Temperature Relationships in Eastern Skunk Cabbage

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***Abstract*:** A laboratory exercise is presented in which students determine where metabolic heat is primarily generated in blooming eastern skunk cabbage (*Symplocarpus foetidus*) plants. Students consider how color, shape, and orientation of spathes, and stage of flower maturation, may affect metabolic heat production and retention of both metabolic and solar heat, and determine whether the production of heat and odor are correlated. They discuss their results in terms of both physiological mechanisms and adaptive functions of heat production.

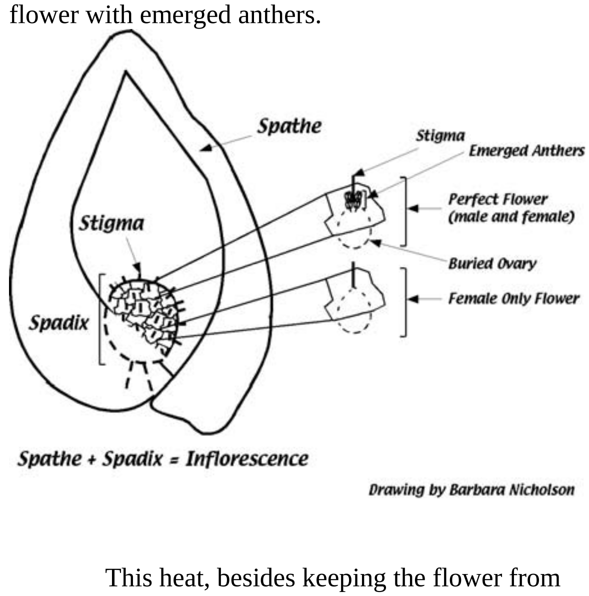
***Keywords*:** **E**cology, skunk cabbage, thermogenesis, pollination, biology majors, biology non-majors

Introduction

The eastern skunk cabbage *Symplocarpus foetidus* is a common perennial plant that lives in wet deciduous forests of eastern North America. Its distribution ranges from southern Canada to the uplands of Tennessee and Georgia and from western Nova Scotia to southeastern Manitoba (Fernald,1950 in Small,1959). It is the first flower to bloom in the spring, emerging from the ground in February and March, when air temperatures vary from –15˚C to +15˚C (Knutson,1974, Molles,2005). Skunk cabbage flowers do not have the appearance of a typical flower. The outer covering of the inflorescence consists of a thick, pigmented bract (called a spathe) with an opening on one side. The interior of the inflorescence has a bulbous fleshy spike called a spadix, crowded with minute petal-less flowers (Mauseth, 2003; FIG 1). Flowers of the skunk cabbage are perfect, having both male and female reproductive parts. In many flowering plants there is a time separation of gender expression, known as dichogamy, that functions to prevent self-fertilization (Richards, 1994). Protogyny is when female function precedes male, and when male function precedes female it is known as protandry (Bertin, 1993). In eastern skunk cabbage, flowers are protogynous, with the female reproductive parts (pistils) becoming sexually mature before the male parts (stamens) (Knutson,1974; Camazine and Niklas,1984).

Living organisms, including both plants and animals, produce heat as a product of cellular respiration, but few plants respire enough or are large enough to be measurably warmer than their surroundings (Knutson 1979). Members of the plant family Araceae, including skunk cabbage, have evolved the ability to metabolically generate considerable quantities of heat. Skunk cabbages can raise the temperature of their flowers to 22 ˚C, even when the surrounding temperatures are much lower than that (Knutson 1979). Temperature elevation in skunk cabbage lasts for approximately two weeks (Molles,2005), corresponding to the maturation of eggs and pollen in the spadix (Knutson,1979). If the spathe is covered by snow during this period, it can melt right through the snow (Knutson,1979). The skunk cabbage has an underground stem that stores large quantities of starch. During heat production, starch is translocated to the flower where it is metabolized at a high rate, generating the heat (Knutson,1974).

FIG 1. Drawing of the spathe and inflorescence of *Symplocarpus foetidus* showing floral parts. Larger drawing shows the spadix during the female-only stage, with stigmas and portions of the styles showing. Smaller drawing shows a single perfect flower with emerged anthers.



This heat, besides keeping the flower from freezing (Knutson,1972; 1974), is thought to attract, shelter, delay, and reward pollinators (Moodie,1976, Seymour *et al*.,2003). It is also believed that the heat assists in the diffusion of carbon dioxide and the skunky odors produced by the plant (Uemura *et al*.,1993). Various pollinators are attracted to both the heat and the odor, and maybe also to the CO_2 given off by the flower. Heat production in *Symplocarpus foetidus* is thought to assist pollination by accelerating the maturation of eggs and pollen in the spadix, by melting any overlying snow cover to expose the spathe, and by attracting a variety of pollinators through the emission of heat, odor and/or CO_2. Since heat production is critical to the reproductive success of skunk cabbage, we designed a lab activity that allows students to investigate some thermogenic relationships that might be found.

Materials and Methods

Skunk cabbage usually grows in moist soils or wetlands, even in small patches of such habitat, so it may be easy to find relatively close to your school. These areas can provide outdoor educational opportunities for students but are usually not considered because of their wet nature. Getting students to enter into these wetlands may pose problems depending on the wetness of the soil. The instructor should choose sites in advance: they must be dry enough to support the weight of an adult walking around the area. All rare and/or endangered plants should be noted and protected during the activity. Students and teachers will need waterproof boots that are mid-calf to knee-high. We have purchased a classroom set of boots covering a range of sizes for students to use during this lab. Boots are sanitized with an antiseptic spray between uses.

Heat production by *Symplocarpus* begins before the spathe opens (personal observation). Initially, all of the flowers on a spadix are female, with only the stigmas and a portion of the styles exposed above the spadix surface (FIG 1). Heat production is most intense during this stage and declines as the stamens erupt and pollen begins to be produced (Knutson,1979). Stamen eruption and pollen release occur from the top of the spadix to the bottom (Camazine and Niklas,1984). In order to capture the most intense heat production by the spadix, timing of this lab is critical. We monitor our central Connecticut skunk cabbage populations on a weekly basis beginning on February 1 to ensure that the lab is conducted during the hottest period. In Connecticut, the period of maximum heat production usually occurs during the third or fourth week in March. Knutson (1972) also reports that heat production peaks during mid to late March in northeast Iowa. When the anthers dehisce, they produce large quantities of pollen, making them easy to identify. With careful observation, the progression from female-only to perfect (male and female) flowers can be documented, and recording this information is useful as it provides information about the stage of spadix maturity. Not all plants in a patch mature at the same time. Although the spadix is clearly visible in FIG. 1, this is not always so, particularly with younger spadices (whose spathes have smaller openings). A simple test to determine which stage the flowers are in is to insert a finger or small paint brush into the spathe opening and brush it across the top of the spadix: if anthers have dehisced, pollen will adhere to the brush or your finger.

Thermodynamics that might be involved

Heat production is energetically expensive for skunk cabbages. Knutson (1974) estimated that the rate of heat production relative to body size in these plants was equivalent to that of a small mammal. Given the large heating cost that these plants experience, it was anticipated that skunk cabbage might have evolved adaptive mechanisms to reduce heat loss, or to acquire additional heat from solar radiation. The spathe itself is very insulative. It is thick and fleshy with large air spaces within its tissues that remind one of Styrofoam. The spathe color and opening orientation may also affect the efficiency of heat gain and loss. We were interested in discovering whether south-facing spathe openings captured more solar radiation than north-facing ones, and whether dark-colored spathes absorbed more solar radiation than light-colored ones. Variation is also present in the width of the spathe opening, and this has implications for heat retention in the spathe. Reportedly the spathe color changes as the flowers mature. Early spathes are yellow-green or yellow in color with few dark mottles, while older spathes acquire darker colors or more dark mottles (Kevan,1989).

Only spathes that are fresh looking, without any obvious tears or other damage, should be measured. A certain percentage of the spadices in a population are “metabolic duds" (personal observation). These bear female flowers in a state of deterioration or abortion, and they will not progress to the perfect stage. They are identifiable by having a flaccid, not turgid, spadix, and by not producing any heat. Students should be informed of the presence of such spadices and instructed not to measure them.

This exercise can be tailored to middle school, high school or college-level students depending on the complexity and length of the investigation that the instructor desires. The laboratory outline presented here was prepared for a course in ecology and evolution for second-year college biology majors.

The Laboratory Exercise

Materials for each group of 3-5 students:

- Clipboard
- Data sheet

- Thermocouple
- Compass
- Ruler
- Small paintbrush or Q-tip cotton swabs
- Dice or random number table (transect method)
- Rope or tape to mark transect lines (transect method)

The type of instrument needed to measure temperature will depend upon the research questions being addressed. For accurate measurements of very small surfaces a thermocouple is the best choice. A thermometer will suffice if you are interested in conducting this lab in a simpler but less precise fashion.

We conducted this lab over a period of two weeks. During the first week students collected data, which were then handed in to the instructor. During the second week students received a pooled data set compiled and summarized by the instructor, and spent their time in the computer lab creating graphs and conducting data analyses.

Groups of students were instructed to work far enough apart that each group measured different plants. Students were instructed to select 10 inflorescences to measure, and six types of measurements were taken at each inflorescence. Students were asked to consider how they choose which inflorescences to measure, to avoid sampling bias. One possibility is for them to measure the first 10 inflorescences they encounter that are easy to reach, undamaged, and are producing heat. Usually the students completed their field measurements in approximately an hour. In larger patches, transect sampling is appropriate and would serve to spread out students and provide a method to randomize samples. Transect lines could be randomized along a baseline using dice or a random number table.

Observations and Measurements

1) Relative strength of the smell emanating from the spathe from a distance of 15 cm (6 inches) from the opening of the spathe. We used the following scale: 0 = no smell is detected, 1 = a slight smell, 2 = moderate smell, 3 = gross, a strong smell. Individuals vary in the sense of smell, so one student in the group should be designated as the "smeller" and conduct all of these observations, being careful to smell each plant from a consistent 15 cm distance in front of the spathe opening.

2) Temperature

a. Air surrounding the spathe, one hand spread distance out from the spathe
b. Ground surface next to the spathe, 3 cm away from the base of the spathe
c. Leaf surface temperature (if a leaf is present): will require a thermocouple
d. Outside wall of floral spathe: will require a thermocouple
e. Spadix surface in the region of the most open flowers

3) Compass direction (NW, N, NE, E, SE, S, SW, W) that the spathe opening was facing. Students could instead measure the direction of the spathe opening relative to the sun azimuth, where 0° indicates that the center of the spathe opening is in the direction of the sun azimuth.

4) Diameter of the opening of the spathe at its widest point.

5) Sex of the flowers on the spadix. If the spathe opening is large enough for this to be seen, determine whether anthers are present and if so, how far down the spadix they can be found. If this can't be seen, insert a finger, paintbrush, or Q-tip cotton swab to test for the presence of pollen. As it is possible to observe the progression from female-only flowers to perfect flowers, each spadix may have only female flowers, only perfect flowers, or both. If students are conducting a detailed study involving different stages of spadix maturation, they may want to consider dissecting the spathe after the remaining measurements are taken.

6) Color of the spathe using the following categories: a) yellow/green (Y), b) predominantly yellow/green with some purple/red mottles (Y/P), c) predominantly purple/red with some yellow/green mottles (P/Y), d) purple/red (P).

Results

Results are reported in a table of data recorded in the field (a completed TABLE 1), a table of class data compiled by the instructor (TABLE 2), and six graphs showing relationships between spadix temperature and other characteristics. Using the individual field data (TABLE 1), bar graphs were drawn showing the temperature of: a) air, b) ground surface, c) leaf surface, d) outside wall of spathe, and e) spadix surface. Individual plants were placed on the X-axis and temperature on the Y-axis (FIG 2). Pooled class data (TABLE 2) were used to graph the following relationships:

1) Spadix temperature and orientation of the spathe opening (FIG 3). Data were grouped into the 8 compass directions and a mean temperature was calculated for each compass direction. Mean spadix temperature was placed on the Y-axis, and the compass points on the X-axis.

TABLE 1. Data collection table used for this lab.

Data Sheet

Skunk Cabbage Lab **Names**______________________________

Flower	Air temp. ˚C	Ground temp. ˚C	Leaf temp. ˚C	Temp. of outside wall of spathe	Temp. of spadix surface	Direction of spathe opening	Diameter of spathe opening (cm)	FlowersFemale, Perfector Both	Relative odor emitted (0-3)	Spathe colors: 1˚/2˚
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										

FIG 2. Example of data collected by a single group in 2003 showing temperature relationships between the air, ground and various parts of the skunk cabbage.

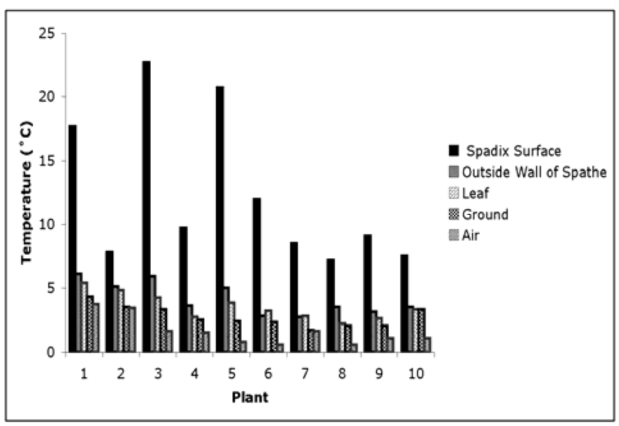


FIG 3. Graph showing the mean temperature of the spadix surface when different orientations of the spathe opening are considered. Data are from Table 2, year 2003.

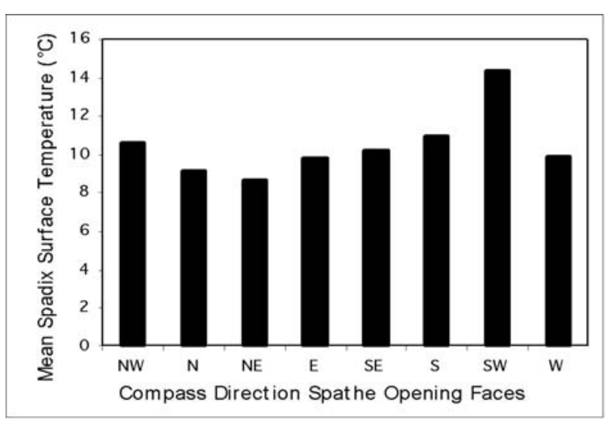


TABLE 2. Summary table of data collected in 2003 and 2004. Mean temp. = Mean temperature, St. Dev. = standard deviation, No. of observations = number of observations.

	2003			2004		
	Mean temp	**St. Dev.**	**No. of obser.**	**Mean temp**	**St. Dev.**	**No. of obser.**
Air	2.5	1.2	70	3.3	1.7	150
Ground	3.5	0.9	70	4.0	1.4	150
Leaf	3.9	1.0	70	5.0	2.5	150
Outside Wall of Spathe	4.5	1.2	70	5.5	3.2	150
Spadix Surface	10.4	6.4	70	13.1	6.7	150

2. Orientation of the Spathe Opening	Mean temp	St. Dev.	No. of obser.	Mean temp	St. Dev.	No of obser.
NE	8.69	5.12	8	9.20	3.76	9
N	9.14	5.57	8	14.07	6.77	22
NW	10.60	1.98	2	12.87	6.88	18
E	9.83	5.92	13	12.86	6.84	23
W	9.87	6.90	6	13.45	5.92	21
SE	10.24	7.10	14	16.41	6.32	15
S	10.93	7.28	12	11.83	8.27	30
SW	14.40	7.38	7	13.47	6.36	12
	sum		70			150

3. Sex of the Spadix	Mean temp	St. Dev.	No. of obser.	Mean temp	St. Dev.	No of obser.
Female	11.98	7.05	30	15.73	6.33	86
Perfect	9.17	5.56	4	9.57	5.44	64
	sum		70			150

4. Diameter of Spathe Opening	Mean temp	St. Dev.	No. of obser.	Mean temp	St. Dev.	No of obser.
0-0.4 cm	12.78	6.91	8	13.93	8.50	6
0.5-0.9 cm	9.65	6.56	8	15.15	7.66	30
1-1.4 cm	12.62	6.81	22	13.31	7.08	51
1.5-1.9 cm	9.59	5.45	16	12.50	5.42	43
2.0-2.4 cm	7.74	6.37	7	11.52	6.15	13
2.5-2.9 cm	8.30	4.83	6	12.58	0.91	4
3.0-3.4 cm	3.45	0.78	2	6.67	3.21	3
>3.5 cm	4.9	-	1			
	sum		70			150

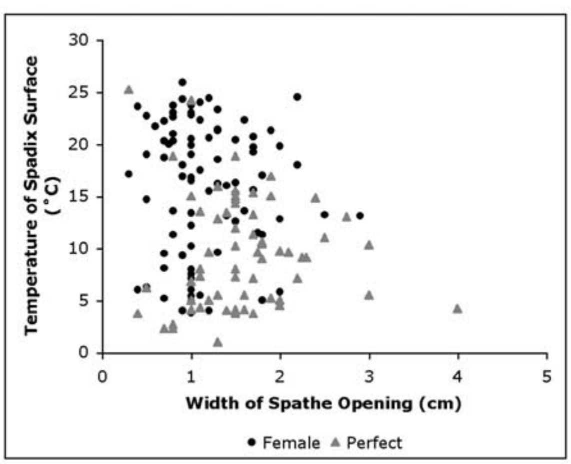
TABLE 2 cont.'d.

5. Color of Spathe	Mean temp	St. Dev.	No. of obser.	Mean temp	St. Dev.	No of obser.
Yellow	12.2	8.39	5	10.48	4.63	4
Yellow/Purple	10.6	7.03	11	13.93	7.11	35
Purple/Yellow	12.55	6.93	28	12.55	6.94	62
Purple	13.67	5.99	26	13.67	5.99	38
	sum		70			139

6. Odor production	Mean temp	St. Dev.	No. of obser.	Mean temp	St. Dev.	No of obser.
None	11.2	7.11	11	12.18	6.77	28
Mild	9.2	5.67	27	14.61	6.8	47
Moderate	10.87	6.85	23	10.58	6.33	32
Gross	11.82	6.57	9	14.04	6.47	29
	sum		70			136

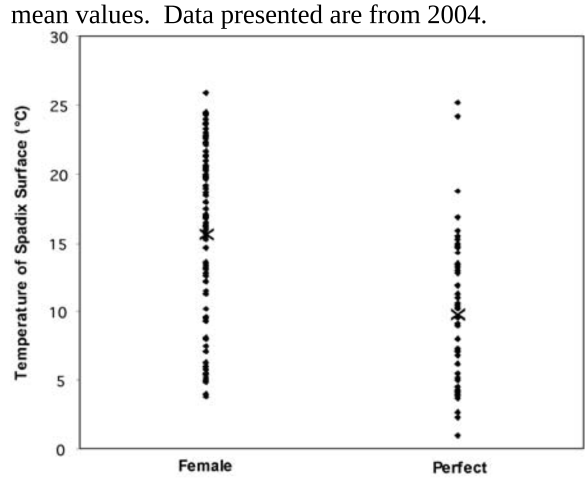
2) Width of the spathe opening and the temperature of the spadix (FIG 4). The data were grouped into width (cm) categories of: 0-0.4, 0.5-0.9, 1.0-1.4. 1.5-1.9, 2-2.4, 2.5-2.9, 3.0-3.5 and > 3.5 cm, and mean spadix temperature was calculated for each category. Width categories were placed on the X-axis and mean spadix temperature on the Y-axis. If different symbols are used for different categories of maturation (female, perfect, both), this will help students to think about how spadix maturation may correlate with width of the spadix opening.

FIG 4. Graph showing the relationship between spadix surface temperature and diameter of the spathe opening, with sex of the flowers indicated. Data presented are from 2004 only.



3) Maturation stage of the open flowers and temperature of the spadix (FIG 5). Mean spadix temperature was calculated for each of the maturation categories. Maturation categories were placed on the X-axis and spadix temperature on the Y-axis. In our sample lab, any spadix producing pollen was designated as perfect, thus we have only two categories: perfect and female.

FIG 5. Graph showing temperature of the spadix surface for female and perfect spadices. “X”s indicate mean values. Data presented are from 2004.



4) Color of the spathe and the mean temperature of the spadix. Data were grouped into four color categories: a) yellow/green, b) predominantly yellow/green with some purple/red mottles, c) predominantly purple/red with some yellow/green mottles, or d) purple/red.

The mean temperature of the spadix was calculated for each category. Color categories were placed on the X-axis in the order above (predicted as less to more effective in absorbing solar radiation) and mean spadix temperature was shown on the Y-axis.

5) Odor production and spadix temperature. The mean spadix temperature was calculated for each odor category. Odor was plotted on the X-axis and mean temperature of the spadix on the Y-axis.

Copies of relevant articles on skunk cabbage were placed on reserve in the library and students were required to refer to several of these in their laboratory reports. They were asked to discuss the following questions, and to attempt to answer "why" questions in terms of both physiological mechanisms and adaptive function.

1) Which parts of the plant were significantly different in temperature from the surrounding air temperature, and which part of the plant was the hottest, suggesting an origin of the heat? Are any of the 10 spadices that you measured not producing heat? Why might this occur?
2) Is there any relationship between the spadix temperature and the orientation of the spathe opening? How might the orientation of the opening affect the temperature inside the spathe?
3) Is there a relationship between the maturity of the open flowers and the temperature of the spadix? Why might the sex of the flowers influence the temperature of the spadix?
4) Is there a relationship between the diameter of the spathe opening and the temperature of the spathe or spadix? Why might this relationship occur?
5) Is there a relationship between the color of the spathe and the temperature of the spadix? Why might this relationship occur?
6) Is there a relationship between the amount of odor production and the temperature of the spadix? Why might this relationship occur?
7) Heat generation in skunk cabbages is metabolically expensive, using large quantities of their stored energy. After conducting this exercise and reading the articles on reserve, what do you feel is the primary adaptive function of skunk cabbages producing heat?

If the primary selective pressures on skunk cabbages were to maximize temperature while conserving heat and reducing metabolic costs, what orientation of the opening, what size of the opening, and what color of the spathe might be optimal for heat conservation and reduction of metabolic costs?

Discussion

Figure 2 is an example of a graph such as those students would generate showing the relationship between air and ground temperature and the temperature of different parts of the skunk cabbage. This graph shows the variability in the data produced by spadices that are in different stages of maturation. The spadix surface is 4.7-16.6˚C warmer than the outer wall of the spathe. Leaves are also slightly warmer than the ground or air, suggesting that some of the heat produced by the spadix is conducted through all parts of the plant. From this figure students can easily see that the spadix is most likely where heat is produced.

Figure 3 presents data for 2003 relating compass direction of the spathe opening to the temperature of the spadix. In 2003, southwest facing spathe openings had the warmest spadices and north and northeast facing spathe openings had cooler spadices than those facing south, southeast, or southwest. Since these data were taken in the morning, it might have been expected that southeast or south-facing spathe openings would have had the warmest spadices, but of course factors such as wind could have had an effect, as well as the particular combination of spadix sexes and spathe opening widths in the plants with openings in each compass direction.

The sex of the flowers is correlated with both the temperature of the spadix and the width of the spathe opening. Figure 4 presents data from 2004. In this graph younger female spadices have narrower openings and hotter temperatures than older perfect (male and female) spadices. In 2004, the mean spadix temperature was statistically significantly different between females and perfect spadices (Mann-Whitney $U = 4226$, $p < 0.001$). In this year females had a mean spadix temperature of 15.7 ˚C, while perfect spadices had a mean spadix temperature of 9.6˚C (FIG 5, TABLE 2). In 2003, females also tended to be warmer than perfect spadices, with mean spadix temperatures of 12˚C, compared to 9.1˚C, respectively, though the difference was not statistically significant (Mann-Whitney $U = 709.5$, $p = 0.194$). Fig. 5 shows the range of temperature values for perfect and female spadices in 2004.

We have found that the spadix is consistently the warmest part of the plant, generally followed by the outer spathe wall, and then the leaf. Spadix temperature correlates best with sex of the flowers (females are on average warmer, though temperature ranges for female and perfect spadices show considerable overlap). There also may be a weak correlation between spadix temperature and diameter of the spathe opening, independent of the correlation between spadix temperature and sex. Color of the spathe was not found to influence the temperature of either the outside wall of the spathe, or of the spadix itself. Odor production was found to be very variable, with no apparent relationship to the temperature of the spadix or the color of the spadix, thus results for these are not presented.

Additional Enrichment Exercises

- Conducting this lab with more detailed observation of the progression from female-only to perfect flowers, and recording the information in more than two or three categories of spadix maturity. This may not be possible to do without significant damage to the spathe and may require dissection of the spathe.
- Temperature regulation in skunk cabbages. Measure spadix temperatures or respiration rate of individuals over a period with varying air temperatures. Knutson (1974, 1979) and Ito *et al*. (2004) report that *S. foetidus* is capable of temperature dependent thermoregulation.
- Duration of heating and survival of the flower. Knutson (1979) reports that each flower produces heat for two weeks or slightly longer. If exposed to temperatures below freezing after this time period, the flower will freeze and die.
- A study of the distribution of the "metabolic duds" to see how frequently these occur in the population.
- Examine the influence of heating on the leaves. Is it possible that in addition to promoting the maturation of eggs and pollen tubes, heat production might also speed up the emergence of the leaves, giving this plant additional time for photosynthesis before the tree canopy establishes? Compare the rates of leaf growth and unfurling in plants with their spadices intact, vs. plants that are "metabolic duds" or plants with their spadices removed.
- Track spathe color and compass orientation of the spathe opening in the same plants from year to year to see if color and/or opening position are genetically (or microenvironmentally) determined, or variable. If these characteristics are found to be constant within the same plant, transplantation experiments could determine whether the microenvironment has an effect.
- Track spathe color and opening widths in a single individual to document darkening of the spathe and increasing opening of the spathe over time.
- Bagging experiments to see if *Symplocarpus foetidus* like its relative *S. renifolius* needs to be cross-pollinated before seeds are produced (Uemura *et al*. 1993).
- Investigation of pollinators and pollination biology. This was part of our earliest versions of this lab, but few pollinators were observed, so that portion of the lab was eliminated. We still have many unanswered questions regarding the role of pollinators in fertilizing *S. foetidus*. Some questions are: 1) Which species are primarily responsible for pollinating skunk cabbage? 2) How many insects currently visit our populations? 3) Does our observation of few pollinators indicate that skunk cabbage has lost many of its pollinators due to urban development?

Examine the role of odor production for anti-herbivory purposes. *S. foetidus* has calcium oxalate crystals in the leaves that are hypothesized to deter herbivores (Knutson,1974). As this plant is particularly abundant in the early spring, when few other leaves and flowers are available to herbivores, odor production might also discourage grazing. In addition to examining plants for signs of insect and mammalian herbivory, the leaves could be offered (along with other leaves without defensive chemicals, perhaps including lettuce and spinach) to insect and/or mammalian herbivores. Care must be taken that the herbivores will have adequate food without needing to eat skunk cabbage leaves, and there may be some danger of poisoning naïve herbivores.

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Call for Applications -- John Carlock Award

This Award was established to encourage biologists in the early stages of their professional careers to become involved with and excited by the profession of biology teaching. To this end, the Award provides partial support for graduate students in the field of Biology to attend the Fall Meeting of ACUBE.

Guidelines: The applicant must be actively pursuing graduate work in Biology. He/she must have the support of an active member of ACUBE. The Award will help defray the cost of attending the Fall meeting of ACUBE.

The recipient of the Award will receive a certificate or plaque that will be presented at the annual banquet; and the Executive Secretary will provide the recipient with letters that might be useful in furthering her/his career in teaching. The recipient is expected to submit a brief report on how he/she benefited by attendance at the meeting. This report will be published in *Bioscene*.

Application: Applications, in the form of a letter, can be submitted anytime during the year. The application letter should include a statement indicating how attendance at the ACUBE meeting will further her/his professional growth and be accompanied by a letter of recommendation from a member of ACUBE. Send application information to: Dr. William J. Brett, Department of Life Sciences, Indiana State University, Terre Haute, IN 47809; Phone: 812-237- 2392; FAX: 812-237-4480; Email: lsbrett@scifac.indstate.edu.