Received: 6 September 2023 | Revised: 30 November 2023 | Accepted: 19 January 2024

DOI: 10.1002/ecy.4268

THE SCIENTIFIC NATURALIST

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Refrigerated flowers in the torrid Mediterranean summer

Carlos M. Herrera

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, Spain

Correspondence
Carlos M. Herrera
Email: herrera@ebd.csic.es

Handling Editor: John Pastor

KEYWORDS: Asteraceae, *Carlina corymbosa*, evaporative cooling, floral thermal biology, floral thermal deficit, Mediterranean climate

Torrid summers are consubstantial with the Mediterranean-type climate that prevails over most of the Iberian Peninsula (Capel Molina, 1981). Daily maximum temperature >40°C and relative humidity <10% occur frequently during the rainless period of 3–4 months that follows springtime. This long harsh season brings considerable hardship to plants, particularly in lowland and mid-elevation habitats. Annuals spend the summer as seeds, while herbaceous and woody perennials halt vegetative and reproductive activity (Thompson, 2005). During July–August the decaying remains of withered annuals lying on a dusty ground, the marcescent foliage of summer-deciduous shrubs, and a generalized dearth of wild flowers all combine to make brown the predominant hue in many Iberian landscapes. It thus comes as a pleasant surprise when such brownish estival carpet is broken here and there by the yellow glittering flowerheads of the thistle *Carlina corymbosa* (Asteraceae; Figure 1A). This perennial herb blooms when hardly any others do and is commonly found in roadsides, open oak woodlands, and clearings in evergreen forests and shrublands, exposed during the daytime to a scorching sunshine. But beyond this visually apprehended peculiarity, the truly outstanding natural history singularity of this thistle is only to be revealed by the sense of touch, more specifically by thermal touch, the perception of temperature of objects in contact with the skin. I discovered by chance that pressing a fingertip on the yellow surface of flowerheads during the hottest period of the day conveyed a cool sensation, as if flowerheads were coolish inside. This observation steered me to articulate the rather counterintuitive hypothesis that during the hottest period of the year, precisely at the time of day when ambient temperature is highest, the flowerheads of summer-flowering *C. corymbosa* thistles have an interior that is cooler than the surrounding air. As shown in what follows, temperature measurements verified this hypothesis.

Instrumental tests were conducted in the field on 1–15 August 2021 and 2023 at two southern Iberian *C. corymbosa* populations growing in open *Quercus ilex* woodlands of central Sierra Morena (760 m above sea level [asl], Córdoba province, "mid-elevation site" hereafter), and in large clearings of *Pinus nigra* forests in the Sierra de Cazorla (1410 m asl, Jaén province, "mountain site" hereafter). The two sites were 155 km apart. Results from the two locations were closely similar, so they will be presented together. Paired measurements of temperature inside individual flowerheads and in the air 2 cm away were taken continuously during periods of 2–5 days. One fine type K thermocouple (exposed junction, 0.2 mm probe diameter, RS PRO Reference 110-4482) was inserted perpendicularly into the flat surface of the flowerhead until it reached the receptacle. A second, similar thermocouple was attached to the flowerhead and its tip kept ~2 cm from the flowerhead's surface. (See Figure 1B for setup.) Wires were attached to the flowerhead and held in place with strips of masking tape. Thermocouples were connected to a battery-powered Omega HH520 data logger/thermometer.

FIGURE 1 (A) Plant of *Carlina corymbosa* in full bloom at the mid-elevation study site, 1 August 2021. (B) Close-up of a monitored flowerhead showing the two thermocouple wires set up for simultaneously measuring temperatures inside the flowerhead (T_{in}) and the surrounding air nearby (T_{out}). Photos (A) and (B) credit: Carlos M. Herrera.

For each monitored flowerhead, paired temperature measurements (within and outside the flowerhead, T_{in} and T_{out} hereafter, Figure 1B) were continuously recorded at either 3-min (2021) or 1-min intervals (2023). Seven different flowerheads were monitored in this way, yielding a cumulative total of 24,519 paired T_{in} and T_{out} records totaling 29.3 flowerhead·days of temperature data (1.9–5.9 days of continuous data per flowerhead; all raw temperature measurements are available in Herrera [2023a]). Preliminary measurements indicated that, during daytime, heating of the exposed probe by solar irradiance led to a rise of 0.2–0.8°C in T_{out} (depending on wind, orientation, and time of day) relative to the air temperature measured with the probe shaded. This effect most likely led to slightly overestimating the thermal deficit inside flowerheads ($\Delta T = T_{in} - T_{out}$) during daytime, but the magnitude of such bias was deemed negligible, and no attempt was made at either shading the external probe or correcting T_{out} values.

Thermal monitoring revealed that the interior of *C. corymbosa* flowerheads was cooler than the immediately surrounding air most of the time. For all monitored flowerheads combined, T_{in} was lower than T_{out} in 88.1% of paired measurements (Appendix S1: Figure S1), the median thermal deficit of the interior of flowerheads relative to the air outside was −3.2°C, and the ΔT interquartile range was −4.9 to −1.2°C, revealing that the thermal deficit was substantial (< -5°C) 25% of the time.

Continuous thermal monitoring of individual flowerheads over several days revealed that both internal temperature and thermal deficit followed regular diel rhythms, as illustrated by the temperature time series for two representative flowerheads, one from each study locality, shown in Figure 2. T_{in} was very similar to T_{out} from early morning through noon, and both temperatures varied in unison over that period. T_{in} and T_{out} became dissociated afterward, and a substantial thermal deficit (ΔT) built up that persisted from noon through at least midnight. The largest ΔT values, approaching −10°C on some days, consistently occurred from noon through early afternoon, coincidentally with the period when T_{out} reached the daily maxima (Figure 2). There also seemed to be a direct relationship between absolute ΔT and maximum air temperature across different days in the life of the same flowerhead, so that in hotter days the absolute ΔT was larger (in Figure 2, upper graph, compare thermal patterns of mild 9–10 August with those of hot 11–14 August).

The finding that flowerheads of *C. corymbosa* undergo a regular diel rhythm of internal refrigeration raises questions about the mechanism permitting these plants to periodically cool their flowers in the torrid weather that prevails during its flowering season, but also on the

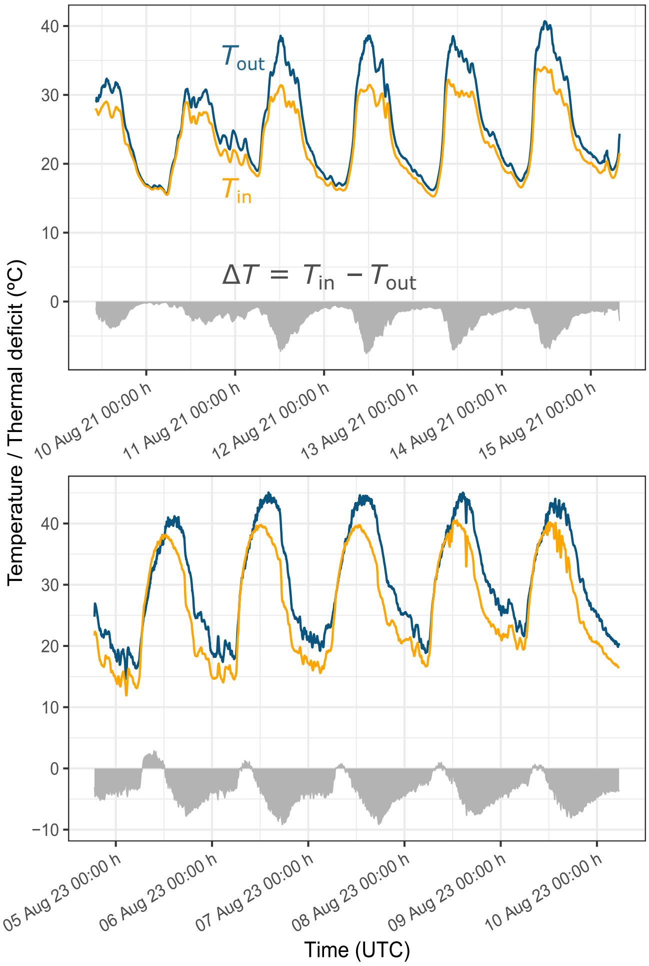

FIGURE 2 Variation of temperature inside flowerheads (T_{in}, orange lines) and the air outside (T_{out}, blue lines) and thermal deficit within flowerheads ($\Delta T = T_{in} – T_{out}$, gray area at bottom of each plot) during the full monitoring period of two representative flowerheads of *Carlina corymbosa*, each encompassing ~5 days (top and bottom graphs are for flowerheads from the mountain and mid-elevation sites, respectively). Original measurements were smoothed for the graphs using a moving average procedure with 10-min sliding window.

possible costs and benefits associated with the species' floral thermal biology. Regarding the possible cooling mechanism, reduced solar irradiance inside these flowerheads due to self-shading (Karban et al., 2023) can be safely ruled out, since substantial thermal deficits persisted also for most of the night (Figure 2). The most parsimonious hypothesis is that periodic flowerhead cooling in *C. corymbosa* was achieved by temporarily enhanced transpiration in the florets and/or receptacle. Weak evaporative cooling has been demonstrated experimentally in flowers of convolvulaceous flowers in a tropical environment, but in that instance the flowers did not reach temperatures lower than the environment (Patiño & Grace, 2002). Cooling by transpiration has been reported for leaves of well-watered plants exposed to sunshine, but actual thermal deficits (i.e., $T_{in} - T_{out} < 0$) are infrequent and much smaller than those exhibited by *C. corymbosa* flowerheads (Cook et al., 2021; Linacre, 1964; Still et al., 2022). The high ambient temperature and low relative humidity faced by *C. corymbosa* presumably augmented the cooling efficacy of transpiration during the hottest part of the day, leading to the large thermal deficits observed. Strong cooling effects arising from intense water evaporation in dry–hot climates have been long used by human cultures from the Mediterranean Basin, Middle East, and Africa as a chilling technique, in the form of sweating pitchers made of porous clay, which typically achieve temperature drops of 5–20°C relative to the ambient temperature ("*botijos*" in Spanish; Chemin et al., 2018; Martínez de Azagra & Del Río, 2015; Zubizarreta & Pinto, 1995). I propose that the large thermal deficit found inside *C. corymbosa* flowerheads at high ambient temperatures was achieved through a "botijo effect." As suggested by one reviewer (Richard Karban), support for this hypothesized mechanism might be found by comparing the cooling ability of plants differing in their access to water, for example, through experimental manipulation of water availability by differential watering.

In addition to the elucidation of the mechanism(s) involved, two striking aspects of the thermal biology of *C. corymbosa* flowerheads deserve attention from a plant ecological perspective. First, since cooling by transpiration involves increased water loss, that *C. corymbosa* plants can afford such water drains during the harshest period of the Mediterranean dry season points to physiological features enhancing efficiency in water acquisition, storage, or retention. Second, the flowerhead cooling system was somehow shut off by plants from early morning through noon, only to be started again at the moment of the day when ambient temperature was quickly approaching the daily maximum. This can be construed as an "intelligent response" (sensu Trewavas, 2003, 2017) directed to prospectively keep flowerhead temperature below dangerous levels that could impair pollen and ovule performance as a consequence of heat stress (Chaturvedi et al., 2021; Zinn et al., 2010). Pollen germination, for example, declines steeply at temperatures >30°C (Orueta, 2002; Seymour et al., 2009). Whether the daily restart of the cooling system was triggered by fast-rising temperature or by increasing solar irradiance could be dissected experimentally by comparing the daily course of T_{in} and T_{out} in flowerheads exposed to different irradiance levels obtained, for instance, by differential shading.

Cooling by transpiration can also have indirect beneficial effects on *C. corymbosa* reproduction via effects on pollinator visitation. Major pollinators of *C. corymbosa* are medium-sized and large endothermic bees in the genera *Anthophora* and *Megachile*, which could risk overheating while foraging in summer sunshine (Corbet & Huang, 2016; Herrera, 2023b; Johnson et al., 2023). Although bees prefer to probe warmer flowers at low ambient temperatures, their preferences shift to cooler flowers at ambient temperatures above ~30°C (Dyer et al., 2006; Norgate et al., 2010; Shrestha et al., 2018). In the hot Mediterranean summer, *C. corymbosa* flowerheads cooler than the air could therefore be more attractive to bees and have greater pollination success. This hypothesis can be evaluated by assessing the possible detrimental effects of artificially raised temperatures inside flowerheads (e.g., by the insertion of battery-powered resistors; Herrera & Medrano, 2017) on pollinator visitation rates, visit duration, and pollen removal and deposition.

ACKNOWLEDGMENTS

I'm indebted to my son, Carlos A. Herrera, for discussion and interpretations of floral cooling from a devil's advocate, physicist's perspective. Richard Karban and Casper van der Kooi provided useful remarks on the manuscript. The research reported here received no specific grant from any funding agency.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Herrera, 2023a) are available in figshare at https://doi.org/10.6084/m9.figshare.24679545.v1.

ORCID

Carlos M. Herrera https://orcid.org/0000-0003-2452-3888

REFERENCES

Capel Molina, J. J. 1981. *Los Climas de España*. Barcelona: Oikos-Tau.

Chaturvedi, P., A. J. Wiese, A. Ghatak, L. Zaveska Drabkova, W. Weckwerth, and D. Honys. 2021. "Heat Stress Response Mechanisms in Pollen Development." *New Phytologist* 231: 571–585.

Chemin, A., V. Dit Vehel, A. Caussarieu, N. Plihon, and N. Taberlet. 2018. "Heat Transfer and Evaporative Cooling in the Function of Pot-in-Pot Coolers." *American Journal of Physics* 86: 206–211.

Cook, A. M., N. Berry, K. V. Milner, and A. Leigh. 2021. "Water Availability Influences Thermal Safety Margins for Leaves." *Functional Ecology* 35: 2179–89.

Corbet, S. A., and S.-Q. Huang. 2016. "Small Bees Overheat in Sunlit Flowers: Do they Make Cooling Flights?" *Ecological Entomology* 41: 344–350.

Dyer, A. G., H. M. Whitney, S. E. J. Arnold, B. J. Glover, and L. Chittka. 2006. "Bees Associate Warmth with Floral Colour." *Nature* 442: 525.

Herrera, C. M. 2023a. "Temperatures Within and Outside Flowerheads of the Summer-Flowering Mediterranean Thistle *Carlina corymbosa* (Asteraceae)." Figshare, Dataset. https://doi.org/10.6084/m9.figshare.24679545.v1.

Herrera, C. M. 2023b. "Thermal Biology Diversity of Bee Pollinators: Taxonomic, Phylogenetic and Community-Level Correlates." bioRxiv Preprint. https://doi.org/10.1101/2023.11.27.568883.

Herrera, C. M., and M. Medrano. 2017. "Pollination Consequences of Simulated Intrafloral Microbial Warming in an Early-Blooming Herb." *Flora* 232: 142–49.

Johnson, M. G., K. Alvarez, and J. F. Harrison. 2023. "Water Loss, Not Overheating, Limits the Activity Period of an Endothermic Sonoran Desert Bee." *Functional Ecology* 37: 2855–67.

Karban, R., D. Rutkowski, and N. A. Murray. 2023. "Flowers that Self-Shade Reduce Heat Stress and Pollen Limitation." *American Journal of Botany* 110: e16109.

Linacre, E. T. 1964. "A Note on a Feature of Leaf and Air Temperatures." *Agricultural Meteorology* 1: 66–72.

Martínez de Azagra, A., and J. Del Río. 2015. "World Map of Potential Areas for the Use of Water Cooling Pitchers (*Botijos*)." *Journal of Maps* 11: 240–44.

Norgate, M., S. Boyd-Gerny, V. Simonov, M. G. P. Rosa, T. A. Heard, and A. G. Dyer. 2010. "Ambient Temperature Influences Australian Native Stingless Bee (*Trigona carbonaria*) Preference for Warm Nectar." *PLoS One* 5: e12000.

Orueta, D. 2002. "Thermal Relationships between *Calendula arvensis* Inflorescences and *Usia aurata* Bombyliid Flies." *Ecology* 83: 3073–85.

Patiño, S., and J. Grace. 2002. "The Cooling of Convolvulaceous Flowers in a Tropical Environment." *Plant, Cell & Environment* 25: 41–51.

Seymour, R. S., Y. Ito, Y. Onda, and K. Ito. 2009. "Effects of Floral Thermogenesis on Pollen Function in Asian Skunk Cabbage *Symplocarpus renifolius*." *Biology Letters* 5: 568–570.

Shrestha, M., J. E. Garcia, Z. Bukovac, A. Dorin, and A. G. Dyer. 2018. "Pollination in a New Climate: Assessing the Potential Influence of Flower Temperature Variation on Insect Pollinator Behaviour." *PLoS One* 13: e0200549.

Still, C. J., G. Page, B. Rastogi, D. M. Griffith, D. M. Aubrecht, Y. Kim, S. P. Burns, et al. 2022. "No Evidence of Canopy-Scale Leaf Thermoregulation to Cool Leaves below Air Temperature across a Range of Forest Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2205682119.

Thompson, J. D. 2005. *Plant Evolution in the Mediterranean*. Oxford: Oxford University Press.

Trewavas, A. 2003. "Aspects of Plant Intelligence." *Annals of Botany* 92: 1–20.

Trewavas, A. 2017. "The Foundations of Plant Intelligence." *Interface Focus* 7: 20160098.

Zinn, K. E., M. Tunc-Ozdemir, and J. F. Harper. 2010. "Temperature Stress and Plant Sexual Reproduction: Uncovering the Weakest Links." *Journal of Experimental Botany* 61: 1959–68.

Zubizarreta, J. I., and G. Pinto. 1995. "An Ancient Method for Cooling Water Explained by Mass and Heat Transfer." *Chemical Engineering Education* 29: 96–99.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Herrera, Carlos M. 2024. "Refrigerated Flowers in the Torrid Mediterranean Summer." *Ecology* 105(3): e4268. https://doi.org/10.1002/ecy.4268