Plants That Warm Themselves

Some plants produce extraordinary heat when they bloom. A few even regulate their temperature within narrow limits, much as if they were warm-blooded animals

by Roger S. Seymour

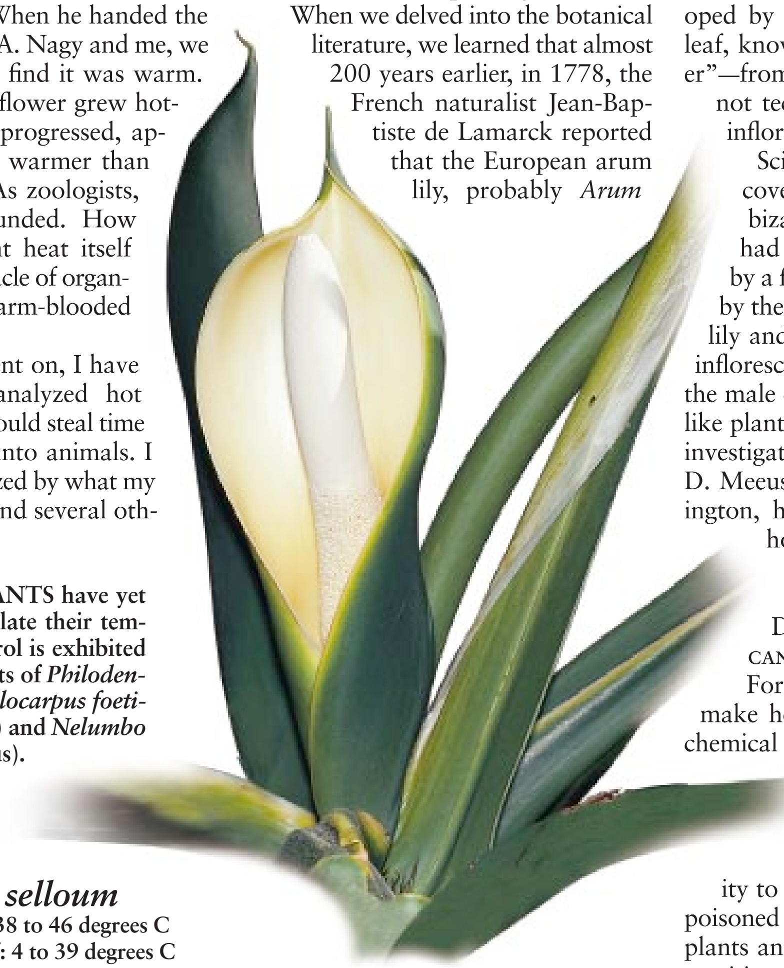
In the spring of 1972 George A. Bartholomew, a leader in the study of animal physiology, invited a group of his students and co-workers from the University of California at Los Angeles to a dinner party. Among his guests was Daniel K. Odell, now of Sea World in Florida. En route to the affair, Dan noticed some striking flowers. They consisted of a rather phallic projection that was about nine inches long and partly enveloped by a leaflike structure. Intrigued, he picked one to show the other partygoers. When he handed the cutting to Kenneth A. Nagy and me, we were astonished to find it was warm. What is more, the flower grew hotter as the evening progressed, appearing to become warmer than the human body. As zoologists, we were dumbfounded. How could a mere plant heat itself more than the pinnacle of organic evolution—the warm-blooded animal?

From that moment on, I have hunted for and analyzed hot plants whenever I could steal time from my research into animals. I continue to be amazed by what my colleagues and I—and several other researchers—have found. Among our discoveries is that some plants produce as much heat for their weight as birds and insects in flight, the greatest heat producers of all. And a few plants actually thermoregulate, almost as if they were birds or mammals: they not only generate warmth, they alter their heat production to keep their temperature surprisingly constant in fluctuating air temperatures.

We were not, it turns out, the first to realize that some plants give off heat. When we delved into the botanical literature, we learned that almost 200 years earlier, in 1778, the French naturalist Jean-Baptiste de Lamarck reported that the European arum lily, probably *Arum italicum,* became warm when it flowered. This plant is a member of the huge family Araceae, which includes *Philodendron,* the kind of plant Dan had plucked. It also includes jack-in-the-pulpit, skunk cabbage and many other familiar plants. In these so-called aroids, or arum lilies, the flowering part is termed a spadix and is not a true flower; it is an "inflorescence," or clustering of small flowers (florets). The aroid spadix, which consists of hundreds of florets assembled on a common stalk, is partly enveloped by a large bract, or specialized leaf, known as a spathe. Dan's "flower"—from *P. selloum*—was therefore not technically a flower; it was an inflorescence.

Scientists had subsequently discovered that other species of this bizarre family heat up, and they had noted weak heat production by a few plants outside the aroids—by the flowers of the Amazon water lily and of the custard apple, by the inflorescences of a few palms, and by the male cones of certain cycads (fernlike plants that resemble palms). Some investigators, among them Bastiaan J. D. Meeuse of the University of Washington, had even uncovered clues to how the cells of various plants generate warmth [see "The Voodoo Lily," by Bastiaan J. D. Meeuse; Scientific American, July 1966].

For instance, they found that to make heat, aroids activate two biochemical pathways in mitochondria, which are often called the power plants of cells. These pathways are distinguished by their sensitivity to cyanide. The one that can be poisoned by the chemical is common to plants and animals; the one that is insensitive to cyanide occurs in heat-pro-



ONLY THREE PLANTS have yet been shown to regulate their temperature. Such control is exhibited by the flowering parts of *Philodendron selloum, Symplocarpus foetidus* (skunk cabbage) and *Nelumbo nucifera* (sacred lotus).

Philodendron selloum
Flower temperature: 38 to 46 degrees C
In air temperatures of: 4 to 39 degrees C
Period of regulation: 18 to 24 hours

GEORGE K. BRYCE

ducing plants, certain other plants, fungi and some unicellular organisms. Both pathways typically use nutrients and oxygen to manufacture an energy-rich molecule called ATP (adenosine triphosphate), which can subsequently be broken apart to provide energy for cellular activities or to produce heat. It is unclear, however, whether aroid cells that warm up generally do so by first making ATP and then breaking it down or by simply liberating heat directly from the pathways without producing ATP as an intermediate.

A "Warm-Blooded" *Philodendron*

We started off looking at *P. selloum* from an entirely different vantage. Instead of examining individual cells or molecules, as most botanists had done, we studied the inflorescences as if they were whole animals. Bartholomew's laboratory at U.C.L.A. conducted comparative studies on heat production and body temperature regulation in animals, and so all the needed equipment and methods were at hand. Furthermore, many *P. selloum* plants were in flower right outside our laboratory window, giving us easy access to our subjects.

Our earliest experiments, driven by sheer curiosity, aimed to do little more than determine whether the inflorescence truly had become as hot as we suspected at the party. We impaled spadices with temperature probes and connected the probes to a machine in the laboratory that recorded temperature continuously. During the measurement period, the air outside averaged about 20 degrees Celsius (68 degrees Fahrenheit), and the spadix temperature remained about 20 degrees C higher, near 40 degrees C (104 degrees F). The inflorescence was, indeed, hotter than its environment and hotter, too, than a person.

By then we were captivated and wanted to know more, such as the range of *P. selloum*'s heat-producing capabilities. Because we could not control the air temperature outdoors, we cut some specimens and put them into indoor cabinets where we could vary the temperature as we chose. Indoors, we could also examine the plant's rate of heat production by the simple expedient of measuring its rate of oxygen consumption. We felt confident in applying consumption of oxygen as a gauge because of the intimate connection between oxygen use and heat generation. In animals, every milliliter of oxygen consumed results in about 20 joules of heat. Thus, the rate of oxygen use can be converted readily to the rate of heat production in watts (joules per second).

We examined the inflorescences at air temperatures ranging from below freezing to uncomfortably hot for humans. At the coldest extremes, some of the inflorescences could not heat up at all. But their temperatures soared to as high as 38 degrees C (100 degrees F) when the environmental temperature was still a cool four degrees C (39 degrees F)—a 34 degree C difference between the inflorescence and the air. The cuttings became hotter still as the air temperature rose further, but the difference between them and their environment became less dramatic. The inflorescences peaked at 46 degrees C (115 degrees F) when the interior of the cabinet was a tropical 39 degrees C (102 degrees F). Further, the estimated rate of heat production decreased as the temperature of the environment increased.

The plant was obviously adjusting heat production to maintain warmth in cold weather and to prevent overheating in hot conditions. The conclusion was startling: these inflorescences did more than produce heat. Like warm-blooded birds and mammals, they were thermoregulating.

Two years after we discovered that *P. selloum* could thermoregulate, Roger M. Knutson, then at Luther College in Iowa, reported that the spadix of the eastern skunk cabbage, *Symplocarpus foetidus,* holds its temperature between 15 and 22 degrees C (59 to almost 72 degrees F) for at least two weeks during February and March, when air temperatures are below freezing. (The plant reportedly melts snow around it.) And just last year at the University of Adelaide in Australia, Paul Schultze-Motel and I discovered that the sacred lotus, *Nelumbo nucifera,* maintains its temperature near 32 degrees C (almost 90 degrees F) for two to four days in the middle of its summer flowering period, even when air temperatures drop to 10 degrees C (50 degrees F). In this case, the spongy, cone-shaped center of the flower, called the receptacle, produces most of the heat. The sacred lotus belongs to a completely different family from *Philodendron* and skunk cabbage, suggesting that thermoregulation evolved independently in aroids and in the lotus.

Why might plants thermoregulate? In birds and mammals, temperature regulation provides the consistent warmth that cells need to carry out biochemical reactions efficiently. Warm-blooded, thermoregulating animals can therefore be active and continue to seek food when cold weather slows the cellular reactions, and hence the activity, of such cold-blooded ani-

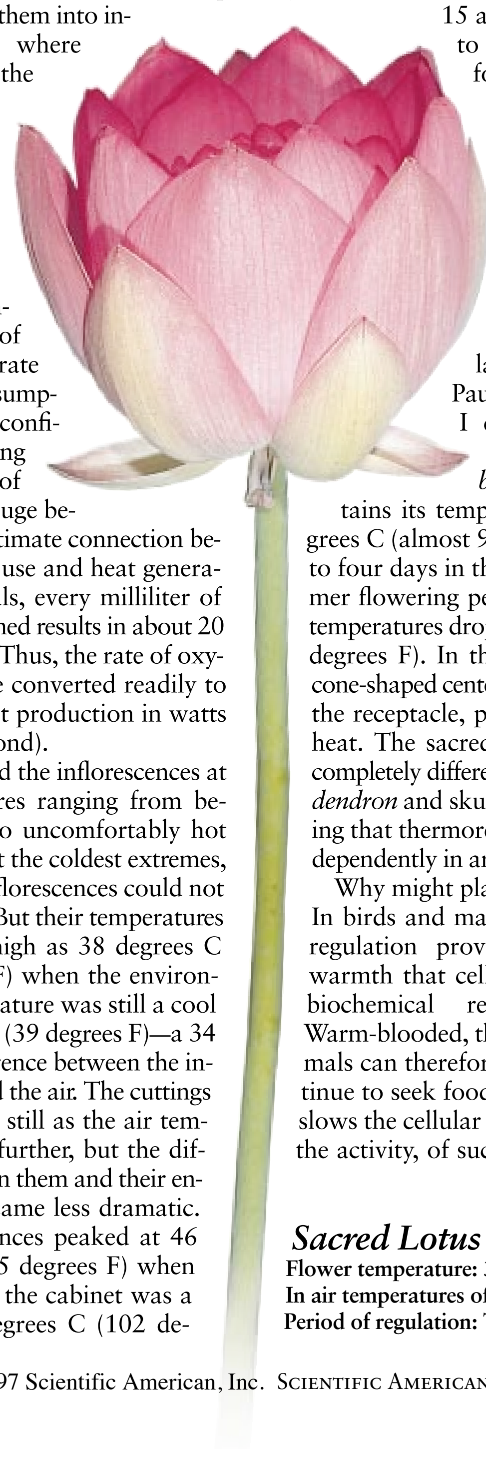
Skunk Cabbage

Flower temperature: 15 to 22 degrees C
In air temperatures of: –15 to 10 degrees C
Period of regulation: Two weeks or more

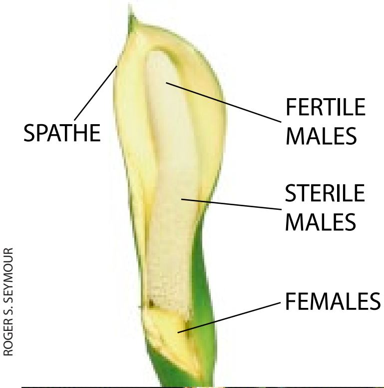
RAYMOND A. MENDEZ *Earth Scenes*

Sacred Lotus

Flower temperature: 30 to 37 degrees C
In air temperatures of: 10 to 35 degrees C
Period of regulation: Two to four days



PATTI MURRAY *Earth Scenes*



ROGER S. SEYMOUR

BEETLES are the natural pollinators of *P. selloum,* whose inflorescence, or flowering part, consists of three types of tiny flowers (florets)—fertile males, sterile males, and females—growing on a stalk (*top left*). During the plant's thermoregulatory period, the leaflike "spathe" around the inflorescence opens, giving the insects access to the florets (*bottom left*). The beetles brush pollen onto receptive female florets. Then, as the plant cools, the spathe folds around some of the insects. Later, the spathe reopens somewhat (*center*), and fertile males release their pollen. The small opening forces escaping beetles to crawl through the pollen (*right*), which sticks to them as they move on to other inflorescences. This convergence of the plant's warming and reproductive periods supports the idea that thermoregulation evolved in *P. selloum* as a reward to pollinating beetles.

GERHARD GOTTSBERGER *University of Ulm*

GEORGE K. BRYCE

GERHARD GOTTSBERGER *University of Ulm*

mals as reptiles. And birds and mammals whose thermostats are set high (close to 40 degrees C) ensure that their tissues can generate energy at the high rates needed for prolonged exercise, such as running or flying. But clearly, we must seek another explanation for temperature regulation in sedentary flowers.

The Value of Thermoregulating

Past work by others has made the reasonable case that aroids and certain other plants heat themselves to vaporize scents that attract insects. Vaporization of attractants could partly explain heating in thermoregulating plants but would not explain why heat production is raised and lowered to keep temperature within a set range. We can suggest two reasons for why thermoregulation evolved in some plant species.

First, it may create a warm, stable environment for pollinators and thereby facilitate reproduction. Large insects that carry pollen from one flower to another typically require high body temperatures for flight, locomotion and social interactions, and they often expend a great deal of energy keeping warm. Those that visit thermogenic flowers would be provided with a fairly steady level of heat directly from the plant. They could eat, digest, mate and function in other ways without having to squander energy of their own to stay warm. Alternatively, the flower itself may require a constant temperature for proper development of its own reproductive structures or to protect sensitive parts from damage that might occur if heat production were uncontrolled.

Either hypothesis could explain why a plant evolved the ability to thermoregulate. Yet the interaction between *P. selloum* and pollinating insects does lend some credence to the idea that thermoregulation in this plant may have been adopted because it abetted pollination. This interaction has been studied closely in Brazil, the plant's native territory, by Gerhard Gottsberger of the University of Ulm in Germany.

The inflorescence of *P. selloum* contains three types of florets. At the top are fertile males that produce pollen. At the base are females capable of producing fruit when they are fertilized. Separating the fertile males and females is a band of sterile males that provide nourishment to pollinating insects and also furnish most of the inflorescence's heat. Tantalizingly, the 18- to 24-hour period of temperature regulation in the inflorescence overlaps the period of female receptivity to pollination. During these hours, the spathe surrounding the spadix opens widely and gives pollen-bearing insects—mainly beetles—easy access to the warm, sterile florets and nourishment. Then the spadix cools, and the spathe closes around it, trapping some beetles inside. After about 12 hours, by which time the female florets are sure to have been pollinated, the flower warms up again, the spathe reopens partway, and the fertile male florets shed their pollen. The pollen sticks to escaping insects, which fly off to repeat the cycle. This sequence promotes cross-pollination and prevents self-pollination; it thereby increases genetic diversity, which favors reproductive success.

In common with *P. selloum,* the sacred lotus maintains high temperatures when the female stigmas are moist and receptive and before the pollen is shed. Heating begins before the petals open widely and ends when opening is complete. The shape of this flower is also appropriate for pollination by beetles. But whether thermoregulation evolved specifically to aid beetles in that endeavor is unclear. The uncertainty arises because we do not know the native habitat of this plant and whether beetles are the main pollinators in that area. Further, the flower clearly is not dependent on beetles; it can be pollinated by other insects after the petals open widely and heat production subsides.

How *Philodendron* Operates

The question of how plants thermoregulate is as fascinating as that of why they do it and was in fact my main concern when I began studying *Philodendron* seriously. To address this problem, I teamed up in the early 1980s with Bartholomew and M. Christopher Barnhart, who is now at Southwest Missouri State University. The answer was not at all obvious, given that plants operate very differently from animals.

In animals, temperature regulation is a complex affair. It requires temperature receptors at many locations in the body, and it demands a nervous system equipped to integrate all the input and to direct various parts of the body to change their activities. For instance, the nervous system often signals animals to adjust to a drop in air temperature by fluffing up their fur or feathers, thereby increasing their insulation and stemming heat loss. This strategy works only to a point, however, and so the animals may also increase heat production as the environment gets colder. Typically they begin to shiver, working their muscles together and forcing them to use ATP. Warming of the body also requires increases in the rates of breathing and blood circulation, in order to increase delivery of nutrients and oxygen to heat-producing tissue.

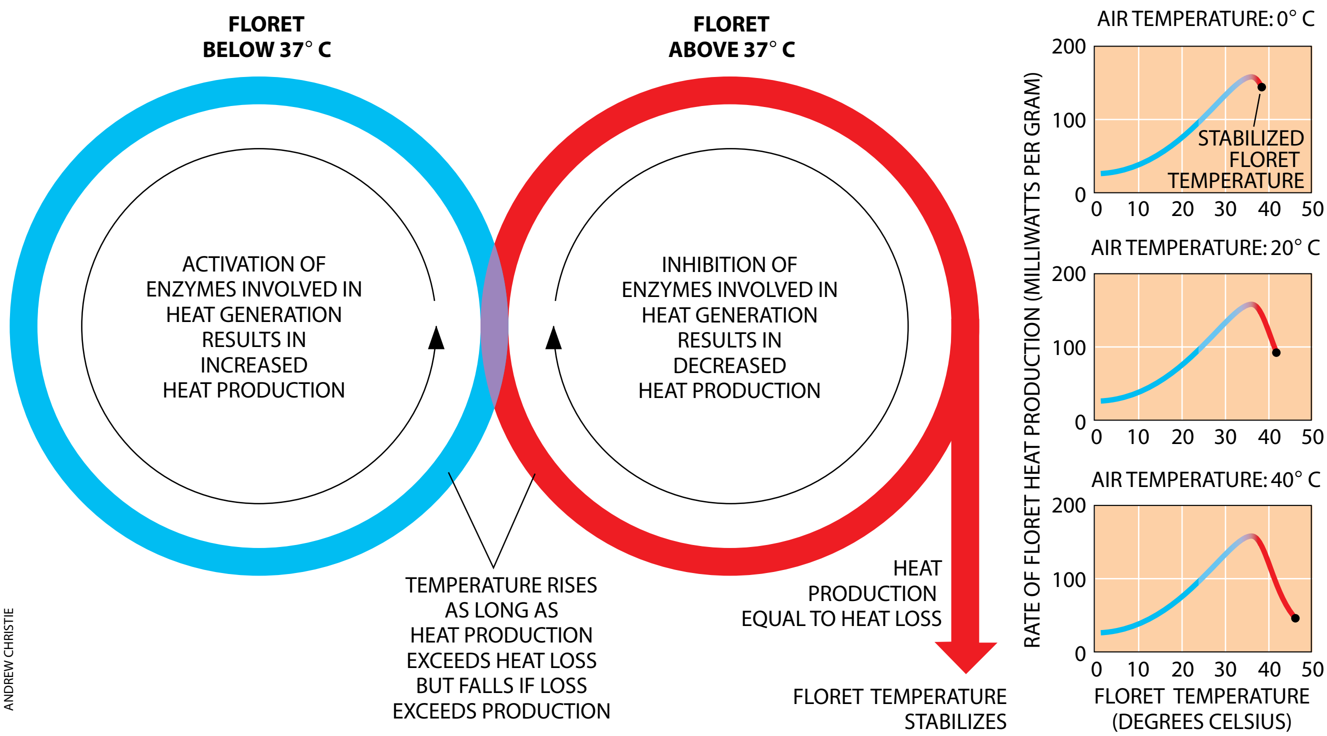
But plants have no fur, no feathers, no nervous system, no muscles, no lungs, no blood and no brain. How, then, we asked, does *P. selloum* raise and lower its temperature to keep the inflorescence in the 38 to 46 degree C range?

We first had to know which part of the inflorescence produced heat, a mystery at the time. We separated the three types of florets from their stalk and measured their oxygen consumption rates. On the basis of these measurements, we calculated the rate of heat production. The sterile males consumed the great bulk of the oxygen we supplied; the fertile males consumed a bit; and the females and the stalk took up almost none. Apparently the sterile florets were responsible for temperature control in the inflorescence. Subsequent studies confirmed this deduction and showed that the florets do not need the fancy temperature-regulating systems of animals. They contain their own thermostats, their own nutrient supplies and their own means of acquiring oxygen.

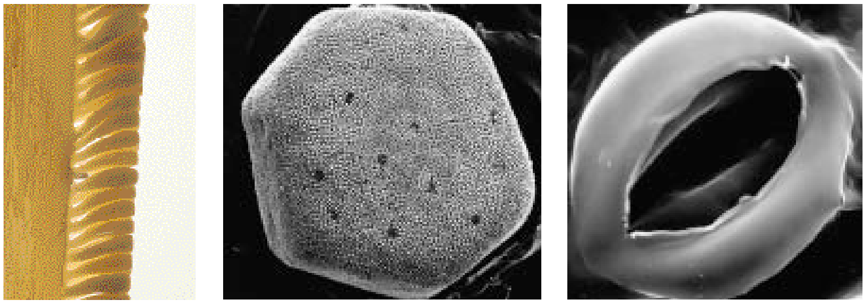
In the experiments revealing the existence of the thermostats we removed sterile male florets from the spadix and put individual florets in incubators kept at set temperatures. On their own, the

How *Philodendron* Achieves a Stable Temperature

The inflorescence of *Philodendron selloum* achieves temperature stability by essentially setting the thermostat of its sterile male florets—the main heat producers—to 37 degrees Celsius (*diagram*). If the temperature of the florets falls below that level, the florets increase their heat production (*left cycle*). As long as heat production surpasses heat loss, the floret temperature rises. As the floret temperature exceeds 37 degrees C (*right cycle*), enzymes needed for heat generation become progressively less active. Their inhibition leads to a decline in heat output. The decline continues until heat production equals heat loss, at which point the temperature stabilizes. The final floret temperature depends on the ambient temperature (*graphs*): If the air is cold, the florets lose heat quickly, so they produce it quickly, and their temperature stabilizes near 37 degrees C. If the air is hot, the florets retain heat, so they produce little of it, and their temperature stabilizes closer to 46 degrees C. *—R.S.S.*



ANDREW CHRISTIE



STERILE MALE FLORETS of *P. selloum* (*left*) take in oxygen through pores called stomates. Several stomates (*dark spheres*) are visible in the center micrograph, highlighting the tip of one floret. The micrograph at the right captures a single stomate.

florets could not warm one another and took on the temperature of the air around them. We could therefore assess how much heat they produced at particular temperatures.

The separated florets generated little heat when they were close to freezing, presumably because the enzymes (biological catalysts) needed for heat production—like most enzymes in living creatures—cannot function quickly when they are very cold. But at warmer temperatures, the florets displayed an interesting pattern of heat generation. (That pattern also occurs when the florets are attached to the spadix, except that in the intact spadix the florets gain added warmth from the heat emitted by one another.) As the temperature of the florets rises, so does their rate of heat production, which leads to further warming. This self-reinforcing increase continues until the florets reach 37 degrees C. At higher temperatures, the florets "turn down the furnace," dropping the rate of heat production steeply.

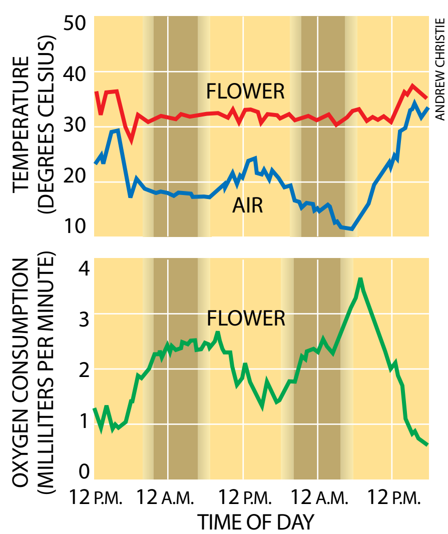
Exactly how far the rate declines depends on the environmental temperature. If the air is cold, say four degrees C, the florets lose heat quickly and their temperature stabilizes at about 38 degrees C (with a high rate of heat generation). On the other hand, when the environment is warm, perhaps 39 degrees C, they lose heat slowly and stabilize at about 46 degrees C (with a low rate of heat production). This pattern is reversible. A floret that has lowered heat production during the warmth of the day can resume generating heat when the temperature drops during the night.

Heat production declines in hot florets probably because the heat itself inhibits the pathways responsible for generating warmth. No one knows whether the high heat acts directly on certain enzymes in the pathways or whether it interferes with enzymatic activity by changing the structure of the membranes that bind the enzymes.

Extraordinary Wattage

Having gained insight into the setting maintained by the florets' thermostat, we began to investigate how the florets obtain the nutrients and oxygen they use during heating and exactly how much heat they produce. Although my earlier studies had estimated heat production on the basis of oxygen use, the results had not yet been confirmed.

It turned out that all the energy devoted to heating in *P. selloum* was present in the florets from the beginning. (This property may not reflect that of other thermoregulating plants, however. The skunk cabbage has to import fuel from the root.) And we were surprised to find that the flowers were "burning" fat, rather than carbohydrate, as had been shown in other aroids. In fact, electron microscopy of the sterile male florets revealed that their tissue contained fat droplets and many mitochon-

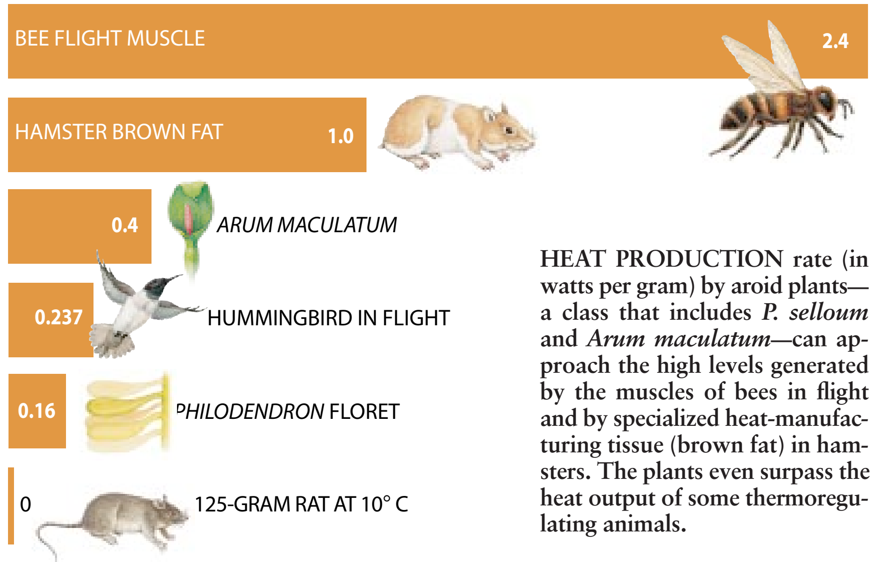


ALL STAGES OF FLOWERING in the sacred lotus are visible in photograph at the right. Temperature regulation begins sometime between the formation of the unopened bud (*right of center*) and the loosening of the petals (*left*), when insects enter the flower. It ends when the petals open fully (*top*). After pollination, the petals fall off (*far right*), and the receptacle, containing the seeds, begins to grow (*green structure near bottom*). The receptacle, visible as the spongy yellow structure in the cross section (*photograph at left*), is also the source of most of the heat. The graph, plotting measurements on one flower, is typical of the data demonstrating that the sacred lotus can actively control its own temperature. The flower maintained a nearly constant temperature (*top*) even though the air temperature fluctuated. Also, the flower achieved this stability by stepping up oxygen consumption (and thus heat production) when the air was cold and stepping it down when the air was warm (*bottom*).

dria—in other words, the tissue was remarkably similar to brown fat, a specialized heat-producing tissue found in mammals. Plant and animal cells typically use mitochondria to incorporate into ATP most of the energy derived from nutrients. But in brown fat and apparently in *P. selloum*'s unusual tissue, nutrients and oxygen are used to make heat directly.

P. selloum's impressive ability to produce heat is perhaps best appreciated by comparing the plant's output with that of other plants and animals. A 125-gram spadix produces about nine watts of heat to maintain a temperature of 40 degrees C in a 10 degree C environment—about the same wattage produced by a three-kilogram cat in the same environment. (Because of this correspondence, I often envision *P. selloum* inflorescences as cats growing on stalks.) A rat weighing 125 grams would produce only two watts, but not for lack of ability; being well insulated by its fur, it would lose less heat to the air and so could conserve its energy for other functions.

On a weight-specific basis, the rate of heat production in *P. selloum* florets approaches the highest rates in flying birds and insects. The florets, which each weigh about eight milligrams, put out 0.16 watt per gram of tissue; the birds and insects emit 0.2 to 0.7 watt per gram. Indeed, when evaluated in this way, aroids in general turn out to be among the greatest heat producers, even if they are compared with animals. The peak performer of the aroids, *A. maculatum,* generates 0.4 watt per gram in its florets, not even an order of magnitude lower than the one watt per gram output of brown fat in Siberian hamsters and the approximately 2.4 watts per gram output of active flight muscles in bees. This bee muscle rate is the maximum I know for animal tissue.



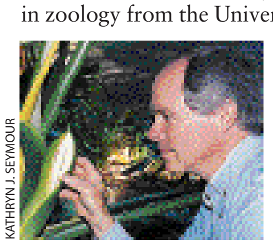
HEAT PRODUCTION rate (in watts per gram) by aroid plants—a class that includes *P. selloum* and *Arum maculatum*—can approach the high levels generated by the muscles of bees in flight and by specialized heat-manufacturing tissue (brown fat) in hamsters. The plants even surpass the heat output of some thermoregulating animals.

The high wattage of *P. selloum* raised the question of how it obtains the requisite oxygen, given that it lacks lungs, a circulatory system and the hormones that step up respiration and circulation in animals. We found that the florets gain the oxygen by simple diffusion from the air, which is normally about 21 percent oxygen. Because oxygen levels inside the florets are below the levels in the air, the oxygen moves down the gradient into the plants. Our experiments show that the diffusion of oxygen begins to decrease only after the oxygen concentration around the florets drops below about 17 percent. This level is almost never reached, however, even when the florets are producing heat at their maximum rate.

My recent anatomical studies have defined the pathway through which oxygen penetrates the florets. A floret is about seven millimeters long and 1.2 millimeters thick (roughly the size of an uncooked rice grain). Incredibly, oxygen enters through only about 170 pores, or stomates, and is distributed through a network of spaces that occupies less than 1 percent of the floret's volume. The diffusion path from the floret surface to each cell is somewhat less than 0.75 millimeter, a distance remarkably similar to the length of the air-filled tubes that supply oxygen to insect flight muscles.

Our work with hot plants demonstrates the power of applying ideas and methods developed in one field of science to another field. Driven by curiosity and logic, my co-workers and I were able to view unusual phenomena without the preconceptions that seem to channel research in well-traveled directions. As a result, we found striking similarities between animals and plants, two groups of organisms usually considered to have little in common. SA

The Author



ROGER S. SEYMOUR, who received his Ph.D. in zoology from the University of California, Los Angeles, is associate professor of zoology at the University of Adelaide in South Australia. In addition to studying heat-producing flowers, Seymour (here shown with *Philodendron selloum*) has recently been concentrating on the physiology of eggs. This is his third contribution to *Scientific American.*

Further Reading

RESPIRATION AND HEAT PRODUCTION BY THE INFLORESCENCE OF *PHILODENDRON SELLOUM* KOCH. R. S. Seymour, G. A. Bartholomew and M. C. Barnhart in *Planta,* Vol. 157, No. 4, pages 336–343; April 1983.

RESPIRATORY GAS EXCHANGE DURING THERMOGENESIS IN *PHILODENDRON SELLOUM* KOCH. R. S. Seymour, M. C. Barnhart and G. A. Bartholomew in *Planta,* Vol. 161, No. 3, pages 229–232; June 1984.

SEXUAL REPRODUCTION IN THE ARUM LILY FAMILY, WITH EMPHASIS ON THERMOGENICITY. B.J.D. Meeuse and I. Raskin in *Sexual Plant Reproduction,* Vol. 1, No. 1, pages 3–15; March 1988.

ANALYSIS OF HEAT PRODUCTION IN A THERMOGENIC ARUM LILY, *PHILODENDRON SELLOUM,* BY THREE CALORIMETRIC METHODS. R. S. Seymour in *Thermochimica Acta,* Vol. 193, pages 91–97; December 14, 1991.

THERMOREGULATING LOTUS FLOWERS. R. S. Seymour and P. Schultze-Motel in *Nature,* Vol. 383, page 305; September 26, 1996.

