INFLORESCENCE INITIATION IN *LOLIUM TEMULENTUM* L.

X.* CHANGES IN ^{32}P INCORPORATION INTO NUCLEIC ACIDS OF THE SHOOT APEX AT INDUCTION

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Summary

Previous studies have shown an increase in RNA at the shoot apex of *L. temulentum* following floral induction, detectable chemically 2 days after induction, and by histochemical means after 1 day. Here, a transient increase in the incorporation of ^{32}P, applied to leaves, into nucleic acids at the apex is shown to occur at about the time when the long-day stimulus is estimated to reach the shoot apex. The increased ^{32}P incorporation due to the long-day exposure occurs throughout the apex, and is not confined to the summit region. Most of the ^{32}P was incorporated into RNA.

There is a marked diurnal fluctuation in ^{32}P incorporation into nucleic acids in both the shoot apex and the leaf primordia, incorporation being highest at midday.

The shoot apex, at this stage of development, appears to be a relatively quiescent tissue compared with the nearby leaf primordia. The leaf primordia incorporate into nucleic acids a much higher proportion of the ^{32}P activity reaching them, and have a much higher activity per unit dry weight than the apex. Changes in the true shoot apex may therefore be masked by the greater activity and mass of associated leaf primordia when "terminal buds" are analysed.

I. Introduction

Earlier studies of the time when the floral stimulus is exported from the leaves of *Lolium temulentum*, and of the velocity of its translocation (Evans and Wardlaw 1966), indicated that the stimulus should reach the shoot apex on the morning after the long day (day II). This is the time at which applications of actinomycin D and 5-fluorouracil are most inhibitory to floral induction in *L. temulentum* (Evans 1964). Increases in RNA in the shoot apex due to long-day treatment could be shown histochemically on day III, at the sites of future spikelet formation (Knox and Evans 1966). Quantitative chemical analysis showed RNA to be the component to exhibit the highest relative rate of increase during the 2 days following the long-day treatment (Rijven and Evans 1967). The present study attempted to establish whether an effect of long-day treatment on nucleic acid metabolism in the apex could be shown during day II, using [^{32}P]phosphate applied to leaves. Similar effects of induction as early as those described here have not been reported for other plants.

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II. Experimental Methods

(a) General

Plants of the strain of *L. temulentum* used throughout this series of studies were grown in 10-cm pots of perlite for at least 5 weeks in 8-hr days of natural light at 25°C day/20°C night temperature, with water and nutrient solution given daily. When the sixth leaf was fully expanded the plants were moved to an artificially lit, humidity-controlled cabinet at 25°/20°C, with 8-hr days at 3500 f.c., and a relative humidity of 85%, to adapt for 3–4 days to these standard experimental conditions.

Details of the methods used changed in the course of the experiments. Those followed in the final experiments, the results of which are considered in detail in the next section, will be described first, and earlier variations on them are then discussed.

When the seventh leaf was just fully grown, the 200–240 most uniform plants were selected and allocated at random to two artificially lit cabinets set at the standard conditions. All lower leaves and tillers were removed, leaving only leaves 5, 6, 7, and 8 on the main shoot. The plants in one cabinet were then exposed to 1 long day by having them under incandescent light of 50 f.c. intensity for 16 hr following the high intensity light period while the short-day controls remained in darkness. At various times during the following day (day II) lots of 10 plants were taken alternately from the long- and short-day cabinets, and ^{32}P was applied to them, as follows. With the aid of a metal mask, a length of 1·5 cm close to the base of the blades of leaves 6 and 7 on each plant was rubbed with a 1% Tween 20 solution, then 10 μl of a solution containing 10 mM citric acid, 2% glycerol, and 3% dimethyl sulphoxide was added to each rubbed area, and finally 10 μl of a carrier-free [^{32}P]phosphate solution was applied to each rubbed area, using a micrometer syringe. The activity of the ^{32}P solutions was about 1–2 mc per millilitre. The applied solutions usually remained entirely within the area rubbed with Tween solution. The treated plants were immediately returned to the standard conditions, the alternate long- and short-day groups being placed together in equivalent positions in the cabinets. After the required interval, the lots of 10 plants were harvested in the order of ^{32}P application and dissected. The apices from each lot were cut across at the base above the youngest leaf primordium showing upwards growth and dropped into ethanol. For some lots the small leaf primordia were also dissected, cut, and put in separate tubes of ethanol. A strict time schedule was followed, plants being treated and dissected at the rate of one per minute. The lots of apices were then extracted and dried, weighed, and their activity counted, as also that of aliquots of the extracting solutions.

Spare lots of plants were dissected 6 days after the long day to check that the short-day controls remained vegetative and that the plants exposed to a long day had initiated inflorescences.

(b) ^{32}P Application

Surfactants have been found to have a highly variable effect on the uptake of ^{32}P by leaves (Parr and Norman 1965). A preliminary experiment with *L. temulentum* showed that rubbing the leaf with a 1% solution of Tween 20 prior to application of ^{32}P resulted in about twice as much activity in unextracted shoot apices after 4 hr

as in plants rubbed with 0·05% Tween 20. A 1% solution was therefore used in all subsequent experiments.

Swanson and Whitney (1953) and Koontz and Biddulph (1957) have shown the marked dependence on pH of ^{32}P uptake following foliar application, uptake being highest at pH 2–3. In a preliminary experiment, addition of 10 μl of 50 mM maleate solution at pH 2 to the area rubbed with 1% Tween 20, before the application of ^{32}P, was found to double the ^{32}P activity in the apices 4 hr later, compared with controls to which water was added. In a later experiment it was found that both maleate and maleic acid solutions could cause damage to the area of application, and thereafter 10 mM citrate buffered at pH 2·5 was used.

Koontz and Biddulph (1957) also found that the addition of glycerol increased ^{32}P uptake. A preliminary experiment showed that the ^{32}P activity in apices of *L. temulentum* 4 hr after application was increased by about 50% when 2% glycerol was added to the maleic acid solution applied to the leaf after rubbing it with 1% Tween 20. Addition of 3% dimethyl sulphoxide to this solution was found to increase ^{32}P activity in shoot apices and leaf primordia by a further 38–44%.

High humidities supposedly increase the uptake and translocation of compounds applied to leaves (Clor, Crafts, and Yamaguchi 1962). The effects of high (85%) and moderate (50%) relative humidities on ^{32}P uptake were compared in two experiments. In both cases the ^{32}P activity in the apices of plants held at the higher humidity was only slightly greater.

The age and position of the leaves to which ^{32}P was applied had a marked effect on the activity subsequently found in the shoot apices. Three to four times as much activity was found in the apices when ^{32}P was applied to the uppermost fully expanded leaf as when the same amount was applied to the leaf below it. The amount translocated from the uppermost expanded leaf to the apex was not affected by the presence or absence of leaves below it, but was affected by the size of the emerging leaf above it, being 50% greater when the emerging leaf was only half to two-thirds expanded than when it was three-quarters or more expanded. In all the early experiments ^{32}P was applied only to the uppermost fully expanded leaf, but in later experiments it was also applied to the leaf below. Although the experimental plants were heavily selected for uniformity, the sensitive dependence on leaf size of ^{32}P reaching the apex may account for much of the variation within treatment groups.

(c) *Extraction Procedures*

The steps followed to remove soluble ^{32}P from shoot apices and leaf primordia were those used by Williams and Rijven (1965). They are set out in Table 1, together with the proportions of total extracted ^{32}P activity removed at each step. At no stage was the material powdered. It can be seen that the 0·2N perchloric acid step used in the early experiments removed a considerable amount of activity. Since some soluble RNA may have been lost at this step, it was omitted from the later experiments, the results of which are given below.

In several experiments, the extracts were bulked and sampled for their activity, to determine the relation between extractable and incorporated ^{32}P in the various treatments.

After extraction and drying, each lot of 10 apices was counted directly on a planchet using a gas flow, end window Geiger-Müller tube. They were weighed on a Cahn electrobalance, and the activity was expressed per unit extracted dry weight.

In some experiments in which high activities in the extracted apices were attained, lots of two apices were treated with deoxyribonuclease or ribonuclease, extracted, and recounted.

TABLE 1

EXTRACTION PROCEDURE FOR APICES AND LEAF PRIMORDIA

The ^{32}P activity removed at each step is expressed as a percentage of the total ^{32}P extracted

Extraction Procedure	Activity Removed from Leaf Primordia (%) (early expts.)	Activity Removed from Apices (%)	
		Early Experiments	Later Experiments
100% ethanol, 70°C, 20 min	12·1	13·3	11·4
70% ethanol, 70°C, 15 min	60·2	54·0	65·1
70% ethanol +0·1N perchloric acid, 30 min on ice	8·4	12·2	17·6
0·2N perchloric acid, 30 min on ice	18·8	20·5	—*
70% ethanol, rinse, on ice	0·2		4·8
100% ethanol, rinse, on ice			
100% ethanol, 30 min	—		0·5
n-Butanol, 70°C, 30 min	0·3		0·3
100% ethanol, rinse			—
Ethanol–ether (3 : 1 v/v), 30 min			0·1
Ether, 15 min			
Ether, 15 min			
Dry in oven, 80°C, 5 min			
Desiccate over silica gel, overnight			

* Step omitted.

III. RESULTS

(a) *Experiments with Long Periods of Exposure to* ^{32}P

Both uptake and translocation of ^{32}P by plants following application to leaves is rapid (e.g. Koontz and Biddulph 1957; Bachofen and Wanner 1962). In an early experiment, significant ^{32}P activity was found in unextracted apices of *L. temulentum* within 30 min of its application to leaves. After 1 hr, activity in the apices increased sharply with increasing time from application.

Three experiments have compared the ^{32}P activity in extracts with that incorporated into nucleic acids in the apices of plants held either in short days or exposed to 1 long day, over a range of times between ^{32}P application and dissection. Figure 1 presents some results from one of these experiments. The amount of ^{32}P incorporated by the apices rose progressively with increase in time from application, and was consistently greater in apices from the long-day plants. The activity in individual apices of short- and long-day plants was counted in the replicates with the smaller difference between them after 9 hr of treatment with ^{32}P and was significantly ($P < 0{\cdot}05$) higher in the long-day apices (Fig. 1).

Activity in the extracts was determined on only one replicate from each treatment but it is clear that the accumulation of extractable ^{32}P in the apices followed a similar course in both the long-day and the control plants. In both it rose

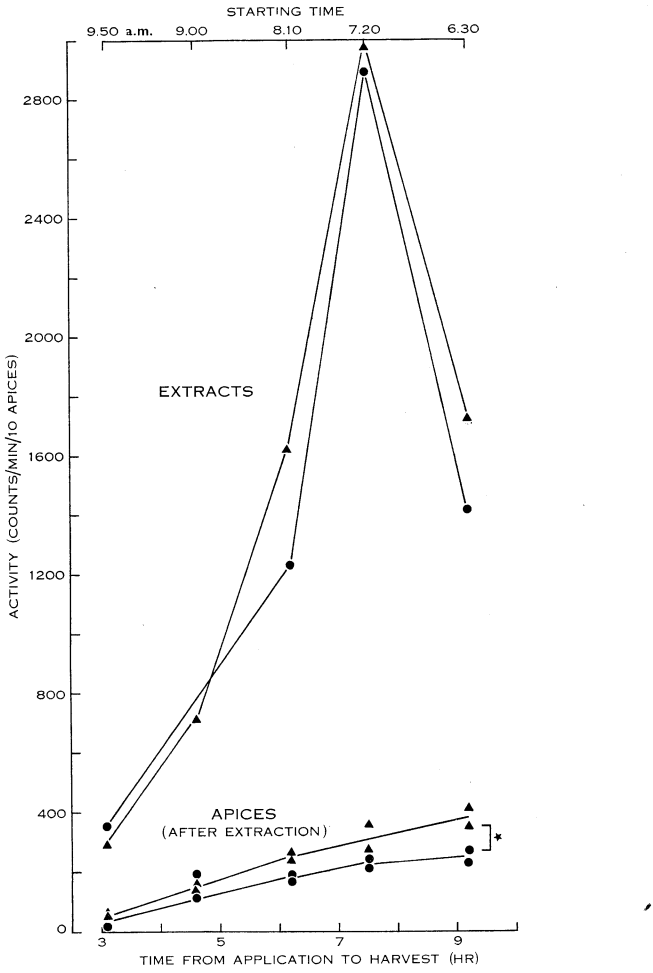

Fig. 1.—^{32}P activity in lots of 10 extracted apices, and in the extracts, as influenced by long-day exposure and time from application of ^{32}P to dissection. All ^{32}P applications were made on the morning of day II; the actual times of application for the first lot in each treatment group are indicated at the top of the figure. Experiment 123. ▲ Plants exposed to 1 long day. ● Short-day controls. * The difference between the ^{32}P incorporated after 9 hr by apices of the two consecutively harvested long- and short-day treatment replicates indicated by the bracket was significant at $P < 0{\cdot}05$.

with increase in time from application of ^{32}P up to $7\frac{1}{2}$ hr, and then declined sharply, suggesting that much of the ^{32}P imported by the apex but not incorporated was re-exported in the late afternoon.

The results given in Figure 1 suggest that ^{32}P activity may have been higher in the extracts of apices from plants exposed to a long day, at least for the later harvests. Similar increases have been found in other experiments, but not consistently in all cases.

A striking feature of these results is the low proportion of ^{32}P in the apices which is incorporated. This ranged between 10·7 and 17·3% for the long-day apices, and between 7·0 and 16·2% for the short-day apices, and suggests that at no time is ^{32}P incorporation by the apices likely to have been limited by ^{32}P levels in them.

TABLE 2

^{32}P ACTIVITY IN EXTRACTED DAY II APICES, EXPRESSED AS COUNTS PER MINUTE PER MICROGRAM OF EXTRACTED DRY WEIGHT, FROM PLANTS EXPOSED TO 1 LONG DAY OR FROM SHORT-DAY CONTROLS

The entries at the top of the two columns for experiment 124 are means for 50 apices, all others are means for 20 apices

Interval between ^{32}P Application and Dissection (hr)	Experiment 123		Experiment 124		Experiment 125	
	Long-day Plants	Short-day Controls	Long-day Plants	Short-day Controls	Long-day Plants	Short-day Controls
3	1·47	0·90	1·95	1·43	2·79	1·83
4·5	5·26	5·55	—	—	—	—
6·25	8·05	6·25	9·38	8·60	—	—
7·5	10·19	8·09	16·10	11·84	18·3	14·7
9·25	12·63	8·83	—	—	—	—
Average dry weight (μg)	2·9	2·9	3·0	2·9	2·9	2·8

The activities in the extracted apices can be given on a unit extracted dry weight basis to reduce effects due to variation at dissection. Table 2 presents the results from Figure 1 in this form, together with the results of the other experiments (124 and 125) with long intervals between application and dissection. With one exception, incorporation of ^{32}P per unit dry weight was higher in apices from plants exposed to the long day, the average increase being 51% for 3-hr exposures, and 29% for 7½-hr exposures to ^{32}P.

Incorporation of ^{32}P into leaf primordia differed in several respects from incorporation into shoot apices. A higher proportion of the ^{32}P in the leaf primordia was incorporated into nucleic acids, usually 40–50% compared with the 7–17% incorporated by the apices. Correspondingly, the activity per unit dry weight in the leaf primordia was far higher than that in the shoot apices of the same plants. Mean values have not been included in Table 2 for comparison with the apices, since there is a pronounced increase in activity per unit weight with increase in leaf primordium weight, as may be seen in Figure 3. In experiment 124, the activity incorporated in the apices 3 hr after ^{32}P application varied between 0·8 and 2·1 counts/min/μg, while that in the leaf primordia varied between 3·1 and 18 counts/min/μg; 7½ hr after application, apices varied between 10·1 and 17·7 counts/min/μg, while leaf primordia varied between 25 and 75 counts/min/μg. Incorporation in the leaf

primordia was somewhat variable, and there was no clear evidence that it was greater in primordia from plants exposed to a long day than in the short-day controls.

The distribution of ^{32}P incorporation within shoot apices was examined by cutting the extracted apices from several treatments into three pieces of about equal length, each piece being about 0·23 mm long, and counting and weighing each lot of 10 pieces. The results are given in Table 3. While the extent of the increase in ^{32}P incorporation is highly variable, it is nevertheless clear that it occurs throughout the apex and is not confined to the summit region. If anything, it is greatest at the base.

In experiments 123–125, digestions with deoxyribonuclease and ribonuclease were made to obtain some indication of the proportions of ^{32}P incorporated into DNA and RNA. Digestions with pancreatic ribonuclease (Worthington) were made with 0·5 mg enzyme per millilitre in 0·1M acetate buffer at pH 6·0, for 2–6 hr at

TABLE 3

DISTRIBUTION OF ^{32}P INCORPORATION IN DAY II SHOOT APICES OF PLANTS EXPOSED TO 1 LONG DAY COMPARED WITH THAT IN SHORT-DAY CONTROLS

Expt. No.	Interval between ^{32}P Application and Dissection (hr)	Part of Apex	Activity (counts/min/μg dry wt.)	
			Long-day Plants	Short-day Controls
122	3	Summit	4·37	2·95
		Middle	4·15	2·40
		Base	3·50	1·51
123	6·25	Summit	5·22	4·53
		Middle	6·72	6·27
		Base	8·27	5·79
123	7·5	Summit	6·76	5·27
		Middle	7·03	6·06
		Base	8·49	7·74

35°C. The results for experiment 125, which were in broad agreement with the others, are indicated below. 35–41% of the ^{32}P incorporated in both long- and short-day apices was removed by the acetate buffer alone, and this proportion did not increase between 3 and 6 hr of digestion. It possibly indicates the proportion of ^{32}P incorporated into soluble (transfer) RNA, including that into the highly labile terminal adenylate (Wicks, Greenman, and Kenny 1965). A further 12–14% of the activity was removed by pancreatic deoxyribonuclease (CalBiochem. Ltd., 1 mg/ml) in 6 hr digestions under the conditions used for ribonuclease, except for the addition of 0·02M $MgCl_2$. Since no Feulgen staining was evident following these digestions, this presumably represents the proportion of ^{32}P incorporated into DNA. Digestions with ribonuclease removed 32–37% more activity than the buffer solution alone. The other 14–16% of activity appeared to be resistant to both ribo- and deoxyribonuclease digestions, in all experiments. Since no Feulgen-positive material remained after deoxyribonuclease digestions, this fraction may comprise RNA resistant to ribonuclease action, as is

that bound to DNA (Huang and Bonner 1965) and also inactive ribosomal RNA (Bell *et al.* 1965).

(*b*) *Diurnal Variation in* ^{32}P *Incorporation*

Eight further experiments were carried out in which the plants were dissected only 3 hr after ^{32}P application, in an attempt to determine the time at which ^{32}P incorporation in the apex is first stimulated by exposure of the plants to a long day. The results given in Figure 1 and Table 2 show that ^{32}P incorporation was relatively slight after this short interval, but increased rapidly with additional time. Hence the considerable variability in the results with 3-hr applications. ^{32}P incorporation in the apices 3 hr after application represented only about 1×10^{-6} of the activity applied to the leaves.

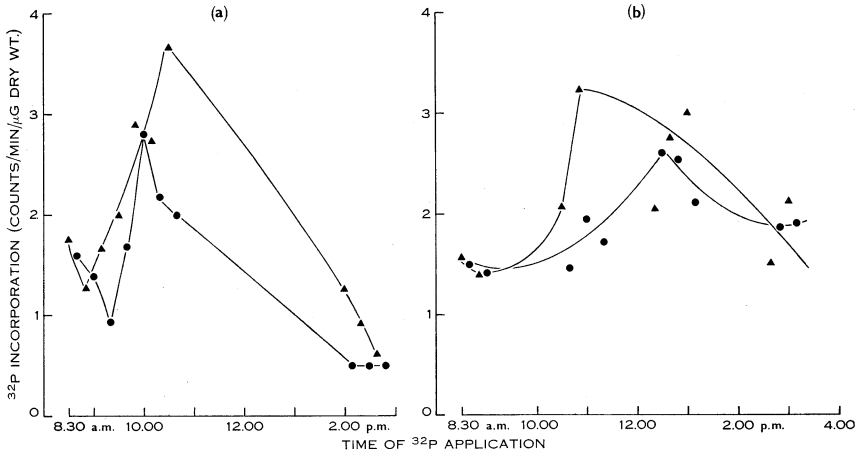

Fig. 2.—^{32}P incorporation into shoot apices 3 hr after leaf application at various times during day II, as affected by long- or short-day exposure during the preceding night. (*a*) Experiment 118: ^{32}P (activity 7×10^6 counts/min) applied only to leaf 7. (*b*) Experiment 122: ^{32}P (activity 5×10^6 counts/min) applied to leaf 7, and the same amount also applied to leaf 6. ▲ Plants exposed to 1 long day. ● Short-day controls.

The results of two experiments are given in Figures 2(*a*) and 2(*b*). In both experiments, as in all the others too, a marked diurnal variation in ^{32}P incorporation was evident. For applications at the beginning of the high intensity light period on day II, incorporation was at an intermediate level (1–2 counts/min/μg), often fell to some extent with later application, and then rose to reach peak values for applications in the middle or second half of the morning. Incorporation following afternoon applications was lower, sometimes extremely low. In two experiments with treatments in which ^{32}P was applied several hours before the beginning of the high intensity light period, or 4 hr later, little was incorporated.

There was no evidence of increased ^{32}P incorporation in apices of long-day plants with applications made at the beginning of the high intensity light period (8.30 a.m.), but an increase could usually be seen for applications near the middle of the morning, as in Figure 2. Comparable increases in ^{32}P incorporation during the morning of day II due to long-day treatment were found in six of the eight experiments,

and a slight increase was found in another. A decrease was found in one experiment, but ^{32}P incorporation in this was at an unaccountably low level in all plants, and, in contrast to general procedure, the treated and control plants were held in different cabinets following ^{32}P application. Over 10 experiments, including the three discussed in the preceding section and the one showing a decrease, the average increase in ^{32}P incorporation by apices due to long-day induction, 3 hr after ^{32}P applications at or close to 10.30 a.m. on day II, was 34·8% ($P = 0{\cdot}01$). In some experiments increases in ^{32}P incorporation were evident for later times of application [e.g. Fig. 2(*a*)].

^{32}P applications were also made on day III in five experiments, mostly in the morning. In all cases there was a significantly higher ^{32}P incorporation in the apices of plants exposed to a long day ($P < 0{\cdot}02$ to $\ll 0{\cdot}01$), the average increase over the short-day controls in the five experiments being 69·1%.

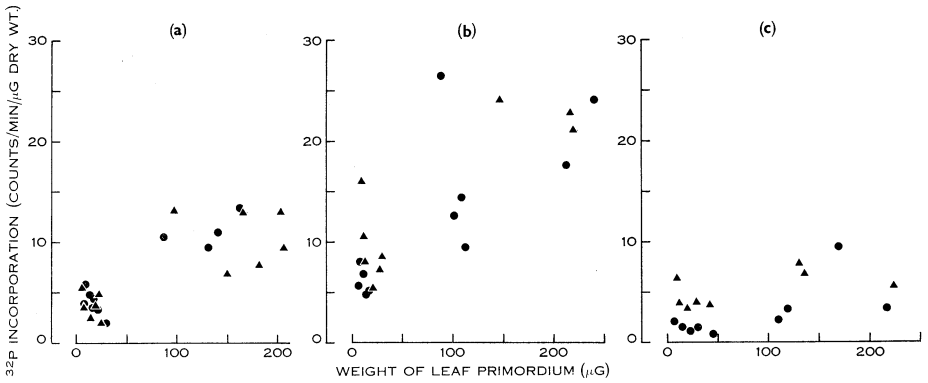

Fig. 3.—^{32}P incorporation into leaf primordia 3 hr after leaf application at various times during day II, as influenced by size of the leaf primordium and by long- or short-day exposure during the preceding night. Experiment 118: ^{32}P (activity 7×10^6 counts/min) applied only to leaf 7. Each point represents an individual leaf primordium. Times of application of ^{32}P are: (*a*) 8.30 a.m.–9.10 a.m.; (*b*) 10.10 a.m.–10.50 a.m.; (*c*) 2.00 p.m.–2.40 p.m. ▲ Plants exposed to 1 long day. ● Short-day controls.

The diurnal fluctuation in ^{32}P incorporation was also evident in the leaf primordia. Figure 3 presents the relation between incorporation and size of the leaf primordium for applications of ^{32}P at the beginning of the morning, in mid-morning, and in mid-afternoon. The data are for the same plants as those for which the incorporation of ^{32}P into apices is shown in Figure 2(*a*). As in all other experiments, there was a tendency for the rate of ^{32}P incorporation per unit weight to increase with increase in size of the leaf primordia, with considerable variation. Because of this variation there is no clear difference in the rate of incorporation of ^{32}P by leaf primordia from short-day controls and from the plants exposed to the long day. However, in the results of several experiments, as in Figure 3(*c*), there is some evidence that ^{32}P incorporation was higher in leaf primordia from plants exposed to the long day.

What is clear from Figure 3 is the sharp rise in incorporation between early and mid-morning applications, and the subsequent fall to low values by mid-afternoon.

IV. Discussion

The results presented above indicate that plants exposed to 1 long day incorporated more ^{32}P into the nucleic acids of their apices than did the short-day controls, when the ^{32}P was applied at mid-morning of the day after the long-day treatment. The average increase for 3-hr exposures to ^{32}P was 35%.

Since an increase was not apparent when the ^{32}P was applied at the end of the low intensity light period, but only when applied some hours after the beginning of the high intensity light period of day II, it can hardly have been due to the low intensity light period acting as a source of energy, but rather to its photoperiodic effects. Moreover, the high proportion of ^{32}P in the apex which was extractable (Fig. 1) suggests that ^{32}P incorporation was unlikely to have been limited by the amount of ^{32}P reaching the apex in either control or induced plants. The fact that ^{32}P incorporation continued to increase beyond $7\frac{1}{2}$ hr after application, while the total ^{32}P in the apices dropped by about 50%, supports this conclusion.

Increased ^{32}P incorporation does not necessarily imply increased nucleic acid synthesis. It could be due to a reduced size, and increased specific activity, of the phosphate or precursor pool in the apex (cf. Cherry *et al.* 1965). However, there is no obvious reason why the long-day treatment should affect the size of the phosphate pool during only part of the day after the long day, except as a secondary effect. The results of a further experiment support this suggestion in that the earliest samples showing a marked increase in ^{32}P incorporation due to long-day treatment showed no difference in the ^{32}P activity of the extracts, whereas later samples did so.

When this problem was investigated by Wicks, Greenman, and Kenney (1965) with livers of adrenalectomized rats, it was found that hydrocortisone on occasions somewhat increased the specific activity of the precursor pool, but increased ^{32}P incorporation into RNA to a far greater extent. They also found that although much of the ^{32}P incorporated by the liver was in the terminal adenylate of transfer RNA, this amount increased only slightly 2 hr after treatment with hydrocortisone, whereas incorporation of ^{32}P into the residue of the transfer RNA increased two- or threefold, as also that into the pre-ribosomal and the DNA-like RNA fractions (Greenman, Wicks, and Kenney 1965).

It seems likely, then, that the transient increase in ^{32}P incorporation observed during the morning of day II in our long-day plants represents increased nucleic acid synthesis as a direct result of the arrival of the floral stimulus in the apex at that time. The results of the digestions with ribo- and deoxyribonuclease are consistent with the suggestion that 80–90% of the activity was incorporated into RNA, and that the increased incorporation due to floral induction occurred in several RNA fractions. These results, therefore, support the conclusion reached from studies with inhibitors such as actinomycin D and 5-fluorouracil (Evans 1964) that RNA synthesis in the apex at the time of arrival of the floral stimulus is an essential component of floral induction.

The results with subdivided apices (Table 3) suggest that the increased RNA synthesis occurred throughout the apices, and was not confined to the summit region. It is clear that the summit is not the prime target of the floral stimulus, and that RNA synthesis in the base of the apex was stimulated on day II by floral

induction. An increase in ^{32}P incorporation by the subtending leaf primordia may also have occurred, although there was no clear evidence in any experiment (cf. Fig. 3) that this is a regular feature of long-day treatment.

The results presented here emphasize the rhythmic nature of shoot apex metabolism. The pronounced diurnal fluctuation in ^{32}P incorporation at the apex was parallelled by that in the leaf primordia. It is unlikely to be due to fluctuations in the amount of ^{32}P translocated to the apex, or in the supply of photosynthate to the apex, as this is unlikely to decrease so sharply in the afternoon as to cause the drop in ^{32}P incorporation then. In fact, Evans and Wardlaw (1966) found no fall in the supply of ^{14}C-labelled photosynthate to the apex in the afternoon. Marked diurnal fluctuations, seemingly endogenous, were also found in the level of soluble amino compounds in apices of *L. temulentum* (Rijven and Evans 1967), but in this case the level rose early in the morning and remained high until the end of the day period. In view of such pronounced diurnal variations in the activity of the apices, variations between experiments in the inductive response to 1 long day could be due to differences in the time of arrival of the floral stimulus in relation to apical metabolic activity.

The relative inactivity of the vegetative shoot apices, previously evident in their low relative growth rates (Rijven and Evans 1967), is emphasized here by the small proportion of ^{32}P which they incorporated into nucleic acids, compared with the leaf primordia, and by the low activity incorporated per unit extracted dry weight. The shoot apex appears to be a relatively quiescent tissue subtended by far more rapidly growing leaf primordia. The late afternoon fall in total ^{32}P activity in the apices, evident in Figure 1, may therefore be due to the demands of rapid leaf growth nearby. The high level of metabolic activity in the leaf primordia, compared with that in the apices, suggests that in the "terminal buds", which have so often been analysed for changes at floral induction, changes in the true shoot apex may well be masked by the greater amount and activity of associated leaf primordia.

V. Acknowledgments

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