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The control of blooming in *Sauromatum guttatum* (Araceae) by darkness[1]

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When an inflorescence of *Sauromatum guttatum* Schott blooms, the spathe unfolds and exposes the spadix. After spathe-opening, the terminal portion of the spadix (appendix) undergoes a dramatic respiratory climacteric (RC) which is characterized by the production of copious quantities of CO_2 and the concomitant warming of the appendix.

In experiments conducted on inflorescences raised under continuous irradiation, we have shown that darkness is the environmental factor which triggers the blooming. The moment of the peak in CO_2 (or heat) production during the RC was used as an index of blooming.

The darkness which triggers the RC is "perceived" by the staminate flowers, borne on the spadix beneath the appendix. Darkness is also involved in (1) regulating the lag time between the inductive dark period and the moment of the peak in the RC, and (2) opening the spathe.

Introduction

During the blooming of *Sauromatum guttatum* Schott (Fig. 1), the spathe of the inflorescence unfolds and exposes the spadix. Spathe-opening, which starts before daybreak, is followed by a dramatic respiratory climacteric (RC) which occurs in the appendix (the sterile, cylindrical, terminal portion of the spadix) in the late morning. Copious amounts of CO_2 are released from the appendix, usually at the expense of a large starch reserve (van Herk 1937*a*). The intense burst of respiration is also accompanied by a simultaneous warming of the appendix. In an extreme case, that of *Schizocasia portei* Schott, where the respiratory substrate seems to be a fatty substance, the temperature of the spadix may reach a level 22° higher than the ambient air temperature (El-Din 1968). Coincident with the development of the climacteric is the production of an unpleasant odor by the appendix (Smith and Meeuse 1966). The mechanism of the respiratory process has been most intensively studied in Eastern skunk cabbage, *Symplocarpus foetidus* (L.) Salis. (Erecinska and Storey 1970). The RC in *Symplocarpus*, however, is quite subdued and this species lacks the specialized appendix.

Depending on the species of arum lily, stench production and the respiratory flare-up may occur either once or on several successive days during the life of an inflorescence (Leick 1915; van der Pijl 1937). Blooming may occur in the morning, e.g. in *Sauromatum guttatum* (van Herk 1937*b*), and *Arum dioscoridis* Sibth & Sm. (our observations); or in the afternoon and early evening, e.g. in *Arum maculatum* L., *Arum italicum* Mill. (James and Beevers 1950; Prime 1960), and *Arum orientale* Bieb. (our observations). We now report experiments which demonstrate the control of blooming of *Sauromatum* by darkness. A preliminary note on some of this work has already appeared (Meeuse and Buggeln 1969).

Materials and Methods

Treatment of Corms and Inflorescences

Sauromatum corms produce two or more palmately lobed leaves which die at the end of a 4- to 5-month growing season. After a brief quiescent period (2–4 months) a corm produces a single inflorescence. Development of an inflorescence to maturity (under greenhouse conditions) generally takes less than a month. A second quiescent period occurs between the death of an inflorescence and the appearance of new leaves.

Plants of *Sauromatum* were grown in the New Botany Greenhouse, University of Washington. As soon as the leaves died, the corms were dug from the soil and brought into the laboratory where the inflorescences were allowed to develop to maturity under continuous fluorescent irradiation ($0.8–1.5 \times 10^3$ ergs $cm^{-2}\,s^{-1}$ from Sylvania "Grow-Lux" and "Lifeline"; Ken-Rad "Coolwhite" lamps) and at 24°–29°C. The size of the inflorescence (height and weight) varied with the size of the corms, e.g. small corms produced small inflorescences, etc., and no effort was made to select inflorescences within a specific size range for experiments.

A mature inflorescence can be expected to have the following characteristics: the base of the spathe becomes

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swollen and turns burgundy in color; the margin of the spathe above the level of the staminate flower zone becomes crimped or scalloped.

When an inflorescence reached maturity it could be triggered to bloom by one of the methods outlined below. Any inflorescence which was not triggered to bloom at this time ultimately underwent a rather "incomplete" blooming. In such cases, the bulbous base of the spathe became weak as a result of the separation of the outer and inner cortex into two laminae. The spathe, which never unfolded, lost its turgidity and sagged around the appendix. Although some stench, heat, and CO_2 were produced, these events occurred at no predictable time.

Corms were frequently placed in a cold box (10°C; 12-h photoperiod at an irradiance of $1.0–4.0 \times 10^4$ ergs $cm^{-2}\ s^{-1}$ from G.E. "White;" Sylvania and Ken-Rad, "Coolwhite" lamps) to retard the development of the inflorescences. There were no noticeable deleterious effects to the corms or inflorescences from 2 months of cold storage.

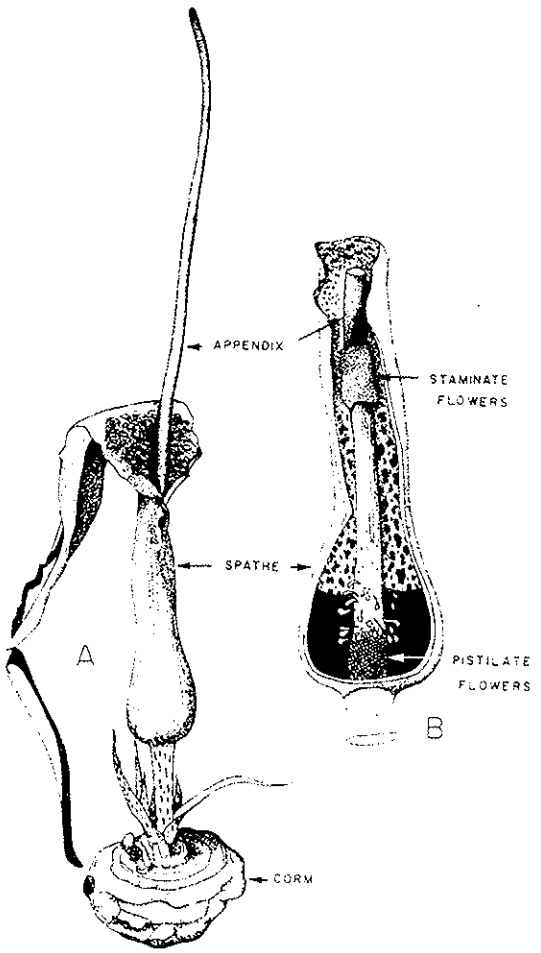

FIG. 1. Drawing of *Sauromatum guttatum* inflorescence. A. The inflorescence in bloom. B. Longitudinal section through the spathe, exposing the spadix.

The experiments were conducted in humidified, plywood cabinets which were supplied with exhaust fans for ventilation. Radiation was provided from opposing banks of fluorescent tubes (G.E. and Sylvania "Coolwhite" and "Daylight"). The irradiance, although constant during any one experiment, varied in the range of 0.8 to 2.0×10^4 ergs $cm^{-2}\ s^{-1}$ between experiments. Earlier data (Meeuse and Buggeln 1969) indicated that the phenomenon under observation, i.e. the moment of appearance of the maximum rate of respiration during the RC, was not influenced by this range of intensities. The temperature of the experimental cabinets varied with the ambient air temperature. During periods of darkness, the temperature ranged from 23° to 25°C; during the light periods, the range was 25° to 28°C.

Measurement of CO_2 Production

Van Herk (1937*b*) and Meeuse (unpublished observations) found that the moments of the maximum rates of CO_2 and heat production during the RC never occurred more than a few hours apart. Under greenhouse conditions, these peak rates were usually reached between 0800 and 1100 h. The moment of maximum CO_2 or heat production was a more useful index of blooming than spathe opening. The latter was unsuitable because the process of opening was continuous, lasting 6 or more hours and lacking clearly defined stages. Also, under some experimental conditions (see below), the RC occurred in the absence of spathe opening.

The following method was used to measure the CO_2 respired from either intact inflorescences or isolated appendices. The inflorescences (or appendices) were placed in Plexiglas cuvettes and air was continuously pumped through the cuvettes and into specially constructed conductivity cells.* As air containing CO_2 was bubbled through a cell, which contained 4 l of 0.125 *N* NaOH, the conductivity of the solution decreased. The solution, then, served as a variable resistance. The magnitude of this resistance was directly proportional to the amount of CO_2 with which the solution had reacted. The system was temperature-compensated to correct for temperature-caused changes in resistance of the NaOH solution. The resistance was ultimately recorded on a Rustrak 0–10 mV recorder (Rustrak Instruments Co. Inc., Manchester, N.H.). Each cell was calibrated by admitting known amounts of CO_2 into the cell and plotting the corresponding recorder readings against grams of CO_2. This conductometric method enabled us to record both the total amount of CO_2 produced by an inflorescence and the rate of production per unit time.

Measurement of Temperature

A direct-reading electronic thermometer (YSI model 43; Yellow Springs Instruments, Yellow Springs, Ohio) was used to measure the temperature of an appendix. Thermometer probes (YSI model 409) were attached to the surface of the appendix with thin strips of polyurethane. The sensors (sensitivity ±0.5°C) were read in sequence as the thermometer input was switched from probe to probe by a motor-driven, recycling, selector switch (designed and constructed by John R. Klima). The temperature was recorded on a "Servo-riter" potentiometric

*Full information regarding the apparatus can be obtained from J.R.K. on request.

recorder (Texas Instruments Co., Houston, Texas) with a full-scale deflection of 0–10 mV and a temperature range of 15° to 35°C. To monitor the ambient temperature, one probe was left permanently attached to a Plexiglas screw-cap tube filled with water.

Experiments and Results

Triggering the RC: Effect of a Single Dark Period

The results of experiments in which mature inflorescences (grown under continuous irradiation) received single dark periods of various lengths, followed by continuous irradiation, are presented in Table 1 and Fig. 2. The minimum length of the dark period required to trigger the RC was 5 h. In this case, the mean lag time, i.e. the time between the start of a treatment which induces the RC and the peak in either the rate of CO_2 production or the temperature rise during the RC, was 47.3 h. The longest lag time (56 h) occurred after a dark period of 24 h.

In a second series of experiments, single 6-h dark periods were given to inflorescences at different times during the "normal" 24-h day. The uniform length of the lag times (Table 2) indicated that the effect of the dark periods was independent of solar time. This result was not unexpected inasmuch as the inflorescences were raised under continuous irradiation. In the absence of a day/night entraining regime, there was no programmed 24-h "cycle of sensitivity" with respect to the effect of a 6-h dark period on the inflorescence. A number of reports have indicated that the amplitudes of rhythmical physiological processes in plants dampen when the plants are held under constant environmental conditions (Schön 1955; Karvé *et al.* 1961; Todt 1962; vanden Driessche 1966; Cumming 1967).

TABLE 1

Lag times for single dark periods of various lengths

Length of dark period, h	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
5	47.3	45–51	±2.6	4
6	43.2	40–48	±2.0	14
12	43.4	41–46	±2.2	8
18*	48.1	(36) 45–55	±5.7	8
24†	56.3	(38) 50–60	±3.0	9
27	46.2	44–48	±1.4	4
30	47.1	42–51	±3.1	6
Continuous darkness‡	46.0	42–50	±3.2	4

*An isolated value, in parentheses, almost rejected at the 90% confidence level by evaluation of the *Q*-test (Dean and Dixon 1951).
†An isolated value, in parentheses, rejected by evaluation of the *Q*-test. The mean and standard deviation have been computed without this datum.
‡Dark periods 50 to 55 h long.

Darkness and the Staminate Flower Zone

We conducted several experiments which demonstrated that the zone of staminate flowers was the part of the inflorescence which "perceived" the inductive dark period. First, selected floral parts (e.g. pistillate flowers, staminate flowers, or appendix) of mature, intact inflorescences were given 6-h dark periods by wrapping pieces of aluminum foil around the spathes to cover the

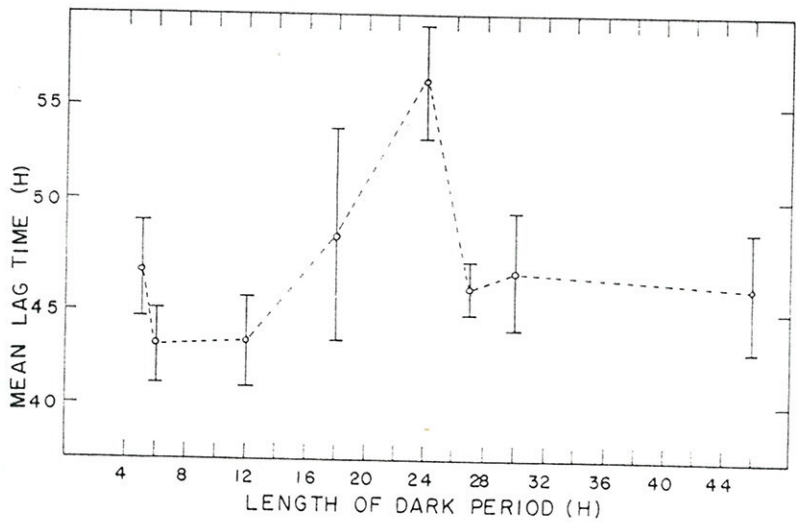

FIG. 2. The relationship between the length of a single dark period and the mean lag time to the peak in the RC. (Standard deviation indicated about each mean.)

TABLE 2

The lag times for 6-h dark periods which were begun at different hours of the day

Hour of onset of darkness	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
0600	41.7	41–43	±1.0	4
1200	42.5	41–44	±1.4	4
1730	42.6	41–45	±2.1	3
1800	41.5	40–44	±1.6	8
1900	42.5	42–43	±0.2	2
2100	41.3	39–45	±2.3	6
2400	42.8	41–44	±1.3	7

TABLE 3

Triggering the RC by darkening the staminate flowers for 6 h

	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
Intact inflorescence	44	43–45	±0.2	3
Upper portion of spathe removed	44.5	44–45	±0.2	2

TABLE 4

The effect of a second dark period, started 24 h after the onset of the first 6-h dark period, on the lag time

Length of second dark period, h	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
0*	43.2	40–48	±2.0	14
1	42.5	39–45	±2.6	4
2	40.1	34–46	±5.0	6
3	35.5	35–36	±0.2	4
4	35.3	34–36	±1.2	3
6	36.0	35–37	±1.0	2

*From Table 1.

TABLE 5

The effect of the time of application of a second dark period (3 h) on the lag time

Start of second dark period, h after beginning first 6-h dark period	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
18	41.7	41–42	±0.2	4
24	35.2	35–36	±0.2	4
30	41.0	39–44	±2.2	4
33	41.7	41–43	±1.0	4

desired regions. At the end of the dark period, the inflorescences were placed in cuvettes and respiration was monitored as described.

Second, the upper portions of the spathes of immature inflorescences were removed at a point just below the staminate flower zones and the cut surfaces were coated with silicone grease. At maturity, a 6-h dark period was given to either the appendix or the staminate flower zone. The staminate flowers were darkened by a black Plexiglass cylinder (3.0 × 3.0 cm), held in place with collars of polyurethane. The appendix was darkened by loosely wrapping it with aluminum foil. At the end of the dark periods, the inflorescences were mounted in cuvettes and respiration was monitored. It should be noted that although spathe removal could be performed on immature (= young) inflorescences without creating any obvious physiological disturbances, the performance of this same operation on mature inflorescences triggered the RC (see experiments below).

Darkening the staminate flowers, either in the presence or absence of the spathe, triggered the RC with mean lag times of 44.0 h and 44.5 h, respectively (Table 3). Darkness was without effect on the other organs.

Role of a Second Dark Period

Mature inflorescences were given an initial dark period of 6 h, then a second dark period of 1 to 6 h (24 h later). A second dark period of 6, 4, or 3 h caused a reduction of the lag time from about 43 h (Table 1) to 35 h (Table 4). A second dark period of 1 or 2 h, when compared with the results of a single 6-h dark period (Table 1), did not significantly reduce the lag time.

The shortening of the lag time was dependent upon the moment of application of the second dark period. A second dark period of 3 h had maximum effectiveness when applied 24 h after the onset of the initial 6-h dark period (Table 5 and Fig. 3).

Under our experimental conditions, the effectiveness of the initial 6-h dark period is independent of solar time (Table 2). The response of the inflorescence to a second 3-h dark period may be governed by a circadian endogenous timing mechanism as the length of the lag time is greatly reduced when a second dark period is given 24 h after an initial dark period (Fig. 3). We suggest that an endogenous clock, dampened during the development of the inflorescence under continuous irradiation, is re-engaged in the inflorescence

at the onset of the first dark period. Several authors have shown that biological rhythms, which have been intentionally dampened, can be restarted by exposing plants to one or more periods of darkness (or irradiation) (Karvé *et al.* 1961; Takimoto and Hamner 1964; Papenfuss and Salisbury 1967).

We found that the length of the dark period required to trigger the RC could be shortened from 5 h to 1 h if the inflorescence received a second dark period (24 h after the start of the first dark period). The mean lag time following pairs of 1-h dark periods was a little longer than the mean times for pairs of 2-, 3-, or 4-h dark periods (Table 6). Single experiments were also conducted with pairs of 5-h, 8-h, and 12-h dark periods. The corresponding lag times were 36, 36, and 37.5 h, respectively.

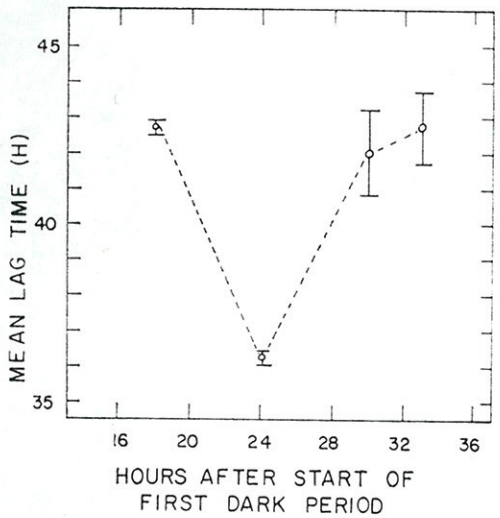

FIG. 3. The relationship between the hour of the onset of the second dark period and the mean lag time to the peak in the RC. (Standard deviation indicated about each mean.)

TABLE 6

The effect on the lag time of two dark periods (less than 6 h apiece) given 24 h apart

Length of each of the two dark periods, h	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
1	40.7	32–48	7.9	5
2	35.0	34–36	1.0	2
3	34.5	33–36	1.6	3
4	33.5	33–34	0.2	2

Response of the Spathe to Darkness

The response of the spathes to single dark periods was quite variable. The spathes did not open if a single dark period was less than 18 h long; they opened incompletely, after 18 h of darkness, and fully after 24 h of darkness. It is interesting that in the latter case, the spathe completed its cycle of opening and shrivelling before the peak in the RC had been reached. The spathe also unfolded after a 27-h dark period, but not after dark periods of 30 or 33 h. Complete spathe opening occurred after pairs of dark periods of 3 h (apiece) or longer.

According to van Herk (1947), the opening of the spathe occurs in response to the hormone, aperiogen. Although the factors which control spathe opening have not been satisfactorily established, we conducted the following experiment which strongly implicated a requirement for darkness. An inflorescence was triggered to bloom by a 6-h dark period. The spathe was removed 10 h after the end of the dark period and cut, transversely, into six pieces which were randomized and then put into water. A second dark period was given to half the sections (24 h after the beginning of the first dark period) while the rest were kept under continuous irradiation. The sections receiving the second 6-h dark period were the ones which opened.

Appendix and the Second Dark Period

An inflorescence was given an initial 6-h dark period, followed 24 h later by a second 6-h dark period given to either the zone of staminate flowers or the appendix. The selective darkening was performed as previously described. In other experiments, a second dark period was given to isolated appendices which had been amputated from inflorescences, 9–14 h after the first 6-h dark period, and placed in water.

TABLE 7

Action of a second 6-h dark period on the appendix

Part of inflorescence receiving second dark period	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
Intact inflorescences				
Staminate flowers	44.2	43–44.5	±0.6	2
Appendix	36.5	36–37	±0.2	2
Isolated appendix	34.8	33.5–37	±0.3	10

TABLE 8
The role of the spathe in triggering the RC

Treatment	Mean lag time, h	Range, h	Standard deviation, h	No. expts.
Complete spathe removal	34.2	33–38	±2.9	10
Slashing the base of spathe	37.2	35–40	±2.2	4

If a second dark period was given to the attached or isolated appendix, the mean lag time was shortened to about 35 h. In contrast, a second darkening of the staminate flowers gave a mean lag time of 44.2 h (Table 7).

Triggering the RC by Spathe Removal

The following experiments were carried out while the inflorescences received continuous irradiation. The spathe of a mature inflorescence was removed at the junction of the spathe and peduncle, and the cut surface was covered with silicone grease. Respiration was monitored as described. A mean lag time of 34.2 h was computed for the interval between the moment of spathe removal and the peak in the RC (Table 8).

Complete removal of the spathe, however, was not required to trigger the RC in mature inflorescences. Fifteen to 20 razor blade slashes (5–8 cm long), made through the swollen base of the spathe and parallel to the main veins, were sufficient to bring about the RC with a mean lag time of 37.2 h (Table 8). Although effective in triggering the climacteric, slashing the spathe did not cause the spathe to open. At the moment, we can only speculate (Buggeln 1969) on the mechanisms involved in inducing the climacteric by rending or removing the spathe.

Discussion and Conclusions

We have studied blooming under controlled conditions to better understand the environmental and physiological conditions which control the process in nature. We have shown that inflorescences raised to maturity under continuous irradiation can be triggered to bloom by darkening only the staminate flowers. We believe that it is the transition from irradiation to darkness which initiates the critical RC-controlling event in the staminate flowers, i.e. the release of calorigen from the staminate flowers (Buggeln and Meeuse 1971). However, as inducing the RC requires a dark period of at least 1 h (Table 6), the biochemical processes involved in the induction may require darkness itself.

Other aspects of the blooming process appear to be at least partially controlled by darkness. A reduction in the lag time results from the effect of darkness on the appendix (Table 7). The evidence also suggests that darkness is required for spathe opening.

We have calculated a range of lag times for *Sauromatum* inflorescences which bloomed under "natural" greenhouse conditions, i.e. about 12-h photoperiod, threshold darkness beginning 1700–1800 h, and RC peak occurring between 0800 and 1100 h. Lag times of 38–42 h elapse between the RC maxima and the hours of threshold darkness on the second evening preceding the RC. Using the same computation procedure Meeuse and Buggeln (1969) found a mean lag time of 40 h for inflorescences which matured and bloomed in the laboratory under a 12-h photoperiod. The lag times obtained under these two 12-h photoperiod regimes are intermediate between the lag times recorded in experiments where inflorescences (raised to maturity under continuous irradiation) bloomed after one or two 12-h dark periods. The lag times in these latter cases were about 43 h and 37 h, respectively.

Although our data indicate that darkness triggers blooming in *Sauromatum*, Matile's (1958) experiments suggest that irradiation is the trigger in *Arum italicum*. He irradiated inflorescences of *Arum* which had been held in continuous darkness, and the inflorescences produced an RC about 24 to 26 h after the onset of irradiation. It is unlikely, however, that irradiation is the "natural" trigger of blooming in *Arum*. A 24- and 26-h lag time would result in a respiratory burst shortly after sunrise. In nature, the RC in both *A. italicum* and *A. maculatum* occurs in the late afternoon! Thus, Meeuse's observations (unpublished experiments) that darkness triggers the RC in these two species of *Arum*, with a lag time of about 22 h, more closely agree with the performance by the plants in nature.

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