed at stamen initials were found in both treatments. However, at this stage the specific activity was higher in the 8-hr treatment. Over the first two stages these values conform with the general observation that higher concentrations of gibberellins are correlated with higher rates of increase of length but at

the third stage they do not. It should be remembered, though, that cell number (Fig. 1) and mean interprimordial distance (Table 3) are relatively constant between the double-ridge and stamen-initials stages whereas both increase markedly between stamen-initials and the elongating-internodes stages: clearly cell division is an important factor at this time.

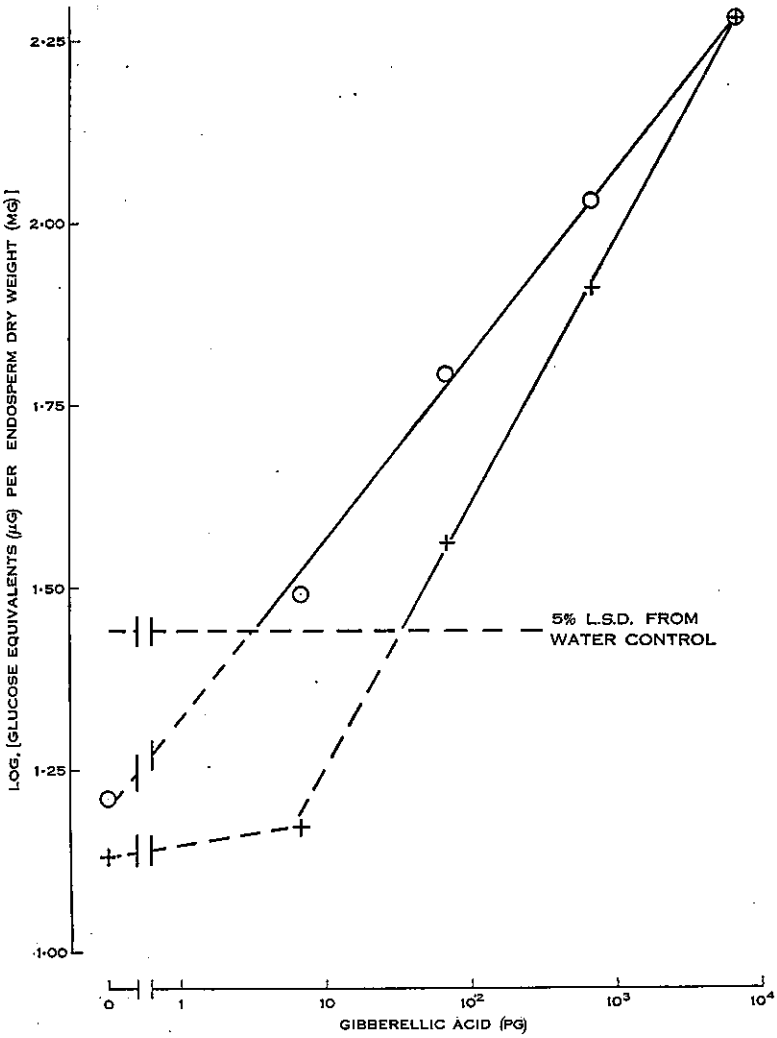

Fig. 4.—Dosage response curves for two standard gibberellic acid solutions in the barley endosperm bioassay.

In those apices where the highest activity of gibberellin-like substance occurred almost the final numbers of primordia were present. Also at this stage of apex development the lemma initial was prominent on many primordia and the dome on which stamen initials appear was greatly enlarged. Often stamen initials were

seen on more than one advanced primordium at this time and it seems likely from the work of Barnard (1955) that stamens may have been initiated in many primordia but that our techniques were inadequate to reveal them.

IV. Discussion

Previously we have measured the growth of the barley apex in terms of primordium number on the apex and also apex length (Nicholls and May 1963). Calculations based on these two measurements gave a constant value to mean interprimordial distance up to the stage of stamen initials, a result carrying with it the implication that a new primordium once formed did not enlarge at all in the

Table 3

GROWTH DATA AND DETERMINATIONS OF GIBBERELLIN-LIKE SUBSTANCES

Stage of Development	Days from Germination	Primordium Number	Apex Length (mm)	Inter-primordial Distance (μ)	Dry Weight per Apex (μg)	Gibberellic Acid Activity	
						Per Apex (pg)	Specific (μg/g dry wt.)
24-hr Light Period							
Double ridge	11	9·5	0·73	76	12·9	25	1·9
Stamen initials	15	19·1	1·63	85	43·6	2100	48
Elongating internodes	19	22·4	3·47	155	244·2	1·4	0·006
8-hr Light Period							
Double ridge	23	14·3	0·85	60	14·0	0·025	0·002
Stamen initials	46	32·7	2·07	63	66·3	170	2·6
Elongating internodes	78	34·1	4·81	142	1148	62	0·055

longitudinal direction of the shoot axis. However, the results presented here (e.g. Fig. 2) show unequivocally that some longitudinal increase does take place, at least within some primordia. Thus there are probably two components contributing to the elongation of the apex in the spikelet phase, namely a net increase in the number of primordia, the major component, and the elongation of these primordia, a minor component.

The finding (Table 3) of a higher concentration of gibberellin-like substances in the apex at the double-ridge stage in plants grown in 24-hr light periods compared with plants grown in 8-hr conditions is compatible with the known biological properties of gibberellic acid, namely increased cell enlargement in treated plants (Brian 1961) and increased growth rates of gramineous apices following gibberellic acid application (Ishikara 1958; Koller, Highkin, and Caso 1960; Purvis 1960; Barbat and Ochesanu 1963). On these grounds the suggestion is made tentatively

that at the double-ridge stage of development the supply of gibberellin-like substances limits growth of the apex.

The most likely modes of increase in cell number in the elongating phase are as follows:

(1) Random or synchronous division of most cells within an internode, the divisions occurring in both instances at approximately equal time intervals. Some cells may be lost from the meristematic group, namely those near the nodal plates which elongate and vacuolate (Poluknina 1960; see also Plate 1, Fig. 2).

(2) An increasing rate of cell division by a few cells as has been shown in cultured root tips by Brown (1959).

Of these possibilities the former, with synchronous cell division occurring, is favoured although it is admitted that the direct supporting evidence is not conclusive. From a similar system, namely the gibberellic acid-induced bolting of the *Samolus parviflorus* stem, evidence has been brought forward by Sachs, Bretz, and Lang (1959*b*) that synchronous cell division is initiated by the application of gibberellic acid. These authors also found that the induced increase in stem length is paralleled by an increase in cell number in the longitudinal direction with no significant increase in cell length, a finding which is consistent with the results reported here for barley (Figs. 1 and 2; Table 1).

The changes in behaviour and organization of cells just discussed are preceded by a higher concentration of extractable gibberellin-like substances and are, at an intermediate stage in their progress, associated with a lower concentration of these substances. This difference in concentration of gibberellin-like substances between apices harvested at the stamen-initials stage and those harvested later may reflect a difference in the rate of utilization, while the rate of supply is assumed to be unaltered in a given set of environmental conditions. This suggestion is supported by the observation that there is a greater decrease in 24-hr plants, where the growth rate is higher, than in 8-hr plants. The changes in concentration of and the requirements for other hormonal substances, as found elsewhere (Harada and Nitsch 1959; Wright 1961), may be involved in this situation.

Assays reported here were based on crude ethyl acetate extracts of barley apices. Taking into account subsequent work with refined techniques, and the now known sensitivity of the bioassay system to GA_1, GA_3, GA_4, GA_7 (Paleg *et al.* 1964) the gibberellin-like substances reported here are most likely to be GA_1 and GA_3. This conclusion draws support from recent work in which GA_3 was identified in the Gramineae (Jones, MacMillan, and Radley 1963).

V. Acknowledgments

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The work was carried out while one of us (P. B. N.) was holding a CSIRO Senior Post-Graduate Studentship.

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STUDIES ON THE GROWTH OF THE BARLEY APEX. II

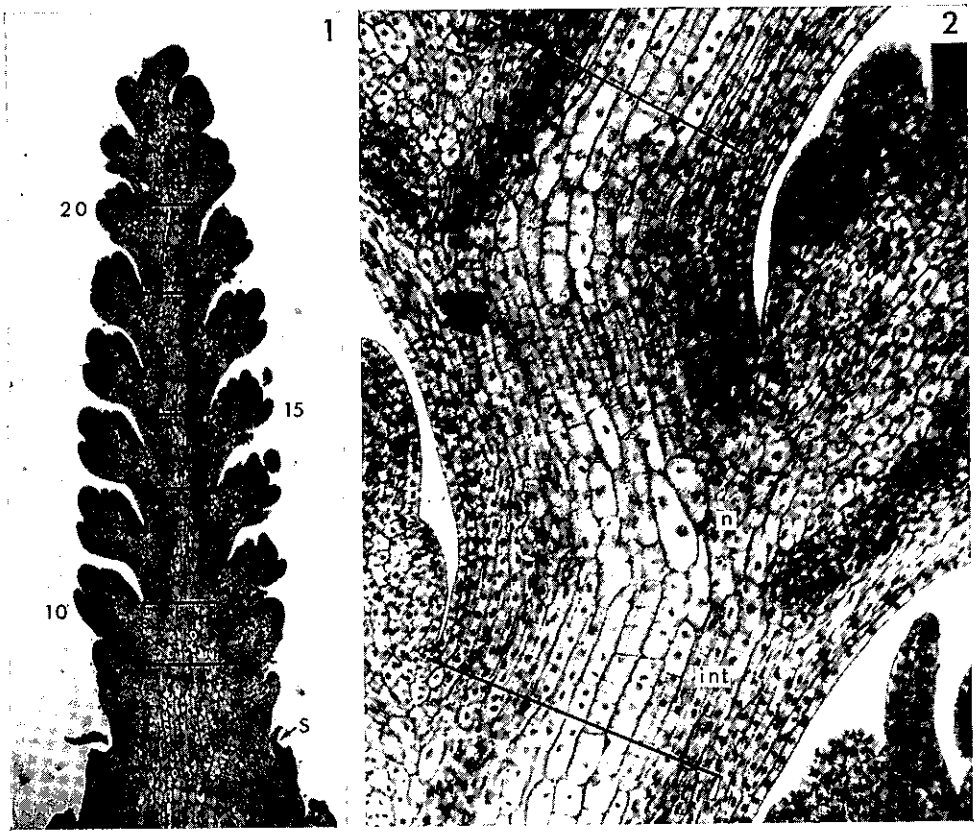

Fig. 1.—Longitudinal section through a 15-day apex (length 2·26 mm) indicating segments 10, 15, and 20 in relation to designated primordia (leaf scar 7 (*S*), primordia 10, 15, 20).

Fig. 2.—Longitudinal section through a 20-day apex in the region of segment 15 (demarcated by the two inked lines). Note the difference in size of the pith cells at the nodes (*n*) and at the internodes (*int*). × 165.)