A RELATIONSHIP BETWEEN PHOTOPERIODISM AND RESPIRATION[1]

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(WITH THREE FIGURES)

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Introduction

The discovery by GARNER and ALLARD (**3**) that many plants have specific photoperiodic requirements for floral initiation has led to considerable research to determine the effect of light in the transition from a vegetative to a flowering condition. It might be expected that this transition would be reflected in some fundamental process in metabolism, possibly in respiration. The results obtained by MELCHERS and LANG (**7**) indicate that some metabolic function, presumably a catabolism of sugar, is involved in the flowering response of *Hyoscyamus niger,* a long-day plant. While BODE (**1**) has reported changes in respiration and photosynthesis, and ROBERTS *et al.* (**9**) have found respiratory changes associated with photoperiodic induction, the results of these workers were obtained long after the flower perimordia had been initiated.

It is the purpose of this study to investigate the metabolic changes, as expressed by respiratory activity, which may be associated with the onset of floral initiation.

Materials and methods

The material in the present study included two short-day plants (cocklebur and Biloxi soybean), two indeterminate plants (Alaska pea and tomato var. Michigan State Forcing), and a long-day plant (Wintex barley). Unless otherwise stated, the experimental material was grown in the greenhouse under a day length that would maintain a vegetative type of growth until the plants were sufficiently mature for experimentation. The plants were then transferred to chambers with controlled temperature and light conditions, and subjected to the photoperiod treatments indicated in table I.

The treatments involving night interruption consisted of day lengths one hour shorter than the short-day treatment with one hour of light added in the middle of the dark period or night. These treatments were particularly useful in providing material comparable to the short-day treatment in hours of illumination and comparable to the long-day material in photoperiodic stimulus. It is well established that a light interruption in the middle of the night period negates the effect of a long dark period both in long-day plants (**2**) and in short-day plants (**5**).

Mature leaves were cut from the plants, brushed lightly to remove contaminants, and circular disks were cut from them. The leaf disks were

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TABLE I

THE DURATION OF THE LIGHT PERIODS GIVEN TO THE VARIOUS PLANTS.

Plant	Short day	Night interruption	Long day
	hrs.	*hrs.*	*hrs.*
Cocklebur	14	13 + 1	16.5
Biloxi soybean	10	9 + 1	14.0
Alaska pea	10	13 + 1	16.5
Tomato var. Michigan State Forcing	10	13 + 1	16.5
Wintex barley	10	9 + 1	12.0

placed in conventional Warburg flasks and their oxygen consumption was determined by the method of KLINKER (**6**). Temperature was held at 27° C.

Preliminary experiments indicated that maximal differences in respiration between treatments occurred at about midday. Thus all respiration readings were started at about 1 P.M. The duration of all respiration determinations was one hour. The leaf disks were then removed from the flasks, placed in a constant temperature oven at 75° C for 15 hours, and weighed. The results of the various experiments are expressed as the Q_{O_2}, *i.e.*, the microliters of oxygen taken up per milligram of dry weight of tissue per hour.

After each series of photoperiod treatments, a group of 7 to 10 plants was transferred to a non-inducing day length, and after three weeks the number of flower primordia was determined by micro-dissection.

Results

THE EFFECT OF PHOTOPERIODS ON THE RESPIRATION OF SHORT-DAY PLANTS

To establish the effect of the light period on the respiratory processes of some short-day plants, Biloxi soybean and cocklebur were subjected to short-day, long-day and night-interruption treatments. The results are shown in table II. It can be seen that in the case of cocklebur, one short day followed by a long night resulted in a decreased rate of respiration,

TABLE II

THE RELATIONSHIP OF PHOTOPERIODISM TO THE RESPIRATION OF SHORT-DAY PLANTS, COCKLEBUR AND BILOXI SOYBEAN. THE Q_{O_2} IS EXPRESSED AS PER CENT. OF THE LONG-DAY CONTROL (VEGETATIVE).

Plant	Days of treatment	Q_{O_2} short day	Q_{O_2} night interruption
Cocklebur	1	90	83
	2	111	97
	3	118	96
Biloxi soybean	1	111	90
	2	123	90
	3	143	90
	4	145	108
	6	119	93

while two or three such photoperiods produced increases up to 18% over the vegetative control. Biloxi soybean did not show an initial depression but exhibited an increase in respiration rate with each short day up to the third day, at which time a maximal increase was observed. Thus, there was an overall increase in respiration rate with floral induction both in cocklebur (18%) and in Biloxi soybean (45%) compared to that of vegetative controls. The night-interruption experiments failed to exhibit an increase, except at one point (Biloxi soybean treated four days), and this difference was too small to be significant. It has, thus, been demonstrated that the photoperiodic induction of flowering in these two short-day plants was associated with an increase in respiratory activity. The same number of

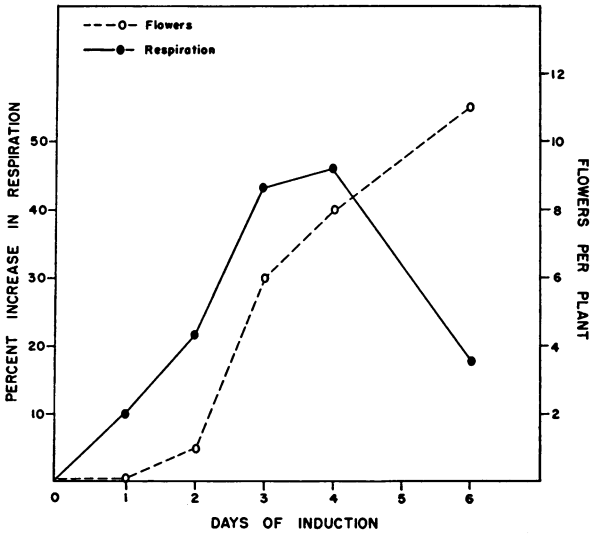

FIG. 1. The effect of number of days of induction on the respiration rate and on the number of flowers induced in a short-day plant, Biloxi soybean.

light hours given as a non-inducing, night-interruption treatment did not evoke such an increase in respiratory activity.

Counts of the number of flower primordia induced in soybean by each number of short days were made after three weeks. The relative effect of each number of short days on respiration rate and on flower induction are compared in figure 1. It can be seen that the greatest rise both in the respiration rate and in the number of flowers ultimately induced occurred with the third day of induction.

THE EFFECT OF PHOTOPERIODS ON THE RESPIRATION OF A LONG-DAY PLANT

To establish the nature of the respiratory response of a long-day plant to photoperiods, Wintex barley was subjected to long-day, short-day, and night-interruption treatments. Figure 2 indicates the respiratory responses

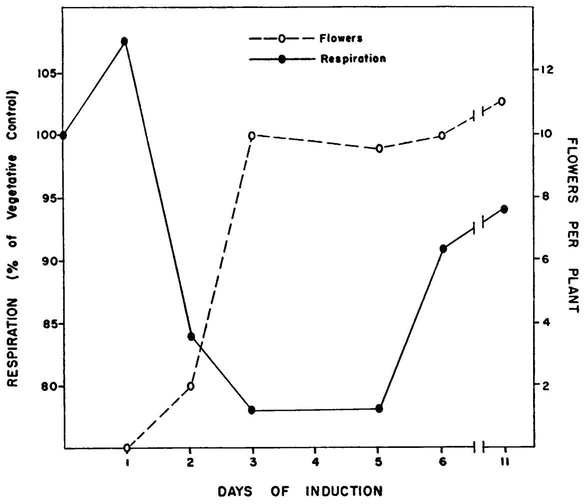

FIG. 2. The effect of number of days of induction on the respiration rate and on the number of flowers induced in a long-day plant, Wintex barley.

exhibited by Wintex barley subjected to long days. It will be observed that a single inducing day-length resulted in an increased respiratory activity whereas subsequent days of induction resulted in decreases up to 21% below the rate of the vegetative control. These results are in contrast to those shown with the short-day plant in figure 1. It appears that the maximal changes in both the flowering and respiratory activities occurred on the second and third days of induction.

In the case of the night-interruption treatments, which are presented graphically in figure 3, it will be observed that while there was a lag in the

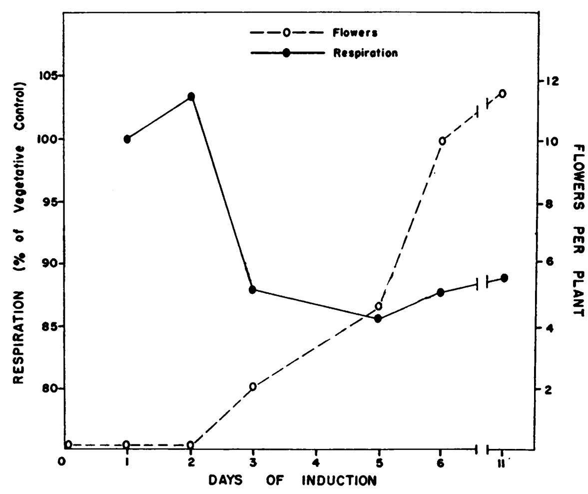

FIG. 3. The effect of number of interrupted nights on the respiration rate and on the number of flowers induced in a long-day plant, Wintex barley.

respiratory response, the number of flowers per plant closely paralleled the respiratory shift. It appears that the night interruption treatment was less effective both in inducing the formation of flowers and in decreasing respiration rate.

It may be stated that at least in the case of Wintex barley there is an overall decrease in the respiration rate with flower initiation. The decrease is observed whether flower initiation is brought about by long photoperiods or by short photoperiods with night interruptions. This decrease is in contrast to the increase in respiration rate demonstrated with the short-day plants tested.

THE EFFECT OF PHOTOPERIOD ON THE RESPIRATION OF INDETERMINATE PLANTS

To determine if the respiratory shifts which had been observed with both the long-day and short-day plants were related to strictly developmental phenomena in the plants, two day-neutral or indeterminate plants, Alaska pea and tomato (var. Michigan State Forcing) were subjected to the three light treatments. The results shown in table III indicate consistently higher respiratory activities in the long-day treatment. Furthermore, the respiration rates of the plants receiving the night-interruption treatment are essentially identical with those of plants receiving the short-day treatment which is very much in contrast to the behavior of the photoperiod-sensitive species.

TABLE III

THE RELATIONSHIP OF PHOTOPERIODISM TO THE RESPIRATION OF INDETERMINATE PLANTS, ALASKA PEA AND TOMATO (VAR. MICHIGAN STATE FORCING).

Plant	Days of treatment	Q_{O_2} short day	Q_{O_2} night interruption	Q_{O_2} long day
Alaska pea	1	4.31	4.33	5.00
	3	4.63	4.55	6.50
	5	4.68	4.75	6.83
Average		4.54	4.54	6.11
Tomato	1	2.67	2.63	2.94
	3	2.72	2.68	3.15
	5	2.77	2.59	3.09
Average		2.72	2.63	3.06

Discussion

On the basis of the experimental evidence presented here, it is proposed that the photoperiodic mechanism by which flowering is induced involves a respiratory shift. There are three lines of evidence to support this hypothesis. First, it has been shown with one long-day and two short-day plants that there is a shift in respiration rate with photoperiodic induction; and upon being induced, the short-day plants exhibited an increase in respiration rate, while the long-day plant exhibited a decrease in respiration rate when compared to their vegetative controls. Second, the night-interruption treatments evoked respiratory rates comparable to the rates in long days in all of the photoperiod-sensitive species tested but not in the indeterminate species, which parallels the effects of night interruption on flowering. And third, a close similarity was found to exist between the flowering and respiratory patterns associated with different numbers of photoinducing treatments.

Long-day and short-day plants exhibited opposite flowering responses to the light interruption of a long dark period. Night interruption of short-day plants did not induce flowering whereas night interruption of the long-day plant did induce flowering. Similarly, night interruption of the short-day species tested did not result in a respiratory shift, whereas night interruption of a long-day plant did evoke such a shift. Night-interruption treatment of indeterminate plants does not alter flowering, and no change in respiration rate was observed.

A relationship has been shown to exist between respiration and photoperiodism at the onset of floral initiation in the photoperiod-sensitive species tested. The present data provide fundamental evidence of the existence of metabolic processes which may be directly involved in the mechanism of photoperiodism in plants.

Summary

Changes in respiratory rates with various photoperiod treatments have been investigated using short-day plants (cocklebur and Biloxi soybean), indeterminate plants (Alaska pea and tomato var. Michigan State Forcing), and a long-day plant (Wintex barley). Respiratory activities expressed as the Q_{O_2} have been determined in long-day, in short-day and in short-day with night-interruption treatments. The results indicate that the respiration rates in leaf disks of long-day plants decreased and those of short-day plants increased with photoinduction. In contrast to these results, the respiratory activities of the indeterminate plants appear to be comparable to the total light received.

The data presented exhibit a correlation between the extent of changes in respiratory activities and the degree of flowering in response to the first few days of photoperiodic induction.

On the basis of the experiments reported, a hypothesis is offered that the photoperiodic mechanism by which flowering is induced involves a respiratory shift.

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