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The Bracts of *Saussurea velutina* (Asteraceae) Protect Inflorescences from Fluctuating Weather at High Elevations of the Hengduan Mountains, Southwestern China

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Abstract

Several members of the subgenus *Amphilaena* (*Saussurea*; Asteraceae) growing at high elevations in the Himalayan region have semi-translucent bracts covering their inflorescences, the function of which is not fully understood. We investigated the thermal benefits of these bracts in *Saussurea velutina* *in situ* in the Hengduan Mountains, SW China, and compared the reflectance spectra and anatomical characters of bracts and rosette leaves in the laboratory. After removal of bracts in the field the average inflorescence daytime temperature was 2.5 °C colder than in control plants with intact bracts. Manually opened treatment inflorescences grew slower and set significantly fewer seeds than control inflorescences with bracts intact. The mesophyll of bracts is a single cell layer with a lower reflectance in the infrared range than rosette leaves. We show that the semi-translucent bracts in *S. velutina* function to ensure warmer temperatures for floral and seed development at high elevations in the Hengduan Mountains.

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Introduction

The alpine zone (4000–5500 m elevation) of the Hengduan Mountains region in SW China, and the eastern region of the Himalaya in Nepal, experiences a summer monsoonal climate with cold rain or sleet, interrupted by short periods of intense solar radiation (Yoshida, 2002). Changeable weather conditions and the short growing season are crucial factors that have influenced the evolution of alpine plants in this area (Ohba, 1988), most of which have specialized morphology for survival in this hostile habitat (Yoshida, 2005). For example, the highly pubescent bracts covering the inflorescence of *Saussurea medusa* (Himalayan “woolly” plant) assist in temperature control and water repellence in the cool humid summer (Tsukaya et al., 2002; Yang et al., 2008). For plant species growing at high elevations, solar energy absorbed by bracts assists in maintaining the temperature of reproductive organs above cold ambient levels, thereby promoting growth and development during brief intervals of warmth (Körner, 2003; Fabbro and Körner, 2004). Two polygonaceous Himalayan plants, *Rheum nobile* and *R. alexandrae* (commonly known as Himalayan “greenhouse” plants), have large semi-translucent bracts covering their racemes (Ohba, 1988). Bracts occur on buds during anthesis and mature fruiting stages; may play an important role in dispersal, pollination, and seed germination (Stuessy and Spooner, 1988; Sun et al., 2008); and may also protect the inflorescences against predators and environmental extremes (Knutson, 1981; Stuessy and Liu, 1983; Evans, 1996). Based on measurements on a single inflorescence on *R. nobile* in Nepal, Omori and Ohba (1999) reported that bracts on the inflorescence elevated the temperature of floral tissues and had insulative effects. In addition, the large bracts of *R. nobile* and *R. alexandrae* have positive effects on the control of sunlight penetration and protect the inflorescence from ultraviolet radiation (Terashima et al., 1993; Omori and Ohba, 1996; Omori et al., 2000; Tsukaya, 2002; Iwashina et al., 2004).

Large, semi-translucent bracts similar to those in *R. nobile* and *R. alexandrae* occur in other plant species in different families, including Ranunculaceae, Caryophyllaceae, and Apiaceae as well as in the genus *Saussurea* (Asteraceae) (Yoshida, 2002). Recently, Kusano et al. (2007) extracted flavonoid compounds from bracts in *S. involucrate* and suggested that bracts may protect inflorescences from UV-B radiation. *Saussurea velutina* is endemic to the Xizang-Qinghai plateau (Shin and Jin, 1999; Fujikawa et al., 2007). It commonly grows above 4300 m, and often occurs at the permanent snow line. It grows to 15–20 cm height in the vegetative phase when its inflorescence is covered by yellow to red colored bracts (Fig. 1a). Upright plants experience conditions that are more closely coupled to ambient atmospheric conditions than low-stature forms (Körner and Cochrane, 1986), and this may explain why the upright forms are rare at higher elevations (Körner, 2003). However, while a number of studies have investigated the effects of bracts, none have tested whether they have any impact on plant fitness in terms of inflorescence growth and seed production. We evaluated the thermal effects and benefits of the bracts of *S. velutina* at high elevations and hypothesized that bracts raise inflorescence temperature and insulate it from weather fluctuations, thereby providing a reproductive advantage to the plant. We tested this hypothesis using field and laboratory studies, including bract removal experiments *in situ*, and by comparing the reflectance spectra and anatomical characters of bracts and rosette leaves.

Materials and Methods

STUDY SITE

The study was done in the alpine zone of Lakaka Pass on Baima Snow Mountain, De Qin County, Yunnan Province, China (28°20'N, 99°05'E, altitude 4560 m). The annual average air temperature recorded at the nearest meteorological station



FIGURE 1. (a) Inflorescence of *Saussurea velutina* under the cover of bracts in the vegetative period, and (b) in the flowering stage.

(28°23'N, 99°01'E, altitude 4290 m), 10 km away, is $-1.0\text{ }^{\circ}\text{C}$ and the yearly precipitation is between 680 and 790 mm with a maximum of 330–405 mm between late June and late August (Wang et al., 2003; Wang, 2006). The difference in mean monthly temperature between the coldest and warmest month is approximately $15\text{ }^{\circ}\text{C}$. The growing season is 10–12 weeks from early June

to early September. The mean air temperature at the study site in summer was extrapolated from meteorological data recorded at the nearest meteorological station from 1982 to 1984 using an adiabatic lapse rate of $-0.767\text{ }^{\circ}\text{C}$ per 100 m (Wang, 2006).

STUDY SPECIES

The genus *Saussurea* is widely distributed in the temperate and subarctic regions of Eurasia and contains about 400 species classified into 6 subgenera. *Saussurea velutina* (subgenus *Amphilaena*) is an herbaceous perennial with a relatively large rhizome system. The plant has basal long, narrow leaves, produces a stem up to 15–20 cm during the vegetative stage and extends a further 20–30 cm during flowering (Fig. 1b). Each stem bears only a single inflorescence. Voucher specimens were deposited in the herbarium of Kunming Institute of Botany, Chinese Academy of Sciences (KUN).

FIELD MEASUREMENT

Effects of Bracts on Floral Thermal Environment

Inflorescence temperature was defined as the internal flower tissue temperature at the ovary (5–10 mm below the surface of the inflorescence) and was measured using three 4-channel thermocouple data loggers (Center 309, data logger thermometer, Center Technology Corp.), each equipped with 4 alloy needle-type sensor probes (1.6–3 mm diameter and an active tip length of 5 mm). These probes were calibrated in ice water before use to assess stability and accuracy (deviation from zero $< 1.0\text{ }^{\circ}\text{C}$, commonly $< 0.7\text{ }^{\circ}\text{C}$). The temperature in the space between bracts was determined in the same way.

To determine the effect of bracts on inflorescence temperature, we removed the bracts in some individuals ($n = 3$) and compared inflorescence temperature with untreated control plants ($n = 3$). Because of damage to one of our thermocouple data loggers, we measured the temperature in the space between bracts for only one inflorescence ($n = 1$). Air temperature (T_a), relative humidity (RH) and solar radiation (I) at the height of the inflorescence (ca. 15 cm above ground) were recorded at 5 minute intervals using an integrated thermistor (I400-104 RH/air temperature sensor, LI-COR Inc.) and a pyranometer (Li-190SA quantum sensor, LI-COR Inc.), both connected to a data logger (Li-1400 data logger, LI-COR Inc.). Wind velocity at 15 cm above ground was recorded every 60 seconds with an anemometer (AVM-07, Prova Corp.). Ambient air temperature and the temperature in the spaces between bracts were recorded at 90 second intervals between 11 and 13 August 2006. All other measurements were made between 8 and 10 August 2007.

Effects of Bracts on Inflorescence Growth and Seed Reproduction

To assess the effects of bracts on inflorescence growth and seed production, three experimental sites were selected in August 2008, each of which had numerous plants whose inflorescences were still surrounded by bracts. At least 12 plants from each site were labeled and divided into 2 groups. In the first group the bracts were carefully opened by hand, folded back and held in place by an elastic band, but not removed. Plants in the second group, the control, each had an intact inflorescence with bracts.

The fruits were collected in September before seed dispersal. In addition, the diameter and height of manually opened and control flower heads were measured using a caliper in the field. Five opened treatment and five control plants were damaged by

TABLE 1

The temperature regime in intact inflorescences (Control) and in inflorescences with bracts removed, and ambient air temperatures at the height of the inflorescence (15 cm) during the experimental period in 2007. Daytime was considered to be from 0800 to 2000 h. Temperature was measured every 5 min for 24 h for 2 days beginning at noon. The minima and maxima are presented as absolute extremes (the single highest and lowest reading).

	Day			Night		
	Air	Control	Removed	Air	Control	Removed
Mean	12.4 ± 3.7	17.1 ± 7.5*	14.6 ± 4.6	6.5 ± 1.1	5.3 ± 1.1	5.3 ± 1.0
Absolute maximum	20.9	31.8	31.9	10.7	11.4	9.1
Absolute minimum	5.4	5.2	5.1	4.7	3.3	3.2

* The data represent the mean values from 3 flowers of each plant category ± s.d.

yaks in the study site. We measured and collected 15 flower heads for each group. The number of flowers and seeds from each inflorescence were counted after air-drying for 90 days. There was a clear morphological difference between seeds and aborted achenes. The latter were small, shriveled, and lacked endosperm.

LABORATORY MEASUREMENTS

Spectral Properties of Bracts and Leaves

The reflectance of reproductive tissues was hypothesized to influence flower temperature (Lacey and Herr, 2005). In order to examine the reflective spectra of bracts in *S. velutina*, 20 plants with bracts covering their inflorescences were collected in July 2006, were sealed immediately in plastic bags, and were transported to the laboratory in an insulated ice box within 24 h and stored at < 5 °C.

Spectral reflectance of the upper surface of leaves and the red and yellow areas of the anatomically lower (sun-exposed) surfaces of bracts, at wavelengths between 400 and 1000 nm, were measured at 3 nm intervals using a Spectral Analysis System (Unispec-sc, PP Systems Inc.). Reflectance was measured ($n = 20$ per plant) on the leaves and bracts of six of the plants with the seemingly healthiest and intact bracts.

$$R_L = [r_L/r_S] \times 100\% \quad (1)$$

where R_L is the reflectance spectrum for each leaf at wavelength λ ; r_L and r_S are the radiance of leaf and reflectance standard at wavelength λ .

$$R_B = [r_B/r_S] \times 100\% \quad (2)$$

where R_B is the reflectance spectrum for each bract; r_B and r_S are the radiance of bract and reflectance standard at wavelength λ .

Anatomical Characteristics of Leaves and Bracts

A total of 12 bracts and 12 leaves were removed from the 6 plants that were used for the inflorescence temperature experiment. The bracts and leaves were fixed on-site in formalin-acetic acid-alcohol (FAA) then observed and photographed using a scanning electron microscope (S-3000N, Hitachi High-technologies Corp.) at Kunming Medical College.

STATISTICAL ANALYSIS

Temperature data for control and treated inflorescences were not normally distributed so these data were analyzed using a Wilcoxon signed rank test. Correlations between air and inflorescence temperatures with incoming radiation were tested

using a Spearman Rank non-parametric correlation test. Differences in diameter, height, and seed production between control and treated flowers were tested using a Paired-Samples *T*-test. All analyses were done using SPSS (version 13.0, SPSS, Chicago).

Results

MICROCLIMATE DURING THE FIELD STUDY

During the study period, the prevailing weather conditions fluctuated among brief clear periods, heavy fog, rain, and hail occurring at any time in a single day. Mean summer air temperature was 4.2 °C. Mean air temperatures 15 cm above ground level during the study periods in 2006 and 2007 were 9.6 °C and 9.5 °C (min./max. 2.3/21.7 °C, 4.7/20.9 °C), respectively, and relative humidity was high, with a mean of 81.9% and 74.7% (min./max. 34.1/100%, 44.0/97.9%), respectively. Ambient air temperature in 2007 was closely correlated with incoming radiation ($r^2 = 0.77$, $P < 0.01$). Wind speed averaged 0.57 m s⁻¹ (min./max. 0/3.1 m s⁻¹).

PLANT TEMPERATURES IN THE FIELD

In 2007, average daytime (0800–2000 h) inflorescence temperature of control plants was significantly higher than those with bracts removed (17.1 vs. 14.6 °C, $Z = -12.551$, $P < 0.01$) (Table 1). In 2006 the average daytime temperature in the space between bracts was 4.6 °C above ambient air temperature, and was as much as 16 °C higher on a clear morning.

There was a significant correlation between inflorescence temperature and solar radiation in both control ($r^2 = 0.86$, $P < 0.01$) and treatment inflorescences ($r^2 = 0.85$, $P < 0.01$). The temperature difference between control plants and those with bracts removed was more than 7 °C for short periods with high radiation. Control plants also warmed up faster with solar radiation (Fig. 2). Temperatures in plants with bracts removed were still higher than air temperature but below the temperatures of control inflorescences during most of the day. However, rain and hail events that occurred at 1400 h and at 1800 h on 8 and 9 August, respectively, obscured these thermal differences (Fig. 2). The temperature of control and treatment inflorescences reached ambient air temperature soon after sunset. There were no significant temperature differences between control and treatment plants during nighttime.

SPECTRAL PROPERTIES OF BRACTS AND LEAVES

The differences between the average reflectance spectra of the bracts and leaves were most apparent in the infrared (IR) part of

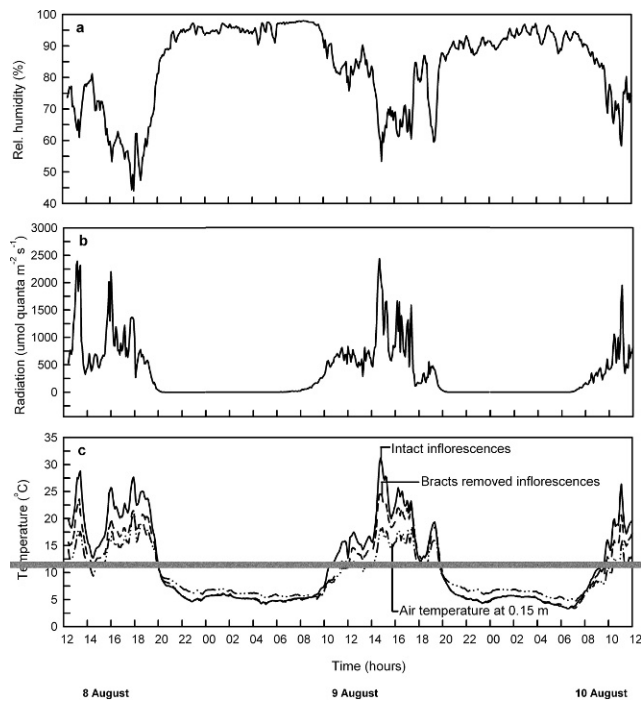


FIGURE 2. Course of environmental variables and temperature of control inflorescences and inflorescences with bracts removed under representative summer weather conditions for this region. Flower temperatures plotted represent mean values for 3 flowers of each plant category ($n = 3$). (a) Relative humidity (%). (b) Solar radiation ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$). (c) Temperature ($^{\circ}\text{C}$) in control and bracts-removed inflorescences and air temperature in the immediate vicinity of inflorescences 15 cm above the ground.

the spectrum (Fig. 3). In the IR range, about 20% of the radiation was constantly reflected by either the yellow or red areas of bracts, but reflectance by the leaves was about 60% (Fig. 3). In the photosynthetically active (PA) range, the reflectance of the yellow area of bract was about 20%, while the red area reflected less than 15% (Fig. 3).

LEAF ANATOMY

Rosette leaves were thicker (190–240 μm) than bracts (40–170 μm). The mesophyll of rosette leaves differentiated to form palisade parenchyma and spongy parenchyma with many chloroplasts as in normal leaves. However, the mesophyll of bracts contained only one layer of cells. These cells have few chloroplasts

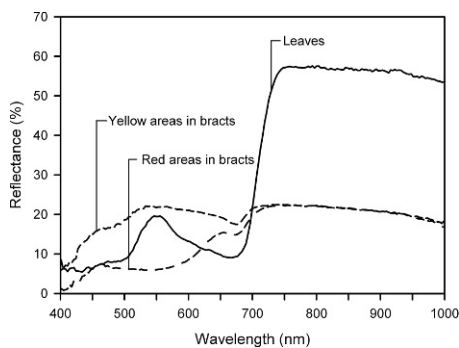


FIGURE 3. Reflectance from the upper surface of leaves and the anatomically lower (sun-exposed) surface of bracts of *Saussurea velutina* (mean for 20 bracts and leaves each).

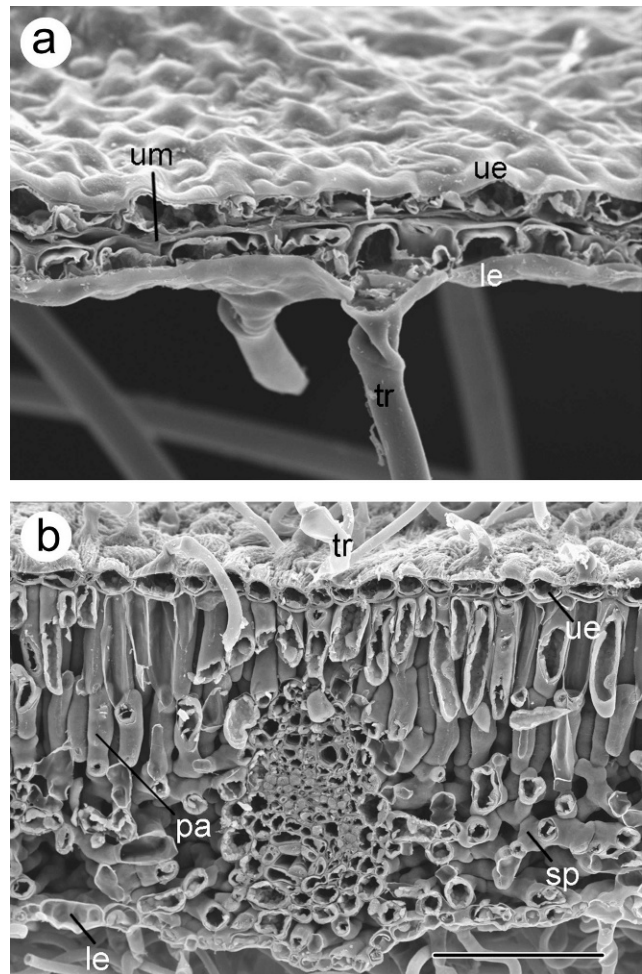


FIGURE 4. Scanning electron micrographs of bract and rosette leaf portions of *Saussurea velutina*. Scale bar = 200 μm . (a) Semi-translucent bract. (b) Rosette leaf. Abbreviations: um, uppermost of mesophyll; ue, upper epidermis; tr, trichome; le, lower epidermis; pa, palisade parenchyma; sp, spongy parenchyma.

(Fig. 4). The lower and upper epidermis of leaves and bracts each consisted of a single layer of cells.

INFLORESCENCE GROWTH AND SEED WEIGHT

The diameter and height of the manually opened inflorescences were decreased by about 30% from 19.52 to 13.90 (mm) ($P < 0.01$) and 20% from 15.35 to 11.95 (mm) ($P < 0.05$), respectively, and mean seed production per inflorescence also decreased significantly from 28.68 to 9.39 (%) ($P < 0.01$) (Table 2).

Discussion

Our data indicate that the bracts in *S. velutina* produce a “greenhouse” effect similar to that reported for *R. nobile*, *R. alexandrae*, and *Eriophorum vaginatum* (Gauslaa, 1984; Omori and Ohba, 1996, 1999; Tsukaya, 2002). Omori and Ohba (1999) reported that the daytime inflorescence temperature of *R. nobile* was about 14 $^{\circ}\text{C}$, and 7 $^{\circ}\text{C}$ higher than ambient air temperature during fair and rainy days. In contrast, we found that the contribution of bracts to overall inflorescence warming in *S. velutina* was much less than the bracts of *R. nobile*. In addition to the warming effect by bracts, the compact structure and dark color

TABLE 2

Effects of manually opening treatments on growth and seed production of inflorescence (mean \pm s.d.). Standard deviation for means of 15 flower heads.

Group	Number of flower heads	Diameter of inflorescence (mm)	Height of inflorescence (mm)	Ratio of the number of seed to flower per inflorescence (%)
Control group	15	19.52 \pm 2.79	15.35 \pm 2.60	28.68 \pm 15.57
Treated group	15	13.90 \pm 4.39	11.95 \pm 2.72	9.39 \pm 9.31
<i>t</i> -test		5.146	2.979	4.227
<i>P</i>		0	0.01	0.001

of the flowering head in *S. velutina* play an important role in inflorescence warming and insulation.

The warming effect by bracts in *S. velutina* was probably due to the anatomical structure and spectral characteristics of the bracts. Bracts in *S. velutina* have only one layer of mesophyll with neither palisade nor spongy form, and therefore are different from rosette leaves both in structure and function. Similar anatomical characters have been described for bracts in *R. nobile* and *R. alexandrae* (Omori et al., 2000; Tsukaya, 2002). Due to the thinner bracts and lack of chloroplast differentiation, bracts in *S. velutina* may scatter and absorb less radiation than green leaves. In addition, bracts in *S. velutina* showed a lower reflectance in the IR range than rosette leaves, a result almost identical to the reflectance in bracts and rosette leaves reported for *R. nobile* (Omori et al., 2000). Based on the similarities between the anatomy and reflective spectra of *S. velutina*, *R. nobile*, and *R. alexandrae*, it is likely that the bracts of *S. velutina* facilitate the transmission of IR radiation which is absorbed efficiently by the inflorescence and results in an elevated temperature within the inflorescence, similar to what Omori et al. (2000) and Tsukaya (2002) reported for the bracts of *R. nobile* and *R. alexandrae*. Meanwhile, the space between *S. velutina* bracts produces a greenhouse effect that result in an elevated temperature within inflorescences. The situation is similar to the warming effect within young catkins of *E. vaginatum* that is due to the greenhouse effect of transparent hairs (Gauslaa, 1984).

We suggested that bracts in *S. velutina* act both as a heat trap as well as a buffer against rapid fluctuations of temperature. However, the temperature of both the control and treatment plants decreased by the same amount as the adjacent air temperature when rain and hail caused solar radiation to drop abruptly. Additionally, there were no observed differences in the nighttime temperature between the control and treatment inflorescences in *S. velutina*, hence the hypothesized protection against radiative cooling by bracts in *S. velutina* was negligible. A similar situation was reported in *S. medusa* from the same region, where the dense bract hairs had little effect on heat retention and aerodynamic resistance within the inflorescence (Yang et al., 2008). In contrast, Omori and Ohba (1999) reported that inflorescences in *R. nobile* were maintained at 1.5 °C above surrounding air temperature during nighttime. In addition, there are well documented reports of some Afro-alpine plant species that have highly specialized morphological traits with insulative properties against radiative cooling (e.g. Hedberg, 1964; Miller, 1986). Meinzer and Goldstein (1985) suggested that only large plant organs with a high heat capacity could show considerable delay in cooling, such as that found in the bracts of *Lobelia keniensis* (Beck et al., 1980; Evans, 1996). *Azorella compacta*, a giant cushion plant in the southern Andes has a thin leaf layer directly overtopping massive woody structures that are able to store heat (Kleier, 2001). *Puya* in the Ecuadorian Andes have their reproductive organs in very dense pockets of pubescent structures

(Miller, 1986). *Rheum nobile* is regarded as the largest alpine herb in the Himalayan region (Ohba, 1988) and it often grows to a height of 150 cm with a 100 cm diameter rosette. Therefore, it seems that bracts and other plant tissues with a high heat capacity may slow convective cooling.

While these Afro-alpine habitats experience freezing temperatures, the prevailing summer monsoon climate in the Hengduan Mountains generally prevents nighttime freezing. If nighttime freezing occurs, the deeply sunken ovaries of *S. velutina* are still protected by the dense thick petals and pappus layer. Furthermore, the adult leaves of *S. medusa*, systematically close to *S. velutina*, have been reported to survive at -5 °C, lower than any temperature experienced by the plant during the growing season (Chen and Lu, 2002). In addition, the Afro-alpine environment is harsh and highly variable (Hedberg, 1964). For example, the greatest daily range of air temperature in some tropical alpine areas was -25 °C to 30 °C (Hedberg, 1964; Evans, 1996). We did not observe such night freezing conditions and extreme fluctuations in weather in our *S. velutina* habitats.

In spite of the rarity of radiative freezing and the relatively calm weather conditions in the study area, plants growing at high elevations in the Hengduan Mountains are exposed to an unfavorable environment. Although irradiance can be intense for short periods, sudden and very irregular weather situations, such as rain, hail, and fog can occur frequently at any time of the day during the wet monsoonal summer, often resulting in a marked drop in air temperature. Low temperature was suggested as the main cause for the inhibition of pollen development in *R. nobile* (Omori and Ohba, 1996). Our results provide evidence that bracts increase reproductive success in *S. velutina* by increasing seed output and thus having a direct positive effect on plant fitness. In alpine and arctic regions, the positive effects of elevated flower temperature on increasing plant growth (e.g. Kevan, 1975; Morison and Lawlor, 1999) and seed set have been reported in several plant species (e.g. Young, 1984; Corbett et al., 1991; Kudo, 1995). In addition, the growing season at these high elevations in the Eastern Himalayas and Hengduan Mountains is only 10 to 12 weeks (Ohba, 1988; Wang, 2006). This means that the time available for flower development in *S. velutina* is less than 8 weeks. Our findings that inflorescences covered by bracts grow faster than manually folded back bracts support previous reports that flower and seed development in several alpine plant species were substantially faster at higher environmental temperature (e.g. Heide, 1992; Alatalo and Totland, 1997; Morison and Lawlor, 1999). Devlin and Witham (1983) suggested that higher flower temperature accelerates the rate of metabolism in the ovary, and thereby increases the rate of carbon transfer to the ovary from the leaves and storage structures. On the other hand, bracts in *S. involucrate*, systematically close to *S. velutina*, were shown to contain many flavonoid pigments (Kusano et al., 2007). UV radiation inflicts biological damage during the cell division and cell differentiation and is deleterious in particular to nucleic acids

(Caldwell et al., 1995). The greater seed set in control plants than in manually opened treatment plants was likely related to the possible protection of reproductive organs against UV radiation by bracts in *S. velutina*.

In contrast, several studies have demonstrated losses in pollen viability resulting from prolonged immersion in water (e.g. Jones, 1967; Eisikowitch and Woodell, 1975; Corbet, 1990; Huang et al., 2002). While some species that grow at high elevations rely on nodding flowers, close their flowers by petal movements, or have other features that protect pollen from wetting (e.g. Sklenář, 1999; He et al., 2006), it has recently been reported that bracts in the dove tree, *Davidia involucrata*, (Nyssaceae) protect pollen grains from rain (Sun et al., 2008). Considering the high humidity in the habitats of *S. velutina* during the monsoonal summer, bracts covering inflorescences in *S. velutina* probably evolved to prevent flowers getting wet and inhibit pathogen infection during the wet monsoonal period. Thus, by contributing to adequate temperature for the success of floral development and possibly reducing rain, hail, and ultraviolet radiation damage to the flowers, the semi-translucent bracts in *S. velutina* are selectively advantageous. Further studies addressing the influence of bracts on the wettability of inflorescences and viability of pollen grains are needed to understand more fully the hydrophobic role of bracts in *S. velutina*.

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