morphology. *Piper* in high-light habitats appeared to produce leaves with thicker mesophyll presumably because thicker mesophyll increases per unit area light absorption and allows the plant to absorb a larger portion of high intensity light. It was surprising that leaf area did not change with habitat as did leaf specific mass. The habitat effect may indicate that there is more change in light levels between upper and lower strata in shade plants than in sun plants, and therefore less benefit to increasing leaf area in the bottom strata.

Frequency of leaf miner attacks was somewhat higher in the shade than in the sun (11.1% vs 8.4%) This is surprising because the higher leaf specific mass that we observed in the sun would actually seem to support more herbivory in the sun, not less, by providing leaf miners greater protection and nutrition. The slightly higher leaf miner attack rate in the shade may have resulted from higher agromyzid abundance in the shade. The difference in attack rate between habitats may not be biologically relevant because herbivory was low on plants in both habitats.

Leaf miner success was strongly related to leaf area and/or to leaf characteristics that covary with leaf area. The success of miners on larger leaves did not appear to be related to larger available leaf area because miner tracks covered only small portions of leaves in both size classes. Rather, leaf miner success may relate to leaf phenology if larger leaves have a longer development period. If immature leaves have lower concentrations of chemical defenses, then leaf miners that spend a larger portion of their development in immature leaves may have greater success. Testing for covariations in nitrogen and carbon-based secondary metabolites, leaf toughness, and water content may further explain differences in leaf miner success across habitats.

If leaf miner success is correlated to leaf development time, then selection should favor adult agromyzis that can detect immature leaves destined to have relatively long development periods. However, the lack of correlation between leaf miner attack rate and leaf area suggest that ovipositing adults lack this ability, perhaps because there are no suitable chemical or physical cues. In any case, it appears that agromyzis oviposit randomly with respect to the probability of larval success. Future studies could look for correlations between attack rates and leaf maturation and compare leaf miner development in mature and immature leaves.

WARMING POTENTIAL IN *DAHLIA* FLOWERS AND CONSEQUENCES FOR INSECT POLLINATORS

JON S. BEADELL, JAMES W. HOURDEQUIN, AND ANITA L. MANNAN

Abstract . The possibility that flowers attract pollinators by creating a favorable thermal environment was examined in *Dahlia*. Parabolic-shaped flowers reflect light inward and warm the region above the central disk where pollinators forage. *Dahlia* exhibited some degree of phototropism and warming effects were most pronounced when flowers faced the sun. In the average time a pollinator spent on a flower, experimental bee temperatures rose 4 °C , suggesting that poikilothermic insects may benefit from the warm micro-environment provided by the flower. There was, however, no significant relationship between the time a pollinator spent on a flower and the difference between flower temperature and ambient temperature.

INTRODUCTION

Dahlia sp. is a sunflower-like plant widely distributed throughout North America yet growing only at high elevations in the tropics. As is typical of composite flowers, *Dahlia* flowers consist of a central disk surrounded by large cupped petals. In sunflowers, these petals may function to warm the reproductive parts of the plant, thereby reducing seed development time and increasing the fitness of the plant. In addition, the reflective petal conformation may produce a warm micro-environment for insect pollinators whose activities are temperature limited.

We hypothesized that the *Dahlia* flower form is similarly adapted for pollinator attraction in high altitude tropical locations where low morning temperatures may limit pollinator activity. We predicted that *Dahlia* flowers are oriented to maximize exposure to the sun. In addition, we expected that petals may serve as parabolic reflectors to warm objects located just above the central disk. Considering the effects of this thermoregulation on pollinators, we predicted that insect temperature should be greater than that due to black body warming alone when located in the parabolic region. As a consequence, insects should spend longer on flowers when the difference between flower and ambient temperature is greatest.

METHODS

We studied *Dahlia* flowers in a patch along the road just east of the Cuerici Biological Station, Costa Rica, on 27-28 January 1996. To determine whether floral temperature regulation occurs in the form of heliotropism or phototropism, we surveyed the orientations of 20 flowers at three times: 0730, 1530, and 0730 the following morning. Differences in orientation were compared with a paired t-test. At 1530, the orientation of 62 flowers located within 2 m of a 50 m stretch of road were surveyed in order to determine the average orientation of flowers.

To assess the effect of petals and floral orientation on the temperature above the central disk, temperature measurements were taken at the surface of the disk following four treatments: with petals at 0, 90, and 180 degrees to the sun and without petals in full sun. Ambient temperatures were also recorded for each trial to control for changes in temperature as the day progressed. Differences between ambient temperature and the temperature above the central disk in the three treatments were analyzed using a one-way ANOVA.

To assess heating effects on pollinators, we caught an average sized bee and immediately measured its internal thoracic temperature with a small diameter thermocouple probe. The bee was then killed, impaled on a temperature probe, and allowed to equilibrate in full sun. The warming of this black body on four flowers with and without petals was recorded over six minutes to estimate warming potential and warming rate. Following each trial, bee temperature was allowed to fall to normal black body temperature. We fit data from both treatments with a third degree polynomial. To determine if warming potential effects bee behavior in nature, two patches of *Dahlia* flowers were observed over a three hour period. For each pollinator, we recorded time spent on flower and temperature of the flower. We used regressions to analyze potential relationships between these parameters. To determine if parabolic petal arrangement affects ovary warming, four flowers with and without

petals were placed in grass and allowed to equilibrate in full sun for 12 minutes. Temperatures were measured at the center of the central disk and these values were compared with a Student's t-test.

Results

There was no change in the orientation of *Dahlia* flowers between 07:30 and 15:30 on the same day ($t = 2.31$, $df = 8$, $P = 0.53$); however, there was a shift in their mean orientation from 184° to 178° between 15:30 and 07:30 the following morning ($t = 2.09$, $df = 19$, $P < 0.02$). This difference probably does not reflect heliotropic motion and is more likely a function of wind or measuring error, estimated at ± 5°. Most *Dahlia* flowers faced south or southeast (Fig. 1), the direction from which the greatest solar radiation was received (pers. obs.).

Temperatures at the surface of flowers directly facing the sun averaged 4.5 °C higher than flowers angled perpendicular to the sun (90°); and 5.5 °C higher than those flowers angled away from the sun (180°; Fig. 2; $F = 9.02$, $df = 2$, $P = .002$). Petaled flowers were 3 °C warmer at the disk surface than flowers with their petals removed (Fig. 2; $t = 2.36$, $df = 7$, $P < 0.001$).

Bee temperature increased an average of 12 °C in six minutes on petaled flowers facing the sun. Bee temperature increased more quickly and leveled off at a higher temperature on flowers with petals than those without (Figs. 3 and 4). Pollinators spent an average of 19 seconds on a flower, however there was no significant relationship between the amount of time a pollinator spent on a flower and the difference between ambient and flower temperature ($r = .008$, $df = 32$, $P = 0.15$, $n=33$). Ovary temperatures were not different in petaled flowers and flowers with their petals removed ($t = 2.45$, $df = 6$, $P = 0.91$).

Discussion

Dahlia flowers are apparently not heliotropic, although plants tended to grow facing the sun. This strategy, combined with a petal morphology that reflects light inward, maximized warming in the parabolic region where pollinators land. Results showing that ovary temperature was unaffected by petal removal suggest that petals do not function to warm reproductive parts.

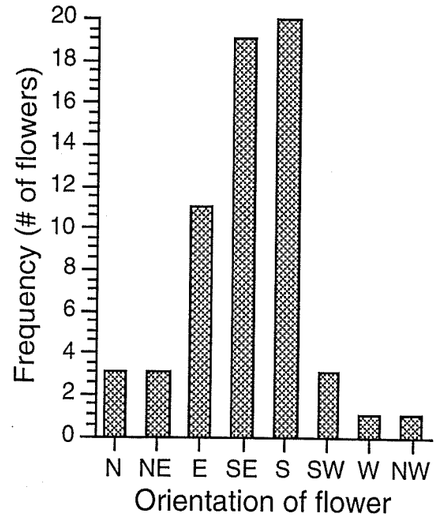

Fig.1. Orientation of *Dahlia* flowers (n = 60) at Cuerici Biological Station, Costa Rica. The strongest solar radiation was received from the south - southeast.

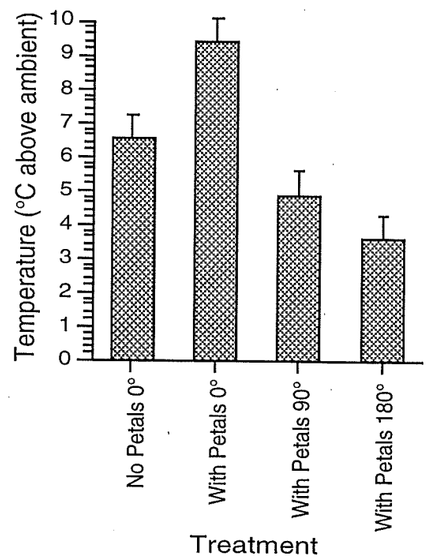

Fig.2. Increases in *Dahlia* flower temperatures over ambient temperature at different angles to the sun and without petals (n = 8).

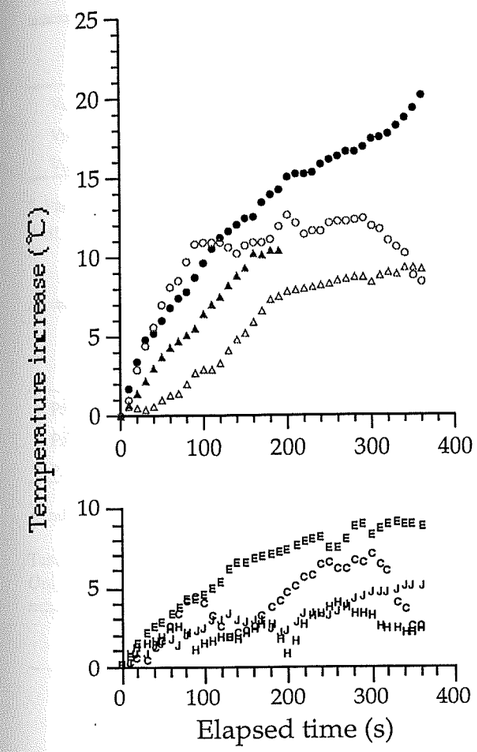

Fig.3. Warming rates of experimental bee on *Dahlia* flowers (Top) with petals (n = 4) and (Bottom) with petals removed (n = 4). The bee began at black body temperature (26.3 °C).

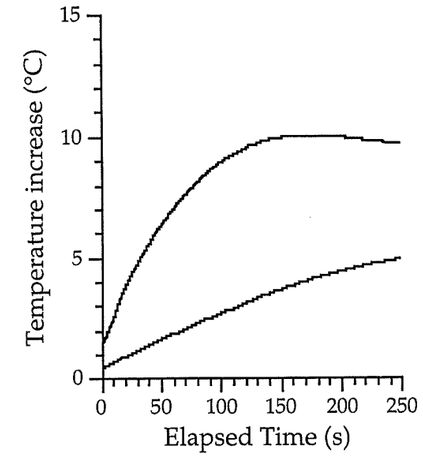

Fig. 4. Curve fitted warming rates of experimental bee on *Dahlia* flowers with (upper curve) and without petals (lower curve). See Fig. 3 for raw data.

The dramatic increase in experimental bee temperature on flowers with intact petals indicates that there is great potential for pollinator warming. Bee temperatures increased by an average of 4°C in the average time (9 seconds) that pollinators in nature spent on flowers. Although experimental bee warming started at relatively low temperatures and did not include metabolic heat production, the wide range over which temperature increased (from 28°C to 40°C) suggests that bees in nature may exhibit similar warming patterns over a smaller temperature range.

Pollinators in nature did not appear to spend longer on individual flowers in the morning when there was the greatest opportunity for temperature increase. It is possible that the benefits of warming are most critical early in the morning, before we began measuring pollinator activity. If pollinators overnight on stems of *Dahlia*, then the critical time for warming on flowers may be the first few minutes before pollinators become active for the day. Alternatively, pollinators may benefit from warming throughout the morning by spreading basking time over a number of flowers and raising their temperature slightly on each one. It is also possible that pollinators are not temperature limited and may function well at cool temperatures or raise their temperature metabolically through flight.

If pollinators are temperature limited, then flowers that can attract pollinators during the cooler parts of the day may have increased reproductive success. Reproductive success would increase if warming in the parabolic region induced pollinators to spend longer on individual flowers and pollinate a greater number of ovules. Another strategy might be to attract pollinators through warming, but to limit nectar production so that pollinators visit a greater number of conspecifics. An understanding of *Dahlia* breeding systems, and specifically whether flowers are obligate outcrossers, could help to distinguish between the relative importance of these two strategies. Future studies could also compare the seed set of *Dahlia* to the seed set of other high elevation flowers to determine whether parabolic shaped flowers have increased reproductive fitness at high elevations.