



# Short communication: thermal regimes in hollow stems of herbaceous plants—concepts and models

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## Abstract

Although there have been studies of the temperature regimes within flowers, micrometeorology within stems seems to have been overlooked. We present ideas, hypotheses, and a diagrammatic model on the biophysical and thermodynamic processes that interact in complex ways to result in elevated temperature regimes within hollow stems of herbaceous plants. We consider the effects of the ambient air around the stems, the possible importance of insolation, and greenhouse effects as influenced by stems' orientation and optical properties, i.e., reflection, absorption, emissivity, translucence, pigmentation, and thermal conductivity. We propose that greenhouse effects contribute significantly to and are influenced by the above phenomena as well as by the gross anatomy (volume:surface ratio; wall thickness), evapotranspiration, and the thermal properties of the gas mixture in the lumen. We provide examples of those elevated temperatures that can be several degrees Celsius above the temperature of the surrounding atmosphere.

**Keywords** Hollow stem · Herbaceous plant · Temperature · Greenhouse effect · Growth

## Introduction

There is a long history of scientific interest in the thermal regimes within structures of herbaceous plants. Metabolic heat generation in the blossoms of Araceae is well studied (Lamarck 1777 (in Cooke 1882); Gibernau et al. 2005; Zhu et al. 2011). The capture of solar radiation by diaheliotropic bowl-shaped (parabolic or spherical-sections) flowers (Kevan 1975, 1989; Kjellberg et al. 1982; Galen 2006; Zhang et al. 2010) has been investigated, especially in Arctic and alpine habitats. Some flowers and inflorescences absorb solar radiation directly (Kevan 1989) and some are notoriously diaheliotropic (e.g., sunflower *Helianthus annuus* (Asteraceae) Atamian et al. 2016). Some, with enclosed calyces or corollas function as microgreenhouses (Kevan 1989; McKee and Richards 1998), which, as with anthesed flowers

(McKee and Richards 1998), we suggest may result in the heating of floral buds and so speed development (see Distifano et al. 2018). Yet other flowers capture convected heat (Kevan 1989).

Despite documentation of those heating mechanisms in floral structures, it seems that heat capture in hollow stems of herbaceous stems has been overlooked. Cooke (1882) in his review of temperatures within plant parts made no mention of stem temperatures, similarly Kerner von Marilaun (1902) mentioned temperatures within flowers but not within stems. Microclimatology within hollow stems seems to have been restricted to studies on CO<sub>2</sub>, as in some alpine plants of Wyoming (Billings and Godfrey 1967) and in bamboo (*Bambusa vulgaris*) (Zachariah et al. 2016).

The importance of hollowness in herbaceous stems in biomechanics relates the ratio of plant mass to buckling strength (Niklas 1992; Niklas and Spatz 2012) as a key parameter. Hollow tubes resist buckling with far less mass than do solid cylinders. Despite that accepted idea, there seem to be no reviews of the incidence of hollowness in stems of herbaceous plants from the viewpoints of taxonomy, biogeography, or seasonality. However, it has been noted that the hollow stems in alpine plants may be an adaptation to recycling respiratory CO<sub>2</sub> for use in photosynthesis (Billings and Godfrey 1967).

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In this manuscript, we present our ideas regarding heating and heat transfer processes in hollow stems of herbaceous plants playing important roles in the complex interactions of form, function, metabolism, and growth (Fig. 1, Box 1).

**Box 1.** Parameters for measuring the microthermic regimes, heating, and heat transfer processes with the hollow

stems of herbaceous plants. We draw special attention to the complex and comprehensive study by Pincebourde and Casas (2006) on the thermal ecology of insect-created leaf-mines. Notations to Fig. 1 refer to Fig. 1 as part of the present paper and followed by letter and number to designate the process identified in Fig. 1. Literature references are made to particularly relevant publications for the particular points noted.

## I. GENERAL

I.1 Time & Date: Required for calculations/estimations of intensity of solar radiation.

I.2 Irradiance (Fig. 1 process A): Direct measurements.

I.3 Ambient air temperature: Direct measurements (re: Fig. 1 process 4).

I.4 Wind speed: Direct measurements for consideration of cooling rates (wind-chill) (re: Fig. 1 process 4) (Pincebourde and Casas 2006).

I.5 Atmospheric saturation deficit: Direct measurements. May influence rates of cooling by transpiration and wind-chill (re: Fig. 1 process 4).

## II. PLANT (STEM) SURFACE

II.1 Orientation: Observation and angular orientation with respect to vertical. This is needed to accommodate angle of incidence of solar radiation.

II.2 Temperatures: Infrared thermometry (Atamian et al. 2016 Fig. 3C; Dietrich and Kömer 2014).

II.3 Emissivity (Fig. 1 processes 1 & 3 outside stem): Infrared thermometry (ratio of energy radiated from stem surface to that which would be radiated by a black body under the same conditions). Needed for accurate non-contact temperature measurements of the stem surface and heat transfer calculations (Ribeiro da Luz and Crowley 2007; Chen 2015).

II.4 Reflectivity (Fig. 1 process 1): Reflectance spectrophotometry by waveband. General reflectance of vegetation is about 15%, but variable between species (e. g., Allen et al. 1969; Gausman and Allen 1973 for near IR; Kevan and Backhaus 1998; Chittka et al. 1994; Omori et al. 2000 for UV to near IR).

## III. PLANT (STEM) CHARACTERISTICS

III.1 Pigmentation: Plant pigments are well studied with respect to their extraction from plant tissue through to their chemistry and molecular genetic expressions (Lee 2007).

III.2 Pigment placement: Surficial, epidermal, mesophilic, etc. affects specular to diffuse reflection and coloration in animal visible range (Kevan and Backhaus 1998; van der Kooij et al. 2016, 2017) and the near IR (Allen et al. 1969; Gausman and Allen 1973).

III.3 Cellular anatomy: Relates to III.2 in respect of pigments in organelles (plastids) or in solution in cytoplasm.

III.4 Heat Conductance (Fig. 1 processes 2la, 2lo & 6) also from outside the stem (Fig. 1 process 4 and re: comments 1.3–5 above) (see Pincebourde and Casas 2006).

III.5 Transmission (Translucence) (Fig. 1 processes 2la, 2lo & 3): See comment III.2 and McKee and Richards (1998); Omori et al. (2000).

## IV. PLANT MORPHOLOGY

IV.1 Stem diameter and length: Direct measurements.

IV.2 Stem wall thickness: Direct measurements.

IV.3 Lumen diameter & volume: Direct measurements. Size of the lumen may influence thermodynamics of heat exchange and movement (Fig. 1 processes 7–10).

IV.3.a *Lumen volume*: Lumen diameter  $\times$  length.

IV.3.b *Septate or not*: Spacing and distance between septa (lumen volumes between septa).

IV.4 Inside wall:

IV.4.a *Smooth, shiny, hairy, pithy*: By observation, scores and possibly measurements. Reflective to insulative properties seem unstudied.

## V. LUMEN ENVIRONMENT

V.1 Temperature: Direct measurements by thermocouples or thermistors.

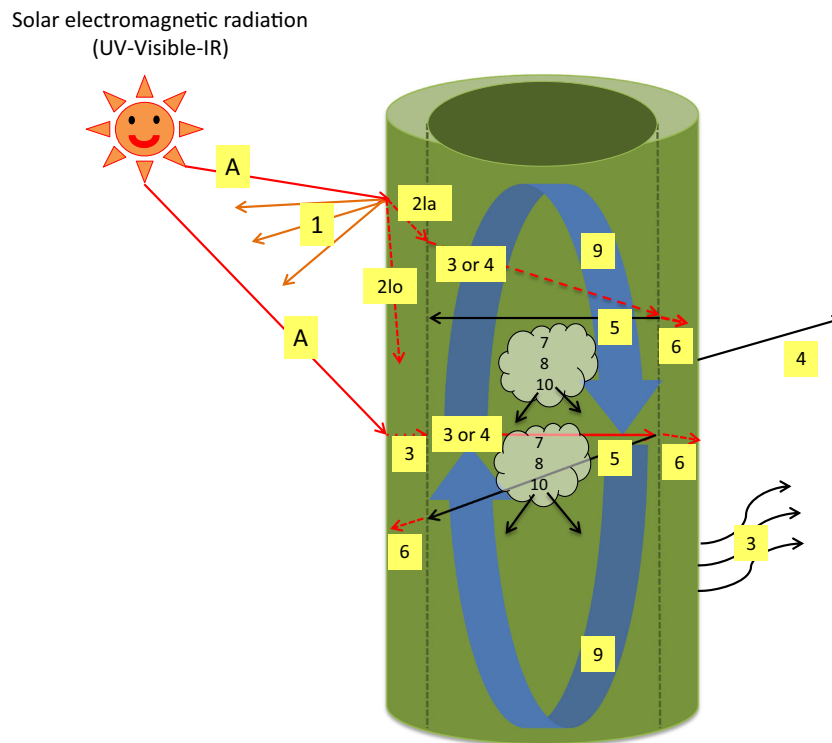
V.2 EM reflection & absorption (Fig. 1 process 5):

V.3 Atmospheric Chemistry (Fig. 1 process 7) as circulating/diffusing (Fig. 1 process 9) greenhouse gas mixture (Billings and Godfrey 1967; Zachariah et al. 2016).

Our interest in hollowness being adaptive for heat gain applies to growth rates of stems in their lofting reproductive structures to conspicuousness for floral presentation, pollination, and then for seed dispersal. We note that although there may be fuel and nutrients for growth and elongation of the above ground parts of herbaceous plants stored in below ground parts (roots, bulbs, corms, tubers, etc.), warmth is needed for metabolism to occur. We hypothesize that hollowness within plant parts promotes heating by the greenhouse

effect, and thereby provides the energy boost needed to accelerate metabolism and growth beyond what might be otherwise feasible at ambient atmospheric temperatures.

For ornamentals, rapid growth is important for stature. Alternating hot and cold stimulates stem elongation in e.g., *Chrysanthemum* production (Carvalho et al. 2002). Spring bulbs (e.g., daffodils, tulips, etc.) grow rapidly, even in cold weather, at rates that exceed those expected by mean ambient air temperatures alone. Similarly, many other tall, showy



**Fig. 1** Plants' stems become warmed by a complex of thermal processes (identified by numbers and letters) involving radiative, conductive, and convective heating. Apart from the influence of the temperature of the ambient air (not shown) is the likely contribution of solar electromagnetic radiation (UV-Visible-IR) (A). Some impinging radiation is reflected (1), some is absorbed (2) and some is transmitted (3) through the tissue (translucence). Absorbed radiation is conducted through the stem's tissue (laterally and longitudinally) (2la; 2lo). It is lost to the stem tissue by radiation (3) and conduction (4) to the outside and inside (lumen) of the stem. Transmitted radiation (3) and/or conducted (4) contributes additional energy to the lumen of the stem. Within the stem, radiant energy (3), like the impinging solar EMR, can be a) reflected (5), b) absorbed by stem tissue (6) from within, and also c) absorbed by the moist atmospheric gas in the

lumen (7). The energy absorbed by the internal atmosphere (7) contributes to the thermal environment within the stem by heat exchange by conduction (8), convection (9), and re-radiation (10). The dynamics of how the thermal environment in hollow stems is generated involves various complex processes that result in the rise in temperature measurable by various thermometric instruments. Heated stems liberate their energy through radiation (measurable as Emissivity; 3) and conduction (4) to the surrounding air (or water in the case of aquatic plants). Some of the heat generated within the stem is conducted elsewhere in the plant by the liquid in conductive tissues (phloem and xylem; 2lo), some of the EMR is used in photosynthesis, and thermal energy is used in metabolism (not shown). Some further explanations and comments are given in Box 1

ornamentals elongate their flowering stems quite rapidly in spring and early summer.

Hollowness is well known in grass culms (Poaceae) and in umbelliferous stems (Apiaceae). That the peduncles of daffodils and tulips, of dandelions and some other Asteraceae are hollow is common knowledge. A casual survey of about 120 species of herbaceous plants (excepting Poaceae) growing in southern Canada (Ontario and Quebec), in northern Manitoba around Churchill, and in Scotland and England in summer 2017 indicates that about 60% have hollow stems. Figure 2 illustrates some hollow stems of common herbaceous plants from southern Ontario, Canada. The anatomy of hollowness ranges from thin-walled and wide lumen tubes, making almost translucent stems (as in *Impatiens* spp., *Taraxacum* spp., *Equisetum* spp., *Fallopia japonica*) to thick-walled stems with or without apparent pith and narrow lumens. Some stems are solid.

## Materials and methods

In 2017, casual surveys were made of herbaceous plants in various locations in Quebec, Ontario, and Manitoba in Canada, in Angus in Scotland, and in Nottingham and Yorkshire in England. The common and conveniently available plants were simply chosen and identified in the field and cut with a pair of secateurs and whether or not they had hollow stems that were noted.

Temperature measurements within hollow stems were made in various locations in Canada (Table 1) by inserting copper-constantan thermocouples (36 gauge 5SRTC-TT-T-36-36 from Omega Canada Inc.) into the lumen of the stems and as left hanging in the air within 2 cm of the point of insertion and in the shade of the study plant. The temperatures from the thermocouples were recorded on an Omega HH147 RS 232 data Logger Thermometer (accuracy  $\pm 0.7$  °C and response time of  $< 0.5$  min (the minimum time interval

**Fig. 2** Representative examples of hollow stems with approximate outside diameters (od) from herbaceous plants: top right, dandelion (*Taraxacum officinale* (Asteraceae)) ca. 3 mm od; top middle, common reed (*Phragmites australis* (Poaceae)) ca. 7 mm od; top left, jewelweed, touch-me-not (*Impatiens capensis* (Borraginaceae)) ca. 5 mm od; bottom right, chicory (*Cichorium intybus*) (Asteraceae)) ca. 4 mm od; bottom middle, water hemlock (*Cicuta virosa* (Apiaceae)) ca. 11 mm od; bottom left, Japanese knotweed (*Fallopia japonica* (Polygonaceae)) ca. 8 mm od. (Photographs from living specimens collected around, Guelph, Ontario, Canada on 7 August, 2018)



between recorded temperatures)) as spot readings alternating between the stem and ambient air. At the same time as the temperatures were being recorded, the general conditions of sunshine and shade were recorded.

The temperatures within and outside the hollow stems were compared statistically by Student's *t* test under the null hypothesis that there is no difference in temperatures.

## Results

From the casual surveys of the incidence of hollow stems from 120 species of temperate zone herbaceous plants, we recorded 75 with hollow stems. Stems that were occluded with pith were scored as solid.

Herein, we report briefly on temperatures within flowering stems of several herbaceous plants (Table 1). In jewel weed (*Impatiens capensis*) with thin, transparent, hollow stems, stem temperature excess of over 3 °C occurs in sunshine, but about −0.5 °C in shade. Black-eyed Susan (*Rudbeckia hirta*) with thicker stems, pith and a narrow lumen, stem temperature excesses in sunshine are about 1.3 °C. In Mastodon flower (*Senecio congestus*) with its wide lumen and pubescent, thin-walled stem can reach 4 °C of stem temperature excess in sunshine. Under cloudy sunshine, the insides of stems of *Anthriscus silvestris* were about 2.5 °C warmer than ambient air. In 2018, we examined dandelions (*Taraxacum officinale*) and found temperatures in flowering stems up to 8 °C warmer than the ambient air in sunshine, but below the temperature of the ambient air in shade.

## Discussion

We propose, in this conceptual paper, that the thermal environment inside hollow stems is determined by several closely linked and complex biophysical interactions that include absorption of solar radiation, reflection of some of that energy, conduction in the stem tissues radially from the radiatively heated stem walls outside to within, liberation of heat by re-radiation and conduction to the lumen of the hollow stems, where it can be absorbed by greenhouse gases (water vapor and CO<sub>2</sub>) and circulated by convection (Fig. 1, Box 1). Cooling, as indicated by stem temperatures that were lower than ambient in shade, may be explained by movement of cool soil moisture in the vascular tissue and by evapotranspiration. The extent to which all the aforementioned thermal processes, all of which require experimental verification, contribute individually to determine the thermal environment inside the stem and the lumen also depends on environmental conditions like ambient temperature and relative humidity, the values of the different geometric parameters that characterize hollow stems, e.g., radial thickness and height of the stem, the stems' thermal properties, e.g., absorptivity and emissivity of interior and exterior stem walls, and thermal conductivity and capacity of the plants' stem tissues. In Box 1, we provide an initial list, with comments, of the parameters which we think contribute to the thermal regimes within hollow stems. The comprehensive study by Pincebourde and Casas (2006) on how modifications of leaf tissue transmittance caused by insect-created leaf mines affected the insects' metabolic activities and body temperatures illustrates the complexity of studying, modeling,

**Table 1** Illustrative temperatures in the stems of several herbaceous plants from Canadian locations under various outdoor conditions

Plant species	Ambient air temperature (A) °C	Temperature in stem lumen (S) °C	Difference (S - A) °C	Student's <i>t</i>	<i>p</i>	N	Conditions and time local DST	Location
<i>Impatiens capensis</i> #1	20.4 ± 1.1	23.4 ± 0.1	+3.1	8.5	<0.0001	9	In sun: 11:15	Avoca, QC; 17 August 2017
<i>Impatiens capensis</i> #2	21.3 ± 0.5	20.7 ± 0.1	-0.6	3.1	0.001	7	In forest shade: 11:30	
<i>Rudbeckia hirta</i>	25.4 ± 0.6	26.7 ± 0.2	+1.2	5.6	<0.0001	8	In sun: 11:45	
<i>Anthriscus sylvestris</i> #1	25.5 ± 0.2	26.8 ± 0.9	+2.4	15.7	<0.0001	7	Cloudy sun: 15:45	Calumet, QC; 17 August 2017
<i>Anthriscus sylvestris</i> #2	24.5 ± 0.4	26.8 ± 0.4	+2.3	13.1	<0.0001	9	Cloudy sun: 15:45	
<i>Senecio congestus</i> #1	16.0 ± 0.5	19.8 ± 0.8	+3.8	10.9	<0.0001	8	In Sun: 16:30	Churchill, MB; 28 August 2017
	14.9 ± 0.2	15.8 ± 0.5	+0.9	5.9	<0.0001	14	Hazy sun: 16:15	
	17.9 ± 0.3	21.7 ± 0.4	+3.8	31.1	<0.0001	16	In Sun: 17:00	
<i>Senecio congestus</i> #2	22.9 ± 0.2	23.2 ± 0.1	+0.3	3.3	0.003	12	Cloudy: 14:00	Churchill, MB; 27 August 2017
	16.3 ± 0.2	17.2 ± 0.3	+0.9	6.9	<0.001	8	Hazy sun: 17:20	Churchill, MB; 28 August 2017
<i>Taraxacum officinale</i>	23.9 ± 0.2	23.9 ± 0.2	0	0.39	0.7	15	Cloudy: 14:20	Churchill, MB; 27 August 2017
	25.8 ± 0.8	30 ± 1.2	+4.2	8.6	<0.0001	9	Bright sun: 11:00	Guelph, ON; 17 May 2018
<i>Taraxacum officinale</i> #1	20.3 ± 0.8	28.3 ± 0.3	+8	21.2	<0.0001	5	Bright sun: 16:20	Avoca, QC; 20 May 2018
<i>Taraxacum officinale</i> #2	18.5 ± 0.2	22.1 ± 0.8	+3.6	4.9	<0.001	6	Bright sun: 16:35	
<i>Taraxacum officinale</i> #3	17.4 ± 0.1	24.6 ± 0.5	+7.2	33.3	<0.0001	7	Bright sun: 16:40	
<i>Taraxacum officinale</i> , 5 plants	25.5 ± 0.3	24.7 ± 0.2	-0.8	10.1	<0.0001	33	Shaded: 11:45	Guelph, ON; 29 May 2018

and understanding the microthermic regimes within plant structures.

Understanding the biological role of hollow stems in plant physiology may have practical implications. A greater understanding of hitherto unknown mechanisms in plant growth may reduce dependence on some resources, because it possibly influences water relations, fertilization and irrigation, plant growth, stature, and mechanical strength against drooping of floral heads, leading to new approaches to resource optimization (heat, hormones, other chemicals) by the floricultural sector, for example. It may also contribute in mitigating the effects of plant diseases and pests.

We expect to explore the intuitive word model and diagrammatically presented interactions (Fig. 1) according to the parameters we identify (Box 1) with respect to the biogeographic, ecological and taxonomic incidence for hollow-stemmed herbaceous plants, the mechanisms of intra-stem thermodynamics, and their implications for plant growth, reproduction and maturation in nature and in floriculture.

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## References

- Allen WA, Gausman HW, Richardson AJ, Thomas JR (1969) Interaction of isotropic light with a compact plant leaf. *J Opt Soc Am* 59:1376–1379
- Atamian HS, Creux NM, Brown EA, Garner AG, Blackman BK, Harmer SL (2016) Circadian regulation of sunflower heliotropism, floral orientation, and pollinator visits. *Science* 353:587–590
- Billings WD, Godfrey PJ (1967) Photosynthetic utilization of internal carbon dioxide by hollow-stemmed plants. *Science* 158:121–123
- Carvalho SMP, Heuvelink E, Cascais R, van Kooten O (2002) Effect of day and night temperature on internode and stem length in chrysanthemum: is everything explained by DIF? *Ann Bot* 90:111–118
- Chen C (2015) Determining the leaf emissivity of three crops by infrared thermometry. *Sensors* 15:11387–11401
- Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vis Res* 34:1489–1508
- Cooke MC (1882) Freaks and marvels of plant life; or, curiosities of vegetation. Chapter XVII temperature. Society for Promoting Christian Knowledge, London, pp 371–382 463 pp
- Dietrich L, Körner C (2014) Thermal imaging reveals massive heat accumulation in flowers across a broad spectrum of alpine taxa. *Alp Bot* 124:27–352
- Distifano G, Gentile A, Hedhly A, La Malfa S (2018) Temperatures during flower bud development affect pollen germination, self-compatibility reaction and early fruit development of clementine (*Citrus clementina* Hort. ex Tan.). *Plant Biol* 20:191–198
- Galen C (2006) Solar furnaces or swamp coolers: costs and benefits of water use by solar-tracking flowers of the alpine snow buttercup, *Ranunculus adoneus*. *Oecologia* 148:195–201
- Gausman HW, Allen WA (1973) Optical parameters of leaves of 30 plant species. *Plant Physiol* 52:57–62
- Gibernau M, Barabé D, Moisson M, Trombe A (2005) Physical constraints on temperature difference in some thermogenic aroid inflorescences. *Ann Bot* 96:117–125
- Kerner von Marilaun A (1902) The natural history of plants: their forms, growth, reproduction, and distribution. Translated from German by FW Oliver, with the assistance of Lady Busk, and Mrs. MF Macdonald, vol 2. Blackie, London
- Kevan PG (1975) Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. *Science* 189:723–726
- Kevan PG (1989) Thermoregulation in arctic insects and flowers - adaptation and coadaptation in behavior, anatomy, and physiology. In: Mercer J (ed) *Thermal physiology 1989*. Elsevier Science Publishing BV, Amsterdam, pp 747–753
- Kevan PG, Backhaus WGK (1998) Color vision: ecology and evolution in making the best of the photic environment. In: Backhaus WGK, Kliegl R, Werner JS (eds) *Color vision – perspectives from different disciplines*. De Gruyter, Berlin, pp 163–183
- Kjellberg B, Karlsson S, Kerstenson I (1982) Effects of heliotropic movements of flowers of *Dryas octopetala* L. on gynoeceum temperature and seed development. *Oecologia* 54:10–13
- Lee DW (2007) *Nature's palette – the science of plant color*. University of Chicago Press, Chicago 432 pp
- McKee J, Richards AJ (1998) Effect of flower structure and flower colour on intrafloral warming and pollen germination and pollen-tube growth in winter flowering *Crocus* L. (Iridaceae). *Bot J Linn Soc* 128:369–384
- Niklas KJ (1992) *Plant biomechanics. An engineering approach to plant form and function*. University of Chicago Press, Chicago xiii + 607 pp
- Niklas KJ, Spatz H-C (2012) *Plant physics*. University of Chicago Press, USA, Chicago, p 426
- Omori Y, Takayama H, Ohba H (2000) Selective light transmittance of translucent bracts of the Himalayan giant glasshouse plant *Rheum nobile* Hook.f & Thomson (Polygonaceae). *Bot J Linn Soc* 132:19–27
- Pincebourde S, Casas J (2006) Multitrophic biophysical budgets: thermal ecology of an intimate herbivore insect-plant interaction. *Ecol Monogr* 76:175–194
- Ribeiro da Luz B, Crowley JK (2007) Spectral reflectance and emissivity features of broad leaf plants: prospects for remote sensing in the thermal infrared (8.0–14.0  $\mu\text{m}$ ). *Remote Sens Environ* 109:393–405
- van der Kooi C, Elzenga JTM, Staal M, Stavenga DG (2016) How to colour a flower: on optical principles of flower coloration. *Proc R Soc B* 283:20160429
- van der Kooi C, Elzenga JTM, Dijsterhuis J, Stavenga DG (2017) Functional optics of glossy buttercup flowers. *J R Soc Interface* 14:20160933
- Zachariah EJ, Sabulal B, Nair DNK, Johnson AJ, Kumar CSP (2016) Carbon dioxide emission from bamboo culms. *Plant Biol* 18:400–405
- Zhang S, Ai H-L, Yu W-B, Wang H, Li DZ (2010) Flower heliotropism of *Anemone rivularis* (Ranunculaceae) in the Himalayas: effects on floral temperature and reproductive fitness. *Plant Ecol* 209:301–312
- Zhu Y, Lu J, Wang J, Chen F, Leng F, Li H (2011) Regulation of thermogenesis in plants: the interaction of alternative oxidase and plant uncoupling mitochondrial protein. *J Integr Plant Biol* 53:7–13