Blazing Blossoms

Investigating the metabolic machinations of heat-generating plants

By RICK WEISS

The first thing you notice about a flowering voodoo lily is its elaborate reproductive structure. The fleshy purple spike, loosely cloaked by a large, hood-like leaf, can reach nearly 3 feet in height — a lush, tropical version of its North American cousin, the jack-in-the-pulpit.

Second, you notice its perfume. "Oh, it's terrible," says Ilya Raskin, who has studied the flower for years. "An absolutely god-awful odor," says Bastiaan J.D. Meeuse, one of the most avid investigators of this putrid plant.

But for all its unique beauty and olfactory insult, a third characteristic of the voodoo lily has kept botanists intrigued for more than 200 years. Put the back of your hand near the blossom and you'll feel waves of heat coming from its hormone-drenched spike. At its metabolic peak, the voodoo lily can warm itself to as much as 14°C above already-toasty ambient temperatures of about 20°C (68°F). Related plants do nearly as well.

"People make jokes all the time about using these plants to heat your house and things like that," says Roger M. Knutson, a botanist at Luther College in Decorah, Iowa, who specializes in heat-producing, or thermogenic, plants. "None of those things have much of a future, I think."

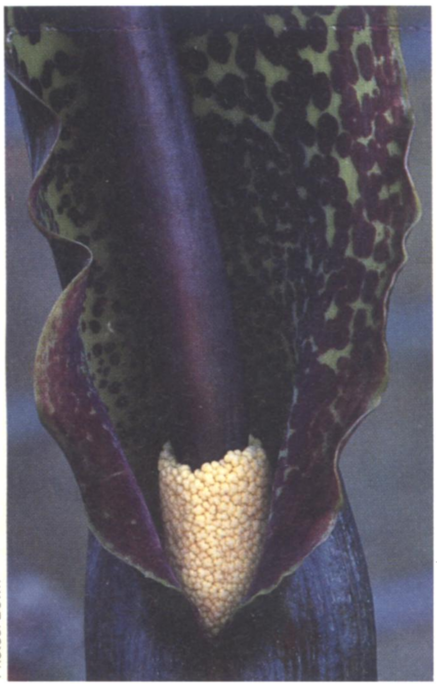
But an improved understanding of thermogenicity in plants could bring other important benefits, Knutson and other researchers say.

For evolutionary ecologists, the plants' temperature-dependent strategies for achieving reproductive success have inspired some of the more innovative experiments in pollination biology — including some involving artificial flowers filled with tiny light bulbs.

Botanical biochemists also have more than a tepid interest in thermogenic plants. They say plants such as the voodoo lily, *Sauromatum guttatum*, promise a better understanding of plant hormone systems involved in flowering — an important area of botany still in its infancy.

In perhaps their most intriguing role, thermogenic plants provide living laboratory vessels for studying traditional and alternative metabolic pathways through which plants convert energy into usable forms. For example, working with Raskin and his colleagues at E.I. du Pont de Nemours and Co., Inc., in Wilmington, Del., Meeuse discovered in 1987 that voodoo lilies produce salicylic acid — the biologically active form of aspirin — and showed that the compound is critical to the plants' heat-producing "respiratory explosion." Meeuse speculates that a better understanding of salicylic acid's role as a regulator of unusual metabolic pathways could lead to the development of new herbicides.

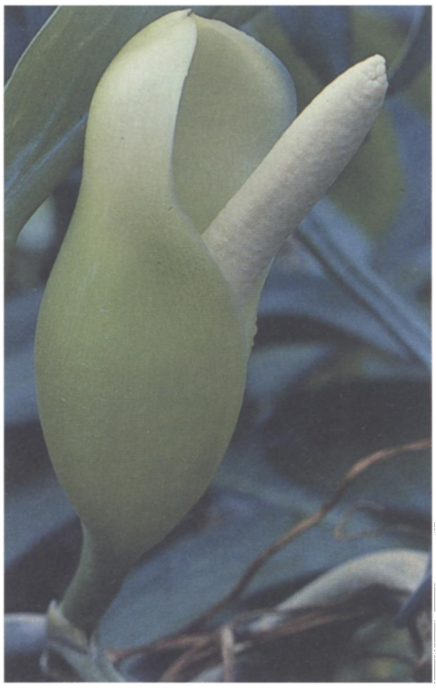
The voodoo lily is "a wonderful, wonderful botanical guinea pig," says Meeuse, a botanist at the University of Washington in Seattle. "These plants work like mad. They respire and respire and respire," giving scientists a precious opportunity to measure reactions that in most plants are either nonexistent or too subtle to notice.



Photos: Bown

The voodoo lily, Sauromatum guttatum, *is beautiful to behold but awful to smell. Native to Southeast Asia and sold in the West as a curiosity, it can generate a metabolic burst rivaling that of a hummingbird in flight.*

Voodoo lilies are by no means the only thermogenic plants; about a half-dozen plant families contain



Philodendrons ("tree lovers") — so called for their propensity for growing up tree bark — feature waxy, fragrant and in some cases thermogenic flowers designed to attract scarab beetles, their insect pollinators.

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some members that generate heat. Among those closely related to the voodoo lily – and most familiar to North American houseplant collectors – are members of the genuses *Dieffenbachia, Philodendron* and *Monstera.* Other thermogenic plants include cycads – the most primitive seed-bearing plants still living – and some palm trees.

With most thermogenic plants native to the tropics (the voodoo lily itself is Southeast Asian), their incentive to produce heat has long puzzled botanists. For a plant faced with limited amounts of food in a competitive environment, heat production would seem a huge waste of energy. "Biochemically speaking, the production of heat is lunacy," Meeuse says.

But experiments have revealed that thermogenicity is valuable indeed – at least in the voodoo lily and its closest relatives, known collectively as arum lilies. Its importance relates to the plant's penchant for pollination by carrion-loving insects. Having produced a malodorous cocktail of amines, skatoles and other aromatic chemicals characteristic of rotting meat, the plant gently warms and disperses this pungent perfume – the better to attract carrion beetles and flesh-feeding flies.

Experiments performed by Fritz Knoll in 1926 confirmed that heat production in arum lilies exists, as Meeuse says bluntly, "to evaporate these horrible, horrible odors."

Knoll made fine, purple glass models of the plant's flower spike, or inflorescence, and put tiny heat-generating light bulbs inside some of them. He painted putrefied blood (mixed with some glycerol to keep it from drying) on both heated and unheated imitation inflorescences, leaving others uncoated. Inflorescences that were warm but blood-free attracted no insects, indicating that heat alone fails as an effective insect attractant. Blood-coated inflorescences – especially those Knoll warmed – did attract insect pollinators, suggesting that odor is the main attractant and heat enhances its effects.

Moreover, says Raskin, once an insect enters one of these fetid flowers, heat "keeps the insects active inside the pollination chamber so they fulfill their pollination requirements."

Active indeed. Temperatures inside these traps can get as high as 44°C, or 110°F. To generate that much heat, the plant needs a metabolic rate "so fierce that it compares favorably with that of a flying hummingbird," Meeuse and Raskin calculate in the March 1988 SEXUAL PLANT REPRODUCTION.

Bown

The malodorous, thermogenic flower of Arum dioscoridis. *In a 1st-century compendium of herbal medicine, the plant's namesake, Dioscorides, recommended mixing it with bullock's dung as a treatment for gout.*

With an evolutionary rationale for thermogenicity thus affirmed, scientists have concentrated on the biochemical reactions through which all this heat is made. "There's a very unusual kind of respiration that goes on in these plants, such that rather than converting the energy of respiration at least somewhat into chemical energy, it is sort of wasted as heat," Knutson says.

Normally, Knutson and others explain, plants use photosynthesis to make starch. Tiny cellular components called mitochondria burn this starch and store the released energy in the form of chemical bonds – typically as high-energy phosphate bonds in the molecule adenosine triphosphate, or ATP. To do this, mitochondria perform a series of electron transfers known collectively as the cytochrome oxidase reaction.

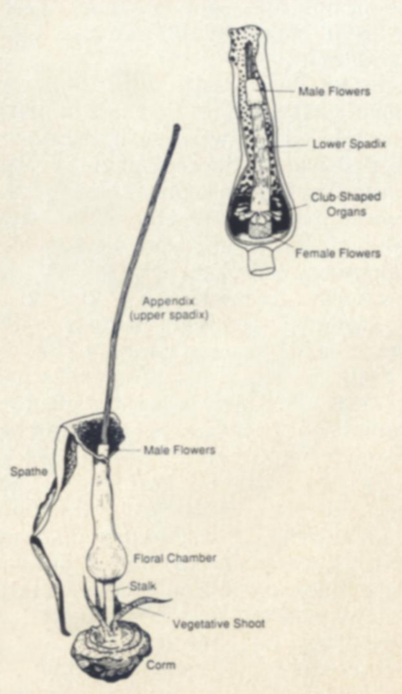
But the voodoo lily and other thermogenic plants feature an alternative electron-transfer pathway, which bypasses most of the classical steps that lead to storage of starch-derived energy in high-energy bonds. Instead, their cells simply emit most of the unleashed energy as heat. Scientists refer to this as a "cyanide-insensitive" respiratory pathway, since cyanide and carbon monoxide – chemicals that block the classical respiratory pathway – do not affect it.

"The voodoo lily circumvents ATP production, so it's just burning things without producing anything except heat," says Raskin. But it does not produce large quantities of heat all the time. Rather, in keeping with its prime purpose of enhancing pollination, the flower's peak heat production coincides with the few days during which flowering occurs.

How does this bit of synchronization occur?

Since 1937, researchers had hypothesized that a plant-produced hormone, synthesized just before flowering, made voodoo lilies "switch" to their alternate, heat-producing respiratory pathway. Botanists dubbed this unidentified substance "calorigen," but it took them another 50 years to characterize calorigen's chemical structure. With two other colleagues, Raskin and Meeuse coauthored a now-classic paper in the Sept. 25, 1987 SCIENCE in which they reported using sensitive chromatography techniques to identify the substance as salicylic acid – the metabolic end-product of aspirin. (Aspirin itself is acetylsalicylic acid; body tissues metabolize it to salicylic acid.) During their experiments, the researchers induced temperature increases of more than 8°C in voodoo inflorescences by injecting them with a solution of salicylic acid.

Two months ago, Raskin and two colleagues from Dupont published the results of further investigations of heat regulation in the voodoo lily. They developed a simplified assay enabling them to monitor changing salicylic acid concentrations in plant tissues. Levels increased almost 100-fold in the day preceding flowering, they found. The next morning,



Voodoo lily inflorescence on its peak day of flowering and heat production. Cross section shows heavily scented floral chamber, which temporarily traps pollinating insects.

"a spectacular metabolic burst" lasting about 7 hours boosted plant-tissue temperatures by more than 12°C. A second salicylic acid increase in another part of the inflorescence yielded a similar burst of thermogenicity lasting 14 hours, they report in the April PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES (Vol. 86, No. 7).

In addition, the researchers added to plant tissues more than 30 chemical analogs of salicylic acid to test each analog's thermogenic potential. With two exceptions, they found that even small changes in salicylic acid's chemical structure removed an analog's ability to trigger heat production. One exception was acetylsalicylic acid (aspirin), which showed about half the heat-producing potential of salicylic acid. The researchers speculate that aspirin's effects in plants, as in people, may result from its conversion to salicylic acid in biological tissues.

Such research has increased botanists' interest in salicylic acid as an important hormone capable of regulating growth and development in both thermogenic and nonthermogenic plants.

"It's long been known that compounds closely related to salicylic acid have been present in plants, such as in willow bark," Raskin says, noting that Native Americans chewed on willow bark to treat fever. "But there's very little we know really about how it is made in plants" or what roles it may play in the plants that produce it.

So far, Raskin says, researchers have found that salicylic acid can stimulate flowering in duckweed – a tiny freshwater herb that forms the familiar green carpet on the surface of stagnant ponds. Other research indicates that the acid advances biosynthesis of ethylene, another plant hormone, and may help plants resist some viral diseases.

Beyond improving scientists' understanding of its role as a hormone, studies of salicylic acid in plants may help solve some nagging mysteries about plant respiration. The acid's ability to trigger heat production in some plants has researchers pondering how salicylic acid regulates these plants' use of traditional and alternative respiratory pathways. Does it do so by turning off ordinary respiration, turning on alternative respiration, or both? Answers to such questions may not appear until scientists identify the key enzymatic components, or oxidases, in the cyanide-insensitive respiratory pathway.

"We're still trying to understand what the alternative oxidase really is," says Lee McIntosh, who studies alternative oxidation and heat-producing proteins at Michigan State University's Plant Research Laboratory in East Lansing. "Some [researchers] have monoclonal antibodies to it now and are close to identifying the [pathway's critical] protein."

If the gene for the key protein were inserted into plants, he speculates, "there would be a lot of things you could think about, like preventing freeze damage in trees and preventing injury in cold-temperature storage."

But the most immediate benefits of studying thermogenic plants may come in the form of new herbicides, Meeuse says. He notes that glyphosate – the most commonly used herbicide in the United States – kills plants by interfering with a series of critical metabolic reactions called the shikimic acid pathway. Plants use this pathway to make many amino acids, vitamins and other essential compounds. "We think there is evidence that salicylic acid is synthesized from shikimic acid in plants," Meeuse says.

Preliminary research in Meeuse's laboratory indicates that glyphosate leads to abnormalities in arum lily flowering, presumably by interfering with salicylic acid production. If scientists can show that salicylic acid does not simply stimulate a cyanide-resistant pathway but also serves as a molecular "switch" regulating classical pathways, it may prove useful as an herbicidal ingredient, perhaps by switching off a plant's normal respiratory pathway.

Meanwhile, researchers intent on developing glyphosate-*resistant* plants (SN: 5/28/88, p.348) continue to report progress with their work, adding to the understanding of these mysterious metabolic pathways. Additional details about plant respiration and hormone regulation seem certain to emerge as biologists apply new gene-transfer techniques to both thermogenic and nonthermogenic plants, researchers say.

And although generations of botanists have studied plant thermogenicity since French naturalist Chevalier de Lamarck first documented the phenomenon in 1778, enough remains unknown to keep a greenhouse full of botanists busy for years.

Says Meeuse, "This whole area is like a mine field of question marks." □

Stalking the stinking hot cabbage

Bown

Eastern skunk cabbage (Symplocarpus foetidus) *can get as much as 35° C above air temperature as its leathery buds poke through spring ice and snow. The distinctive leaf shape traps and circulates heated air around the bud.*

Perhaps the most common thermogenic plant native to temperate climes is the Eastern skunk cabbage – so named because of the odor its leaves release when bruised. It is among the first plants to poke through spring snow and ice along the Eastern Seaboard, in part because of its ability to melt through that frosty crust, notes Deni Bown, author of *Aroids: Plants of the Arum Family* (1988, Timber Press, Portland, Ore.).

Researchers remain uncertain of thermogenicity's primary role in Eastern skunk cabbage, says Joseph M. Patt, a botanist at Rutgers, the State University of New Jersey in Piscataway. (Western skunk cabbage, which grows in the U.S. Southwest and along the West Coast, is not thermogenic.) However, he and others say, Eastern skunk cabbage's ability to maintain remarkably constant temperatures over a wide range of environmental conditions has attracted botanical attention for years.

"You could make money betting that these plants, at a particular stage of development, are going to be from 20° to 22°C over a very broad range of environmental temperatures," says Roger M. Knutson of Luther College in Decorah, Iowa. Insight into how Eastern skunk cabbage regulates its temperature may lead to a better understanding of control processes more generally present in plants, he says.

Adds Patt: "People might at first think [such studies are] rather esoteric. But there's so little we know about plant hormone levels and regulators of flowering. The research is very important in that way." – *R. Weiss*