PHYSIOLOGY OF GROWTH IN THE WHEAT PLANT

IV.* EFFECTS OF DAY LENGTH AND LIGHT-ENERGY LEVEL

By R. F. WILLIAMS† and C. N. WILLIAMS†‡

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Summary

This study describes the effects of short- and long-day treatments at two light-energy levels on the growth of a spring wheat.

Classical growth analysis revealed a complex interacting pattern with time. Treatment effects on the relative growth rate were dominated by those on net assimilation rate, which was increased both by high light energy and long days.

The growth of successive leaf primordia and of the inflorescence of the primary shoot is described. The pattern was greatly changed by day length, there being 13 foliage leaves in short days and 7 or 8 in long days.

The early growth of each leaf primordium was exponential, the exponent decreasing with leaf number. The duration of this phase increased from about a week in leaf 3 to 5 weeks in leaf 13. The relative growth rates of the primordia then rose to maxima whose values were approximately twice those for the exponential phase. The maxima occurred two or three days before leaf emergence, and the rates then fell to zero.

The patterns of growth were very similar for the two long-day treatments, but, for the low-energy, short-day treatment, all growth processes tended to be slower than in the parallel high-energy treatment.

The double-ridge stage of floral induction was advanced about 3 weeks by the long-day treatments, but occurred at the same apex volume. However, long-day apices were squat and pyramidal, whereas short-day apices were long and had many more foliar members at induction.

Inflorescence growth tended to be exponential and rapid with long days, but slow and falling away from exponentiality with short days. Initial relative growth rates of the inflorescence were similar to those of their presumptive flag leaves.

I. INTRODUCTION

Previous papers of this series have been concerned with quantitative aspects of the growth of a spring wheat in a controlled environment. Williams (1960) described the early growth of the primary shoot and, in particular, established the pattern of growth of successive leaf primordia on its apex. Williams and Rijven (1965) extended this description to the changes in DNA, RNA, proteins, and cell

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† Division of Plant Industry, CSIRO, P.O. Box 109, Canberra City, A.C.T. 2601.

‡ Present address: Faculty of Agriculture, University of Malaya, Kuala Lumpur.

wall materials of the fourth leaf from an early stage to full maturity. More recently, Williams (1966*a*) has described later phases of the growth of the primary shoot and of its inflorescence.

The technique of serial reconstruction, first described by His (1888) has played a prominent part in this programme, and promises to be very useful for the descriptive analysis of the effects of treatment on plant growth. Our understanding of the growth processes may be furthered by studying ways in which the general pattern of growth can be modified by factors of the external environment, or by experimental manipulation of appropriate test plants. Consequently, in planning the experiments to be described, treatments were selected for their known major effects on morphogenesis rather than for their intrinsic interest. The change of the shoot apex from the vegetative to the reproductive state is clearly a major one, and in spring wheat it is greatly accelerated by long days. Day lengths of 8 and 24 hr were therefore selected for comparative study. The quantity of light energy received has morphogenetic effects on leaf growth, tiller numbers, and upon root–shoot ratios, so this factor was varied by contrasting 4 with 8 hr per day of natural light. This was done for each of the day-length treatments. Two temperature treatments were imposed on the short-day treatments in one experiment. However, the selected temperatures (20/15°C *v.* 25/20°C) had much less effect than anticipated, and the higher temperature was excluded from the second experiment.

II. Experimental Procedure

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

Two experiments were conducted in successive years, their sowing dates being February 9, 1961, and February 1, 1962. In each, a spring wheat (*Triticum aestivum* L. cv. Nabawa) was grown in a series of controlled environments, but with natural light during the "day" periods. The duration of sampling period varied somewhat with treatment, but, in general, covered the first 30 days of growth in 1961 and the second 30 days of growth in 1962.

Grains within definite weight ranges (50–55 mg in 1961, and 55–60 mg in 1962) were set to soak on the sowing dates (day 0) and those with the coleoptile and seminal roots just showing were set out in moist perlite in 4-in. pots on day 1. The basic replication throughout for each harvest class was four replicates of six plants. Hoagland No. 2 nutrient solution, but with the ammonium dihydrogen phosphate at half the usual strength, was used daily throughout the experiments to water the pots, and these were also periodically flushed with tap water.

For the 1961 experiment, dry weight samples were taken for the whole grain as soaked on day 0, for the embryo and rest of grain on day 1, and for leaf 1, rest of shoot, roots, and rest of grain on day 4. Thereafter, harvests were made when the successive leaves of the primary shoot had emerged on more than half of the plants of a given treatment. Thus for treatment 8S (see Fig. 6) harvests were taken on days 4, 10, 14, 19, 25, and 30, when leaves 1–6 respectively of the primary shoot had emerged. The occasions for which specific organs were measured for volume or weight will be apparent from the tables and figures.

The first harvests of the 1962 experiment were taken when the sixth leaf of the primary shoot had appeared on more than half of the plants of each treatment. These harvests were thus comparable with the final harvests of the 1961 experiment. There is reasonable agreement between the experiments with respect to many attributes of growth. However, certain discrepancies appear which will be discussed in the results section. Subsequent harvests of the 1962 experiment were based on the times of emergence of leaves 7–10, or at comparable time intervals for those treatments (long-day) which produced fewer than 10 leaves on the primary shoot. Inflorescence dry weights were determined only for the long-day treatments.

In both experiments, the leaves were dissected at the ligule, and the "stem" fraction included the scutellum and the leaf sheaths. All dissected parts were dried at 80°C in an oven with forced draught.

For the 1961 experiment, leaf area was determined by making positive prints on auto-positive contact paper, but from direct measurements in 1962. Areas (A) of individual leaves were based on the regression:

$$A = 0{\cdot}91L \,.\, \tfrac{1}{2}\,(x_{0.25} + x_{0.75}),$$

where L was the length, and $x_{0.25}$ and $x_{0.75}$ the widths one-quarter and three-quarters of the way along the leaf blade. When it was not possible to measure all of the leaves, a subsample only was measured, and the rest estimated from the area–weight ratio.

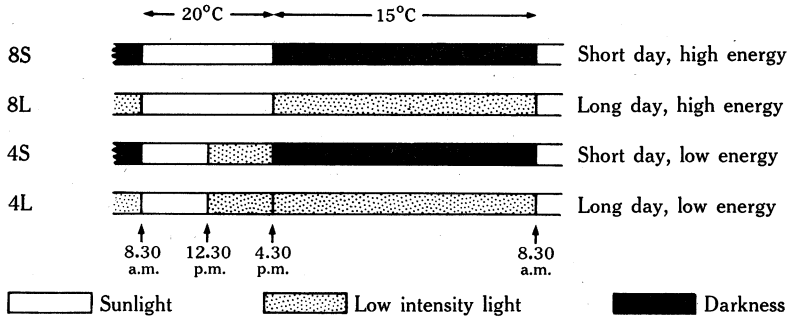
For later stages of growth, particularly in the 1962 experiment and in the long-day treatments, the leaf sheaths and stems made increasing contributions to the photosynthetic area. These contributions were estimated from products of length and average diameter of these approximately cylindrical organs.

(*b*) *Volume Integration*

That part of the apex of the primary shoot which was inside the emerging leaf at harvest was dissected out and fixed in formalin–acetic acid–alcohol. The 24 axes of each harvest class were later graded by length for the outermost leaf primordium or for the inflorescence where there were no leaves. The nine largest and the nine smallest axes were discarded, and only the six "median" axes were embedded for sectioning. These median axes were very uniform and, in general, only one was eventually used for the estimation of volumes. The volume integration procedures are fully described by Williams (1960), and his regression equation (*loc. cit.* p. 405) was used for the larger primordia. The tannic acid staining schedule of Sharman (1943) was used throughout. This is superior to the iron alum haemotoxylin and erythrosin procedure used earlier, because it stains the cell walls, even of meristematic tissues.

(*c*) *Treatments*

The four treatments which were imposed for both experiments constitute a simple 2×2 factorial design in which two light-energy levels are compared for both short- and long-day plants. The accompanying diagram defines the treatments, and it will be noted that the high- and low-energy treatments were obtained by exposing the plants to 8 and 4 hr of sunlight respectively.



Short-day plants received 8 hr of light, and the long-day plants received continuous light. The low-intensity lighting was from incandescent lights giving 25–30 f.c. at plant level. The 1961 experiment had two additional short-day treatments in which the temperature regime was 25/20°C (i.e. 25°C for the 8 hr "day" period, and 20°C for the night period). In all other treatments the temperature regime was 20/15°C.

III. Results

(a) *Basic Growth Data for the Whole Plant and Its Parts*

With the exception of the total leaf area data of Table 4, the primary data of the two experiments are presented in graphical form. This permits treatment comparisons to be made chronologically as well as for comparable growth stages (e.g. the time of appearance of a specified leaf of the primary shoot). Figures 2, 3, 4, 11, 13, and 15 use logarithmic scales because these are appropriate to growth data covering such extensive ranges in size. Most of these figures also use the conventional method of indicating minimum significant differences ($P = 0{\cdot}05$ and $0{\cdot}01$), but it should be noted that these apply, strictly, only to comparisons within treatments. They underestimate the differences for treatment comparisons to an unknown extent, because true replication is not possible when environments are simulated in single cabinets. However, treatment effects tend to be so large relative to these differences that there is no doubt that they are meaningful.

Table 1

VISIBLE LIGHT ENERGY FOR THE LEAF-APPEARANCE INTERVALS OF THE FOUR MAIN TREATMENTS FOR THE 1961 EXPERIMENT

The visible light energy was taken as 45% of the total energy of sunlight recorded plus 7% of that supplied by the supplementary incandescent lighting

Treatment	Light Energy ($cal.cm^{-2}day^{-1}$) for Leaf-appearance Interval			
	2–3	3–4	4–5	5–6
8S	190	171	138	205
8L	205	174	141	208
4S	78	76	115	107
4L	88	72	117	116

Close inspection of the figures, and especially of Figures 6 and 11, suggests that the two experiments conducted in successive years, and having a common harvest based on the appearance of leaf 6, link up remarkably well. Except in Figures 11–14, however, the time scales have not been directly linked. Such discrepancies as occur seem to be referable mainly to differences in natural light intensity experienced in the two years. However, their presence points to the need to stress the fact that, although temperature was fairly rigorously controlled, light fluctuated with the degree of cloud cover from day to day. Since the leaf appearance intervals were sometimes quite short — from 4 to 8 days — it is not surprising that the visible light-energy data of Table 1 are rather variable. Unfortunately, no total energy records were kept for early 1962, but some indication of a difference in the light regime for the two years is given in the bright sunshine data of Tables 2 and 3. These records are for whole days, and are not limited to the experimental periods of sunlight (8.30 a.m. to 4.30 p.m.). For this reason there is no point in attempting

to arrive at sunshine values for treatments 4S and 4L. The outstanding fact to be noted is that, for leaf-appearance interval 2–6 there was considerably less bright sunshine per day in 1961 than in 1962.

TABLE 2

HOURS OF BRIGHT SUNSHINE (CAMPBELL-STOKES) PER DAY FOR THE LEAF-APPEARANCE INTERVALS OF TWO TREATMENTS OF THE 1961 EXPERIMENT

Treatment	Sunshine (hr/day) for Leaf-appearance Interval				
	2–3	3–4	4–5	5–6	Mean (2–6)
8S	8·3	5·8	5·1	9·7	7·1
8L	7·8	5·8	5·1	9·7	7·0

TABLE 3

HOURS OF BRIGHT SUNSHINE (CAMPBELL-STOKES) PER DAY FOR THE PRE-HARVEST PERIOD, AND FOR THE LEAF-APPEARANCE INTERVALS OF TWO TREATMENTS OF THE 1962 EXPERIMENT

Treatment	Sunshine (hr/day) for Leaf-appearance Interval					
	Mean (2–6)	6–7	7–8	8–9	9–10	Mean (6–10)
8S	8·9	9·4	7·1	8·0	8·7	8·3
8L	8·9	9·6	6·9	7·8	8·7	8·2

Figure 1 shows that tillers did not begin to appear until the third week of growth. Tiller numbers increased quite slowly in the low light-energy treatments, but rapidly with high energy. The numbers were depressed by long days, and there was a spectacular increase with the short-day, high-energy treatment (8S).

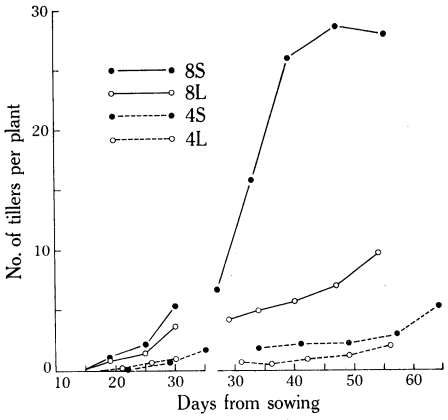


Fig. 1.—Numbers of visible tillers per plant as determined by light-energy level and day length. For a full description of the treatments see Section II(*c*).

The dry weight data of Figures 2 and 4(*a*) are for the whole plant, including roots, but excluding the rest of the grain. They exhibit high initial rates of increase while the seedling is dependent on seed reserves, but there is a rapid transition to

lower steady rates based on photosynthesis alone (cf. Williams 1960). The rates decline further after about day 30, but the experiments did not continue long enough to judge if they would settle down to another steady rate such as that suggested for field-grown wheat by Williams (1964, fig. 6·3).

The high-energy treatment had much the greater effect on the weight of the whole plant; this was eight times that for the low-energy treatment after about 50 days. Length of day had no effect at this stage, though long days consistently increased plant weight during the first 4 weeks (the 1961 experiment). Figure 3 shows this effect of long days to extend to the 1962 experiment when the weight of the primary shoot alone is considered. The only serious discrepancy between the dry weight data of the two experiments is that for the long-day, low-energy treatment.

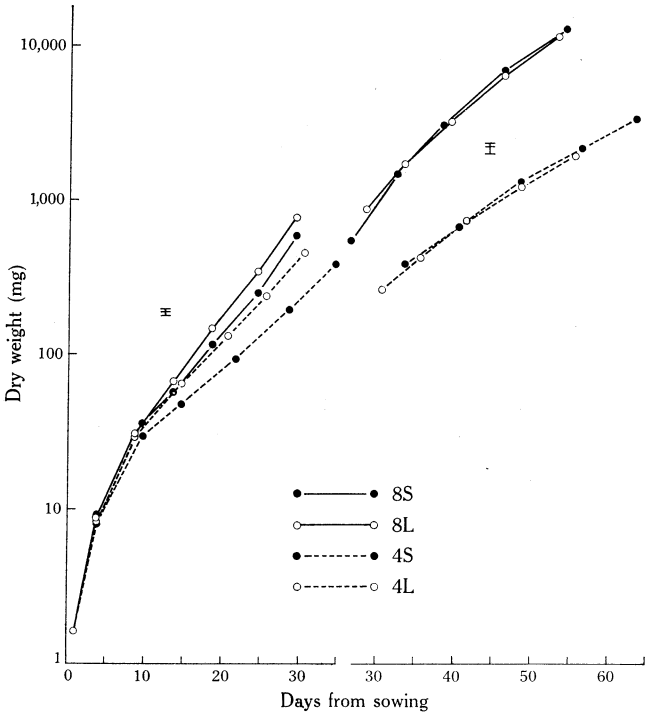


Fig. 2.—Dry weight per plant as determined by light-energy level and day length.

There was an early effect of the higher-temperature treatment (Fig. 4), based on accelerated growth during the period of dependence on seed reserves. Thereafter the dry weight curves were parallel.

Dry weight data for leaves, stems, and roots are given separately on an absolute scale in Figure 5. They show remarkably different patterns of response to day length and light-energy level. Thus there were large increases in stem weight with long days, but negligible effects of energy level. Long days also had a large effect on leaf weight, though there were also consistent increases with the high-energy

treatment. Root weight, on the other hand, was greatly increased by the high-energy level, but much less affected by day length. When attempting to interpret these

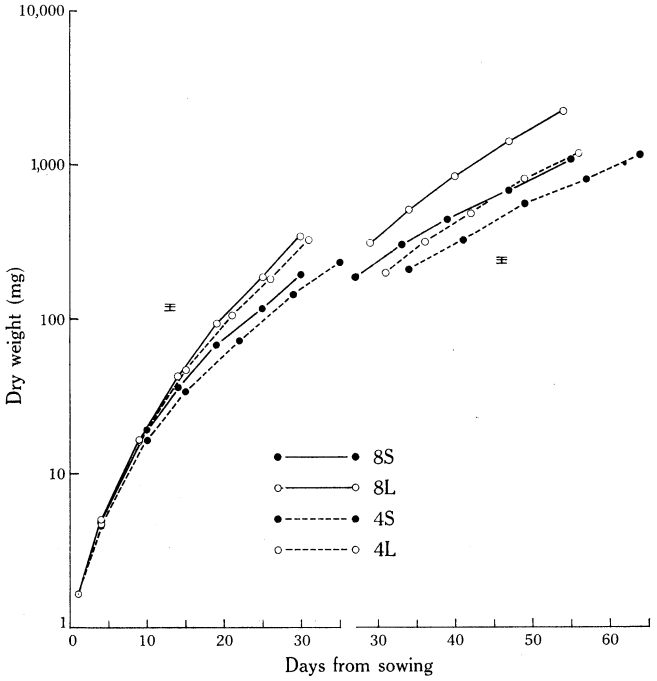


Fig. 3.—Dry weight of the primary shoot as determined by light - energy level and day length.

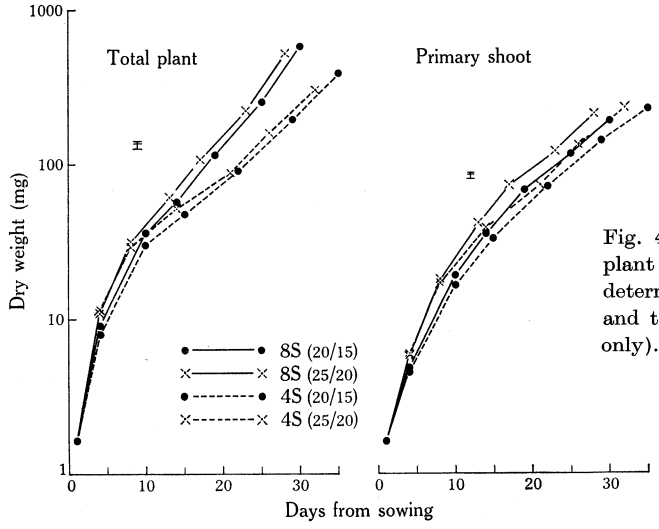


Fig. 4.—Dry weight of the whole plant and of the primary shoot as determined by light-energy level and temperature (1961 experiment only).

responses it is necessary to remember that the "stem" fraction includes the leaf sheaths, and is dominated by them during early vegetative growth, especially in short days when the true stem remains small. It is now well established that roots

tend to suffer most when treatment results in a shortage of carbohydrates. This is well shown in the short-day, low-energy treatment whose roots virtually ceased growing for a period following the exhaustion of seed reserves.

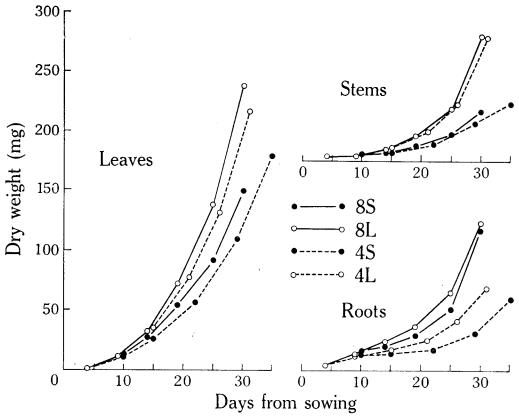


Fig. 5.—Dry weights of the leaves, stems, and roots as determined by light-energy level and day length (1961 experiment only).

The ratios of the weights of the principal plant parts to the total plant weight are plotted additively to produce the diagrams of Figure 6. The patterns are very similar for the two light-energy treatments, except that the root weight ratios fall

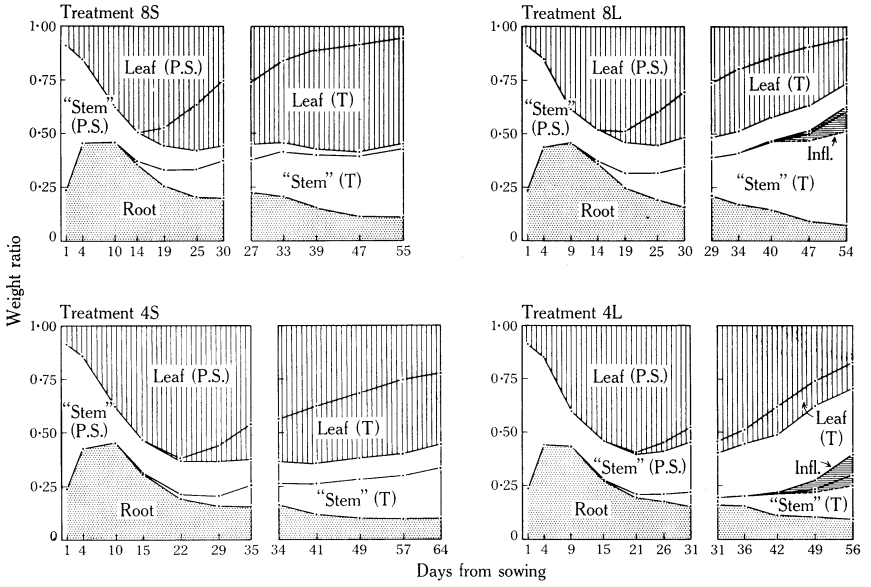


Fig. 6.—Dry weight ratios of principal plant parts plotted additively for wheat plants subjected to two light-energy levels and two day-length treatments. *P.S.*, primary shoot; *T*, tillers.

more rapidly with time and the tillers contribute much less to the leaf and stem weight ratios in the low-energy treatments (4S and 4L). With long days there were decreases in the leaf weight ratio and corresponding increases in the stem weight

ratio from the third week onwards. The inflorescence weight ratios attained values of 0·12 and 0·14 at anthesis for treatments 8L and 4L respectively but would be negligible for the short-day treatments. Inflorescence volumes for the primary shoots of these treatments are presented below.

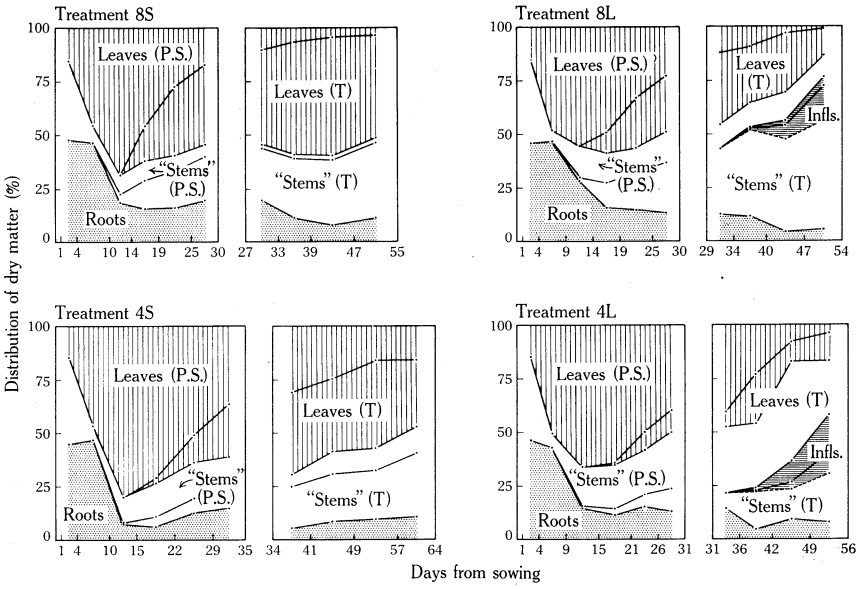


Fig. 7.—Indices of distribution of dry matter between the principal plant parts of wheat plants subjected to two light-energy levels and two day-length treatments. *P.S.*, primary shoot; *T*, tillers.

The distribution indices of Figure 7 were obtained by expressing the increments in dry weight of leaves, stems, etc. for each interval as percentages of the total dry weight increment for that interval. Taken in conjunction with Figure 6 they provide a descriptive account of the changing patterns of growth as affected by treatment.

TABLE 4

TOTAL LEAF AREA PER PLANT AT THE TIMES OF APPEARANCE OF THE LEAVES INDICATED

Treatment	Leaf Area (cm²) in 1961 Experiment			Leaf Area (cm²) in 1962 Experiment		
	Leaf 2	Leaf 4	Leaf 6	Leaf 6	Leaf 8	Leaf 10*
8S	4·79	23·8	122·2	177·2	741	2743
8S (25/20°C)	5·28	24·6	134·9			
8L	4·39	32·9	162·5	174·0	581	1169
4S	4·53	27·0	104·2	117·8	368	805
4S (25/20°C)	5·01	27·6	87·3			
4L	4·24	30·3	99·6	76·6	185	269

* Anthesis in 8L and 4L.

Leaf area was determined primarily as a basis for growth analysis, but the data of Table 4 show that treatment effects were considerably different to those on total

dry weight (Fig. 2). Thus long days ultimately had little effect on dry weight, but greatly reduced the final leaf area. The data also show reasonable agreement between the two sets of values for leaf-appearance 6.

(*b*) *Growth Analysis*

Growth has been examined in terms of the classical concept of relative growth rate, R_W (Fig. 8) and its two components, the net assimilation rate, E_A (Fig. 9) and leaf area ratio, F_A (Fig. 10). In Figures 8 and 9 the earliest values for each treatment are those for leaf-appearance interval 2–3. This interval was the first for which E_A values were meaningful, for the first leaf was only approaching maturity as the second leaf appeared. However, there were earlier values for R_W covering early seedling growth. From the beginning of the second day from soaking to the appearance of the first leaf, the mean value of R_W was 0·549, but for leaf-appearance interval 1–2 the mean had fallen to 0·236, and for interval 2–3 (Fig. 8) it was 0·125 with a range of 0·094 (4S) to 0·158 (8L).

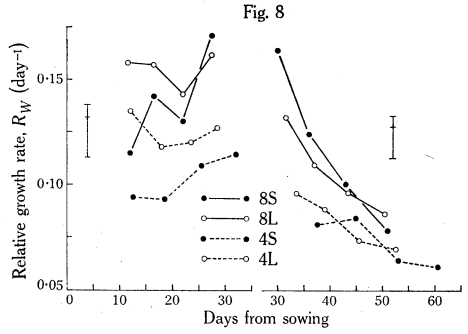
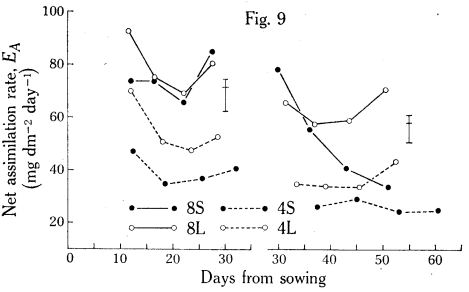
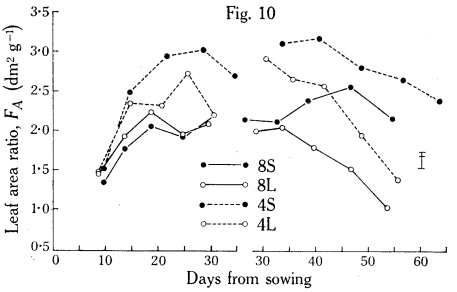


Fig. 8.—Relative growth rate of the whole plant (dry weight basis) as determined by light-energy level and day length.

Fig. 9.—Net assimilation rate as determined by light-energy level and day length.

Fig. 10.—Leaf area ratio as determined by light-energy level and day length.





The growth analysis (Figs. 8–10) reveals a remarkably complex interacting pattern. In general, R_W is seen to be greatly affected by treatment between days 10 and 30, but fairly constant with time (except in treatment 8S where it rises). Later, however, the downward trends with time tend to dominate the picture and treatment effects are reduced.

Figure 9 shows that E_A fell with time in all treatments but relatively more in 8S and less in 8L. For the two low-energy treatments, E_A fell to about half the initial value, but was consistently higher in 4L than in 4S (Fig. 9). For leaf-appearance

interval 2–3, E_A was also greater in 8L than in 8S, but this effect was absent for the next five intervals. There seems little doubt that the high level of tillering in 8S with the consequent high degree of self-shading was responsible for the fall in E_A after day 30. The plants of 8L had fewer tillers and, with the onset of stem elongation and heading, leaf display was more favourable and perhaps accounts for the maintenance of high E_A values up to anthesis.

It will be clear from comparisons within Figures 8, 9, and 10 that treatment effects on R_W are dominated by those in E_A. Indeed, treatment effects on F_A are almost invariably in the opposite sense, and so tend to reduce rather than supplement the effects of E_A on R_W. In three of the treatments, however, the late falls with time in R_W are determined by falls in F_A. Only with treatment 8S is this fall determined by a fall in E_A. This, as has already been suggested, was probably due to excessive self-shading.

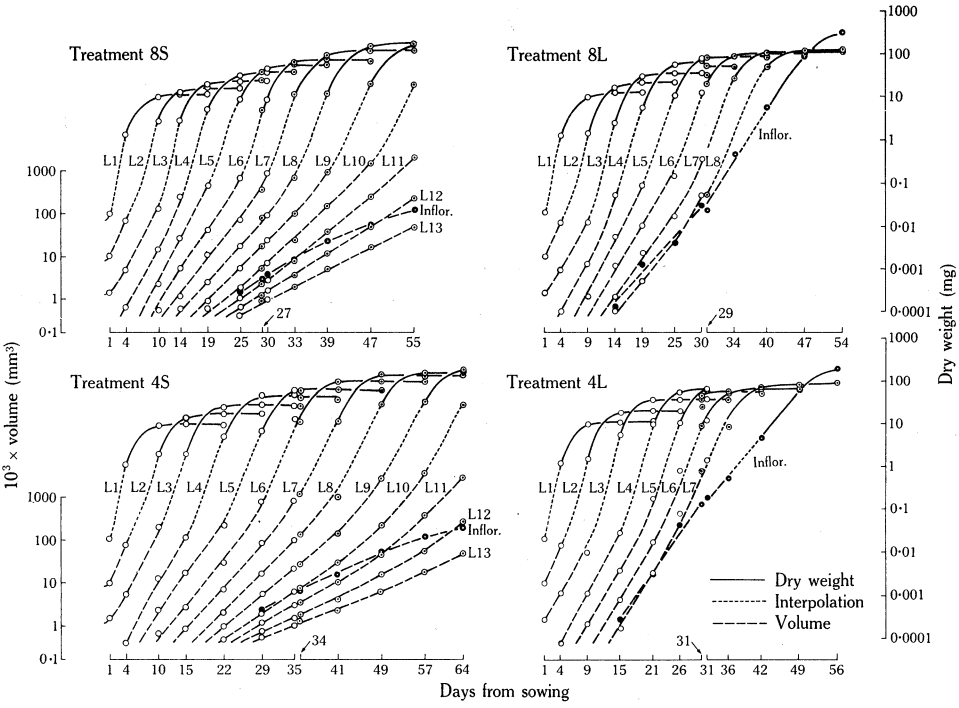


Fig. 11.—Volume and dry weight changes for successive leaves (L1, L2, etc.) and the inflorescence for wheat plants subjected to two light-energy levels and two day-length treatments. The first dry weight values coincide with the times of emergence of the leaves.

(c) *Pattern of Growth at the Shoot Apex*

Most of the effects of treatment so far described have concerned the net production of dry matter, and its distribution to tillers on the one hand, and to leaves, stems, roots, and inflorescences on the other. Such effects have frequently been reported (Evans, Wardlaw, and Williams 1964) in other species, but in less detail or with less emphasis on quantitative description. Figure 11 extends this

account to a description of the growth of successive leaf primordia and of the inflorescence of the primary shoot, as these are affected by the four light treatments. Williams (1966*a*) has already provided such a description for a single set of environmental conditions very similar to those of treatment 8L of the present study.

TABLE 5

ATTRIBUTES OF THE PRIMARY SHOOT RELATING TO FLORAL INDUCTION AND INFLORESCENCE DEVELOPMENT

Treatment	Leaves on Primary Shoot	Double-ridge Stage			Days from Sowing to Anthesis
		Days from Sowing	Apex Length (mm)	$10^3 \times$ Apex Volume (mm^3)	
8S	13·0	47	1·13	48	—
8L	8·4	26	0·64	42	54
4S	12·8	49	1·10	41	—
4L	7·4	23	0·63	46	56

In preparing Figure 11, the data for the two separate experiments were fused together by minor adjustments of the time scales. Perfect agreement was scarcely to be expected even though the common harvest within each treatment was taken on the day upon which more than half of the sixth leaves had emerged from within

TABLE 6

LENGTHS OF LEAF PRIMORDIA ON PRIMARY SHOOT APICES OF PLANTS FROM TREATMENT 8S (SHORT-DAY, HIGH-ENERGY TREATMENT)

Lengths are based on serial sections of "median" plants, and are numbers of 10 μ transverse sections from the tip to the half-junction with the next outside leaf

Leaf Appearance Stage	Days from Sowing	Length of Primordium									
		8	9	10	11	12	13	14	15	16	17
6	27	84	39	19	14	8					
7	33	—	88	46	24	16	11	8			
8	39	—	—	114	56	29	18	12	9		
9	47	—	—	—	150	66	32	22	15	13	9
10	55	—	—	—	—	138	64	27	19	13	11

leaf five. The best fit of the data was obtained by an overlap of one day for treatments 8S and 4L, and by inserting a gap of one day for treatments 8L and 4S. This device achieved excellent continuity, and permitted the drawing of smooth curves for all leaf primordia.

The pattern of growth at the shoot apex is greatly changed by day length. Thus at the high-energy level, the number of foliage leaves on the primary shoot was reduced from 13 to 8, and at the low-energy level from 13 to 7 by the long-day

treatment. Mean values are given in Table 5, together with other information on floral initiation. However, it is not easy, at an early stage of development, to determine which is the presumptive flag leaf for a given shoot. This is illustrated in Table 6, which gives primordium lengths for treatment 8S. For this treatment, double ridges were present on or about day 47, but even then there was no discontinuity in the sequence of primordium lengths, though some of the upper primordia were destined to become foliar ridges of the inflorescence. Eight days later, primordia 12 and 13 had doubled in length, but younger primordia had increased by only 25% or less. Primordium 13 would thus seem to be the presumptive flag leaf. Of the relatively few apices examined in this way, all those from treatment 8S had this pattern, but one from treatment 4S had only 12 presumptive foliage leaves. The experiment was not continued long enough to confirm these predictions.

TABLE 7

LENGTHS OF LEAF PRIMORDIA ON PRIMARY SHOOT APICES OF PLANTS FROM TREATMENT 8L (LONG-DAY, HIGH-ENERGY TREATMENT)

Lengths were obtained as in Table 6. The double-ridge stage was attained on day 26

Leaf Appearance Stage	Days from Sowing	Length of Primordium							
		3	4	5	6	7	8	9	10
2	9	96	26	12					
3	14	—	190	48	22	10			
4	19	—	—	309	77	30	14	7	
5	25	—	—	—	352	90	42	18	12
6	30	—	—	—	—	630	176	20	10

For treatments 8L and 4L, on the other hand, the flag leaf had developed fully by the final harvest (anthesis). With 8L, 60% of the plants had eight leaves, and 40% had nine; but for 4L, 60% of the plants had seven leaves, and 40% had eight. The length data of Table 7 (treatment 8L) indicate quite clearly that primordium 8 was the presumptive flag leaf. Primordia 9 and 10 stopped growing as soon as double ridges appeared.

The changing pattern of leaf growth as affected by leaf number and treatment is shown in the relative growth rate data of Figure 12. The pattern is the same for all treatments during the period of dependence on seed reserves though there is less evidence of a change in pattern resulting from the exhaustion of these reserves, about 10 days after sowing, than was the case in the earlier study (Williams 1966*a*, fig. 7). However, this could be explained by the fact that the early experiment was conducted in winter, when light-energy levels were presumably lower. The low-energy treatment (4S) gives most evidence for an adjustment of pattern (notably for leaves 4 and 5), and this is also the treatment with the lowest E_A values (Fig. 9).

Williams (1960) found that, apart from the seed-reserve effects already mentioned, the early growth of each leaf primordium was exponential, but that the exponent decreased with leaf number in a rather discontinuous manner. Figure 12 shows that the duration of the exponential phase varies from about a week

in leaves 3 and 4, to as much as 5 weeks in leaves 12 and 13 of the short-day treatments. The exponential phase of growth for leaves 1 and 2 no doubt occurred wholly or in part during the growth of the embryo. However, none of the treatments of the present experiments show much evidence of discontinuity in the decrease of the exponent with leaf number. This is best seen in Figure 14 where the initial values for successive primordia (from the fourth onwards) are plotted on a larger scale, together with the relative growth rates for the inflorescences. These initial values can be taken as measures of the relative rates of growth on the flanks of the shoot apex, for the earliest available volumes for the primordia tend to be dominated by the contribution of the tunica layers of the apex (Williams 1960). The trends in these curves (Fig. 14) seem to be identical for the high-energy treatments (8S and 8L) as far as the eighth primordium, but no explanation can be offered for the near absence of trend with 4L.

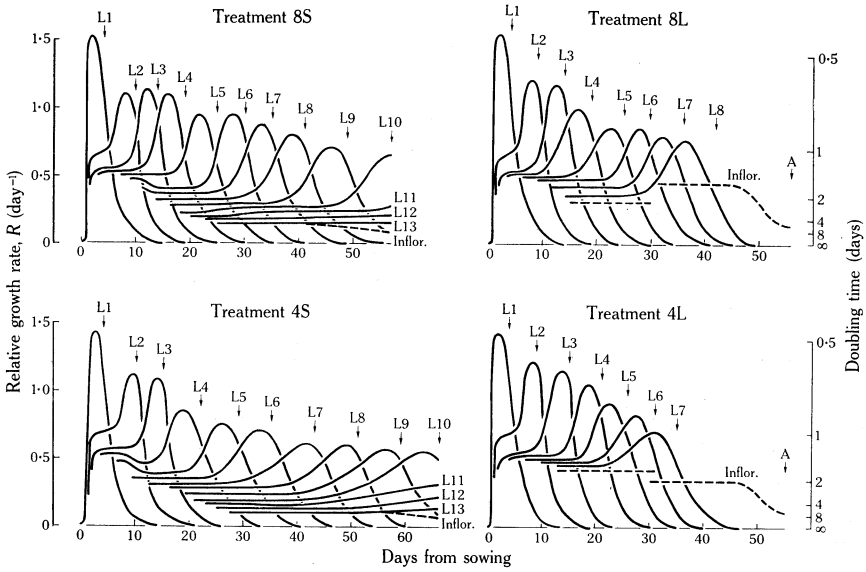


Fig. 12.—Relative growth rates for successive leaves (L1, L2, etc.) and the inflorescence of the primary shoot of wheat plants subjected to two light-energy levels and two day-length treatments. The arrows mark the times of emergence of the leaves, and *A* indicates time of anthesis in the long-day treatments.

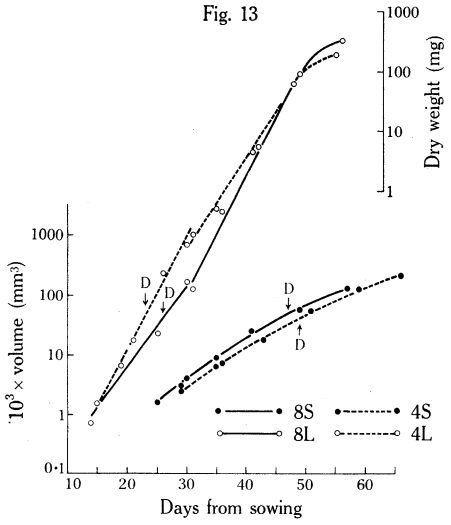
Following the early exponential phase of growth, the relative growth rates of the leaf primordia rise to maxima whose values are approximately twice those for the exponential phase (Fig. 12). The maxima occur 2 or 3 days prior to leaf emergence, and the rates then fall to zero. The maxima decrease with increasing leaf number, and the duration of successive phases of the growth rate curves increases considerably.

No remarkable differences occur between the general patterns of growth for the two long-day treatments (Fig. 12), except the difference in numbers of leaves already noted. However, the patterns are rather different for the short-day treatments. Thus, from the third leaf on, all relative rates of change tend to be lower,

and progress through the successive phases is retarded for the leaves of treatment 4S. The net result is that the ninth leaf of the primary shoot of this treatment appeared 2 days later than the tenth leaf of treatment 8S.

(*d*) *Inflorescence Growth*

The volume and weight data for inflorescence growth are plotted on logarithmic scales in Figures 11 and 13, but treatment comparisons are best made in the second of these. Inflorescence volumes for stages prior to initiation are those for whole apices above the level of junction with the presumptive flag leaf.



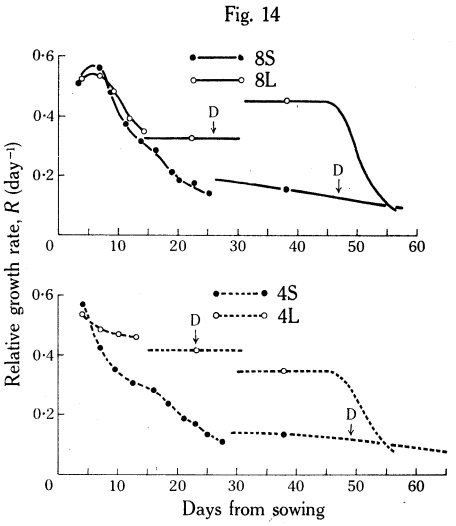


Fig. 13.—Volume and dry weight changes in the inflorescence of the primary shoot as determined by light-energy level and day length. *D* marks the double-ridge stage of floral initiation.

Fig. 14.—Relative growth rates for the inflorescence of the primary shoot as determined by light-energy level and day length. At the left are shown the initial rates for successive leaf primordia. These may be taken as indices of the relative rate of change on the flanks of the shoot apex. *D* marks the double-ridge stage of floral initiation.

The double-ridge stage of floral initiation was advanced about 3 weeks by the long-day treatments (Table 5), but occurred in all treatments when the apex volume had attained the same value. In spite of this, the apices were almost twice as long in short-day as they were in long-day plants, and their form was very different in the two cases. Long-day apices were squat and pyramidal, as depicted by Williams (1966*a*, plate 2, fig. 2). Short-day apices were long and thin and had many more foliar ridges when double ridges first appeared. Furthermore, swelling of the spikelet primordia began much higher on the apices in these treatments.

Williams (1966*a*, fig. 6) found that inflorescence growth was almost strictly exponential for more than 4 weeks under the long-day conditions of his experiment, and this is confirmed in the long-day treatments of the present experiments (Fig. 13) if allowance is made for the composite character of the evidence. However, the slopes of the successive segments (for 1961 and 1962 respectively) are appreciably different within treatments.

For the short-day treatments, the continuity of the data for the two years is satisfactory, but growth is very slow and is not exponential. Extrapolation of these curves, and of those for relative growth rate (Fig. 14) suggest that, in the absence of any dramatic change in the trends, inflorescence growth might cease altogether within 100 days of sowing. Furthermore, the dry weight would then be of the order of only 1% of that of a mature ear. It is probable, therefore, that these inflorescences would have aborted, and that further growth would have been expressed in continued tillering.

The relative growth rates of Figure 14 stress the discontinuity in inflorescence growth for treatments 8L and 4L in the two seasons, but there is no justification for accepting mean values in their stead. Such values would in fact obscure the remarkable agreement that exists between the initial relative growth rates for the inflorescences (all treatments) and those for the youngest leaves (the flag leaves) with which they are associated. This agreement is less surprising if, as suggested above, the initial leaf values can be taken as measures of the relative rates of growth on the flanks of the shoot apex. Early inflorescence growth would thus seem to be close to exponential, the exponent being determined by that of the most active part of the apex at the time of transition from vegetative to reproductive growth.

IV. Discussion

Since the primary purpose of this study was to describe the effects of certain light treatments on the pattern of growth at the shoot apex in wheat, no attempt will be made to comment fully on their effects on other attributes of the growth of the test plants or to relate them in detail to the literature. Indeed, effects of light intensity and length of day figure prominently in the comprehensive review by Evans, Wardlaw, and Williams (1964) on the environmental control of growth in grasses. Perusal of that review will show that there are many parallels to the responses reported above. However, there is also much confusion in the literature because it is seldom possible to disentangle the effects of treatment on vegetative growth on the one hand from those on reproductive development on the other.

In this respect the present study is no exception, and attention has already been drawn to the complex interacting pattern revealed by the growth analysis (Figs. 8–10). A simpler case is provided by the response in terms of tiller production (Fig. 1), where the dominant effect is the promotion of tillering by the high-energy treatment. It is less obvious whether the reduction in tillering with the long-day treatment is to be regarded as a secondary effect of the promotion of flowering by that treatment, or as a primary effect on vegetative growth which is later modified by the onset of reproduction. As a way around this problem, Evans, Wardlaw, and Williams (1964) suggested that grasses with a vernalization requirement should be grown without vernalization in order to study day-length effects on strictly vegetative plants.

Ryle (1966*a*, 1966*b*) has conducted such a series of experiments with three perennial grasses — cocksfoot, meadow fescue, and perennial rye-grass. The plants

were given no vernalization or short-day treatments, and no stem elongation or inflorescence development occurred. Increasing the photoperiod in a number of ways, including the use of a "light-break" in the middle of the dark period, increased leaf length and sometimes leaf width, but decreased the rate of production of leaves. However, the rate of production of new leaf surface increased with photoperiod. Increasing the photoperiod also decreased the rate of tillering. These effects were most pronounced in cocksfoot and least in perennial rye-grass, but all may be regarded as effects on vegetative growth.

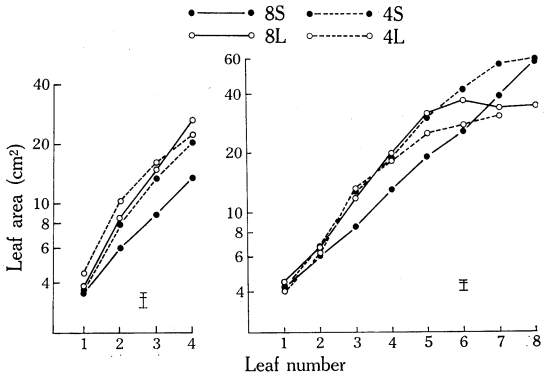


Fig. 15.—Areas at maturity for successive leaves of the primary shoot as determined by light energy-level and day length. Values for the first four leaves of the 1961 experiment are shown to the left. Other values are for the 1962 experiment.

The areas of successive leaves on the primary shoot of wheat in the present experiments are presented in Figure 15. While this index of growth response is marginal to the purposes of the paper, it is a sensitive one, and illustrates the interactions between treatments and with time which have to be reckoned with when treatments have multiple effects. There are also marked differences in response in the two years (for leaves 1–4) which throw some light on the discrepancy in response to long days at the low-energy level. Figure 15 shows that leaves 1 and 2 responded very little in 1962 to either light-energy level or to day length. In 1961, however, even leaf 1 was increased in area by long days at the low energy level. The area of leaf 2 was greatly increased in 1961 by both long days and the low-energy treatment, and these effects were maintained for leaves 3 and 4. These differences in response can reasonably be referred to the fact that the early leaves were growing during a period of sunny weather in 1962, but in cloudy weather in 1961.

Figure 15 also shows that the long-day effect on individual leaf area is reversed from about leaf 4 at the low-energy level, and after leaf 6 at the high-energy level. Since Ryle (1966*a*, 1966*b*) found this effect to increase continuously with increasing leaf number, it is likely that the reversal is a secondary effect, possibly determined by competition for energy substrate between leaf and stem in the long-day plants.

In one of his experiments, Ryle (1966*b*) established quite large positive effects of long days on the net assimilation rate of cocksfoot grown in a simulated sward. He thought it unlikely that there was a direct effect of day length on photosynthesis, but that the long-day effect on leaf display resulted in a more efficient interception of light. This interpretation has been advanced above for the late increase in E_A with

long days (8L *v.* 8S in Fig. 9), but there may be other explanations for the early increases with long days at both energy levels, and for the consistent and quite large increases at the low-energy level. Friend, Helson, and Fisher (1967), using Marquis wheat, also reported an increase in E_A when their 8-hr day length was supplemented by low-intensity light.

A feature of the day-length treatments of the present experiments is that, for short days, the plants entered the sunlit period from darkness, but, for long days, they did so from low-intensity light. This difference could conceivably affect the timing of stomatal opening, and Mansfield (1963) has shown, with soybean, that night lengths of the order of 12–16 hr are probably the most favourable for stomatal opening during the first few hours of a subsequent period of light. Then, too, Brun (1962) has claimed that when the duration of the previous dark period ranged from 4 to 12 hr, the stomatal-opening response time for banana leaves gradually decreased from about 25 min to less than 5 min, irrespective of the dark-period temperature. However, Mansfield (1962), who provides the only direct evidence known to the authors, has shown for *Xanthium pennsylvanicum* that the rates of opening of stomates in high light were significantly *slower* following a period in low-intensity light than following darkness. Thus there is little ground for supposing that the long-day increases in net assimilation rate reported here were contributed to by earlier opening of the stomates for the "day" period.

TABLE 8

LENGTH OF LEAF SHEATH AS AFFECTED BY LIGHT-ENERGY LEVEL AND LENGTH OF DAY

Treatment	Length (cm) of Leaf Sheath			
	1	2	3	4
8S	2·2	2·8	4·5	7·3
8L	3·5	7·3	12·1	18·0
4S	3·5	6·3	9·1	12·0
4L	4·3	9·0	12·4	15·1

Another consideration arising from the specific long-day treatments used is that the long-day plants received 16 hr of low-intensity light over and above that received by the short-day plants. Clearly, this extra energy could have contributed to the long-day effects on net assimilation rate. However, it can be shown in terms of visible light energy (Table 1) that the additional energy accounted for only 1·9% of the total in the high-energy series, and for about 3·6% in the low-energy series. It seems unlikely that this level of additional energy could account for all of the effect.

Yet another possibility is that the long-day stimulus to leaf and stem (mainly leaf sheath) growth (Fig. 5) constitutes a cause rather than an effect of the initial increases in E_A at both energy levels, and for the continuing increase at the low-energy level. King, Wardlaw, and Evans (1967) have shown recently that photosynthesis by the flag leaf of wheat is regulated directly by the demand for assimilates elsewhere

in the plant, and they quote many papers in which effects on the rate of photosynthesis are interpreted in terms of "sink" strength of various organs. Table 8 gives mature leaf-sheath lengths for the first four leaves of the 1961 experiment. These demonstrate the potential magnitude of this component of sink strength as affected by day length. However, it would be premature to speculate further on the possible interaction of this factor with others involved in the response to the light treatments of these experiments. In their study of leaf growth in Marquis wheat, Friend, Helson, and Fisher (1962) conclude that control of leaf growth by hormonal mechanisms sensitive to photoperiod seems more probable than does control by internal competition. However, these mechanisms may well be complementary, not mutually exclusive.

In discussing the patterns of growth at the shoot apex presented above, little more can be done than point to unexplained phenomena which could be of general interest. Why, for instance, do the initial growth rates of successive leaf primordia fall with time (Fig. 14), though less so with treatment 4L? Is it connected with the increasing number of primordia, all of which are dependent on the same pool of energy substrate? What is the mechanism which keeps the growth of the leaf primordium exponential for periods of up to 5 weeks, and at a rate which seems to be determined by that of the flanks of the shoot apex at the time of differentiation of the primordium in question?

Williams and Rijven (1965) suggested that each leaf primordium in turn escapes from some form of growth limitation by entering upon a phase of more rapid growth, and in so doing assumes a dominant role in the control of the vegetative apex. With the onset of reproduction, this role is lost, for presumptive foliar ridges never enter a phase of more rapid growth (Williams 1966*b*). However, the apex itself (now the presumptive inflorescence) grows exponentially, at least for a time, and dominates the growth of the shoot. We need to know more about this change from growth dominated by foliar activity to growth which is the expression of cauline activity. What, for instance, is the role of growth substances in this situation?

V. Acknowledgments

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