STUDIES ON THE GROWTH OF THE BARLEY APEX

I. INTERRELATIONSHIPS BETWEEN PRIMORDIUM FORMATION, APEX LENGTH, AND SPIKELET DEVELOPMENT*

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[*Manuscript received March* 5, 1963]

Summary

A detailed study has been made of the morphology of the spring-barley apex from shortly after germination to shortly before heading. The effects of 8- and 24-hr light periods and three levels of soil-moisture tension were examined with reference to the total number of primordia initiated on the main stem, the length of the apex, and the rate of spikelet development.

For the environmental conditions explored it was found that the initiation of double ridges occurred when the apex was a particular length (0·45 mm), and that the initiation of internode elongation, the appearance of stamen initials on the most advanced spikelet, and the cessation of primordia formation occurred concurrently.

I. INTRODUCTION

The morphology of the gramineous shoot apex is already well documented (Bonnett 1937; Evans and Grover 1940; Sharman 1947; Bremer-Reinders 1958), and it is clear that the spike is a branched system bearing fertile and infertile branches. However, when relating work on barley to that on other members of the Gramineae the following differences should be taken into account. In barley, the main shoot axis does not differentiate into a terminal spikelet, and primary branches are terminated by an ovary. In wheat, the main shoot axis differentiates into a terminal spikelet, and it is the secondary branches, not the primary, that are terminated by ovaries. In rye, ryegrass, and oats the arrangement is similar to that in wheat.

The interrelationships between growth processes such as primordium formation, apex length, and spikelet development have been the subject of much study. At the appearance of spikelet initials the apex length in *Triticum* spp. is the same over a range of vernalization treatments (Cooper 1956) and a similar correlation over a range of light periods has been observed in spring wheat (Gott 1961). In contrast the apex length at the appearance of spikelet initials in *Lolium temulentum* L. decreases with increasing day length (Evans 1960). A second relationship has been observed by Evans (1960) in *L. temulentum* grown in different photoperiods,

* 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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namely between the apex length and the development of the spikelets, and a similar correlation can be deduced from data on Wintex barley reported by Borthwick, Hendricks, and Parker (1948). The proposal developed here that the onset of internode elongation is correlated with the cessation of primordium formation and that these changes coincide with a particular stage of spikelet development draws support from studies on *L. temulentum* and *T. vulgare* (Cooper 1951, 1956), Petkus rye (Gott, Gregory, and Purvis 1955; Purvis 1960), and Wintex barley (Borthwick, Hendricks, and Parker 1948). If these interrelationships hold under different conditions it follows that the number of spikelets formed on the apex will depend upon the rates of two processes—spikelet initiation and spikelet development. Determinations of the number of spikelet branches on a spike have revealed a constant number in *L. temulentum*, indicating that rates of primordium initiation and spikelet development are similarly affected by photoperiod (Evans 1960). In contrast there are wide variations in the number of spikelets formed in Petkus rye, e.g. in the spring variety the number of spikelets increases with decreasing day length, indicating that the two determining rates have responded differently (Gott, Gregory, and Purvis 1955).

Most drought studies on cereals have been made on the later stages of inflorescence development, a situation commented on by Gott (1961). Exceptions have been those investigations (Milthorpe 1950; Amer and Williams 1958) showing that immature tissues can tolerate higher intensities of dehydration than more mature tissues with a large proportion of vacuolated cells. Observations on plants other than cereals have indicated the kind of information that might be profitably collected about inflorescence development under water stress. Thus the translocation of materials from the stem to the younger leaves at the shoot apex of a tomato plant is considered to be interrupted by drought (Gates 1955*a*, 1955*b*; 1957). In addition, floral initiation, and development of initiated flowers, in apricots have been shown to be delayed by soil-moisture stress (Brown 1953).

Studies reported here have a bearing on these matters, especially the interrelationships between several parameters of growth and development, measurable on shoot apices, of spring barley grown in different light periods and soil-moisture regimes.

II. Materials and Methods

Two varieties of barley (*Hordeum vulgare* L.) were used, namely Prior "A" and C.I. 5611, although only results with one, Prior "A", are reported in detail. Seeds were sown in a loam–sand mixture in 4-in. polythene pots and plants were grown in a controlled-environment cabinet.

The root medium was prepared by mixing four parts of Urrbrae loam with one of sand. Steam sterilization was carried out and then batches of 80 kg dry weight (sufficient for 100 pots) of soil were mixed as required with mineral nutrient supplement and brought to about 14% moisture content. The final moistening to field capacity was done after the wet soil had been added to pots and its moisture content accurately determined. When moisture-stress experiments were conducted the soil in each pot was covered with aluminium foil to minimize evaporational loss.

The cabinet used had space on its shelf for 100 pots arranged in 10 rows. Pots within rows (blocks) were re-randomized, and the position of each row was changed on a cyclic pattern every second day so as to reduce positional variance arising from known gradients of light intensity and temperature across the rows. The soil-moisture stress treatments were: W_0, no stress; W_1, stress increasing up to 5 atm, thereafter no stress; W_2, stress increasing up to 15 atm, thereafter no stress. At first, watering coincided with re-randomization of pots but as plants grew water was added daily.

The light source for the cabinet comprised 34 "Cool-White" fluorescent tubes (Philips TLF 80/33) separated from the body of the cabinet by a sheet of glass. The light intensity was 2500 f.c. (140 cal/cm^2/24 hr) in the centre of the shelf falling to 2000 f.c. (105 cal/cm^2/24 hr) at the corners, measured at the leaf surface. Supplementation with incandescent light was achieved by replacing four pairs of fluorescent tubes with four incandescent strip lamps (B.G.E. 150 W). In this arrangement the light intensity at the surface was composed of 2450 f.c. (135 cal/cm^2/24 hr) fluorescent light plus 120 f.c. (163 cal/cm^2/24 hr) incandescent light.

Temperature was maintained at $17\pm1\cdot5$°C, with a gradient of $1\cdot5$°C between air inlet (through one side of the cabinet) and air outlet (through the other). Relative humidity was maintained at 85 ± 5%.

A scoring technique was employed to assess the stage of development of the inflorescence. In the vegetative state the assessment was based on the shape of the apical dome; in the reproductive state it was based on the stage of development of the most advanced spikelet primordium. Scores allotted to the respective stages were as follows:

1·0, early vegetative (dome short);
2·0, late vegetative (dome elongating);
3·0, double ridges (spikelet primordium visible);
4·0, triple mound (lateral spikelet primordia);
5·0, glume initials;
6·0, lemma initials;
7·0, stamen initials;
8·0, awn initials;
9·0, late floral.

The term "primordium formation" is used here to refer to the formation of all lateral appendages on the main axis, and "primordium number" to refer to the total number of lateral appendages whether mature or just initiated. Apex lengths were measured from the tip of the main axis to the base of that primordium immediately above the uppermost recognizable leaf (Nicholls 1962). In the early vegetative stage this measure lacks precision because the dome's size is related to plastochrone phase at the time of measurement and because the oldest simple ridge primordium does not develop into a recognizable leaf immediately the next simple ridge primordium appears.

For convenience the development of the apex is referred to one of three phases: vegetative, spikelet, and elongating. The vegetative phase is bounded by germination at one end and the appearance of double ridges at the other; the spikelet phase by the appearance of double ridges and the appearance of stamen initials; the elongating phase by the appearance of stamen initials and the cessation of peduncle elongation.

III. Results

The growth of the barley apex is reported here in terms of three processes: primordium formation, increase in apex length, and development of the inflorescence.

(*a*) *Primordium Formation*

In one experiment of the series fluorescent light alone was used; in another incandescent light was added to the fluorescent. In both experiments lighting was continuous. From the data in Figure 1(*a*) it can be shown that the rate of

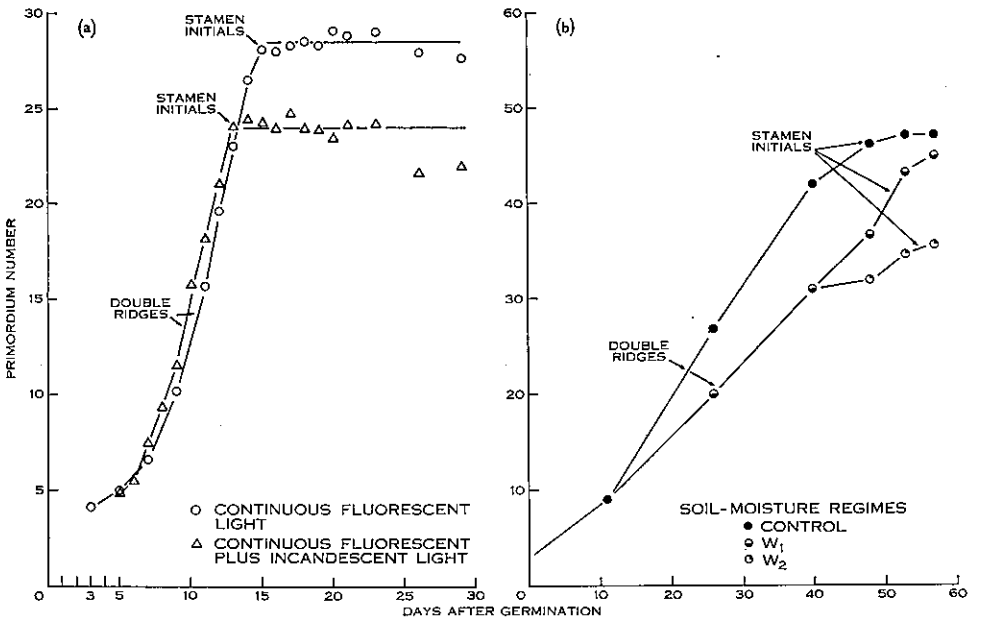

Fig. 1.—(*a*) Changes in primordium number on main axis under continuous fluorescent light and continuous fluorescent plus incandescent light regimes. The first appearances of double ridges and stamen initials are indicated. (*b*) Changes in primordium number for 8-hr fluorescent light periods and under different soil-moisture regimes. First appearances of double ridges and stamen initials are shown. Stress ceased for treatment W_1 on day 40 and for treatment W_2 on day 48.

primordium formation was slow at first in both instances but that early there was a marked increase in rate from about 0·5 to 3·5 primordia per day. Primordium formation stopped abruptly in both conditions.

When fluorescent lighting was supplied for day lengths of 8 hr, however, rate of primordium production was much slower as can be derived from the slopes of curves in Figures 1(*b*) and 1(*a*). The maximum rate in 8-hr day lengths was 1·15 primordia per day. The numbers of primordia produced when different soil-moisture regimes were applied are also shown in Figure 1(*b*), and the most evident effect was a reduced rate while soil-moisture stress existed. When water stress was relieved in the W_1 treatment, primordium formation continued until approximately the same number of primordia had been formed as in the controls although in the W_2 treatment the final number was most probably less.

(b) Increase in Apex Length

The apex length when plants were grown under continuous fluorescent light is plotted against time in Figure 2*A*. Although the linear regression coefficient

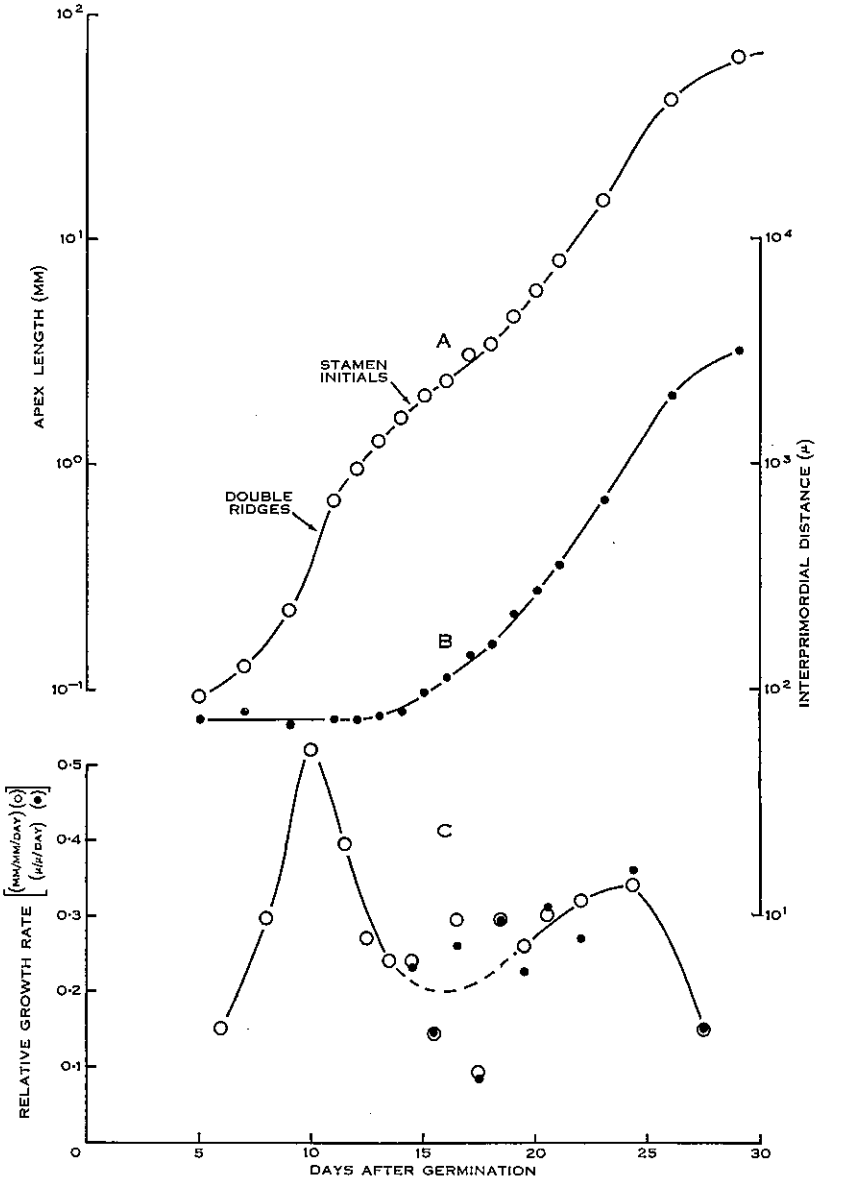

Fig. 2.—Some primary and derived estimates of growth of the main stem of barley growing under continuous fluorescent light and with ample water supply. The first appearances of double ridges and stamen initials are shown. *A*, changes in apex length with time (○); *B*, changes in mean interprimordial distance, calculated from apex length and primordium number, with time (●); *C*, increase in apex length/unit length/unit time (○) and increase in interprimordial distance/unit distance/unit time (●), i.e. the relative growth rate curves corresponding to *A* and *B* respectively.

is significant, further analysis indicates a significant scatter of means about a straight line and it is possible that the plot arises from the summation of two overlapping sigmoid curves. The latter concept draws support from an examination of the plot of increase in apex length per unit length which shows two peaks (Fig. 2 *C*). Furthermore when interprimordial distances are plotted against time two phases are apparent (Fig. 2*B*). In the first the mean interprimordial distance is approximately constant and hence the increase in apex length during this time is due mainly to the addition of new primordia. In the second interprimordial distance increases and, moreover, since the increase in interprimordial distance per unit distance follows

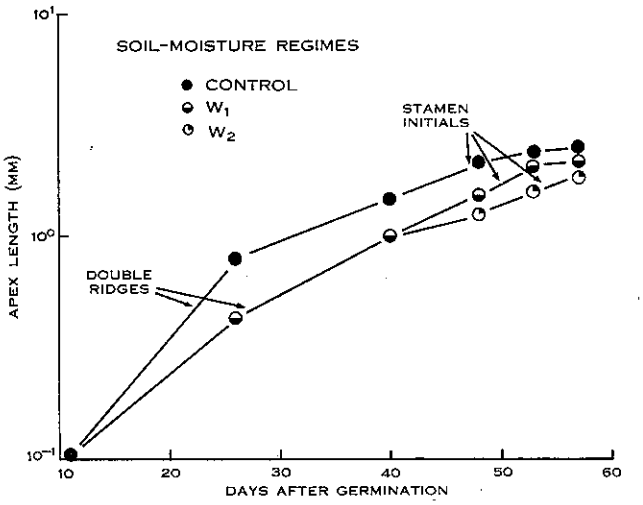

Fig. 3.—Changes in apex length in 8-hr fluorescent light periods and under different soil-moisture regimes. The first appearance of double ridges and stamen initials are shown. Stress ceased for treatment W_1 on day 40 and for treatment W_2 on day 48.

closely the increase in apex length per unit length (Fig. 2*C*), it seems likely that the increase in apex length during this time is due mainly to the increasing interprimordial distance. It is to be noted that stamen initials first appear at the point of transition from the first to the second phase of interprimordial distances.

If fewer measurements of apex length are made over a shorter period of development these complex interrelationships may not be observed. This is the situation with results from plants grown in fluorescent light of 8-hourly periods (Fig. 3). Nonetheless these curves do serve to illustrate the points that with shorter light periods the rate of increase in apex length is decreased (cf. Fig. 2*A*) and that during soil-moisture stress the rates are further reduced.

It appears from these results and those of the preceding section that both the rate of primordium formation and the rate of increase in apex length are, up to the appearance of stamen initials, similarly affected by reduced light periods and

by water stress. The dependence of apex length (y) on the number of primordia on the apex (x = primordium number less leaf number) was therefore explored. Soil-moisture stress was without effect on the relationship although light regimes did alter it as the following linear regressions show:

$$\text{24-hr light period:} \quad y = 0{\cdot}076x - 0{\cdot}043;$$
$$\text{8-hr light period:} \quad y = 0{\cdot}060x + 0{\cdot}012.$$

The difference in slope of these two lines is significant and it follows that inter-primordial distance (slope) is influenced by the length of the light period but not by the soil-moisture regimes applied in these experiments.

TABLE 1

INFLORESCENCE STATUS

Harvest Time (days)	Stage of Inflorescence Development* with Soil-moisture Regime W_0		Harvest Time (days)	Stage of Inflorescence Development*		
				Fluorescent Light for 8 Hr and with Soil-moisture Regimes:		
	Continuous Fluorescent Light	Continuous Fluorescent plus Incandescent Light		W_0	W_1	W_2
8	—†	1·7	11	1·0	1·0	1·0
9	2·0	2·2	26	3·0	2·7	3·0
10	—†	3·0	40	5·3	3·0	3·0
11	3·0	3·4	48	7·7	6·0	4·0
12	3·7	5·2	53	8·0	7·0	6·0
13	5·2	6·5	57	8·0	8·0	7·0
14	6·2	7·1				
15	7·0	7·9				
16	7·5	—†				
19	>8·0	—†				

* See Section II for details of light and soil-moisture regimes, and for stages of inflorescence development to which the scores listed correspond.

† Not assessed.

(c) *Development of the Inflorescence*

The stages of inflorescence development are recorded in Table 1 for selected treatments at several harvest occasions. An examination of this table reveals that the environmental factors have affected the rate of inflorescence development in a similar direction to that already noted for rate of primordium formation and for rate of increase of apex length. Hence it is pertinent to examine closely interrelationships between specific stages of inflorescence development, apex length, and primordia formation.

The important morphological marker points on the inflorescence scoring scale are 3·0 and 7·0, indicating double ridge formation and the appearance of stamen initials respectively. Using the data of Table 1 and other similar results these two

marker points can be positioned with respect to apex length (see Fig. 2*A* and Fig. 3) and primordia number (see Figs. 1(*a*) and 1(*b*)). Double ridges were observed only on apices whose lengths were 0·45 mm or more, irrespective of day length and soil-moisture regime. The appearance of stamen initials coincided with the cessation of primordium formation whatever the environmental history of the plants.

In addition to measuring inflorescence development on the basis of the most advanced spikelet primordium, observations were also made on the rate of development of all spikelets on an inflorescence. These are expressed as days^{-1} between

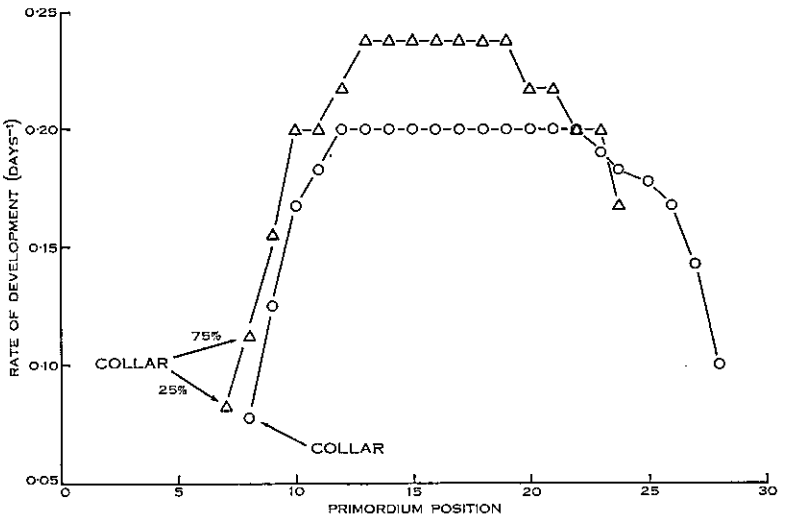

Fig. 4.—Rate of development of all spikelets, measured as days^{-1} between the first appearance of the spikelet as a simple ridge and the appearance of stamen initials on that organ, produced on inflorescences of barley under continuous fluorescent light (○) and continuous fluorescent plus incandescent light (△). The positions of the collar nodes were as shown.

the appearance of a floral organ as a simple ridge and the appearance of stamen initials on that same organ. Data from plants grown in continuous light (either fluorescent or fluorescent plus incandescent) are recorded in Figure 4. Under both light regimes the rate of development of spikelets becomes progressively slower towards both the apical and basal ends of the inflorescence, the collar spikelet being the slowest. The higher rates for spikelets developing in fluorescent plus incandescent light is also an observation of interest.

IV. Discussion

In those day-length and soil-moisture regimes studied, double ridges were first visible when the apex length reached 0·45 mm. Thus apex length *v.* time curves, which reflect the difference between rates of primordium formation and the rates of development of simple ridges into recognizable leaves, are probably good measures of the progress of apices towards double ridges. The imposition of soil-moisture

stress consistently reduced the slope of the apex length *v.* time curves and the difference between stressed and unstressed plants became significant at pF values as low as 3·0. Decreasing the light period from 24 to 8 hr also decreased the slope. Thus moisture stress and decreasing light periods both reduced primordia formation more than they reduced the rate of progression from a simple ridge to a recognizable leaf. Although these two environmental factors produce the same end result, there is no *a priori* reason to suppose, however, that their mechanisms of operation are the same.

TABLE 2

FINAL APPORTIONMENT OF PRIMORDIA BETWEEN LEAVES AND SPIKELETS OF BARLEY SUBJECTED TO VARIOUS LIGHT AND SOIL-MOISTURE REGIMES

Light Regime*	Soil-moisture Regime*	Primordium No.	Leaf No.	Spikelet No.
24 hr, fluorescent	W_0	28·5	7·1	21·4
	W_1	25·5	6·9	18·6
16 hr, fluorescent	W_0	34·5	7·3	27·2
	W_1	31·5	8·3	23·2
8 hr, fluorescent	W_0	47·3	15·2	32·1
	W_1	45·0	14·8	30·2
24 hr, fluorescent	W_0	28·5	7·0	21·5
24 hr, fluorescent plus incandescent	W_0	24·0	6·8	17·2

* For details see Section II.

Again, in these environmental conditions the appearance of the first stamen initials coincided with the cessation of primordium formation. It follows that the number of spikelets per inflorescence may indicate the influence of environmental factors on the rate of primordium formation relative to the rate of spikelet development between the double-ridge stage and the stamen-initials stage. Observed values for spikelets per inflorescence are recorded in Table 2. From these it may be concluded that decreasing the light period (more spikelets) improves the ratio of the rate of primordium formation relative to the rate of spikelet development, whereas the imposition of water stress (fewer spikelets) decreases the ratio of primordium formation relative to spikelet development. Thus moisture stress and decreasing light periods both reduce rates of primordium formation and of development of these primordia but it is the relative effects on these rates that determine how many leaves and how many spikelets there will be.

Although increases in dry weight (Gates 1955*a*, 1955*b*) and in stem length (Slatyer 1957) of tomato plants continue at relatively high levels of soil-moisture tension, Stocker (1960) has reviewed results of several workers showing, as is demonstrated here, a reduction in the rate of growth processes at slight soil-moisture deficits. But little information is available on the influence of soil-moisture

tensions on morphological patterns and it seems appropriate to mention two such observations. Two abnormalities were occasionally observed on the apex either separately or together. The first was a failure in the formation of a primordium on an apex at the double-ridge stage of development and hence the subsequent absence of a spikelet, and later, a grain at that position. The second was the rotation about the longitudinal axis of the plane of insertion of the simple ridges produced after watering up; and hence at maturity the ear showed a discontinuity in its plane of symmetry at that point. Possibly the stage of the plastochrone when soil-moisture tensions became critical determined whether both, one, or neither of the abnormalities occurred. Similar perturbations can be induced by surgical means (Snow 1951).

It has been demonstrated that the rate of development of spikelets becomes slower toward the basal end of the spike. When a double ridge first appears there appears to be at least two simple ridges between it and the youngest recognizable leaf. Further detailed examination of these "in between" ridges will be necessary before speculation about factors influencing their development can be rewarding.

The separation of morphological development of the barley plant into two phases, vegetative and reproductive, on the basis of the appearance of double ridges is commonly accepted. However, Bonnett (1935) claimed that the two phases were also characterized by non-expanding and expanding stem internodes respectively. In the present study stem-internode elongation was not observed until the appearance of stamen initials (see also Borthwick, Hendricks, and Parker 1948). More detailed anatomical studies to be reported in a subsequent paper will cast some light on this situation; in brief, it appears that a little cell extension occurs in the pith of the inflorescence prior to the formation of stamen initials although cell division does not begin before this stage.

Similar water-stress experiments to those detailed here were conducted under 16- and 24-hr light periods and continuous fluorescent light experiments were, in the main, repeated using fluorescent plus incandescent lighting. The series was also repeated using another barley variety (C.I. 5611). Although C.I. 5611 developed at slower rates, and displayed slightly modified responses to soil-moisture tensions, the main findings presented here were amply confirmed (Nicholls 1962). In particular those morphological correlations emphasized in this paper were always observed, thus giving added weight to the suggestion that a study of metabolic changes in those organs concerned at critical stages could well lead to a deeper understanding of the growth of the barley apex.

V. Acknowledgments

The Prior seed used was from a single plant selection bulked by Dr. D. Aspinall of the Plant Physiology Department, and the original Prior seed, as well as the variety C.I. 5611, was supplied by Dr. K. W. Finlay of the Agronomy Department. This work was carried out while one of us (P.B.N.) was holding a C.S.I.R.O. Senior Post-Graduate Studentship.

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