

Heliocaminiform structures: plant organs that function as microgreenhouses

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Abstract

Plant structures that enclose trapped air are morphologically and taxonomically diverse. They range from pubescence (trichomes) on various parts of plants to flowers, inflorescences, stems, culms (above-ground jointed stems of grasses), petioles, peduncles, scapes, fruits, bracts, leaves, galls, algal pneumatocysts, moss sporophytes, lichen podetia, and fungal fruiting bodies. Despite being familiar, such structures have not been studied systematically until recently when their complex thermodynamic functionality as microgreenhouses has been recognized. We propose the term “heliocaminiform” (Greco-Latin origin for “sun-room”) provides an umbrella term that describes form and function. Almost all the hollow structures we have examined have elevated internal temperatures of several degrees C above the surrounding air in sunshine, but those are abolished under cloud or at night. The potential importance for the additional heat is presumed to be in growth, maturation, reproduction, sexual function, and overall fitness of the plants. There seem to be no experimental studies on those effects even though they may help explain aspects of plants’ responses to climate change and to phenological mismatches with symbionts (mutualists and herbivores) as ecologically co-dependent partners. Our review and observations opens a remarkably new and hitherto surprisingly neglected avenue in botany which we hope others will explore.

Key words: micrometeorology, plant temperature, botany, heliocaminiform, greenhouse effect, thermoregulation

Introduction and etymology

Hollow structures have been little studied by botanists even though widespread and diverse. They occur in Angiospermae (e.g., in stems, culms, flowers, inflorescences, fruits, petioles, peduncles, spadices, and galls with or without additional pubescence), moss sporophytes, lichens (podetia and thalli), Phaeophyta (pneumatocysts), and fungi (stipes and caps). Several recent papers have pointed out the possible importance of such hollow structures in the lives of some plants and their symbionts (Kevan et al. 2018; van der Kooi et al. 2019; Coates and Kevan 2021) with their contributing significantly to heat budgets, growth, maturation, and reproduction through the microgreenhouse effect. A few studies propose that photosynthetic gas exchange (especially CO₂) is ameliorated and adaptive within hollow structures (e.g., some subalpine plants (Billings and Godfrey (1967) (Table 1, row 34), wheat (*Triticum aestivale* (Poaceae)) culms (Bornemisza-Pauspertl et al. 1984), the inflated stems of *Eriogonum inflatum* (Polygonaceae) (Osmond et al. 1987), and algal pneumatocysts (Table 1, row 39). With such a broad array of structures across so many phylogenetic lines, it is appropriate that formal recognition be given to the structures and how they may function. We propose a term and its definition as follows: **Heliocaminiform** structures are small, hollow parts of plants (*sensu lato*) that function as microgreenhouses. The term derives from the Greco-Latin word “heliocaminus” in reference to the solar heated room

in the palace of Roman emperor Hadrian (b. 24 January 76 – d. 10 July 138) who reigned from 117 to 138. It is also recorded that Tiberius (Roman emperor Tiberius Caesar Augustus b. 16 November 42 BC—d. 16 March AD 37) commissioned the building of greenhouses for cucumber growing earlier. Readers interested in that early history of greenhouses may wish to consult Pliny the Younger (1900) (1st Century AD; Firth (1900) translator) and Justinian (1904–1909) (5th Century AD; Monro and Buckland (1904–1909) translators)).

The aim of this review is to provide a comprehensive, but not exhaustive, list of heliocaminiform structures in plants (*sensu lato* to include algae, lichens, and fungi) derived from a broad review of available literature and our own experiences, with evidence, if available, of passive heating by the greenhouse effect. With that list compiled, we provide a discussion of the morphological and phylogenetic breadth of the phenomenon with the hope that others will be motivated to embrace the concept in their botanical considerations for research and teaching.

Results

We present our findings in Table 1 which lists more than 40 higher taxa (family or above) that produce, or probably produce, heliocaminiform structures. Most of the examples we provide (Table 1, rows 1–38) are from flowering plants

Table 1. Examples of possible heliocaminiform structures of botanical interest: Magnoliophyta (Angiospermae or Flowering Plants) arranged by Family in alphabetical order; *Equisetum* (Equisetales); Phaeophytales (brown algae); Bryophyta, lichens and fungi.

	Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
1	Magnoliophyta (Angiospermae)	Many	Many	Hollow floral buds that may open with reflexed petals or expose reproductive structures in anthesis in zygomorphic, stereomorphic, urceolate, or actinomorphic flowers are probably heliocaminiform prior to full anthesis. Most trap and semi-trap blossoms are hollow prior to anthesis. There are various species that close when shaded but reopen when re-insolated (see rows 11 and 23).	See van der Kooi et al. (2019) , van Doorn and van Meeteren (2003) , van Doorn and Kamdee (2014) , van Doorn and Kamdee (2014) .
2		Amaryllidaceae		Many species with hollow stems. Observed temperatures within the stems of <i>Narcissus papyraceus</i> 5.80 ± 0.70 °C in the sun, and 1.15 ± 0.78 °C in shade, within a study greenhouse. <i>Narcissus</i> sp. (daffodil form) grown on University of Guelph campus gardens had stem interiors up to 6.6 °C warmer than ambient air in sun and ranged from to + 2.7 °C to -0.2 °C in shade. The epicalyx bract of some species may form a heliocaminiform structure.	Kevan & Coates unpublished from University of Guelph Greenhouse, Winter 2019. No records have been discovered.
3		Anacardiaceae	<i>Pistacia vera</i>	Hollow galls may buffer extreme heat from adverse effects on aphids living within.	Martinez (2009) .
4		Apiaceae	Many species <i>Anisotome latifolia</i>	Hollow stems are characteristic of many species. We have made intrastem temperature measurements in cow parsley (<i>Heracleum maximum</i>). In sunshine we found temperatures up to about 5 °C in the stems. Large, divided, smooth leaves forming enclosed cavity beneath and becoming warmer than ambient temperatures on sub-Antarctic Campbell Is.	Kevan and team 2018–2019 casual spot checks in Avoca, QC and McMillans Corners, ON. Little et al. (2016) .
5		Apocynaceae	<i>Asclepias syriaca</i>	Hollow fruits (follicles) attain temperatures excesses of over 13 °C in sunshine but the effect is abolished at night and under cloudy conditions. The balloon plant milkweed (<i>Asclepias</i> (a.k.a <i>Gomphocarpus physocarpa</i>) produces inflated, papery follicles when in fruit.	Kevan & Coates unpublished from Guelph & Cambridge, ON from summers 2019-2021.
6		Araliaceae	<i>Stibocarpus polaris</i>	Large, hairy leaves forming enclosed cavity beneath and becoming warmer than ambient temperatures on sub-Antarctic Campbell Is.	Little et al. (2016) .
7		Arecaceae	Many species	The maturing inflorescences of many palms are held within hollow spadices (bracts) which split at anthesis.	No records found on thermal relations.
8		Asphodelaceae	<i>Bulbinella rossii</i>	Large, smooth leaves form enclosed cavity beneath and those, and the leaves, become warmer than ambient temperatures on sub-Antarctic Campbell Is.	Little et al. (2016) .

Table 1. (continued).

Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
9	Asteraceae	Many species	<p>Hollow stems and scapes are known in various species. Temperatures in hollow stemmed <i>Cirsium setosum</i> may reach 2.66 ± 0.631 °C above ambient. Within the hollow peduncles of <i>Taraxacum officinale</i> temperatures may reach 6.07 ± 1.81 °C in sunshine: the effects are abolished at night or under cloudy conditions. In <i>Parnassia salicifolia</i>, internal temperature of stems of 4 study plants reached a maximum of 4.65 ± 0.59 °C above ambient temperature.</p> <p>In stems of <i>Gerbera jamesonii</i> temperature excesses during the day in greenhouse grown plants can reach 4 °C. <i>G. jamesonii</i> varieties have inconsistent hollowness, so the temperature range an individual may experience may vary even within a given cultivar and stem.</p> <p>Temperatures with the hollow stems of <i>Rudbeckia hirta</i> (also variable as to hollowness) in sunshine were about 2 – 4 °C above ambient</p> <p>The hollow stems of <i>Zinnia</i> spp. reached up to 2 °C warmer than ambient air.</p> <p>The bracts around the inflorescences of <i>Saussurea velutina</i> have been shown to protect the reproductive structures from fluctuating weather conditions in high mountains.</p>	<p>Kevan et al. (2019) for <i>C. setosum</i>, <i>T. officinale</i>, <i>P. salicifolia</i> in Magadan oblast, Russia. Results for <i>T. officinale</i> in Guelph, ON remain unpublished from 2019-2022 Kevan and his team.</p> <p>Kevan and Coates, (2020), COHA Connections. Understanding how temperatures within plants affect their growth. https://cohaconnections.ca/understanding-how-temperatures-within-plants-affect-their-growth/</p> <p>Kevan, Smith and Humphrey unpublished data from spot checks from roadside plants near Bell. Falls and Harrington, QC in 2018 and 2019.</p> <p>Zinnias grown on University of Guelph campus, Larson & Coates, unpublished from 2019.</p> <p>Yang and Sun (2009).</p>
		<i>Pleurophyllum</i> spp	Hirsute to downy large leaves form enclosed cavity beneath and that, and the leaves, become warmer than ambient temperatures on sub-Antarctic Campbell Is.	Little et al. (2016).
10	Balsaminaceae	<i>Impatiens glandulifera</i> and <i>I. capensis</i>	<p>In Ontario, the hollow, septate stems of <i>I. glandulifera</i> reached up to 8 °C warmer than ambient air under direct sunlight. Under partially cloudy conditions, the effect was reduced to 4 °C. In Perthshire shady woodlands temperatures within the stems reached 2 – 3 °C.</p> <p>Within the hollow stems of <i>I. capensis</i> temperature excesses of 2 - 4 °C were recorded in sunshine but were only 1 – 2 °C under natural semi-shade.</p>	<p>Coates unpublished for ON records from 2021, Kevan unpublished Scottish records from 2019 for <i>I. glandulifera</i>.</p> <p>Kevan unpublished data from Grenville-sur-la-Rouge, QC from summer 2019.</p>
11	Brassicaceae	<i>Lesquerella</i> spp. <i>Caulanthus</i> spp.	<p>Hollow siliques and in <i>L. arctica</i>, the flowers close epinastically when the sun is obscured by cloud.</p> <p><i>Caulanthus inflatus</i> and <i>C. hallii</i></p>	<p>No records found on thermal relations; Kevan (1970).</p> <p>Both desert-adapted species have specialized inflated stems. No studies on temperature regimes within have been made. https://www.youtube.com/watch?v=CVpjLRNo1jc</p>
12	Bromeliaceae	<i>Puya</i> spp.	Comparisons of temperature excesses between differentially pubescent species at different altitudes and between experimentally denuded plants indicate the importance of the pubescence.	Miller (1986)
13	Campanulaceae	<i>Platycodon grandiflorus</i>	Balloon flowers become inflated as the floral buds approach anthesis. Various species of <i>Campanula</i> produce inflated floral buds.	No records found on thermal relations.

Table 1. (continued).

Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
14	Cannabaceae	<i>Cannabis sativa</i>	Some cultivars have hollow stems. Preliminary observations noted 3.5 °C temperature excess within the stems in sunshine at an air temperature of 27 °C.	Kevan et al. unpublished from near Greenfield, ON 2020.
15	Caryophyllaceae	<i>Silene</i> spp.	Hollow syncalyces of <i>S. uralensis</i> , and <i>S. sorensensis</i> in the High Arctic may attain temperature excesses within of up to 2.5 °C, 6.2 °C respectively under sunny conditions but the effect is abolished when it is cloudy.	Kevan (1970, 1989, 2019).
16	Cleomaceae	<i>Isomeris arborea</i>	Hollow fruits.	No records found on thermal relations.
17	Cucurbitacea	<i>Cucurbita</i> spp.	Hollow peduncles and petioles of <i>C. pepo</i> in flower attained temperature excesses up to 9 °C in sunshine but the effect is abolished under cloud and at night. Highest temperature differences occurred during 10AM -2PM.	Coates unpublished from 2020-2021, Cambridge, ON.
		<i>Echinocystis lobata</i> . Possibly <i>Ecballium elaterium</i> .	Hollow fruits of <i>E. lobata</i> in sunshine but the effect is abolished at night and under cloudy conditions. On a sunny day (with incident light of 1.165 x 10 ⁵ LUX), we recorded temperatures within fruits at 8.29 ± 0.48 °C warmer than ambient air. On cloudy days (e.g., with incident light 1.4 x 10 ⁴ LUX) that average was reduced to 0.09 ± 0.19 °C. <i>E. elaterium</i> fruits may attain hyperbaric pressure within as part of building up temperature excess within as part of the explosive means of seed dispersal.	Kevan and Coates unpublished data from <i>E. lobata</i> in summers 2019-2021 at Washington Creek, ON. No records found on thermal relations.
18	Cyperaceae	<i>Carex</i> spp	The inflorescences are contained in involuclral bracts until anthesis.	No records found on thermal relations.
19	Ericaceae	<i>Vaccinium (Oxycoccus)</i> spp.	Hollow fruit.	No records found on thermal relations.
20	Euphorbiaceae	<i>Hevea brasiliensis</i>	Explosively dehiscent 3-lobed, 3-seeded capsule (somewhat hollow).	No records found on thermal relations.
		<i>Ricinus communis</i>	Hollow stemmed.	No records found on thermal relations.
21	Fabaceae	Peas and beans	Hollow pods are characteristic of numerous species and cultivars of legumes. Notable are <i>Baptisia</i> spp., <i>Sutherlandia frutescens</i> (balloon pea), and <i>Pisum sativum</i> (garden pea).	No records found on thermal relations.
22	Fagaceae	<i>Quercus</i> spp.	Hollow galls.	No records found on thermal relations.
23	Gentianaceae	<i>Gentiana</i> spp., <i>Gentianella</i> spp.	Hollow flowers as in bottle gentians. <i>Gentiana</i> spp.) and in <i>Gentianella amarella</i> produce flowers that close when clouds obscure the sun.	Unpublished field observations by Kevan et al. (2018) for <i>Gentiana</i> spp. from alpine Colorado (<i>G. algida</i>) and <i>G. clausa</i> in Ontario and for <i>Gentianella amarella</i> from Churchill, MB. We have found no records of intrafloral temperatures.
24	Iridacea	<i>Crocus</i> spp.	McKee and Richards (1998) report that illuminated flowers attain internal temperatures of about 3 °C and than purple and white flowers warm more than do yellow ones.	McKee and Richards (1998).
		<i>Iris</i> spp.	Hollow stems, flower, and fruits.	No records found on thermal relations.
		<i>Oncoclycus</i> spp.	Hollow flowers attain temperature excesses of about 2.5 °C in morning sunshine. The flowers are used as sleeping places by pollinating bees.	Sapir et al. (2006).

Table 1. (continued).

Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
25	Lamiaceae	<i>Eriophyton wallichii</i>	Extensive and dense pubescence on leaves of this Himalayan plant dampen temperature fluctuations.	Peng et al. (2015).
26	Liliaceae		Many species have hollow stems. The flowers of <i>Tulipa</i> spp. close at night and when the sun is obscured by clouds.	No records found on thermal relations.
27	Malvaceae	<i>Abelmoschus</i> spp.	Fruits are hollow capsules.	No records found on thermal relations.
28	Moraceae	<i>Ficus</i> spp.	Ripening fruits are thick-walled and hollow. Comparative studies of 11 species in Panama indicate temperature excesses of 2 – 3 °C of fruit from about 5 – 50 mm in diameter in which insolational heat gains were naturally reduced by evapotranspiration, especially in larger figs, to below the lethal levels for the inquiline pollinating wasp larvae.	Patiño et al. (1994)
29	Orchidaceae		Many orchid flowers present enclosed parts, notably the slipper orchids (Cypripedioideae). <i>Serapias vomeraceae</i> attains temperature excesses of about 3 °C above ambient air temperature, a phenomenon that is associated with early morning pollinating activity of bees that sleep the night in the flowers.	We know of no records of temperature regimes in slipper orchid flower, see Dafni et al. (1981) for <i>S. vomeracea</i> .
30	Orobanchaceae	<i>Pedicularis</i> spp.	Hollow flowers of <i>P. langsдорфii</i> and <i>P. capitata</i> develop temperature excesses up to about 6 °C in sunshine, an effect that is abolished in cloudy weather.	Kevan (1970, 1989, 2019a, 2019b).
		<i>Rhinanthus</i> spp.	Hollow stems may attain internal temperatures several degrees warmer than the ambient air. Pubescence of the plants contributes to the effects (see also row 3). Yellow rattle owes its common name to the hollow capsules in which the seeds develop and rattle around loose until released. Flowers and capsules are probably both heliocaminiform structures.	Meier (1995). We know of no records of temperature regimes in this genus.
31	Plantaginaceae	<i>Antirrhinum</i> spp. & <i>Linaria</i> spp.	Common name “snapdragon” indicates this flower opens and closes when squeezed laterally. Differences in pigmentation, as in cultivars of <i>Antirrhinum</i> , may alter the amount of heat trapped within the corolla but our preliminary records have not provided clues as to the effects of colouration. Temperature excesses within the flowers range up to 4.5 °C in sunshine midday in the University of Guelph Bovey greenhouse, but were abolished in shade and cloudy weather.	Photograph of research site appears in Kevan, Coates (2020).
32	Poaceae	Many species	Hollow culms, as in <i>Avena sativa</i> from Magadan, Russia attain temperature excesses within of about 4 C in sunshine and for <i>Phragmites australis</i> temperature excesses with culms of 6.3 °C. The thermal regimes in the boot (reproductive structures enclosed in the developing flag leaves (bracts) and husks as in maize (<i>Zea mays</i>) seem not to have been investigated but we recorded temperature excesses of about 1-2 °C in ears on a production field margin in 2023.	Kevan et al. (2019) for <i>A. sativa</i> ; Coates unpublished, ON., for <i>P. australis</i> in summer 2021. Kevan & Coates, unpublished data from Skunks Misery, ON, August 2023.

Table 1. (continued).

Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
33	Polygonaceae	<i>Rheum</i> spp.	Several high-altitude species produce overlapping translucent, achlorophyllous bracts that act as microgreenhouses and protect the inflorescence from UV light. The stems, as in many <i>Rheum</i> spp., are hollow.	Bojian and Grabovskaya-Borodina, (2003); Omori and Ohba (1996); Omori et al. (2000); Iwashina et al. (2004); Tsukaya 2002; Song et al. (2013,).
		<i>Reynoutria japonica</i>	Japanese knotweed has septate stems, with large hollow cavities that may reach to 4.6 °C warmer in the sun during the day, and down to -3.6 °C below ambient temperature at night.	Kevan & Coates, unpublished data from Cambridge, ON (Riverside Park) 2021.
		<i>Rumex</i> spp.	Several species have hollow flowering/fruitlets stems. For <i>R. patientia</i> internal statistically significant temperatures excesses of 3.99 ± 0.84 (t = 77.58 p < 0.001) and 4.45 ± 0.74 C (t = 19.76, p < 0.001) were measured in plants growing in sunshine in Belgrade, Serbia	Kevan & Coates unpublished from 2020.
		<i>Eriogonum inflatum</i>	Has specialized inflated stem parts below the inflorescence. The gas composition within has been proposed to ameliorate photosynthetic activity.	Osmond et al. (1987)
34	Ranunculaceae	<i>Nigella damascena.</i>	Hollow fruits studied on garden plants had mean temperature excess of 5.5 ± 0.4 °C in sunshine Mature pods split and so disperse their seeds: high temperatures may contribute to the drying of ovary wall and development of seeds.	Kevan & Coates unpublished from Cambridge, ON summers 2020-2021
		<i>Thalictrum pubescens</i>	Hollow stems can attain internal temperatures of about 4 - 5 in sunshine.	Kevan and team unpublished from Grenville-sur-la-Rouge, QC, 2–8 August 2019.
		<i>Delphinium barbeyi</i>	Hollow stems may be reach 30–37 C while ambient temperatures are 13–16 C. The effect is abolished at night and in shade.	Billings and Godfrey (1967) from high altitudes (subalpine at 3100 m) in the Medicine Bow Mts, WY. They invoke the greenhouse effect.
35	Salicaceae	<i>Salix</i> spp.	The pubescence of the catkins (aments) probably acts to result in microgreenhouse effects which differ between the sexes.	Kevan (1990). See main text under "pubescence" for other references.
36	Sapindaceae	<i>Koeleruteria</i>	Hollow, inflated capsular fruit.	No records found on thermal relations.
37	Solanaceae	<i>Physalis</i> spp.	Hollow syncalyces of <i>P. heterophylla</i> and <i>P. virginiana</i> may attain temperature excess of up to 10.0 °C in sunshine but the phenomenon is abolished under cloudy conditions. In experimental greenhouse trials at the University of Guelph, the temperatures within the hollow syncalyces of <i>P. peruviana</i> reached 6.6 °C warmer than the surrounding air temperature in sunny weather. At night, the temperatures within the same hollow syncalyces were about 1-2 °C cooler than the surround air.	Kevan et al. unpublished from Cambridge, ON, Guelph summer & fall 2018 & 2019. Li et al. (2019) recorded somewhat similar conditions in <i>P. floridana</i> in their detailed study.
		<i>Capsicum</i> spp.	Hollow fruits of <i>C. annuum</i> may attain temperatures excesses of up to about 4 – 6 °C in greenhouse conditions even without insolation. They may be generating heat metabolically but this effect has yet to be investigated.	Coates and Kevan (2020).
38	Equisetales	<i>Equisetum</i> spp.	<i>Equisetum</i> spp. have hollow stems which have been investigated for biomechanical properties.	Niklas (1992); Niklas and Spatz (2012).

Table 1. (concluded).

Major taxon	Family	E.g., genus & species	Temperatures within hollow structures	Notes & references
39	Phaeophyta	Phaeophyceae	<p>Preliminary checks on the internal thermal regimes in fertile shoots of sporophytes of <i>E. arvense</i> indicate temperature excesses of only 1 - 2 °C in sunshine but -1 °C in roadside shade. Similar results were found for <i>E. hylemale</i> involving more detailed preliminary study, no statistical differences were found.</p> <p>Pneumatocysts in <i>Fucus</i>, <i>Macrocystis</i>, <i>Nereocystis</i>, <i>Sargassum</i> are well-known and usually explained as aiding in buoyancy of the photosynthetic lamina. As far as we are aware, temperatures have not been measured in pneumatocysts until now but ambient temperature regimes affect the gas (notably CO₂) within.</p>	<p>Kevan unpublished from Grenville-sur-la-Rouge, QC summer 2019 from roadside. <i>E. arvense</i>. Preliminary results by Coates & Kevan for <i>E. hylemale</i> at Skunk's Misery, ON 10 August, 2022.</p> <p>See King (2001); Supratya et al. (2020); Liggan and Marton (2020). Temperatures within the pneumatocysts of <i>Fucus vesiculosus</i> and <i>Nereocystis luetkeana</i> were recorded at ca. 4 °C in sunshine on the coast of Washington in July, 2023 (Fig. 5).</p>
40	Bryophyta	<i>Sphagnum</i> spp.	Sporophytes explosively release spores when insolated. Temperatures within remain unstudied.	Kimmerer (1994)
41	Lichens	<i>Cladonia</i> spp. and <i>Cladina</i> spp.	Hollow podetia. Preliminary measurements from a Laurentian forest site at Bell Falls, Avoca, QC, Canada indicate up to ca. 4 C temperature excess within in sunshine in <i>Cladonia cristatella</i> .	Kevan, unpublished casual observations, summer 2021; Tikhmenev, E, Personal communication, 2021
42	Fungi	<i>Catherellus</i> and <i>Craterellus</i> , <i>Morchella</i> spp., and many basidiocarp fungi.	Hollow stipe or pileus. Most fungi known to have hollow structures grown in shaded environments so microgreenhouse effects from insolation probably do not apply. The structure of the Nidulariaceae suggests that thermal relations and possibly insolation may play a role in maturation.	No records found on thermal relations.

Note: Many of the values presented for internal temperatures are based on unpublished spot-checks as explained in Materials and Methods in various localities over the years 2018–2023. The values represent the approximate ranges of values one might expect when making more detailed studies.

Fig. 1. Pubescence and heliocaminiform function.**Left:** Old man cactus (*Cephalocereus senilis*) at Desert Botanic Garden, Phoenix, AZ. (Table 1, row 13).**Middle:** Woolly louswort (*Pedicularis lanata*) from Arctic tundra (Barrow, Alaska) (Table 1, row 30).**Right:** Pussy willow (*Salix discolor*) male catkins in anthesis. Credit NVK Nurseries (Table 1, row 35).

in which the phenomenon is known from flowers (petals and sepals) and inflorescence pubescence (see also van der Kooi et al. 2019), fruits, stems, and culms (including peduncles) (see also Kevan et al. 2018), bracts (including achlorophyllous bracts, flag leaves in Poaceae (Table 1, row 32), involucre bracts in Cyperaceae (Table 1, row 18), and spadices in Arecaceae) (Table 1, row 7). Pubescence may be present on many plant parts, notably leaves, bracts, stems, inflorescences and so on (Table 1), where it differentially responds to irradiation by absorption and reflection at various wavebands and insulational trapping of heat within (e.g., Table 1, rows 6, 9, 12, 13, 30, 35). We also note that pneumaocysts of phaeophytes may function as heliocaminiform structures while also providing buoyancy for access to light (Table 1, row 39). Kimmerer (2003:118) notes that “On a hot summer day, if you’re very quiet, you can witness the smallest discernable sound I know—the “pop” of Sphagnum capsules. It’s hard to imagine that a sound emitted by a capsule only one millimeter long could be audible. Their capsules, tiny urns on short stalks above the moss, explode like a popgun. The heat of the sun builds up air pressure inside the capsule, until the top blows off, propelling the spores upward.” Presumably it is insulational heating and desiccation that causes the phenomenon. A few fungi produce hollow basidiocarps but we found no references to thermal regimes within them (Table 1, row 42). Some lichens are notoriously tolerant of high temperatures but the thermal regimes within their hollow podetia and thalli seem not to have been investigated until recently (Table 1, row 41).

Discussion

Our discussion draws generalizations from data presented in Table 1. We start with considerations of plant pubescence,

which may be present on almost any aerial part of plants before remarking on flowers, inflorescences, calyces, bracts, fruits, galls, stems etc. of Magnoliophyta. We note that some brown algae (Phaeophyta) produce hollow pneumatocysts, some fungi have hollow parts (Table 1, rows 39 and 42, respectively), as do some lichens (Table 1, row 41) and that they may have heliocaminiform functionality.

Plant pubescence

Plant pubescence comes about through unicellular to complex multicellular trichomes (Fig. 1). It is important for temperature modification of flowers in some species but has been studied only in a few (Table 1 rows 12, 30, 35 and below). Floral trichomes have been intimated in restrictive pollinator visitation (Kerner 1878) and general plant pubescence in herbivore defence (Levin 1973). Levin (1973) also addresses some aspects of phytogeography and pubescence but does not invoke micrometeorological functionality.

Thick pubescence can heat underlying structures in cool, high-elevation environments by increasing the boundary layer of air adjacent to the leaf and reducing convective heat loss (Meinzer and Goldstein 1985), i.e., the greenhouse effect with trapped air within and differential radiative structures (trichomes) without.

We have not reviewed the wide diversity of proposed functions for which experimental evidence is lacking (UV and irradiation protection, moisture accumulation and retention, differential growth by solar aspect and/or compass direction, and perhaps heat accumulation) for pubescence in Cactaceae (Table 1, row 13). However, two studies (Meier 1995; Miller 1986) have evaluated the impact of pubescence on the thermal dynamics of reproductive structures and the downstream impacts on plant reproductive fitness. In the Andes Miller (1986) records that species of *Puya* (Bromeli-

aceae) from high elevations produce denser pubescence than those occurring at lower elevations. More glabrous (i.e., with less pubescence), low-elevation taxa tended to track ambient temperatures while high-elevation pubescent taxa tended to be warmer than ambient conditions. Unmanipulated plants of *Puya hamate* maintained temperatures 2–3 °C higher than ambient night-time conditions while those denuded of pubescence did not, indicating insulating properties of the pubescence. Finally, north-facing (warmer) inflorescences had elevated seed production compared to south-facing (cooler) inflorescences, providing a link between temperature and fecundity (Miller 1986) (Table 1, row 12). Meier (1995) recorded temperatures within stems and inflorescences of two High Arctic species of *Pedicularis*, *P. lanata* and *P. hirsuta* (Orobanchaceae) with respect to the heat available to herbivorous larvae of *Olethreutes inquietana* (Lepidoptera: Tortricidae) and *Gonarticus arcticus* (Diptera: Scathophagidae) living within the stems. She found temperature excesses of several degrees C, and by removing the pubescence on *P. hirsuta* found that temperature excesses were reduced and of shorter duration (Table 1, row 30). The thermal dynamics of inflorescences with respect to pubescence have also been studied in two Himalayan taxa. Although the woolly inflorescence of *Saussurea medusa* (Asteraceae) may be 5.9 °C warmer than ambient air temperatures, it is unlikely to be due to pubescence, but rather the compact architecture of the inflorescence itself (Yang et al. 2008). Removal of pubescence in situ and in controlled conditions had negligible impact on heat retention, and thus Yang et al. (2008) posited that pubescence functions mostly to repel water and/or to reflect UV light (Table 1, row 9). In the Himalayan mint (*Eriophyton wallichii* (Lamiaceae)), flowers are covered by densely pubescent leaves. Pubescent control leaves absorb slightly more visible light than experimentally shaved leaves, and consequently are significantly warmer (Peng et al. 2015). Peng et al. (2015) authors also evaluated pollen viability and seed production in control plants and those with experimentally lifted leaves, but from these treatments it is difficult to assess the direct effect of pubescence on fitness (Table 1, row 25). Together those studies in Himalayan taxa suggest that pubescence may be less important than leaf architecture in mediating floral temperatures and heliocaminiform effects.

The idea that pubescent flowers, inflorescences, stems, and bracts function as heliocaminiform “hairy heat traps” to warm floral structures was recognized in willows (Krog 1955; Budel 1957; Kevan 1970; Mølgard 1982; 1989). In Alaska, woolly willow catkins may be 15–25 °C warmer at ambient air temperatures of 0 °C, and removal of pubescence reduces temperatures by about 60% relative to unmanipulated catkins (Krog 1955). In willows, sex-based differences in pubescence create disparities in inflorescence temperature with pistillate catkins having denser pubescence and, on average, being significantly warmer than staminate catkins (Kevan 1989) (Table 1, row 35).

Flowers and Inflorescences

Heliocaminiform flowers and inflorescences are discussed in the review by van der Kooi et al. (2019) who comment on the effects of colour, floral form, cellular features,

pubescence, and corolla opening and closing (Fig. 2). More recently, Zhang and Tang (2023) observed thermal images of 18 alpine flowering species and recorded a maximum of 11 °C difference between the center and the edge of some blooms, especially in Asteraceae. Many flowers start their development as hollow buds comprising their calyces and corollas and enclosing the reproductive organs. Our review of the literature has uncovered remarkably few examples of the temperatures within floral buds but many studies (not cited) in which the micrometeorology of ambient conditions, especially air temperatures, in close proximity to budding flowers on trees, shrubs, and herbs have been made. We suggest that greater attention to internal temperatures within immature floral structures may help understandings of the development, maturation, and fertility of the reproductive structures within and to issues of sexual compatibility. It is known that the temperatures of floral reproductive organs can have profound influence on pollen viability, compatibility in fertilization, and stigma receptivity over the period of floral development from early bud to complete anthesis (Distefano et al. 2018 for *Citrus clementina* flowers allowed to develop in incubators).

Calyces

As noted above, calyces contribute structurally to the hollow forms of floral buds in many plant species and so, presumably and potentially to heliocaminiform effects. Table 1 lists various taxa of plants in which the flowers produce especially well-developed calyces that continue to enclose the corolla after anthesis as proximally connate sepal(s) or as a symsepalous calyx, sometimes referred to as a syncalyx. The syncalyx of many species of *Silene* presumably function as microgreenhouses, as shown for two Arctic species (Kevan 2020) (Table 1, row 15). The inflated syncalyces of *Physalis* spp. become heated in sunny weather with the effect of accelerating growth and maturity of the fruit within (Li et al. 2019) (Table 1, row 37).

Bracts

The translucent and sometimes achlorophyllous terminal leaves of various plants have been demonstrated to function in UV protection of the reproductive structures within, and to allow the plants to accumulate heat by the greenhouse effect, e.g., bracts of *Saussurea velutina* (Asteraceae) (Yang and Sun 2009) (Table 1, row 9) and *Rheum* spp. (Polygonaceae) (Omori and Ohba 1996; Omori et al. 2000; Iwashina et al. 2004; Tsukaya 2002; Song et al. 2013) (Table 1, row 33) at high elevations in the Himalayas. The involucrel bracts, well known in many Asteraceae, enclose air spaces that likely become warm and protect the inflorescence within. Similarly, the large leaves of sub-antarctic and high mountain megaherbs have also been suggested to form air-filled spaces that function as microgreenhouses, heating, and protecting the blossoms developing within (Little et al. 2016; Table 1 rows 4, 6, 8, 9, 33).

Another form of bract is exemplified by the flag leaves that characteristically enclose the developing reproductive structures (flowers and fruiting heads) in Poaceae (Table 1, row 32) at the boot stage (i.e., when the immature inflorescence is

Fig. 2. Hollow flowers and heliocaminiform function.

Top: Translucent syncalyces and corollas of *Silene uralensis* (photo from Aiken et al. 2007) and *S.sorensenis* (Caryophyllaceae) (photo from Aiken et al. 2007) (Table 1, row 16) (above) and *Pedicularis langsdorfii* (photo by Paul Sokoloff, Creative Commons License) (Table 1, row 30) and *P. capitata* (Orobanchaceae) (below) (photo by Alison Cassidy, Creative Commons License) (Table 1, row 30) (below) (see Kevan 2020).

Bottom left and right: Various colours of flowers of snapdragons (*Antirrhinum majus*) growing in the experimental greenhouse at the University of Guelph. Temperatures within the enclosed petals of the flowers as measured with thermocouples (visible fine wires attached to Omega OM-HL-EH-TC datalogger) are up to 4.5 °C warmer than ambient air (Table 1, row 31).



enclosed within the bracts) may contribute through the microgreenhouse effect to the rapidity of growth and maturation, but we have found no records of this. The same idea may apply to the papery bract, perhaps an epicalyx, that encloses the floral buds of various Amaryllidaceae, such as the familiar daffodil and narcissus (Table 1, row 2). We also suggest that the spadices that enclose the reproductive organs of many palms (Arecaceae) and the involucre bracts of sedges (Cyperaceae) may function similarly while affording protection (Table 1, row 7 and 18, respectively).

Fruits

We note that various plants produce hollow fruits with translucent outer walls (pericarps) (Fig. 3). Those that we have examined (i.e. *Asclepias syriaca* (Table 1, row 5), *Nigella damascina* (Table 1, row 34), and *Echinocystis lobata* (Table 1, row 17) attain elevated internal temperatures in sunshine, sometimes amazingly high (e.g., in follicles of *A. syriaca*). There are numerous plant taxa that produce hollow, heliocaminiform fruit and suggest themselves for further study, notably in such important families as Fabaceae (Table 1, row 21), Brassicaceae (Table 1, row 11), Cucurbitaceae (Table 1, row 17), some Solanaceae (Table 1, row 37), and a few Ericaceae (Table 1, row 19). *Koelreuteria* appears to be similar with its inflated capsular fruit with seeds inside but it remains unstudied for the possibility of heliocaminiform function (Table 1, row 36).

We know of no general review of hollowness in fruits and, apart from our preliminary records (Table 1), we have found no records of temperature regimes within them.

Galls

Few studies have been made on the physical conditions within hollow galls, even those with obviously translucent walls, as the well-known oak-apple (Connald 1908) (Table 1, row 22). Cynipid wasp larvae inhabit the galls, e.g., *Biorhiza pallida* in Europe, *Amphibolips confluenta* in eastern North America, and *Atrusca bella* in western North America. One of the best studied galls is the goldenrod ball gall induced by the fly, *Eurosta solidaginis* (Diptera: Tephritidae). It occurs conspicuously on the stems of various species of goldenrod, *Solidago* spp. (Asteraceae) (Table 1, row 9). Layne Jr. (1991, 1993) notes that the galls, which are thick-walled and probably not translucent, in sunshine can attain temperatures up to 5 °C above ambient air temperatures and do buffer the conditions within in hot summer and cold winter conditions. The pistachio horn gall is induced by aphids, *Baizongia pistaciae* (Hemiptera: Pemphigidae) on pistachio (*Pistacia* spp. (Anacardiaceae)). The galls are large and inhabited by large numbers of aphids. Martinez (2009) records that the galls buffer the inhabitants from extremely high ambient temperatures and insolational heating (Table 1, row 3). With about 13 000 species of gall-inducing organisms known, it is surprising that so little is recorded about the physical conditions within their homes.

Stems

In our initial studies of possible heliocaminiform structures in plants, we were surprised to find no general review

in the botanical literature from the mid-19th century until today about the occurrence of hollowness in plant stalks (stems, culms, and so on) and little that pertained to the temperature regimes within them (Fig. 4). Billings and Godfrey (1967) proposed that hollow stems in sub-alpine plants may act as greenhouses and ameliorate gas exchange for photosynthesis, growth, and maturation. Stems of wheat (*Triticum aestivum* (Poaceae)) are also hollow and provide for ameliorated gas exchange and photosynthesis (Bornemisza-Pauspertl et al. 1984). *Eriogonum inflatum* (Polygonaceae) has specialized, inflated, zone of the stem which has also been proposed to function similarly (Osmond et al. 1987). Neither of the latter studies includes information on temperature relations. The remarkable hollow stems of *Caulanthus* spp. (Brassicaceae) have not been studied with respect to their potential for heliocaminiform function (2020 (<https://www.youtube.com/watch?v=CVpjLRNo1jc>)).

Kevan et al. (2018) present a model for the complex thermodynamic interactions within stems and we have followed up with more intense studies, the results of which are briefly summarized in Table 1. We have been surprised to find that temperatures in insolated and shaded stems of *Equisetum* spp. do not seem to differ from one another nor much from the surrounding air (Table 1, row 38). We conjecture that rapid evapotranspiration (the stems shrivel rapidly when cut) may offset any heating by heliocaminiform function in sunshine.

Algae

Pneumatocysts in *Fucus*, *Macrocystis*, *Nereocystis*, *Sargassum* are well-known hollow structures in some brown algae (Phaeophyta) (Fig. 5). They are usually explained as aiding in buoyancy of the photosynthetic lamina. As far as we are aware, temperatures have not been measured in pneumatocysts until now, but ambient and internal temperature regimes probably affect the gas (notably CO₂) within (King 2001; Supratya et al. 2020; Liggan and Marton 2020) (Table 1, row 39). Preliminary results from the coast of Anacortes, WA, USA, show temperatures with the pneumatocysts of bladder wrack (*Fucus vesiculosus*) and bull kelp (*Nereocystis luetkeana*) (Fig. 5; Table 1 row 39) were about 4 °C warmer than the ambient air under sunny conditions.

Bryophytes

The sporophytes of *Sphagnum* spp. comprise tiny urns on stalks above the main gametophyte moss (Fig. 5). Presumably the insolation heats and expands the air within the capsule until the capsule bursts and releases the spores upwards (Table 1 row 40 (Kimmerer (2003:118))). The extent to which this heliocaminiform phenomenon occurs in mosses remains to be studied.

Fungi

A hollow stipe or pileus, or both is characteristic of some fungi, notably *Catherellus* and *Craterellus*, *Morchella* spp., and other basidiocarp fungi (Fig. 5). Most fungi known to have hollow structures grown in shaded environments so microgreenhouse effects from insolation probably do not apply.

Fig. 3. Helioaminiform fruits and fruiting structures.

Topmost: Ground cherry (*Physalis* spp.) fruits grow within hollow, translucent calyces. In greenhouse trials at the University of Guelph, the temperatures within the hollow calyces reached 6.6 °C warmer than the surrounding air in sunny weather. During the night, the temperatures within the same hollow calyces were on average 1-2 °C cooler than the surround air. (Table 1, row 36).

Next Below: Three-day trace of temperatures within *Physalis* fruiting structures during cloudless conditions.

Left: *Asclepias syriaca* plant with follicles instrumented with thermocouples (fine wire leads shown). The follicles reached temperatures up to 13 °C warmer than ambient air during our studies.

Within bottom four illustrations:

Right: Longitudinal sections of milkweed (*Asclepias syriaca*) follicle with thermocouple wires and probe inserted through the follicle wall into hollow interior and **Left (above)** and immature follicle with visible air space surrounding developing seeds and air pockets in the wall (**below**).

Left: Wild cucumber (*Echinocystis lobata*) fruits are hollow as they mature. On a sunny day (incident light = 1.165×10^5 LUX), reached an average of 8.29 ± 0.48 °C warmer than ambient air. On a cloudy day (incident light = 1.4×10^4 LUX) averaged only 0.09 ± 0.19 °C warmer than ambient air. (Table 1, row 17).

Right: Hollow capsule of *Nigella damascena* can attain internal temperatures of 5.5 ± 0.4 °C in sunshine as the grow and mature (Table 1, row 34).

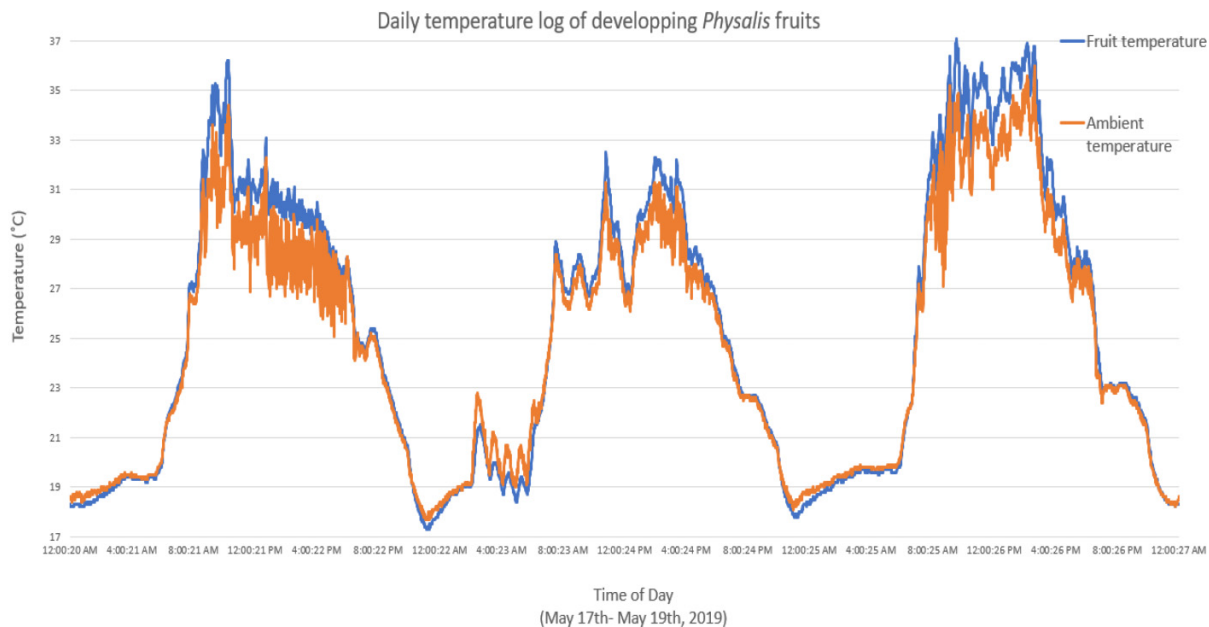


Fig. 3. (concluded).



The structure of the Nidulariaceae suggests that thermal relations and possibly insolation may play a role in maturation (Table 1 row 42).

Lichens

Lichens show an amazing array of forms and tolerance to heat and desiccation (Lange 1953, 1954) (Fig. 5). Among foliose and fruticose *Cladonia* spp. are numerous examples of species that are hollow within, especially within the podetium that supports the ascocarp. *Thammodia* spp. (worm or bone lichens), some *Hypogymnia* spp. (e.g., *H. tubulosa* the powder-headed tube lichen) and *Alectoria* spp. are also known to have hollow thalli. Species of *Letharia* (wolf lichens) may be hollow within the fruticose thalli. Although hollow structures may be common within vegetative and reproductive structures of lichens we know of no review of the subject nor of its functionality in lichen growth and reproduction (Table 1 row 41).

Conclusion

The capacity of plants to thermoregulate passively through the effects of differential trapping of radiative heat (insolation, the microgreenhouse effect, and insulation) within various somewhat translucent structures is widespread and diverse in nature but has not been reviewed until now. The structures range from pubescence through to more or less entirely enclosed, air-filled bracts, flowers, fruits, stems, leaves, algal laminae pneumatocysts, moss sporophytes, lichen podetia, fungi and galls. Our review illustrates that there have been few studies that have been made to test the hypotheses that hollow structures can and do act as microgreenhouses. We posit that the similarity in form and function across the diverse array of plants (*sensu lato*) (Table 1) warrants a new descriptive and inclusive term “heliocaminiform” for the phenomenon. We postulate that the same complex processes as are described particularly for stems by Kevan et al. (2018) apply to the form and function of heliocaminiform structures

Fig. 4. Heliocaminiiform stems, culms, peduncles and petioles.

Top: Plant stem thermometry in a commercial horticultural operation for gerbera daisies (Van Geest Brothers Limited in Grimsby, ON). *Gerbera jamesonii* Rendez-Vous (left) and Toast (right). The plastic box contains an Omega OM-HL-EH-TC datalogger recording internal stem temperatures of 4 flowers and adjacent ambient air temperatures by fine thermocouples (wires barely visible). A Reed Environmental Meter SD-9300 records light, with the light sensor suspended above the plants (right). In full sunlight, temperatures within the hollow Rendez-Vous stems can be up to 10.2 °C warmer than ambient air but within the somewhat hollow/pithy Toast stems are up to 4.7 °C warmer than ambient air. (see also [Table 1](#), row 9).

Next illustrations down: Left: Temperature recording from hollow stemmed *Ptarmica salicifolia* in Magadan, Russia. Blue wires are from thermocouples inserted in the peduncle or hung in adjacent the ambient air and connected to the Omega RDXL4SD data logger. Study plants had temperature excesses ranging from 1.23 ± 0.53 °C to 4.65 ± 0.59 °C. ([Table 1](#), row 9 and [Kevan et al. 2019](#)).

Right: Dandelion (*Taraxacum officinale*) and Omega OM-HL-EH-TC datalogger in the field. Stem temperatures in sunshine range from 1.9 °C (as shown on datalogger screen) to 8.6 °C warmer than ambient air temperatures. The maximum temperature difference was recorded when incident light was between 1.00×10^5 and 1.16×10^5 LUX. ([Table 1](#), row 9 and [Kevan et al. 2019](#)).

Below: Longitudinal section of a dandelion (*Taraxacum officinale*) stem (10X mag.). The inner walls of the stem is pale and shiny but not wet.

Top row: *Phragmites australis* (Arundinoideae) in roadside ditch (**left**) by College Ave., Guelph, ON (**left**). It is considered invasive. Its hollow stems (culms) (**centre**) grow rapidly up to 5 m tall. The hollow culms are septate (intermodally compartmented) and when growing are pale green becoming woody in maturity. On **right** a thermocouple is shown inserted into the culm. ([Table 1](#), row 31).

Next row down: The petioles of *Cucurbita pepo* are hollow and warm by heliocaminiiform effects ([Table 1](#), row 17). On **left** is shown a peduncle with thermocouples inserted (wire leads visible) and on **right** is shown a peduncle broken open to display the large hollow interior.

Bottom row: Far left: *Rumex patienta* hollow stem with a septum at the leaf node in Belgrade, Serbia. **Mid-left:** Instrumentation in place in stem in full sun and at a similar height in the shade of leaves (ambient air temperature) ([Table 1](#), row 32). **Mid-right:** Hollow stem and petioles of Himalayan balsam (*Impatiens glandulifera*) (Photo courtesy of: Prof. Joe Caffrey, Director, INVAS Biosecurity Ltd., 44 Lakelands Avenue, Stillorgan, Co Dublin, Ireland). **Far-right:** hollow stem of Giant Hogweed (*Heracleum mantegazzianum*) as typical of many Apiaceae ([Table 1](#), row 4) (Photo by: Leslie J. Mehrhoff, University of Connecticut, Bugwood.org).



Fig. 4. (concluded).



in general, including those exhibited by animals (e.g., lepidopteran cocoons (Kevan et al. 1982), insect pilosity (Downes 1964)).

Our results (Table 1) and discussion demonstrate the hitherto unrecognized botanical novelty of the phenomenon and points to the need for further studies of diversity of helio-

Fig. 5. Possible heliocaminiform function in Brown Algae (pneumatocysts), *Sphagnum* moss, fungi and lichens.

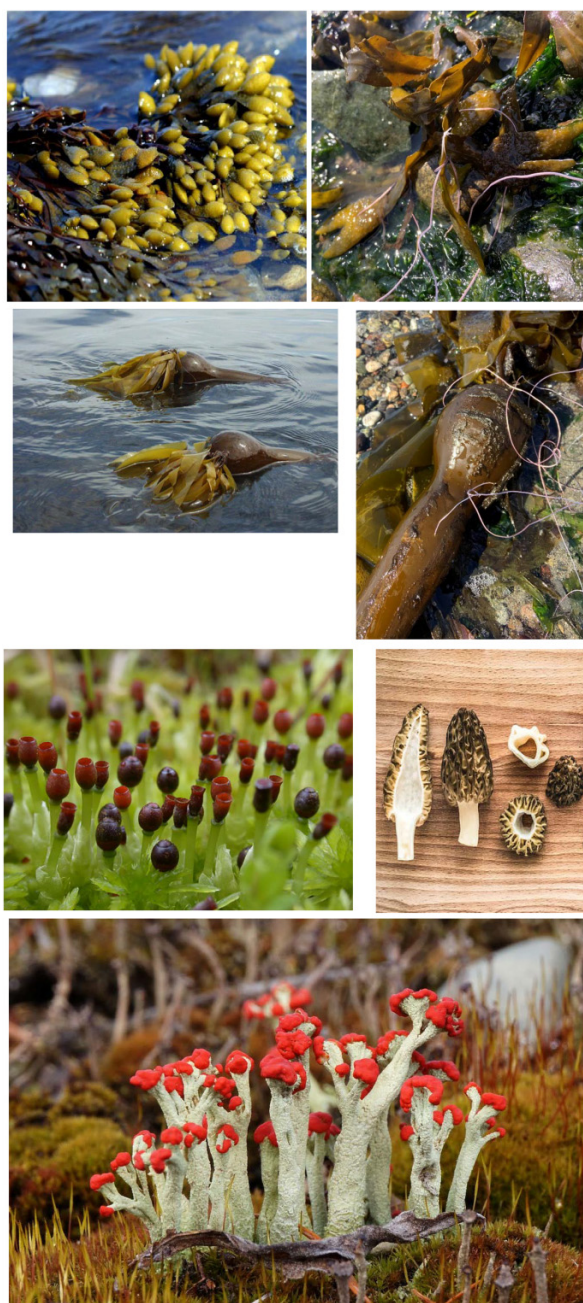
Top: Pneumatocysts of *Fucus vesiculosus* (bladder wrack) in intertidal waters (photo by Caleb Slemmons (Creative Commons Flickr)) (Table 1 row 39) **(left) and right** with thermocouples inserted in intertidal waters in Anacortes, Washington, USA 16:44 10 July, 2023. Maximum observed temperature difference between ambient air and within pneumatocysts was 3.9 °C under sunny conditions, 4:44 PM July 10, 2023.

Next row down: Pneumatocysts of bull kelp (*Nereocystis luetkeana*) at low tide showing inflated, hollow and buoyant properties **(left)** (photo by Caleb Slemmons (Creative Commons Flickr) (Table row 39) and as washed to shore **(right)**, at Washington Beach Park, Anacortes, Washington, USA 16:22 14 July, 2023 **and right** showing wire thermocouples inserted into hollow pneumatocyst and in adjacent air (photo by C. Coates): maximum recorded temperature difference was 4.4 °C under sunny conditions.

Next row down: Left: Dark unexploded and exploded sporophytes of *Sphagnum fimbriatum* (dark and hollow), unexploded (pale and open) <https://www.britishbryologicalsociety.org.uk/bryophyte-of-the-month/sphagnum-fimbriatum/> (Photograph by J. Sleath, accessed 30 August, 2023) (Table 1, row 40).

Right: Hollow stipitate fruiting structure of morel (*Morchella esculenta*) <https://www.growforagecookferment.com/foraging-for-morel-mushrooms/>(Table 1, row 42).

Bottom: British soldier lichen, upright podetia are hollow but no data we have found suggest heliocaminiform function (Table 1, row 41) <https://www.flickr.com/photos/ikewinski/16913799510> Creative commons.



caminiiform structures in plants. It is clear that additional studies to generalize the impact of pubescence are needed. It appears that the ecological role of pubescence on the microclimate is dynamic and habitat-specific: pubescence impacts temperature, water relationships, and protection from UV irradiance and herbivory. For flowers and inflorescences, the importance of solar warming has been reviewed recently (van der Kooi et al. 2019) and the microgreenhouse effect explained (Kevan 2020). Surprisingly, there have been few studies on the temperature regimes inside buds of any kind, floral, calyx, leaf, or bracts. That seems a neglected part of plant micrometeorology which, when further studied, may shed light important aspects of the mechanisms and effects of thermoregulation for the development and maturation of plants' sexual functionality. Equally surprising is the lack biogeographic, evolutionary, or ecophysiological consideration of hollowness in stems. It has been suggested that hollow stems occur more frequently in cool conditions (such as in Arctic, Subarctic, and alpine regions) than in temperate to tropical regions (Kevan and Coates 2021).

Process and product

Plants become warmed by a complex of thermal processes (Kevan et al. 2019) involving radiative, conductive, and convective heating. Apart from the influence of the temperature of the ambient air is the likely contribution of solar electromagnetic radiation (UV-Visible-IR). Some impinging radiation is reflected, some is absorbed and some is transmitted through the tissue (translucence) about which little seems to be known. Absorbed radiation is conducted through the stem's tissue (laterally and longitudinally). It is lost to the stem tissue by radiation and conduction to the outside and inside (lumen) of hollow structures. Transmitted radiation and/or conducted heat contributes additional energy to the lumen. Within the stem, radiant energy, like impinging solar EMR, can be (a) reflected, (b) absorbed by wall tissue from within, and also absorbed by the moist atmospheric gas in the lumen. The energy absorbed by the internal atmosphere contributes to the thermal environment within the heliocaminiiform structure by heat exchange by conduction, convection, and re-radiation. 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 structures liberate their energy through radiation (measurable as Emissivity), conduction to the surrounding air (or water in the case of aquatic plants), and evapotranspiration. Some of the heat generated within hollow structures is conducted elsewhere in the plant by the liquid in conductive tissues (phloem and xylem), some of the EMR is used in photosynthesis, and thermal energy is used in metabolism.

The additional heat resulting from heliocaminiiform processes must positively affect photosynthetic metabolism. That, coupled with the enriched gas mixture within hollow structures (e.g., stems of *Mertensia ciliata* (Boraginaceae)

(Billings and Godfrey 1967), *Triticum aestivale* (Bornemisza-Pausperl et al. 1984), and *Eriogonum inflatum* (Osmond et al. 1987 (and see above and Table 1 row 33)) would contribute to speed and extent of growth, maturation, and reproduction. There are many plants with hollow structures, especially stems. Such forms are probably multifunctional and for stems include compressional, torsional, and bending strength (Niklas 1992; Niklas and Spatz 2012) and rapidity of growth, especially in early development. Those features, coupled with capacity for internal heating through heliocaminiiform effects, and retention of gases that enhance photosynthetic biochemical reactions illustrate multifunctionality. Although the woody walls of mature stems probably do not allow for heliocaminiiform effects, they loft reproductive organs above the canopy, so aiding in pollination and subsequent seed dispersal. An extreme example is the Bambusoideae (Poaceae) spp., known to include the fasted growing plants on Earth and appreciated for use from salads to scaffolding but we are unaware of any observations on the temperatures or other conditions (e.g., gaseous) within bamboo culms.

Biothermometry has been applied to plants through direct measurements and by remote IR thermometry. For flowers, the means of warming under cool conditions have been recently reviewed (van der Kooi et al. 2019) and include solar basking by orientation of plant parts to face the sun, closing of leaves or floral parts and so retaining heat, adaptations that emulate translucent miniature greenhouses and, in some special cases, metabolic heating. For other plants parts, notably stems, Kevan et al. (2018) show that hollowness imbues plants with elevated temperatures in sunny conditions. Cooling under heat stress is less understood. Apart from the orientation of leaves by paraheliotropism to reduce solar heating, cooling is attributed to transpirational heat loss (i.e., heat loss by the evaporation of water through stomata, akin to sweating (e.g., *Equisetum* spp. Table 1, row 38, corn sweat, some fruit and galls). The cooling effect of trees is not simply by shading but includes transpiration and may involve paraheliotropism. Those phenomena are increasingly invoked for mitigation of heat in urban landscapes. Herbaceous plants may also exhibit paraheliotropism and so reduce incident solar heating stress, but, additionally, show growth responses mediated by interacting heat and light sensitivities that result in heat avoidance. Thus, plants, although apparently static and passive, show remarkable capacities to regulate their internal temperatures by a complex variety of strategies. Those include solar heating, as in diaheliotropic solar furnaces (Kevan 1989), microgreenhouse effects (Kevan et al. 2018; Kevan 2019a, 2019b, 2020), metabolic endothermy (van der Kooi et al. 2019) and concomitant cooling by evapotranspiration (as noted above and referred to as the swamp cooler effect (Galen 2006)), paraheliotropism and adaptive morphogenesis (Crawford et al. 2012). Thus, plants, although apparently static and passive, show remarkable capacities to regulate their internal temperatures by a complex variety of strategies. Thus, plants are, as Michaletz et al. (2015) argue, but from the viewpoint of metabolism, limited homeotherms!

Phenology, climate change, and phenological mismatches

There are increasing amounts of information in the modern scientific literature on the observed effects of climate change on plant distributions and to a lesser extent growth rates (Post 2013) but fewer studies on the micrometeorological basis of concomitant effects in phenological mismatches between plants and their symbionts (other plants, herbivores, mutualists). Recent papers have pointed out the consequences of recently documented phenological mismatches in pollination through pollinator availability and activity and flowering times (Høye et al. 2013; Miller-Struttman et al. 2015; Wheeler et al. 2015). There have been major advances in micrometeorology and the effects of ambient temperatures, and other factors, on the growth and productivity of plants, especially for agriculture and forestry (Jones 2013). It is acknowledged that intraplant thermal regimes influence reproductive fitness of plants directly through the growth and presentation of the sexual organs (flowers and inflorescences) and indirectly through performance of the vegetative parts. There are surprisingly few studies on how supporting structures (stems, petioles, peduncles, culms etc.) capture and use ambient heat (including solar radiation) to enhance their presentations for pollination (by insects or by wind) or for seed/fruit dispersal (mostly by wind) (Kevan et al. 2018). In short, there appears to be major gaps in knowledge linking climate change with whole plant phenology, vegetative productivity and reproductive fitness. We suggest that studies are urgently needed to better understand the form and function of plant structures in terms of their abilities to develop micrometeorological environments that seem assuredly influenced by climate changes but have rarely been studied in that context. What is emerging in studies about the issues noted above are the complex and dynamic interrelationships between climate change, ambient meteorological and micrometeorological conditions, the micrometeorology within individual plants and within their reproductive structures and the knock-on effects on their symbionts (mutualists and herbivores) as ecologically co-dependent partners. In this study we have concentrated on the hitherto unrecognized diversity of heliocaminiform structures and the microgreenhouse effect by which plants may respond to climate change at global to highly localized (including within plant parts) levels.

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Data availability

All relevant data are within the paper.

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Author contributions

Conceptualization: PGK, CC

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Methodology: PGK, CC

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Competing interests

The authors declare that there is no conflict of interest regarding the publication of this paper.

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