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The Circadian Rhythm of Leaf Movement of Coleus blumei x C. frederici, a Short Day Plant.
II. The Effects of Light and Temperature Signals[1, 2]

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Abstract. **The phase response curve for the circadian rhythm of leaf movement of *Coleus blumei* x *C. frederici*, a short day plant, is generally similar to those reported for other organisms. An increase in the duration of the light signal caused an increase in the extreme values of the phase response curve and shortened the time for transition from maximum delays to maximum advances. Experiments with 2 light signals showed that the overt rhythm of leaf movement represents the rhythm of the light sensitive oscillator even during the transient period that followed the first light signal. A temperature decrease of 7° for 8 hr caused only a transient phase shift in the following 2 cycles but not in the steady state. The combination of such a temperature decrease and a light signal showed that only the overt rhythm of leaf movement was disturbed by the temperature decrease whereas the light sensitive oscillator was free running. A temperature decrease of 11° for 10 hr caused a steady state phase shift and affected the light sensitive oscillator as well.**

One of the problems involved in circadian rhythms in biological systems is how they are used as the time scale for photoperiodic responses, such as flowering in some of the higher plants. To approach this problem, a preliminary knowledge is required of the mechanism of entrainment by light-dark cycles and to what extent the overt circadian rhythm reflects the rhythm of the light sensitive oscillator. [The light sensitive oscillator, or the A-oscillator, is an innate entity, not yet physically localized, which responds to the light-dark regime, and on which the overt circadian activity, the B-oscillator, is locked (13).]

In order to study the mechanism of entrainment by light-dark cycles many workers have used the effects of single light pulses on the phase of an otherwise free running circadian oscillation [summarized by Aschoff (1) and Pittendrigh (11)]. This method was applied also to the rhythm of leaf movement of the day-neutral-plant *Phaseolus multiflorus* (9) and the rhythm of petal movement of the short-day-plant *Kalanchoe blossfeldiana* (3, 4). The results of these studies have shown that the effect of light signals on the rhythm of higher plants is similar to what is known for other organisms. However, for *K. blossfeldiana*, Bunning and Zimmer (3) concluded that the overt rhythm of petal movement cannot be dissociated from the light sensitive oscillator, whereas Engelmann and Honegger (4) concluded that the coupled oscillator model fits unequivocally their results.

Since the time measurement process in a photoperiodically sensitive plant occurs when the plant is still in the vegetative stage, it seems necessary to study the circadian rhythm before the plant flowers. This paper reports a detailed study of the behavior of the circadian rhythm of leaf movement in a short-day-plant, *Coleus blumei* x *C. frederici*, as affected by single light or temperature signals of different durations. This study suggests that the overt rhythm of leaf movement entrains by light signals and is locked to the light sensitive oscillator: separation between the overt leaf movement rhythm and the light sensitive oscillator occurs only after a temperature pulse.

Materials and Methods

The method for leaf movement recording and conditions of plant growth were as previously described (5).

A standard procedure was adopted of entraining the plants by 3 to 4 cycles of 12 hr light and 12 hr dark (LD 12:12) at 21 ± 1°, perturbing them with a light signal of 1300 ft-c or a temperature decrease, and then subjecting them to dim light of 10 ft-c for another 4 cycles at 21 ± 1° unless otherwise stated.

In preliminary experiments 1 or 2 hr of light perturbations, given at different clock times, did not

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cause any shifts in the circadian rhythm of leaf movement. Therefore 4 and 8 hr signals were used The controls used for all light signal experiments were plants entrained to LD 12:12 and transferred to dim light of 10 ft-c at the end of the last main light period. The results of 3 such control runs each containing 5 plants, were not statistically different and were pooled together to be used as a unit. A few of the light signal experiments were repeated and the results are included in the tables and the figures.

The terminology and designations used in this paper are as described by Pittendrigh (12): The last day in light-dark cycle is defined as Day 0. Day 1 is the first day in constant light or dark, Day 2 the second, and so on. Subjective day and subjective night are the first and second halves, respectively, of the circadian cycle. Circadian time, or the CT scale, is the time scale of the circadian rhythm. The scale measures the full circadian cycle of the organism and runs from CT 0 to CT 24. One CT unit is equal to the free running period divided by 24 hr. CT 12 corresponds to the time at which the lights were turned off on Day 0 in a light-dark cycle of 12 hr light and 12 hr dark.

Results

Single Light Signals Lasting 4 Hr. Plants entrained to three LD 12:12 cycles were interrupted by 4-hr light signals applied during the night of Day 0 and Day 1. In several experiments, marked by an asterisk in table I, the light signals were preceded by dim light, contrary to the general procedure of a preceding dark period. Changing the standard procedure was necessary in the case of light signals interrupting the late Subjective night 1, since the absence of a "light on" signal in a rhythm under 24 hr dark period, caused a 3-hr delay; this is avoided in the presence of dim light (5). The results show that having dim light preceding the light signals (table I, light signals at hr 1200 eastern standard time) did not change the amount of phase shift compared to having dark preceding them. The only difference noted was that more cycles were needed to reach a steady state phase shift when dim light preceded the light signal.

The results summarized in table I and figures 1 and 2 show the following characteristics of the response to 4-hr light signals: A) The maximum steady state phase shift resulting from a 4-hr light signal was about 6 hr for delays and 8 hr for ad-

Table I. *Phase Shifts of Time of Minimum Leaf Position Resulting From 4-hr Light Signals*

Plants were kept in light-dark cycles of 12 hr light and 12 hr dark prior to the 4-hr light signals. Day 0 is the last day with a 12 hr light period. Constant dim light of 10 ft-c followed the light signals which were given at various carcadian times (CT) either during the Subjective night of Day 0 or on Subjective day 1. Each value is the mean time of minimum leaf position of 5 plants ± Standard Error (S. E.). The phase shift ($\Delta\ \Phi$) is calculated by subtracting the mean of the perturbed cycle from the control.

Time of onset of light signal		Daily means (EST) and phase shifts ($\Delta\Phi$) in hr											
		Day 1			Day 2			Day 3			Day 4		
EST	CT	EST	S.E.	$\Delta\Phi$	EST	S.E.	$\Delta\Phi$	EST	S.E.	$\Delta\Phi$	EST	S.E.	$\Delta\Phi$
Control		2348	± 0.39		2200	± 0.23		2154	± 0.53		2116	± 0.45	
Subjective night 0:													
2000	1200	0512	± 0.52	—5.4	0354	± 0.64	—5.9	0224	± 1.07	—4.5	0124	± 1.08	—4.2
2200	1408	0400	± 0.50	—4.2	0300	± 0.54	—5.0	0224	± 0.81	—4.5	2230	± 0.30	—1.3
2300	1512	0600	± 0.70	—6.2	no data			0400	± 0.95	—6.1	0330	± 1.80	—6.3
2300	1512	0400	± 0.32	—4.2	0336	± 0.51	—5.6	0506	± 0.33	—7.2	0406	± 0.46	—6.8
2400	1616	0454	± 0.32	—5.1	0206	± 0.31	—4.1	2336	± 0.26	—1.7	1800	± 0.00	+3.2
0100	1720	0448	± 0.58	—4.0	0200	± 0.74	—4.0	2336	± 0.40	—1.7	2230	± 0.86	—1.3
0200	1824	1848	± 0.37	+5.0	1700	± 0.44	+5.0	1542	± 0.49	+6.2	1300	± 0.55	+8.2
0200	1824	2024	± 1.10	+3.4	1630	± 0.29	+5.5	1530	± 0.66	+6.4	no data		
0400	2032	2306	± 0.33	+0.7	2000	± 0.42	+2.0	1936	± 0.66	+2.3	1736	± 1.20	+3.6
0400	2032	2130	± 0.23	+2.4	1736	±0.67	+4.4	1612	± 0.49	+5.7	no data		
0600	2240	2336	± 0.40	+0.2	2154	±0.40	+0.1	2036	± 0.81	+1.3	1848	± 1.25	+2.4
Subjective day 1:													
0800	0048	0036	± 0.26	—0.8	2312	± 0.37	—1.2	2200	± 0.20	—0.1	2042	± 0.75	—0.5
1200	0456	0248	± 0.37	—3.0	0048	± 0.45	—2.8	0024	± 0.92	—2.5	2318	± 0.75	—2.1
1200[1]	0456	2300	± 0.40	+0.8	2324	± 0.81	—1.4	0100	± 0.41	—3.1	2336	± 0.60	—2.4
1600	0872	0418	± 0.38	—4.5	0418	± 0.25	—6.3	0330	± 0.75	—5.6	no data		
2000	1288	0600	± 0.00	—6.2	0536	± 0.52	—7.6	0430	± 0.28	—6.6	0318	± 0.25	—6.1
2400[1]	1704	2436	± 0.40	—0.8	0136	± 0.61	—3.6	0336	± 0.51	—5.8	0218	± 0.85	—5.1
0200[1]	1912	2400	± 0.57	...	0218	± 0.33	—4.3	1318	± 1.35	+8.6	1318	± 0.25	+7.9
0400[1]	2120	2354	± 0.51	...	1912	± 0.20	+3.8	1848	± 0.63	+3.1	1748	± 1.15	+3.4

[1] Dim light started at the end of the main light period.

vances. B) The transition from maximum delays to maximum advances occurred during the late subjective night. The slope of the transition line was slightly different when signals were given on Day 0 or Day 1. For Day 0 the transition from maximum delays to maximum advances was between CT 15.1 and CT 18.2, whereas for light signals given on Day 1 it was between CT 17 and 19.2. C) When the system was delayed, a steady state was achieved by the second cycle in constant dim light. When the system was advanced, it took 3 to 4 cycles to reach the steady state condition. This is similar to the response of the *Drosophila* eclosion rhythm (14, fig 7). D) The amplitude of the rhythm was generally not affected much by the light signals except for a transient damping following a light signal at hr 2400 EST; this is evident from the example shown in figure 1 and from a comparison of the amplitude of each plant on the last day in light-dark cycle and on the third cycle in dim light.

Single Light Signals Lasting 6 to 8 Hr. Six and 8-hr light signals were concentrated around the region of transition from maximum delays to maximum advances on Subjective night 0. With 8-hr light signals, the system attained its maximum phase shift, which was 12 hr (table II and fig 2,3). The nature of this transition from maximum delays to maximum advances was abrupt rather than gradual as with the 4-hr as well as the 6-hr light signals. Perturbing the system with 6-hr light pulses gave values intermediate between those for 4 and 8 hr (table II and fig 2).

Two Consecutive Signals. Experiments were conducted to elucidate which of the following empirical models applies to the circadian rhythm of

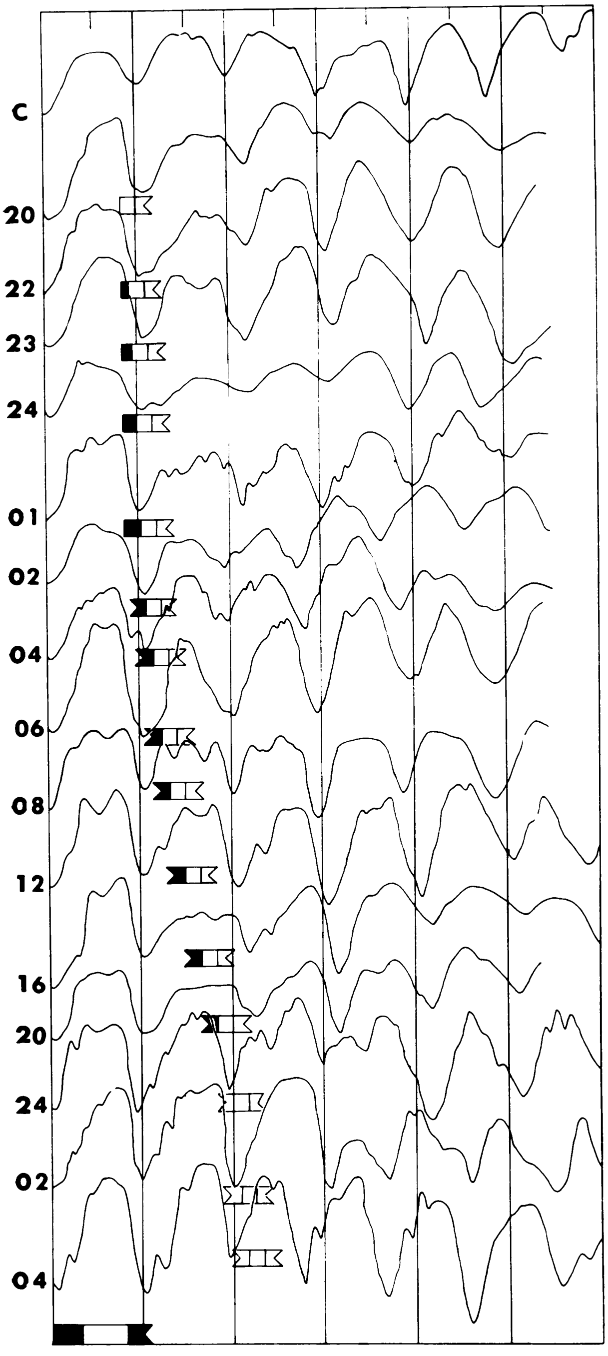

FIG. 1. Tracings of the nyctinastic leaf movement of *Coleus* before and after single light signals. Plants entrained to LD 12:12 (lights on at 0800 EST) were given 4-hr light signals after which they were exposed to dim light of 10 ft-c. Each curve represents the individual leaf movement of 1 plant. The uppermost tracing is the control (C). Vertical numbers indicate the hr in EST of the beginning of the light signal. Empty bars below each tracing indicate the light signal. Black and white bars below indicate the last dark:light cycle, respectively. Vertical lines are 24 hr apart and indicate hr 2400.

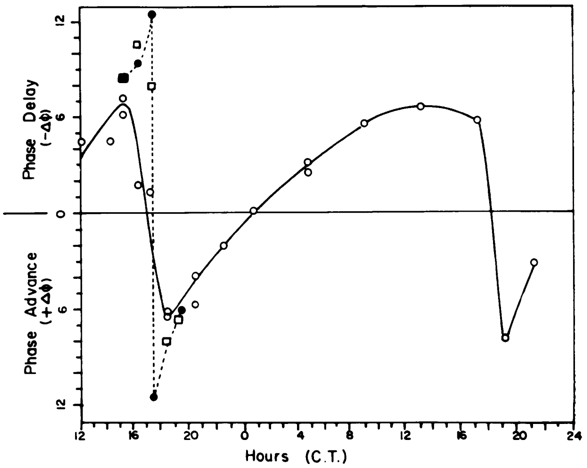

FIG. 2. Phase response curves for the nyctinastic leaf movement of *Coleus blumei* x *C. frederici.* Each point on the curve represents the steady state phase shift ($\Delta\Phi_{ss}$), based on the third cycle after the light signal for delays, and on the fourth cycle in the case of advances. Each point is an average of 5 plants and represents 1 experiment. ————. and ○: 4-hr light signals. — — — and ●: 8-hr light signals. □: 6-hr light signals.

Table II. *Phase Shifts of Time of Minimum Leaf Position Resulting From 6 and 8-hr Light Signals*

Plants were kept in light-dark cycles of 12 hr light and 12 hr dark prior to the light signals. Day 0 is the last day with a 12 hr light period. Constant dim light of 10 ft-c followed the light signals which were given at various circadian times (CT). Each value is the mean time of minimum leaf position of 5 plants ± Standard Error (S.E.). The phase shift (ΔΦ) is calculated by subtracting the mean of the perturbed cycle from the control, which is given in table I.

Time of onset of light signal		Daily means (EST) and phase shifts (ΔΦ) in hr											
		Day 1			Day 2			Day 3			Day 4		
EST	CT	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ
a. 6-hr light signals:													
2300	1512	0512	± 0.58	—5.4	0500	± 0.41	—7.0	0624	± 0.60	—8.5	no data		
2400	1616	0518	± 0.49	—5.5	0700	± 0.57	—9.0	0830	± 0.30	—10.6	0624	± 0.47	—9.2
0100	1720	0730	± 0.87	—7.7	0848	± 0.83	—7.8	0848	± 0.63	—7.9	0530	± 0.76	—8.3
0200	1824	2024	± 0.51	+3.4	1618	± 0.43	+5.7	1354	± 0.55	+8.0	1130	± 0.86	+9.7
0300	1828	1812	± 0.47	+5.6	1530	± 0.34	+6.5	1412	± 0.31	+7.7	1448	± 0.31	+6.4
0600	2240	2200	± 0.33	+1.8	1924	± 0.40	+2.4	2048	± 0.56	+1.1	1912	± 0.73	+2.0
b. 8-hr light signals:													
2300	1522	0918	± 0.44	—9.5	0500	± 0.00	—7.0	0536	± 0.67	—7.7	0506	± 0.43	—7.9
2400	1616	0918	± 0.28	—9.5	0736	± 0.66	—9.6	0618	± 0.63	—8.5	0630	± 0.77	—9.3
0100	1720	1342	± 0.25	+10.1	0900	± 0.41	+13.0	1000	± 1.20	+11.9	0942	± 0.55	+11.5
0300	1928	2100	± 0.41	+2.8	1800	± 0.57	+4.0	1612	± 0.47	+5.7	1130	± 0.50	+9.7
1400	0664	0230	± 0.50	—2.7	0500	± 0.41	—7.0	0600	± 1.03	—8.1	0730	± 0.50	—10.3

Table III. *Phase Shifts Resulting From Two Signals*

Each tabulated value is the mean time of minimum leaf position ± Standard Error (S.E.). The number of plants for each experiment is given in parentheses. The phase shift (ΔΦ) is calculated by subtracting the mean of the perturbed cycle from the control, which is given in table I. A. Two successive light signals (each 4 hr in duration) were given. The first was given during the night of Day 0 and the second during the night of Day 1. B. A temperature signal (7° decrease for 8 hr or 11° decrease for 10 hr) was given during the night of Day 0. This was succeeded by a 4 hr light signal during the night of Day 1.

	Onset of signal		Daily means (EST) and phase shifts (ΔΦ)													
	1st	2nd	Day 1			Day 2			Day 3			Day 4			Day 5		
	EST	EST	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ	EST	S.E.	ΔΦ
A. Two successive light signals:																	
(4)	0400	2200	2245	± 0.25	+1.0	1200	±0.41	+10.0	0245	±0.50	—4.2	0523	±0.68	— 6.2	0500	±0.59	—6.0
(6)	0400	2200	2109	± 0.17	+1.7	1715	±0.40	+ 4.8	1400	±0.71	+7.9	1208	±0.18	+ 9.0			
B. Temperature signal succeeded by light signal:																	
7° temp. decrease																	
(5)	2200	...	0200	± 0.00	—2.2	2400	±0.76	— 2.0	2148	±0.49	...	2000	±0.20	+ 1.2			
(4)	2200	0200	0248	± 0.37	—3.0	0124	±0.29	— 3.4	2348	±0.58	—1.9	1700	±0.46	+ 4.2	1324	±0.28	+7.6
(1)	2200	0200	0200	±	—2.2	0100		— 3.0	1500		+6.9	1330		+ 7.7	1300		+8.0
11° temp. decrease																	
(5)	2330	...	0348	± 0.49	—4.0	2436	±0.51	— 2.6	2400	±1.26	—2.1						
(5)	2330	0130	0224	± 0.51	—2.6	0624	±0.25	— 8.4	0454	±0.60	—7.0	0424	±0.67	— 7.2	0224	±0.26	—5.4

leaf movement in *Coleus*: A) The overt rhythm of leaf movement is the manifestation of the underlying light sensitive oscillator, including the transient phase which follows a light signal, as suggested by Bunning and Zimmer (3), or B) The steady state phase shift reached by the third and fourth cycle reflects the immediate response of the light sensitive oscillator, the view of Pittendrigh *et al.* (11, 13).

The experiments were essentially those described by the above-mentioned authors. They were designed so that only delays would be predicted by the first hypothesis and advances by the second. It is apparent from the response to 4-hr light signals that the region of minimum leaf position marks the transition region from maximum delays to maximum advances; perturbations before and at minimum leaf position cause delays, whereas perturbations after, until CT 0, result in advances. Therefore the first 4-hr light signal was started at 0400 EST of Day 0 and the second one at 2200 of Day 1. According to the hypothesis that the overt rhythm of leaf movement represents the underlying light sensitive oscillator, the second light break should cause a delay since it started at the minimum leaf position; according to the second hypothesis the reference point of minimum leaf position on the A-oscillator occurs 3 hr earlier (according to a steady state phase shift of + 5.8 hr for single light signal, table I). The second light signal should therefore cause an advance.

The results summarized in table IIIA and figure 4 fit Bunning's model for the behavior of the leaf movement rhythm. They show that the steady state phase shift of 4 plants (table IIIA first row and fig 4 upper tracing) which were at the minimum leaf position when the 2nd light signal started, was a delay of 6 hr, exactly the amount of phase shift caused by a single light signal at this phase of the overt rhythm, when not previously perturbed. A group of plants in the same experiment (table IIIA bottom row and fig 4 lower tracing) which reached their minimum leaf position about an hr earlier than the average of the first set of plants, showed an advance of 8 to 9 hr, a magnitude characteristic of the response to single light perturbation at this phase of the overt rhythm. The advance, according to the second hypothesis should be run in the order of +3 hr.

In view of these results, the question arises whether one can distinguish between the light sensitive oscillator and the overt rhythm in *Coleus* leaf movement. To answer this question a method designed to separate the light and temperature effects similar to that suggested by Pittendrigh *et al.* (13) was used. Plants entrained by light-dark cycles, then kept in dim light, received a 7° temperature drop (from 21°–14°) for 8 hr, starting at hr 2300 EST on Day 0, where according to Wagner (15) there was a significant response to a low temperature pulse in *Phaseolus multiflorus* leaf movement. The results show (table IIIB) that the first 2 cycles after the temperature pulse were delayed by about 2 hr, but that this delay did not persist into the third and fourth cycle. Figure 5, middle tracing, indicates that lowering the temperature in this manner did not change the actual pattern of the leaf movement.

In another experiment the same temperature decrease was followed by a 4-hr light signal at hr 0200 EST on Day 1. If the transients recorded during the first 2 cycles after the temperature perturbation indicated the position of the light sensitive oscillator, the light signal would start at CT 17.04 and should cause a delay of about 5.1 hr (table I); but if the light sensitive oscillator was not actually

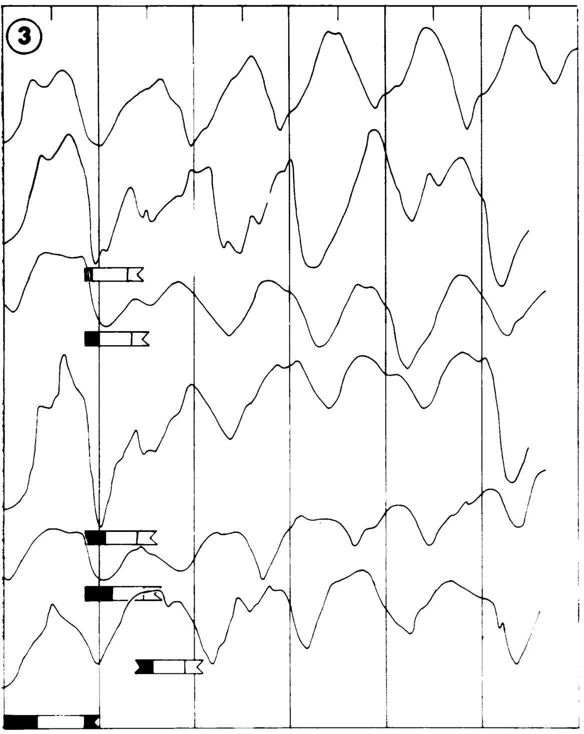

Fig. 3. Tracings of the nyctinastic leaf movement of *Coleus* before and after 8-hr light signals. Other specifications as in figure 1.

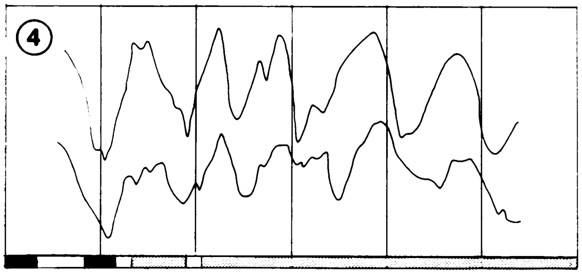

Fig. 4. Samples of leaf movement tracings of *Coleus* before and after 2 successive light signals each lasting 4 hr; the first one started at hr 0400 and the second at hr 2200 EST. Top figure represents the group of plants in which the second light signal started at the time of minimum leaf position. Bottom figure represents the group of plants in which the second light signal started after the time of minimum leaf position.

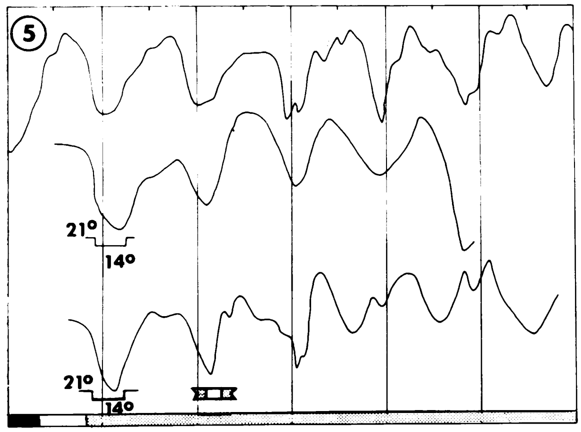

Fig. 5. Samples of leaf movement tracings before and after a temperature decrease of 7° followed by a light signal. Top: A control sample of leaf movement at a constant temperature of 21° and under constant dim light of 10 ft-c. Middle: A sample of leaf movement tracing before and after a temperature decrease of 7° for 8 hr, starting at hr 2200 EST. Plants were kept in dim light of 10 ft-c. starting at the end of the main light period. Botton: Temperature decrease as above followed by a 4-hr light signal starting at hr 0200 EST.

perturbed, as the steady state phase indicated, then the light signal would fall at CT 19.12, as in the control, and should result in a phase shift of +8 hr. The results summarized in table IIIB and the sample of leaf movement tracing in figure 5, show that indeed the response was as if the light sensitive oscillator was not disturbed at all; the steady state phase shift was an advance of about 7.6 to 8 hr.

In another experiment in which the temperature was lowered to 10° for 10 hr, there was a steady state delay of about 2 hr. When the same temperature pulse was followed by a 4-hr light signal starting at hr 0130 EST of Day 1, there was a delay of about 7 hr, a predictable response of the light sensitive oscillator (table IIIB). Lowering the temperature to 10° for 10 hr also diminished the amplitude of the leaf movement rhythm for the following 2 cycles (about 48 hr). This indicates that the physiological processes involved were disturbed. This is not surprising since *Coleus* is a subtropical plant whose optimal temperature for growth is about 30°.

Discussion and Conclusions

A phase response curve to light signals based on the steady state phase shift is presented for the rhythm of leaf movement of *Coleus blumei* x *C. frederici,* a short day plant in its flowering response (8). The phase response curve of *Coleus* is similar to those of other organisms as summarized by Aschoff (1) and Pittendrigh (11). Light perturbations occurring during the first half of the Subjective day and early Subjective night delay the circadian rhythm of leaf movement, while those occurring during the late Subjective night advance it. The transition from maximum delays to maximum advances occurs at the beginning of the second half of the Subjective night. When the system is phase delayed after a light signal, it takes 1 to 2 cycles to reach the steady state free running period. On the other hand, in the case of advances the system does not reach its steady state until the third or the fourth cycle.

The duration of the light pulse also determines the amount of phase shift; the maximum amount of phase shifting with 4-hr light signals is about half of the maximum phase shift with 8-hr light signals. The amount of phase shift with 6-hr light signals is between these two. In addition, the transition from maximum delays to maximum advances is gradual in the case of the 4-hr and 6-hr light perturbations, but it is abrupt when the system is perturbed with signals of 8-hr duration.

An increase in the amount of phase shift as a result of an increase in the duration of the light signal has also been reported for the luminescence rhythm in *Gonyaulax* (6, 7), leaf movement rhythm of *Phaseolus multiflorus* (2) and *Kalanchoe* petal movement rhythm (Engelmann, unpublished). Most of the light signals were administered at 1 specific clock time. The results, for several clock times, have been obtained with the eclosion rhythm of *Drosophila* (10) and *Pectinophora* egg hatching rhythm (Horn, unpublished).

An experiment using 2 consecutive light signals indicates that the overt rhythm of leaf movement, which undergoes transient shortening or lengthening of the free running period, accurately reflects the behavior of the light sensitive oscillator. A 7° temperature decrease perturbs the overt rhythm of leaf movement but apparently does not affect the light sensitive oscillator. Therefore light signals given after such a temperature decrease result in a response characteristic of the phase of the underlying light sensitive oscillator and not of the overt B-oscillator. One can speculate that light sensitive and temperature sensitive oscillators exist in *Coleus* plants as 2 separate entities normally locked together, the A-oscillator driving the B-oscillator as in the case of *Drosophila* (12, 13). Bunning and Zimmer (3) concluded that the overt petal movement of *Kalanchoe* flowers represents the immediate response of the light sensitive oscillator. They followed the rhythm for 1 to 2 cycles after the second light signal. Engelmann and Honegger (4) studied the same plant with the same method, but followed the rhythm for 5 cycles after the second light signal. Their results are different from the previously mentioned authors' in the sense that they support the model of the 2 coupled oscillators system; phase shifting by the second signal could be explained only on the basis that transients following the first light signal are due to the B-oscillator regaining phase with the light sensitive oscillator. However, some of their results could not be explained by this model, and they suggested that 2 rhythms were initiated by a given light signal, one by the light on signal and another by the light off signal. Thus, a model involving 2 coupled oscillators can be applied to circadian rhythms in higher plants. The difference between the *Kalanchoe* petal movement and *Coleus* leaf movement is that in the latter the A and B oscillators are unlocked from each other only after a temperature perturbation, but not after light signals, where the overt rhythm is a true manifestation of the light sensitive oscillator.

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Literature Cited

1. Aschoff J. 1965. Response curves in circadian periodicity. In: Circadian Clocks, J. Aschoff, ed. Amsterdam: North Holland Publishing Company. 95–111.

2. BÜNNING, E. AND I. MOSER. 1966. Response-Kurven bei der circadianen Rhythmik von *Phaseolus*. Planta 69: 101–10.
3. BÜNNING, E. AND R. ZIMMER. 1962. Zur Deutung der Phasenverschiebungen und "Transients" nach exogener Störung endogener Rhythmen. Planta 59: 1–14.
4. ENGELMANN, W. AND H. W. HONEGGER. 1967. Versuche zur Phasenverschiebung endogener Rhythmen: Blütenbewegung von *Kalanchoë blossfeldiana*. Z. Naturforsch. 22B: 200–04.
5. HALABAN, R. 1968. The circadian rhythm of leaf movement of *Coleus blumei* x *C. frederici*, a short-day-plant. I. Under constant light conditions. Plant Physiol. 43: 1883–86.
6. HASTINGS, J. W. 1964. The role of light in persistent daily rhythms. In: Photophysiology. A. C. Giese, ed. Academic Press, New York and London. 333–61.
7. HASTINGS, J. W. AND B. M. SWEENEY. 1958. A persistent diurnal rhythm of luminescence in *Gonyaulax polyedra*. Biol. Bull. 115: 440–58.
8. KRIBBEN, F. J. 1955. Zu den Theorien des Photoperiodismus. Beitr. Biol. Pflanzen. 31: 296–311.
9. MOSER, I. 1962. Phasenverschiebungen der endogenen Tagersrhythmik bei *Phaseolus* durch Temperatur und Lichtintensitätsänderungen. Planta 58: 199–219.
10. PITTENDRIGH, C. S. 1960. Circadian rhythms and the circadian organization of living systems. Cold Spring Harbor Symp. Quant. Biol. 25: 159–84.
11. PITTENDRIGH, C. S. 1965. On the mechanism of the entrainment of a circadian rhythm by light-cycles. In: Circadian Clocks. J. Aschoff, ed. Amsterdam: North Holland Publishing Company. 277–97.
12. PITTENDRIGH, C. S. 1967. Circadian systems. I. The driving oscillation and its assay in *Drosophila pseudoobscura*. Proc. Natl. Acad. Sci. U.S. 58: 1762–67.
13. PITTENDRIGH, C. S., V. G. BRUCE, AND P. KAUS. 1958. On the significance of transients in daily rhythms. Proc. Natl. Acad. Sci. U.S. 44: 965–73.
14. PITTENDRIGH, C. S. AND D. H. MINIS. 1964. The entrainment of circadian oscillation by light and their role as photoperiodic clocks. Am. Naturalist 98: 261–94.
15. WAGNER, R. 1963. Der Einfluss niedriger Temperatur auf die Phasenlage der endogenen tagesperiodischen Blattbewegungen von *Phaseolus multiflorus*. Z. Botan. 51: 179–204.