Thermoregulating lotus flowers

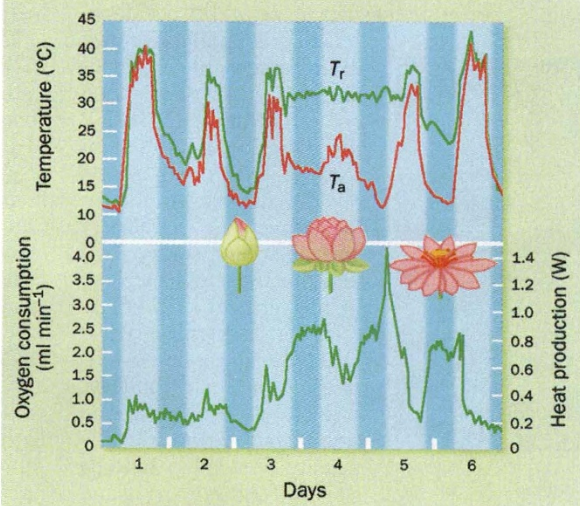
SIR — The sacred lotus, *Nelumbo nucifera* Gaertn. (Nelumbonaceae; see cover), not only produces a significant amount of heat during the sequence of flowering, but also regulates its temperature with an unexpected precision. We report that in air temperatures varying between 10 and 30 °C, the flowers remain between 30 and 35 °C throughout a 2–4-day period. Thermal stability is achieved by increasing the rate of heat production in proportion to the decrease in ambient temperature, a pattern identical to that in homeothermic birds and mammals. The homeothermic episode begins before petal opening and continues through the period of stigma receptivity. It may enhance and stabilize flower development and perhaps reward insect pollinators with a warm, equable environment.

Heat production by flowers and cones is known to occur in many species of the aroid family[1], and in a few water lilies[2], palms[3], and cycads[4]. Although records of heat production are common, observations of temperature stability are limited to two species of aroid: *Philodendron selloum*[5] and *Symplocarpus foetidus*[6]. Temperature regulation in *Nelumbo* has apparently evolved independently. *Nelumbo* flowers are protogynous and have a variable sequence of anthesis that favours outcrossing via insect pollinators[7]. A conical receptacle that contains several carpels forms the bottom of an otherwise empty floral chamber before the petals open (see figure). Stamens grow around the receptacle and are initially pressed close to it by the petals, but are released when the petals open fully.

We measured receptacle and ambient air temperatures and oxygen-consumption rates continuously in 19 flowers in the Adelaide Botanic Gardens. Early buds were at ambient temperature, but a small unregulated temperature rise appeared in closed flowers a few days before the main episode of heating (see figure). Then a 'homeothermic' period of high, regulated temperatures began in many cases 1 or 2 days before the flower opened, and continued for 2–4 days in association with presumed female receptivity (moist stigmas). Temperatures and oxygen consumption started to decline after the petals opened fully and pollen was shed.

During the homeothermic period, receptacle temperature (T_r) is regulated in a narrow range (30–35 °C) at ambient air temperatures (T_a) of between 10 and 30 °C. At $T_a = 10$ °C, $T_r = 30$ °C and at $T_a = 30$ °C, $T_r = 35$ °C. At $T_a > 30$ °C, T_r rises and remains a few degrees higher than T_a. Meanwhile, oxygen-consumption rate (hence heat production) is inversely related to T_a (see figure). Maximum heat production is about 1 W at a T_a of 10 °C.

Temperature regulation in *Nelumbo* apparently occurs at the cellular level by a steep, temperature-induced, reversible inactivation of the heat-producing metabolic pathways, as has been observed in thermoregulating *Philodendron*[8]. Briefly, when the flower enters its homeothermic period, it heats itself to at least 30 °C. Above this temperature, further increases in T_r markedly decrease the rate of heat production. Temperature equilibrium is reached when the rate of heat production equals the rate of heat loss. At low T_a, therefore, the rate of heat loss is high and T_r stabilizes near 30 °C. At higher T_a, heat loss decreases, so T_r rises slightly and reduces the rate of heat production until equilibrium is reached. Conversely, as T_a drops, heat loss increases, the flower cools slightly and increases heat production. The homeothermic period therefore relies on small changes in flower temperature within the region just above 30 °C. Regulation depends directly on T_r and indirectly on T_a, but apparently not on time of day or light cycle. Temperature stability over 2–4 days indicates complete reversibility of the responses.



An example of temperatures of the receptacle (T_r) and ambient air (T_a), and rates of oxygen consumption throughout a complete episode of thermogenesis in the sacred lotus. Stages of flowering and light cycle are indicated. Note the constancy of T_r and the reciprocal changes in T_a and oxygen-consumption rate between days 3 and 5. Temperatures in and around the flowers were measured with thermocouples and oxygen-consumption rate was measured with a flow-through respirometry system. Oxygen consumption is converted to heat production assuming 21.1 J per ml of oxygen[12]. The flowers were shielded from direct sunlight with an umbrella.

Laboratory measurements on cut flowers show that the receptacle is responsible for about half of the heat production, and the petals and stamens about a quarter each. A respiratory quotient of 1.0 indicates that carbohydrate, probably starch, is oxidized in all three tissues. Starch is present in *Nelumbo* staminal appendages, which, until now, have been thought to be the major site of heat production[2,7,9].

Common explanations for heat production in flowers are that it enhances the evaporation of floral scent that attracts insects[1,7], that it protects flowers from cold[10], or that it is a reward for pollinators, particularly endothermic flying insects[8]. Schneider and Buchanan[7], among several others, have concluded that the floral structure and pattern of anthesis of *Nelumbo* were appropriate for beetle pollination. They found that beetles were important pollinators in several Texas populations, but bees appeared important in another. Beetles that were trapped overnight fed and copulated in the floral chamber and were released unharmed the next morning to carry the pollen away. One function of thermal stability, therefore, may be a direct energetic reward to pollinators. The environment in the floral chamber would maintain a high body temperature for the insect and promote not only feeding, digestion and reproductive behaviour, but also suitable body temperatures for flight. Many insects, including beetles and bees, require thoracic temperatures above 30 °C to initiate flight[11], and the flower could be directly preparing them for departure, thus eliminating their requirement for endogenous heat production.

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