J Plant Res (2002) 115:263–268
Digital Object Identifier (DOI) 10.1007/s10265-002-0030-1

SHORT COMMUNICATION

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Thermal insulation and accumulation of heat in the downy inflorescences of *Saussurea medusa* (Asteraceae) at high elevation in Yunnan, China

Received: January 22, 2002 / Accepted: April 2, 2002 / Published online: June 18, 2002

Abstract Himalayan snowball plants, which are considered to be an extreme form of downy plants, have very dense trichomes on well-developed bracts that surround the inflorescences. It has been postulated that the downy inflorescences of these plants might serve to keep the interior of inflorescences warmer than the outside and, thus, to protect reproductive cells from low temperatures in their Himalayan habitat. In the present study, we examined the downy inflorescences of *Saussurea medusa* Maxim. in native habitats in the high alpine zone of the Henduan Mountains in Yunnan, China, and we analyzed the temperature within inflorescences after absorbance of light energy. *S. medusa* is pollinated by bumblebees and we found that its inflorescences accumulated heat not on the inside, but, rather, on the upper surfaces. The thick hollow stems and the overlapping bracts with obvious epinasty might serve not only to retain heat, but also as an insulator to protect the inside against overheating, with apparent local warming of flowers that are located at the tops of plants, which are cone-shaped. We made a model that mimicked the warming of inflorescences, providing support for the hypothesis that the downy bracts of *S. medusa* have two functions: thermal insulation to protect the inside of flowers and the accumulation of heat on the upper surfaces of the inflorescence. Such a system might be effective in attracting pollinators and also in protecting tissues from extreme variations in temperature.

Key words Alpine plants · Downy plants · Heat insulation · Pollination · *Saussurea* · Thermography

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The forms of some alpine and arctic plants reflect their adaptation to frigid environments (Krog 1955; Körner 1998; Morris and Doak 1998). In particular, in the alpine zone of the Sino-Himalayan region, which is characterized by high precipitation in summer, some plants are characterized by unusual specialized morphology (Ohba 1988). Adaptive morphology of two types, in particular, has been recognized. These types are exemplified by Himalayan glasshouse plants, which are characterized by the semi-translucent bracts that cover their inflorescences, and Himalayan snowball plants, which are characterized by highly pubescent bracts that surround their inflorescences (Ohba 1988). The translucent bracts of glasshouse plants, *Rheum nobile* Hook.f. & Thomson (Polygonaceae) and *R. alexandrae* Batalin, insulate the insides of inflorescences against the cold (Terashima et al. 1993, 1995) and protect the insides of inflorescences from the damaging effects of ultraviolet light (Omori and Ohba 1996; Omori et al. 2000; Tsukaya 2002).

The highly pubescent inflorescences (or synflorescence) of Himalayan snowball plants, which are an extreme form of downy plants (Tsukaya and Tsuge 2001), are thought to represent an adaptation that supports blooming during the monsoon season at low temperatures in alpine zones (Kikuchi and Ohba 1988; Tsukaya et al. 1997; Tsukaya and Ohba 1999). Several species of *Saussurea* that are distributed in the high alpine zone of the Himalayas and Southwest China have very similar, downy inflorescences, for example, *S. gossipiphora* D. Don, *S. graminifolia* Wall. ex DC., *S. laminamaensis* Kitam., *S. laniceps* Hand.-Mazz., *S. medusa* Maxim., *S. nishiokae* Kitam., *S. simpsoniana* (Field. & Gardner) Lipsch., *S. spicata* Ludlow ex Kitam., and *S. topkegolensis* H. Ohba et S. Akiyama (Fujikawa 2000; Fujikawa and Omori 2000; Ohba and Fujikawa 2000). Wuenscher (1970) reported that the thick boundary layer formed by dense hairs on a plant's surface can effectively reduce the diffusion of heat away from the plant and, as we showed previously, downy inflorescences of *Salix* and

Magnolia are effective in keeping the insides of the inflorescences warmer than the outside (Tsukaya and Tsuge 2001). Thus, it has been proposed that the dense trichomes on bracts might act to protect the primordia of the reproductive organs from the cold (Ohba 1988; Tsukaya and Tsuge 2001). It has been also proposed that downy, warm inflorescences might be attractive to insects and, in particular, to pollinators (Ohba 1988). However, this proposal has been controversial. Tsukaya and Tsuge (2001) opposed this hypothesis, noting that the arrangement of downy pubescent bracts is generally looser at the flowering stage than the earlier stages when gametogenesis is underway.

In the present study, to clarify the roles of the downy bracts and cauline leaves of Himalayan snowball plants at the flowering stage, we examined flowering specimens of *Saussurea medusa* in two native populations at altitudes from 4,465 to 4,620 m, near a pass of Mount Baima Xueshan, north Yunnan, China, on 26 and 27 July 2001. We also collected individual plants, and dried voucher specimens were deposited in the Herbarium of the Kunming Institute of Botany of the Chinese Academy of Sciences (KU) and at the University of Tokyo (TI). Pollination of flowers by bumblebees was observed from 1330 to 1500 hours on 26 July and from 1200 to 1330 hours on 27 July 2001.

The native habitats of *Saussurea medusa* were generally steep slopes composed of rough-edged stones (1 to 2.5 cm in length), which were easily displaced. Individual flowering plants were scattered at a distance from one another in most

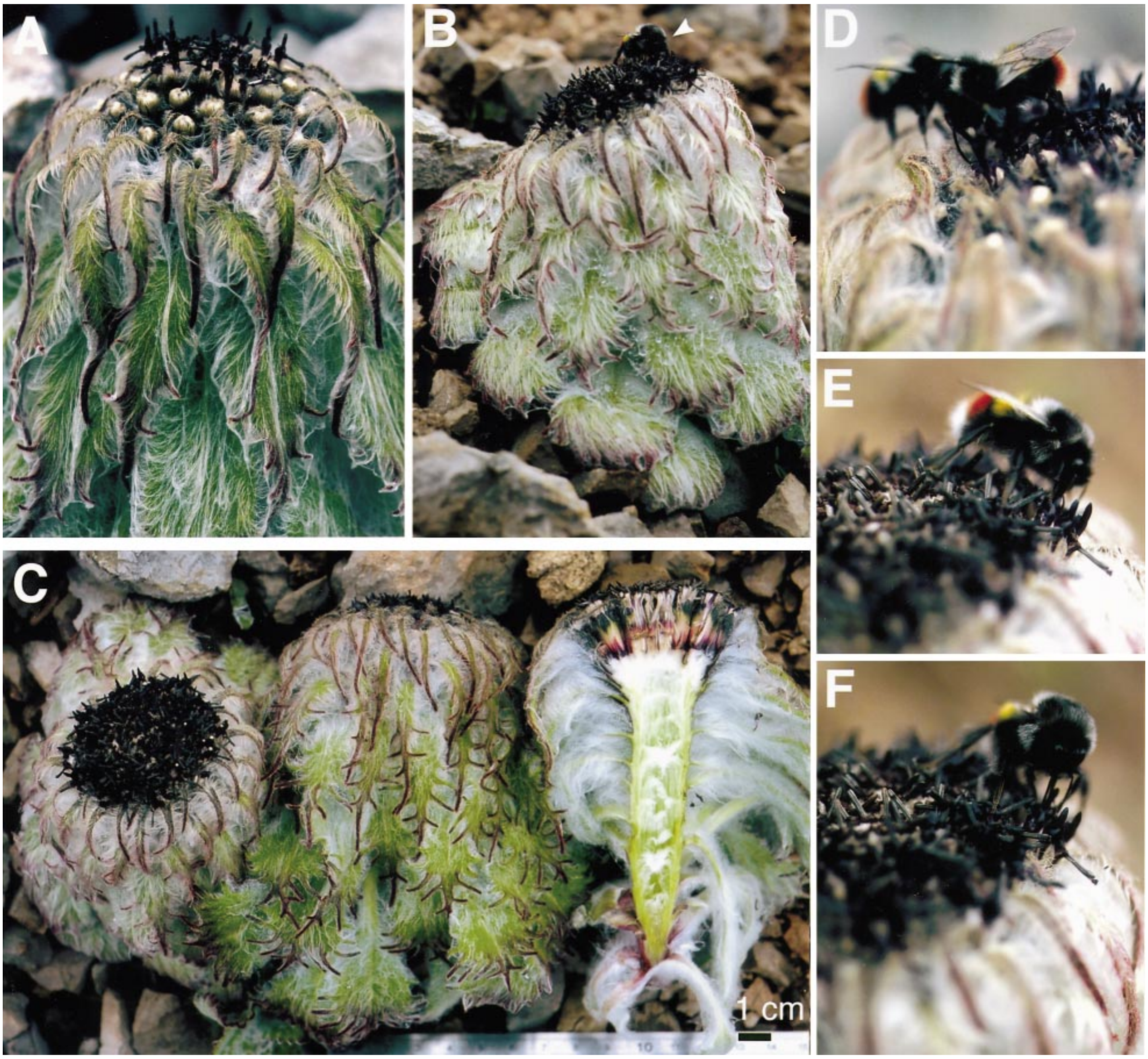

Fig. 1A–F. Native habit and gross morphology of downy inflorescences of *Saussurea medusa* and visits by bumblebees. **A** Gross morphology of flowering individuals. Note the highly pubescent bracts and cauline leaves that surround the inflorescence, as well as the obvious epinasty of bracts and cauline leaves. **B** An inflorescence with flowers and a pollinating bumblebee (*arrowhead*). **C** Longitudinal section of *S. medusa* showing hollow internodes, adjacent to intact flowering specimens. *Bar* 1 cm. **D–F** Bumblebees visiting flowers of *S. medusa*. Photographs were taken in the native habitat of *Saussurea medusa* (4,610 m; near a pass of Mount Baima Xueshan, north Yunnan, China) of the habitats that we examined. Blooming flowers were dark purple, whereas the other parts of plants, including flower buds, were covered with white hairs (Fig. 1). The air temperature at one habitat was 17.4 °C at 1245 hours on 27 July (it was cloudy). During our observations of two separate populations, the inflorescences of *S. medusa* in both populations were frequently visited by bumblebees [*Bombus* (*Psithyrus*) *chinensis* (Motawitz); Fig. 1B]. No other species was observed to visit the inflorescences, but one butterfly (*Parnassius* spp.) was observed to fly around the plants in one population. Bees landed directly on inflorescences without touching any other parts of the plants (e.g., cauline leaves) and remained on an inflorescence for more than 1 min at most. These observations suggest that the bees precisely recognized the positions of the flowers on the plants.

When flowering plants were examined by hand, the upper surface of all flowering inflorescences (nine of nine) felt warmer than the other part of the plants. Therefore, using transplanted specimens, we examined the distribution of heat accumulated by the downy inflorescences with a thermograph (Neothermo TVS-600; Avionics Japan, Tokyo), while measurements of light intensity were made with a light meter (LI-250; LI-COR Inc., Lincoln, Ne., USA). Temperatures were also measured with a digital thermometer (CT-700SD; CUSTOM Inc., Tokyo) equipped with a needle-type sensor probe (LK-310; CUSTOM Inc.), as described earlier (Tsukaya and Tsuge 2001). We found that when white light at approximately $125\,\mu E\,m^{-2}\,s^{-1}$ (incandescent lamp) was incident on two opposite sides of the plant, from an angle of 45° above the flowering plant in both cases, heat accumulated rapidly and predominantly on the upper surface of the inflorescence on which the flowers were arranged (Fig. 2). This thermograph confirmed the apparent accumulation of heat by *Saussurea medusa* in its native habitat. Three minutes after the start of the irradiation with white light, the temperature of the upper surface of the entire inflorescence was 41.0 °C whereas that inside the inflorescence (half way up the inflorescence, inside the bracts) was 34.0 °C. The warming effect was completely dependent on the intensity of light and, in darkness, the inflorescence was not warmer than other parts of the plant, or even than the soil into which plants had been transplanted (data not shown). The lack of a heating system in the inflorescences of *S. medusa* is similar to the lack of such a system in the downy inflorescences of *Salix* and *Magnolia* that we have described previously (Tsukaya and Tsuge 2001), and in another downy species of *Saussurea*, *S. gossipiphora* (Takayama 1993).

The inside of plants remained at more moderate temperatures than the surface during irradiation (Fig. 2B), perhaps because of an insulating effect of the downy bracts and leaves. As shown in Fig. 1C, the internodes of *Saussurea medusa* are hollow and there is considerable air space among the cauline leaves and bracts, which might act as an insulator of the deep interior of the plants. Alternatively, the air spaces between the downy cauline leaves and bracts might accumulate heat because of solar radiation, and might act as a conduit for warm air to the upper parts of inflorescences.

To confirm the proposed warming and insulating effects of the downy structure of *Saussurea medusa*, we made models of flowering *S. medusa* using 1-mm-thick felt and monitored increases in temperature in and on the models upon irradiation with white light. To mimic the structure of flowering *S. medusa,* the model was conical, with a hollow "stem" surrounded by heat-insulating "leaves" (Fig. 3A). A felt cylinder of 1 cm in diameter and 8 cm in height was covered with leaf-shaped pieces of felt. Three types of "leaves" were designed, having the same contours as the actual leaves and bracts of *S. medusa*. "Lower leaves" had triangular (broadest at the tip) "blades" of 2.8 cm in length and 3 cm in width with "petioles" of 4 cm in length and 5 mm in width. "Upper leaves" had similarly triangular "blades" of 2.8 cm in length and 2.8 cm in width with "petioles" of 1.5 cm in length and 3 mm in width. "Bracts" resembled "upper leaves" in shape, but lacked "petioles". In the longitudinal direction, the center of each "leaf" was backed with a paper strip 1 mm in width, which mimicked a midrib. We attached 16 "lower leaves", 34 "upper leaves", and 16 "bracts" via their bases to the felt "stem" in a helical manner with 4-mm spaces from base to top (Fig. 3A). The density of the "leaves" roughly mimicked that of actual leaves. The top of the model was capped with a cone of felt with 3 cm in radius and 2 cm in height. We made two models, one using pale green felt (shown in Fig. 3B) and one using white felt (Fig. 3C). Models were kept at room temperature (23.5–27.0 °C) before exposure to sunlight ($1{,}120$–$1{,}680\,\mu E/s/m^2$; measured with a light meter LI-250). During a 10-min irradiation with sunlight from one side of the models, temperatures were measured at three points on the models (as indicated in Fig. 3A) with a digital thermometer (CT-700SD) equipped with a needle-type sensor probe (LK-310). The distribution of heat in the model mimicked that in *S. medusa*, with the greatest and fastest warming at the top of the model and, simultaneously, below the "bracts" half way up the models (Fig. 3B, C). Although differences in terms of warming patterns between the two parts were not obvious, there was a tendency for the top part to become slightly warmer than the region below the "bracts" when the model was made with pale green felt (Fig. 3B). The dark purple flowers of *Saussurea medusa* (Fig. 1) might be more effective for accumulation of heat than the pale-colored felt of our models. Warming deep inside the model (at the bottom center of the cylinder) was much slower than that at the two higher positions, as expected. At all points examined, the kinetics of warming could be represented by logarithmic curves (Fig. 3). Although the models are different from real plants in terms of the absence of water in the model, if we postulate that the observed warming patterns of the models reflect those of *S. medusa,* we can divide the role of the downy structure of flowering *S. medusa* into two distinct functions: namely, local warming of flowers situated at the top of the plant and insulation of tissues deep within the plant.

The local warming of flowers can be easily understood as a pollination strategy of plants in a cold alpine zone. As described above, bumblebees frequently visited the flowers of *S. medusa*, which grows at a low density of individuals on slopes with poor vegetation. *Adonis ramosa* Franch. is known to attract Diptera pollinators by heat from to solar radiation (Kudo 1995). *S. medusa* might attract pollinating bumblebees to its warm inflorescences and warmth might promote the activities of bumblebees on them. However, because bumblebees are known as “hot-blooded insects” and are able to keep their body heat high even under low temperature, warmth itself might not be such an attractive

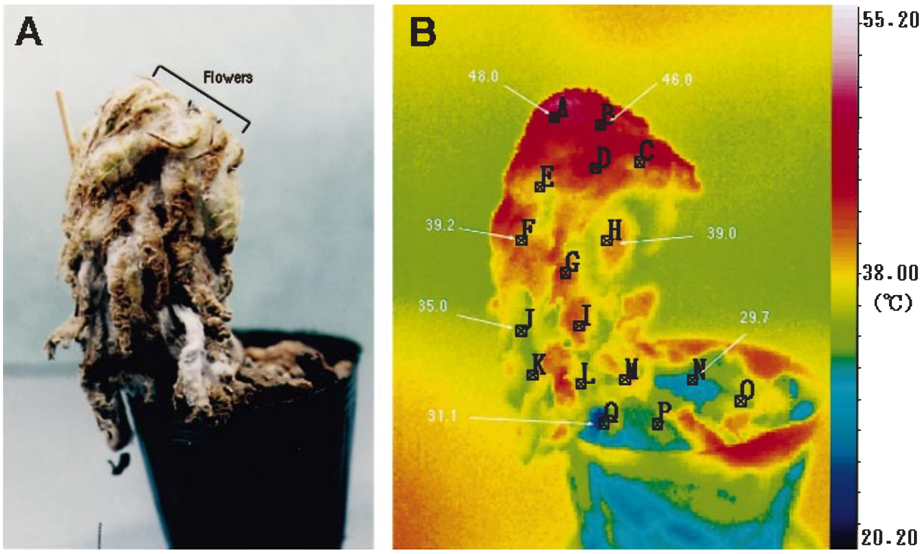

Fig. 2A,B. Thermographic image of *Saussurea medusa*. **A** Photograph of a plant in a vinyl pot. **B** Thermograph of the individual shown in **A**. The *far-right column* shows the colors that indicate surface temperatures. Temperatures, at sites indicated by letters of the alphabet, were as follows: *A* 48.0; *B* 52.0; *C* 40.6; *D* 43.1; *E* 38.7; *F* 39.2; *G* 42.0; *H* 39.0; *I* 40.4; *J* 35.0; *K* 35.0; *L* 36.0; *M* 38.5; *N* 29.7; *O* 36.0; *P* 33.1; *Q* 31.1 (°C)

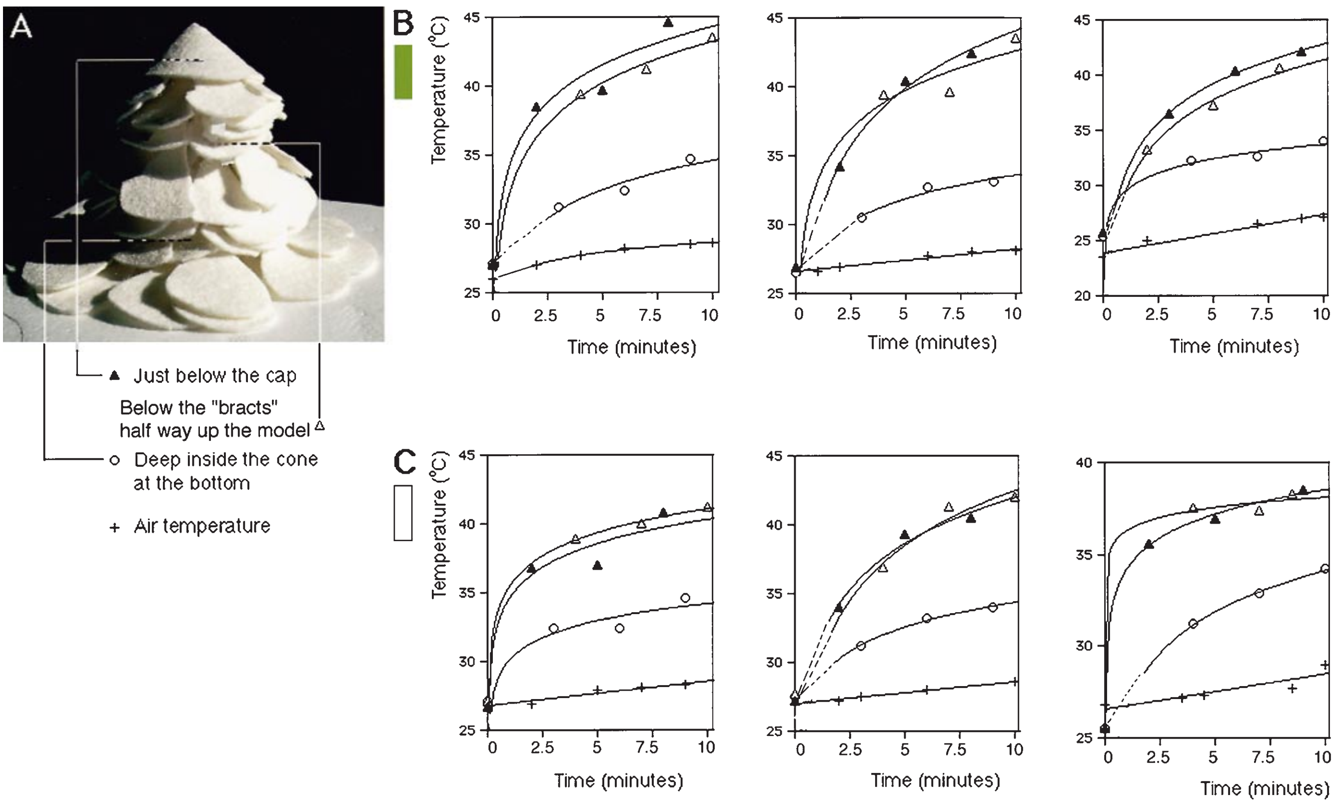

Fig. 3A–C. Simulation of warming effects using models that mimicked the downy structure of *Saussurea medusa.* **A** Lateral view of a model used for simulations. Temperatures were measured at points indicated by the *symbol* used in **B** and **C**. **B, C** Three independent sets of results from the pale-green model (**B**) and the white model (**C**). Curves were drawn on the assumption that the increases in temperature with time were logarithmic except in the case of *broken lines*, which are simple connections from data points to time zero factor for the bumblebees. Bumblebees might be attracted by the nectar of *S. medusa* and might locate flowering inflorescences of *S. medusa* by monitoring heat as infrared radiation (see Fig. 2). Thus, *S. medusa* might be an insect-pollinated plant that attracts pollinators not only by its resources (nectar) or attractive color, but also by heat. Also, the other downy species of *Saussurea* were observed to be visited by bumble bees, namely, *S. gossipiphora* (observed on 18 August 1997, around Tangnag, Solukhumbu district, East Nepal, altitude 4,600 m), *S. spicata* (observed on 3 September 1999, around Yak Kharka, Mustang district, West Nepal, altitude 4,600 m) and *S. simpsoniana* (observed on 16 August 1997, around Khare, Solukhumbu district, East Nepal, altitude 4,750 m and on 1 September 1999, around Yak Kharka, Mustang district, West Nepal). The observed pollinator in the present study was *Bombus* (*Psithyrus*) *chinensis*, which is known to show cleptoparasitism. Further experiments in the field involving, for example, attraction of bumblebees by warmth and cleptoparasitism of *B. chinensis* around pollination of *S. medusa,* are needed to examine this interpretation.

The effects of insulation of tissues inside plants seem to reflect a meaningful adaptation of alpine plants to their harsh environment. As reported previously (Takayama 1993; Tsukaya and Tsuge 2001), temperatures inside warmed downy bracts reached from several to more than 20 degrees above the air temperature, but soon decreased again to air temperature when light intensity decreased. Such large changes in temperature might be harmful to plant organs. Thus, the heat-insulating effects of downy bracts might protect organs in the plant's interior from abrupt and large changes in temperature.

Pubescent plant organs have various functions (Levin 1973; Johnson 1975). We previously proposed that a major role of dense trichomes on downy plants might be protection from low temperatures of reproductive cells at the early stages of gametogenesis (Tsukaya and Tsuge 2001). The present study suggests that the entire structure of flowering specimens of *Saussurea medusa* might play a role at the flowering stage. The downy conical structure is effective for the warming of flowers arranged at the top of the inflorescence, and it might also be effective in keeping mild conditions in terms of temperature inside the plant as a result of its insulating effect not only to retain heat, but also to protect the tissue against excessive heating. A full understanding of the roles of the unusual morphological features of alpine plants in the adaptation to their harsh environment will help us to clarify the background of the morphological biodiversity of plants. The present study provides a foundation for such studies.

Acknowledgments The term "downy plants" (Tsukaya and Tsuge 2001) was proposed to describe plants that display a type of convergent evolution by Dr. Ann M. Körner of Bioscript (Hamden, CT, USA). The authors thank Professor H. Ohba of the University Museum of the University of Tokyo and Dr. S. Akiyama of the National Science Museum, Japan for discussions on Himalayan plants and for giving the authors the opportunity to join expeditions to alpine regions of Yunnan, China and the Himalayas in Nepal. Dr. M. Ito of the Sapporo Institute of Technology (Sapporo, Hokkaido, Japan) and Dr. P.H. Williams of the National History Museum (London, UK) kindly identified the bumblebees. The Nagoya branch of Avionics Japan Inc. kindly lent a thermograph (Neothermo TVS-600) for the present study. Models of *Saussurea medusa* were skillfully constructed by Ms. K. Kabeya of the National Institute for Basic Biology, Japan. The botanical expeditions were supported by Grants-in-Aid for Fundamental Scientific Research from the Ministry of Education, Science and Culture, Japan, and laboratory studies were supported by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan, and by a grant from the Bio-Design Program, Ministry of Agriculture, Forestry and Fishes of Japan.

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