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The ecological role of orientation in tropical convolvulaceous flowers

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Abstract Flowers of *Ipomoea pes-caprae* and *Merremia borneensis* show a preferred orientation, pointing in the general direction of the sun but not exactly tracking the sun. They demonstrated no diurnal heliotropism but strong seasonal heliotropism. The possible effects of this non-random orientation on the heat balance of the flower and the possible consequences on pollination were studied by measuring gynoecium temperature and insect visitation. Differently treated flowers were used to measure gynoecia temperature along with the microclimate: intact flowers, flowers with corollas removed, flowers with the stile and stamens removed, shaded flowers, and flowers constrained to be facing away from the sun. The lowest gynoecium temperature was achieved when the flowers were not constrained and not greased. It is concluded that the natural position of the flower, as well as transpiration, ensures that the temperature of the gynoecium does not reach dangerous levels. Insects preferentially visited sunlit flowers that were free to adopt their natural orientation.

Keywords Heliotropism · Pollination · Convolvulaceae · Morning glory · Tropical flowers

Introduction

Heliotropism of flowers, the movement of flowers to face the sun, has been observed in alpine, arctic and subarctic regions (Hocking and Sharplin 1965; Kevan 1972, 1975; Smith 1975; Kjellberg et al. 1982; Stanton and Galen 1989; Kudo 1995; Krannitz 1996; Totland 1996). These regions are characterised by low temperatures and a short growing season for plant growth and reproduction.

Some explanations have been proposed for the occurrence of heliotropism in flowers:

1. The pollinator attraction hypothesis (Hocking and Sharplin 1965; Hocking 1968; Smith 1975; Kudo 1995) holds that the warmth associated with full insolation of the flower is a direct reward for pollinators.
2. The growth promotion hypothesis (Kevan 1972, 1975; Kjellberg et al. 1982; Kudo 1995) assumes that effective absorption of solar energy and the consequent rise in temperature has a favourable effect on pollen germination, growth of the pollen tube and seed production.
3. The cooling hypothesis, appropriate to flowers in hot climates, assumes that the position of flowers is adjusted to avoid overheating (Lang and Begg 1979).

In Brunei, a tropical country, flowers of *Ipomoea pes-caprae* (the Beach Morning Glory) and *Merremia borneensis* (Convolvulaceae) appeared to face the sun (personal observations). *I. pes-caprae* is usually found along the coast on beaches and sandy isolated patches within 500 m from the sea shore. *M. borneensis* in some places is found as a sympatric species with *I. pes-caprae*, as well as along roads, disturbed and grassy areas or in the canopy of secondary vegetation.

In this paper we investigate whether flowers of *I. pes-caprae* and *M. borneensis* are indeed heliotropic, and if so, what might be the ecological relevance of the phenomenon. This involved measurement of the orientation of flowers and also some experimental manipulations to

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examine the effects of corollas and flower angle (orientation and inclination) on temperatures of the gynoecium.

Materials and methods

Plant material

This study was carried out on flowers of *I. pes-caprae* (L.) Sweet ssp. *brasilensis* (L.) Oostr., and *Merremia borneensis* Merr., two species belonging to the family Convolvulaceae. Members of the Convolvulaceae are mostly twining herbs or shrubs, comprising about 85 genera and 2,800 species. Their flowers are radially symmetrical and trumpet-shaped (Fig. 1). They are short lived, lasting less than one day. In these species and many others the corollas open only in the morning (hence the common name, Morning Glory), wilt around noon and fall early in the afternoon. Then the sepals close, assuming the shape of the developing bud (Van Steenis 1953).

Study site

Flowers of *M. borneensis* were studied at the main entrance to the campus of the University of Brunei Darussalam (4°58.6′N 114°53.8′E, elevation 2 m). Two sites were in the Tutong district, Brunei, in January 1999 and one site was along the road between Lundu and Sematan, Sarawak, Malaysia, in September 1998.

Flowers of *I. pes-caprae* were studied at a sandy area located on the campus of the Universiti of Brunei Darussalam, (114° 53.8′ E 4° 58,6′ N, elevation 2 m) and on different beaches along the west coast of Borneo including Pantai Meragang, Pantai Berakas, Pantai Sungai Liang in Brunei Darussalam, and Pantai Siar, Lundu, Sarawak, Malaysia (1°40′N 109°52′E) in November and December 1997, August, September, December 1998 and in January 1999.

Field measurements

Temperature and microclimate

Temperatures were measured on: intact flowers, flowers with corollas removed, flowers with the style and stamens removed, shaded flowers, flowers constrained facing the sun and facing away from the sun, and greased flowers to restrain evapotranspiration.

Because it was not possible to measure the temperature of all types of flowers in one experimental run, there were two different types of experiments:

- Experiment type I: flowers with corolla removed versus intact corolla (only flowers of *M. borneensis*).
- Experiment type II: flowers maintained in their natural position, facing the sun versus flowers constrained 180° to the normal orientation, facing away from the sun (flowers of *I. pes-caprae* and *M. borneensis*).

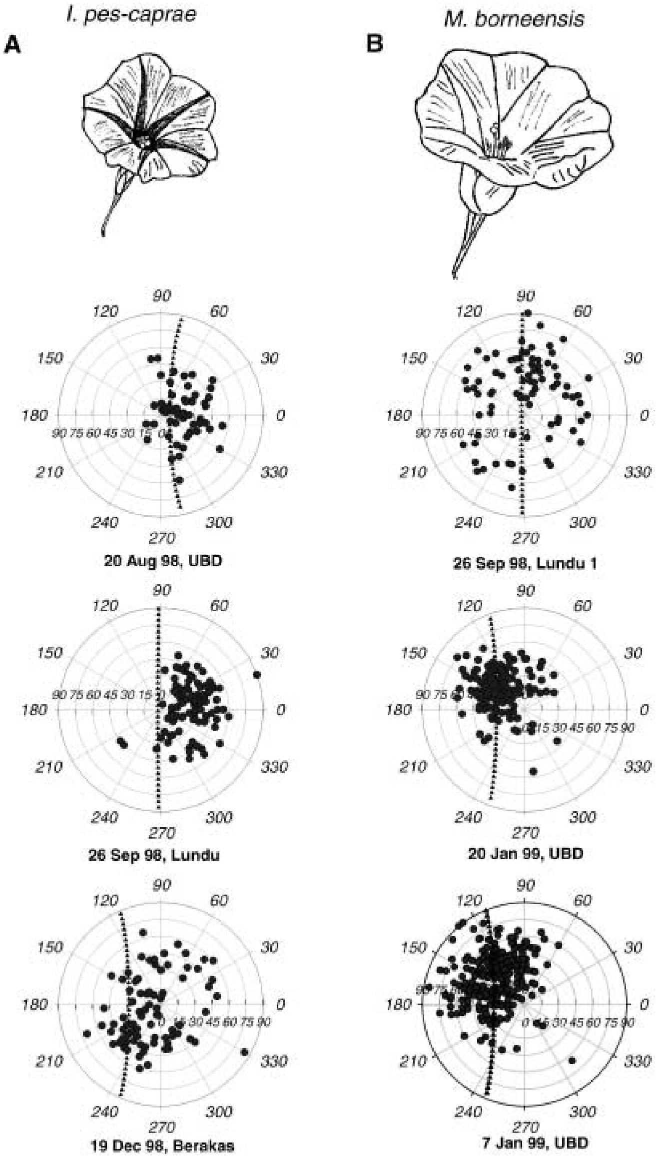

Fig. 1 Distribution of the orientation of flowers of **A** *Ipomoea pes-caprae* and **B** *Merremia borneensis* for different locations and times of the year. Each *filled circle* represents the orientation of a single flower described by its inclination angle and azimuth angle. All measurements were done between 0900 and 1400 hours. The corollas were shed in the afternoon. The *triangles* represent the sun-path on that particular day and at that particular location: University Brunei Darussalam (UBD) campus; Lundu, Sarawak, Malaysia and Pantai Berakas, Brunei

Between 10 and 19 flowers were used per experiment. Half of them were mechanically constrained by attaching the peduncle to an arch made of wire and inserted in the ground at about 10 cm from the flower. Half of the constrained and half of the naturally oriented flowers were greased with silicone gel to prevent transpiration.

Temperatures were measured using copper-constantan thermocouples (0.5 mm diameter) inserted in the centre of the gynoecium (T_{gy}), in the corolla (T_{co}), or in the interior (T_{in}) (in accordance with the type of experiment) of each flower.

Inclination of the flowers, i.e. the angle from the horizontal, was measured with a clinometer (SF-02920, Suunto, Espoo, Finland). Orientation was measured with a compass (MC-1, Suunto, Finland). To assess the measurement error of the inclination and orientation a test was performed. A total of 100 readings were taken from the same flower. The variance was calculated and the standard deviation was estimated as ±3.0° for the orientation and ±1.4° for the inclination.

Flower azimuth and inclination angle were tested using Rayleigh's test (Forseth and Ehleringer 1982). The null hypothesis for azimuth was that the flowers came from a population uniformly distributed around a circle, i.e. no direction was preferred. If the null hypothesis was rejected, the conclusion was that there was a mean population direction, i.e. a particular direction was preferred. The null hypothesis for the inclination angle (the angle from the horizontal) was that the population had a mean angle of 0°, i.e. the flowers were vertical, corollas facing the zenith.

Table 1 Mean of the azimuth and inclination angles on different dates and at different locations for flowers of *Ipomoea pes-caprae* and *Merremia borneensis*. The null hypothesis for azimuth was that the flowers came from a population uniformly distributed around a circle. The null hypothesis for the inclination angle was that the populations had a mean inclination of 0°. *n* Sample size, *Az* calculated mean azimuth ±95% confidence interval for the population mean direction, *P* probability, *Ho* null hypothesis (*r* rejected, *a* accepted), *a'* calculated mean inclination angle ±95% confidence interval for the population mean inclination angle. The azimuth was measured from 0–360°, with 0°=north, 90°=east, 180°=south, and 270°=west. The inclination was measured from the horizontal (0–90°), with 0°= a vertical flower with the corolla facing the zenith and 90° a horizontal flower with the corolla facing north, east, south or west. UBD Universiti of Brunei Darussalam

Species	Dates	Location	*n*	*Az* (degrees)	*P*	*Ho*	*a'* (degrees)
Ipomoea pes-caprae	*20 Aug 1998	UBD	60	9±15	<0.001	*r*	29±4.0
	23 Aug 1998	Highway	66	356±71	<0.117	*a*	28±1.4
	23 Aug 1998	Meragang	108	36±12	<0.001	*r*	39±2.7
	*11 Nov 1997	UBD	16	190±39	<0.001	*r*	42±2.6
	*3 Dec 1997	UBD	16	161±33	<0.001	*r*	34±1.0
	*6 Sep 1998	Meragang	95	348±22	<0.009	*r*	26±5.1
	26 Sep 1998	Lundu	99	4±10	<0.002	*r*	36±10.2
	12 Dec 1998	Berakas	23	89±36	<0.005	*r*	37±4.1
	17 Dec 1998	Meragang	38	223±39	<0.008	*r*	40±4.8
	18 Dec 1998	Sungai Liang	33	255±	<0.154	*a*	40±4.2
	19 Dec 1998	Berakas 1	37	188±47	<0.029	*r*	34±2.8
	19 Dec 1998	Berakas 2	46	232±34	<0.002	*r*	39±4.5
	25 Jan 1999	Berakas 2	61	239±39	<0.001	*r*	24±3.4
	25 Jan 1999	Berakas 3	32	213±23	<0.001	*r*	28±3.5
Merremia borneensis	26 Sep 1998	Lundu 1	83	84±22	<0.001	*r*	46±3.3
	26 Sep 1998	Lundu 2	51	177±49	<0.0352	*a*	41±3.6
	7 Jan 1999	UBD	278	141±5	<0.001	*r*	42±1.7
	20 Jan1999	UBD	167	116±9	<0.001	*r*	35±1.5
	20 Jan 1999	Tutong 1	23	164±17	<0.001	*r*	41±5.5
	20 Jan 1999	Tutong 2	25	199±28	<0.001	*r*	20±–

* Indicates that the date in the table corresponds to the grouping of several days: 18, 21, 22 August=20 Aug; 5, 7 September=6 Sept; 9, 10, 11, 12 November=11 Nov; 4–10 January=7 Jan; and 19, 20, 22, 23, 24 Jan=20 Jan

To establish if the flowers track the sun, the angle between the solar beam and the central axis of the flower was calculated from the angles mentioned above. This is hereafter called the angle of incidence. Differences in orientation and inclination between hours were tested with Watson's U^2 test (Forseth and Ehleringer 1982), a two-sample non-parametric test. The null hypothesis for flower azimuth was that the two samples came from two populations that had the same direction. If the null hypothesis was rejected, the conclusion was that the flowers had different orientation at different times of the day. The null hypothesis for the flower inclination angle was that the two samples had the same angle from the horizontal.

Insect visitation

Insects (Hymenoptera) visiting the flowers were counted for 10- to 60-min periods over several days. Only when the insect remained in the flower for more than 3 s was it counted.

For *M. borneensis*, all the observations were done at the University of Brunei campus from plants climbing on bushes. For each day of observations two groups of flowers were selected. One group was from plants growing behind the bushes (not facing the sun) and the second group was from plants growing in the front part of the bush (facing the sun). The plants behind the bushes had no flowers, so excised flowers were placed where they might have occurred (over the course of measurements they did not wilt). Within these two groups there were different treated flowers: intact flowers, flowers with corollas removed, and flowers with the style and stamens removed. To determine if the number of visiting insects per flower was the same for both conditions, the differences in mean number of insects per flower were examined with a one-way analysis of variance (Minitab 12.3).

For flowers of *I. pes-caprae*, observations of insect visitation were done at Meragang Beach. In this case several flowers were tethered east and the same number were tethered west.

Results

Determination of flower heliotropism

The position (azimuth and inclination) of flowers of *I. pes-caprae* and *M. borneensis* is represented with polar plots for different dates and locations (only a few of them are shown in Fig. 1). In the majority of cases the flowers were pointing in a 'preferred' direction (Table 1). However, in two of the samples (Highway on 23 August and Sungai Liang on 18 December) for *I. pes-caprae* the flowers were not oriented in a particular direction at all. The mean inclination angle for *I. pes-caprae* varied between 21° and 45°, and for *M. borneensis* between 20° and 46° (Table 1).

Solar tracking

To explore the possibility that the flowers were solar trackers, the position (azimuth and inclination angle) of *I. pes-caprae* flowers was measured three times per day for 4 days. The flowers were definitely oriented to a preferred angle (Table 2). However, flowers of *I. pes-caprae* did not track the sun during the day (data were tested with Watson's U-test but found to be not significant). The orientation of these flowers appears to be determined by the position of the sun during the year. In the period before the equinox, when the sun was in the northern part of

Table 2 Mean flower azimuth and inclination for *I. pes-caprae* on four different dates and at three different hours of the day (except for 20 August, with only two sampled hours) at Meragang Beach, Brunei. The null hypothesis for azimuth was that the flowers came from a population uniformly distributed around a circle. The null hypothesis for the inclination angle was that the populations had a mean inclination of 0°. *n* Sample size, *Az* calculated mean azimuth ±95% confidence interval for the population mean direction, *Ho* null hypothesis whether rejected (*r*) or accepted (*a*), *a'* calculated mean inclination angle ±95% confidence interval for the mean angle. The azimuth was measured from 0–360°, with 0°=north, 90°=east, 180°=south, and 270°=west. The inclination was measured from the horizontal (0–90°), with 0°=a vertical flower with the corolla facing the zenith and 90° an horizontal flower with the corolla facing north, east, south or west

Dates	Time of day (h)	*n*	*Az* (degrees)	*P*	*Ho*	*a'* (degrees)
18 Aug	0700	19	3±36	<0.004	*r*	20±6.0
	1000	22	348±29	<0.001	*r*	25±5.8
	1300	21	8±27	<0.001	*r*	22±5.9
20 Aug	0700	13	348±31	<0.001	*r*	25±6.1
	1200	15	3±27	<0.001	*r*	27±8.7
21 Aug	0700	20	21±33	<0.002	*r*	29±4.7
	1000	16	35±22	<0.001	*r*	28±7.8
	1300	21	32±49	<0.001	*r*	36±8.9
22 Aug	0700	22	3±20	<0.001	*r*	31±6.2
	1000	22	6±23	<0.001	*r*	34±7.0
	1300	22	359±26	<0.001	*r*	37±7.8

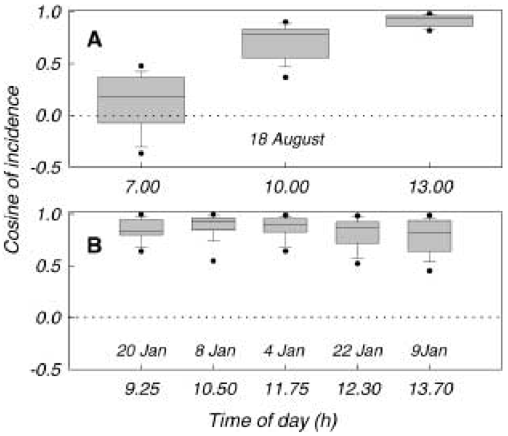

Fig. 2 Cosine of angle of incidence between the solar beam and the central axis of flower for flowers of **A** *I. pes-caprae* at different hours of the day on 18 August 1998 on Pantai Meragang, Brunei, and **B** *M. borneensis* at different hours of the day on different dates on the campus of UBD. The cosine would be 1.0 for perfect solar tracking. The number of flowers per location and date varies from 25 to 278 flowers. Note that the *x*-axis is not the same in each case (the time of day at which the measurements were done). *Vertical boxes* with error bars (*vertical lines*) representing statistical values. The boundary of the box closest to zero indicates the 25th percentile, the *line* within the box marks the median, and the *boundary* of the box farthest from zero indicates the 75th percentile. *Whiskers* above and below the box indicate the 95th and 5th percentiles

the sky, the flowers tended to point north, but after the equinox, when the sun was in the southern part of the sky, the flower tended to point south (Fig. 1).

A useful test for solar tracking is to examine the behaviour of the cosine of the angle of incidence of solar radiation impinging on the flower. If the flowers were tracking the sun, the cosine of incidence would be close to 1.0 during the whole day. For flowers of *I. pes-caprae*, the value fluctuated from 0.67 in the morning (at low solar altitudes) to almost 0.92 at solar noon, implying a deviation of 48° to 22° (Fig. 2A). The cosine of incidence for the flowers of *M. borneensis* was close to 1.0 with almost no difference between sampling times (Fig. 2B).

The temperature of the gynoecium was related to the orientation of the flower. Five experimental runs of the experiment type I were performed for *M. borneensis* and all showed the same trend. Only one day (23 January 1999) is shown for *M. borneensis* in Fig. 3. Naturally oriented flowers were cooler (41.0°C) than constrained flowers (44.2°C) during the sunniest period (Fig. 3A). This suggests that the corolla is like a parasol when the flower faces the sun, and without it the solar beam hits the underside of the flower, increasing the temperature of the gynoecium. When the incident radiation was diffused (cloudy periods) the effect of temperature diminished (Figs. 3A, C). When flowers were prevented from transpiration (evaporative cooling) but kept in their natural position, there was an increase in the temperature of the gynoecium from 41.0°C to 47.1°C relative to the naturally oriented flower in the sunniest period, yet the effect of preventing transpiration alone was less than the effect of changing the orientation (180° from the natural position). The calculated cosine of incidence for the flowers in this experiment indicates that the naturally oriented flowers are almost facing the sun, i.e. cosine of incidence close to 1.0 (Fig. 3B). The trend of calculated cosine of incidence for the constrained flowers was opposite to the one for naturally oriented flowers and this seems to have an effect on the thermal balance of the flower (Fig. 3A, B). Still the gynoecium temperature follows the pattern of irradiance during the day (Fig. 3C). In conclusion, the lowest temperatures were recorded in gynoecia of flowers that were not manipulated. Evidently, both transpiration and orientation play a role in cooling the flower. The patterns of gynoecium temperature and microclimate for *I. pes-caprae* were similar (data not shown for simplicity of presentation).

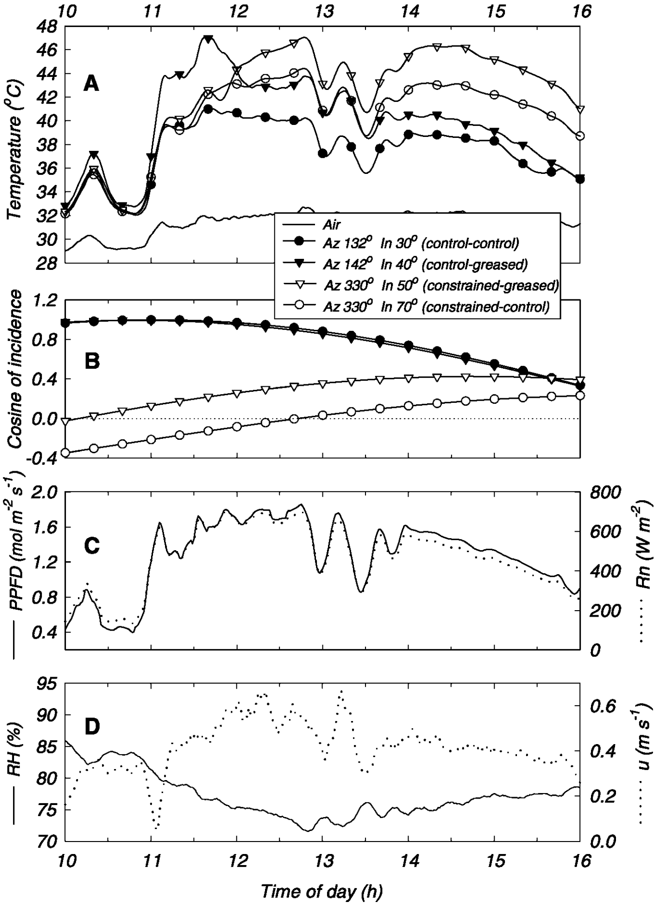

Fig. 3A–D Gynoecium temperature, cosine of incidence and microclimate for flowers of *M. borneensis* under different treatments on 23 January 1999. The treatments were a combination of constrained, transpiring and non-transpiring corolla and sepals. **A** The temperature course of different treated flowers. **B** The cosine of angle of incidence for the different treated flowers. **C** Photosynthetic photon flux density (PPFD; *continuous line*) and net radiation (R_n; *dotted line*). **D** Relative humidity (RH; *solid line*) and wind velocity (*u*; *dotted line*)

Figure 4 shows the mean values of excess temperature according to the orientation during the day. Naturally transpiring flowers of *M. borneensis* normally oriented had the lowest mean values of excess temperature (6.7 K), and non-transpiring constrained flowers had the maximum mean value (12.8 K) again suggesting the cooling effect of transpiration and the shading effect of corollas on the temperature of the gynoecium (Fig. 4A).

For *I. pes-caprae* on 7 September (Fig. 4B), the minimum mean value (1.6 K) of excess temperature was obtained when flowers were normally transpiring and oriented to the west (270°) and the maximum mean value of excess temperature was obtained for non-transpiring flowers oriented east (7.3 K) when normally transpiring flowers were oriented east (90°).

For *M. borneensis* (Fig. 4C), the normally-transpiring intact flowers had an excess temperature (gynoecium) of 6.7 K, while the non-transpiring flowers with the corollas removed had an excess temperature as high as 11.4 K. These results suggest that corollas are not only important for the pollination process but also contribute to maintaining the gynoecium temperature at tolerable low levels.

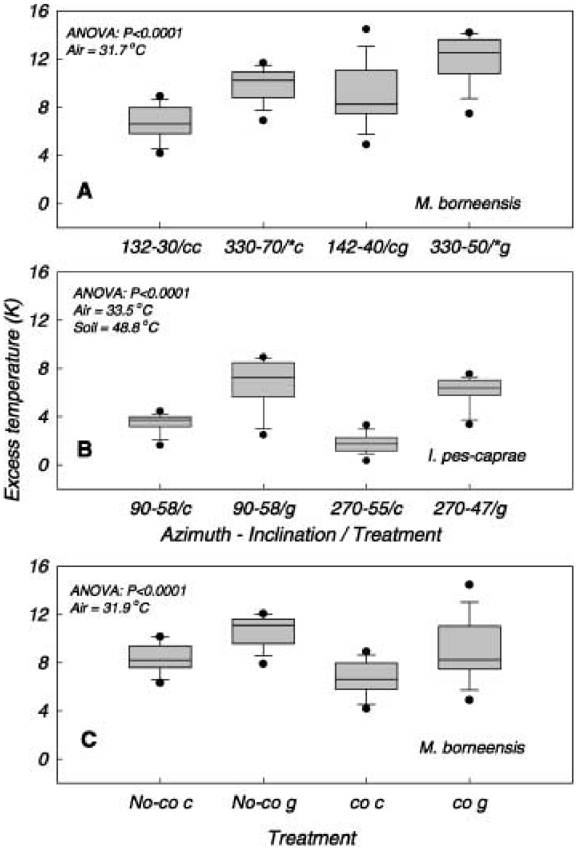

Fig. 4A–C The excess temperature of the gynoecium for treated flowers. Plots include only data when PPFD≥900 µmol m^{-2} s^{-1}. **A** The excess temperature for *M. borneensis* treated flowers according to the position (azimuth orientation) on 23 January. Naturally oriented transpiring flowers (*cc*), constrained transpiring (**c*), naturally oriented non-transpiring (*cg*), and constrained non-transpiring (**g*). Mean excess temperature of each flower was used for comparison (one-way analysis of variance) and they were significantly different. **B** The excess temperature for treated flowers of *I. pes-caprae* according to the position (azimuth orientation) on 7 September 1998. Flowers oriented east normally transpiring (90°–58°/*c*), oriented east non-transpiring (90°–58°/*g*), oriented west transpiring (270°–55°/*c*), and oriented west non-transpiring (270°–47°/*g*). Mean excess temperature of each flower was used for comparison (one-way analysis of variance) and they were significantly different. **C** The excess temperature for treated flowers of *M. borneensis* on 23 January 1998. Flowers with the corolla removed normally transpiring (No-co *c*), flowers with the corolla removed non-transpiring (No-co *g*), intact flowers transpiring (co *c*), and intact flowers non-transpiring (co *g*). Mean excess temperature of each flower was used for comparison (one-way analysis of variance) and they were significantly different. *Vertical boxes* with error bars (*vertical lines*) representing statistical values. The *boundary* of the box closest to zero indicates the 25th percentile, the *line* within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. *Whiskers* above and below the box indicate the 95th and 5th percentiles

Table 3 Mean number of flower visitors per flower in two direction classes (*E* east, *W* west) for *I. pes-caprae* at Meragang Beach, Brunei for 3 days in September 1998. Observations were done on sunny days. Insects preferred to visit west-facing flowers (*P*<0.04, one-way analysis of variance)

Date	Mean angle	Mean azimuth	Orientation	Number of insects	Number of flowers	Time observed (min)	Insects per flower
7 Sept	44	64	E	35	25	60	1.4
7 Sept	45	301	W	29	8	60	3.625
2 Sept	45	120	E	0	5	60	0
2 Sept	45	320	W	74	5	60	14.8
13 Sept	45	270	W	130	8	45	16.25
13 Sept	45	140	E	0	5	45	0
13 Sept	45	90	E	38	8	45	4.75

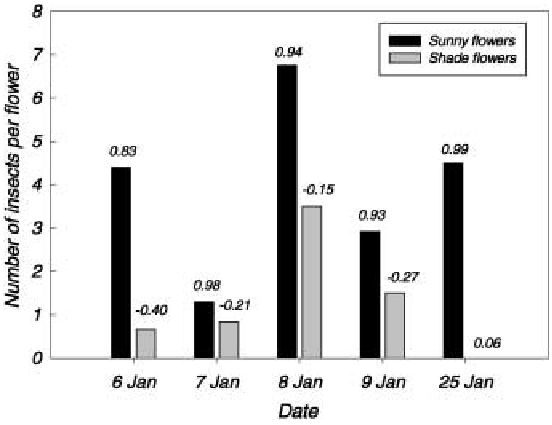

Fig. 5 Mean number of insect visitors per flower in sun and shade on different dates. The mean cosine of incidence is the number on top of each column (1.0 denotes a flower pointing directly at the sun). The differences between the insect count were significant (*P*<0.04, one-way analysis of variance)

Insect visitation

There were several types of insect visitors: pollen feeders (very small bees) and potential pollinators (small to big bumble bees, and wasps). Only two classes are considered here, pollen feeders and potential pollinators.

The relationship between flower direction and frequency of flower visitors is shown for *M. borneensis* in Fig. 5. The average number of visiting insects per flower was high for flowers facing the sun. When flowers were in the sun, potential pollinators preferred the flowers to be intact (*P*<0.01). Some days, the abundance of pollen feeders was higher than the abundance of potential pollinators and they preferred flowers with the corollas removed (*P*<0.01). For example, on 24 January 76% of the insects visiting flowers with the corolla removed were pollen feeders whereas 96% of the insects visiting intact flowers were potential pollinators and 99% of the insects visiting flowers with the stamens and pistils removed were potential pollinators. This result strongly suggests that potential pollinators of *M. borneensis* are attracted by the perceived brightness of corollas in the sun. Furthermore, some potential pollinators (for example, *Ameglia anomala*) visited the removed corollas that had been discarded on the ground. Few insects visited flowers in the shade (plants growing behind the bushes) either intact, or with the corolla or the stamens and pistils removed (*P*<0.01, one-way analysis of variance).

A summary of the relationship between flower orientation and frequency of insect visitors is presented for *I. pes-caprae* in Table 3. The average number of insect visitors per flower was higher for flowers facing west than for flowers facing east and the differences were significant (*P*<0.04, one-way analysis of variance).

Discussion

This paper presents evidence for the non-random orientation of two tropical convolvulaceous flowers, *M. borneensis* and *I. pes-caprae*, and demonstrates that this adaptation enables them to lower the risk of overheating of the gynoecium whilst ensuring pollination by insects. There were two instances in which orientation was random, but both were in areas of disturbances: a parking lot and a beach with shifting sands.

Although most of the flowers faced the sun during the hours of maximum solar radiation (morning to early afternoon) they did not show diurnal movements to follow the sun, and therefore are not classical solar trackers or heliotropic flowers. A leaf or a flower is traditionally considered to be a solar tracker or heliotropic when it moves in response to the *diurnal* movement of the sun across the sky (Ehleringer and Forseth 1980) or “the diel bending or turning response of plants directly to and with the sun”

However, there is strong evidence for a ‘seasonal heliotropism’ as flowers point towards the north or south parts of the sky, depending on the time of year. This appears to be the first record of seasonal heliotropism in the absence of diurnal heliotropism. Possibly different mechanisms are involved in this kind of heliotropism.

In contrast to flowers of the arctic and alpine species, the warming of the flower is unlikely to be a reward for the insect pollinators because the temperature of the air in these tropical lowlands is high enough to promote activity of pollinators. Then the question arises why a tropical flower faces the sun. There has been some discussion in the literature. For example, flowers of *Drosera tracyi*, from the wet savannas in Florida, have inflorescences that face the morning sun. It was suggested that this pattern of heliotropism is an evolutionary anachro-

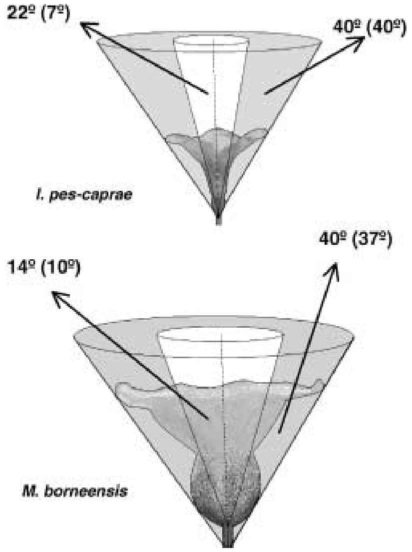

Fig. 6 The parasol effect and critical angles. There is a critical range of angle within which the solar beam will not enter the corolla tube (and thus warm the gynoecium from the inside) and will not strike the lower region of the flower and thus warm the gynoecium from the outside). This range is 22–40° for *I. pes-caprae* and 14–40° for *M. borneensis*. In *parentheses* are shown the angles calculated from photographs, corresponding to the critical angles, and depending on the exact shape of the corolla tube

nism because it apparently has no function (Wilson 1994).

The surface of the convolvulaceous corolla is highly reflective. Flowers with corollas facing the sun were more attractive to the potential pollinators than the corollas in the shade facing away from the sun. Pollinators discriminated among flowers on the basis of the position relative to the sun, and probably not because of the warm temperature on the flower chamber. However, facing the sun directly could be detrimental if the flower did not have cooling mechanisms. A notable difference between the tropical convolvulaceous flowers and all the known heliotropic flowers is that heliotropism is a mechanism to increase the temperature of the flower chamber, thus promoting pollination, fertilisation, growth, and seed set.

Kevan (1989) suggested that corollas of some flowers provide a parasol for the gynoecium, but when the orientation of the flower is changed, for instance rotated 180°, the effect of the corolla as a parasol disappears.

Based on the shape of the flowers it was possible to calculate critical angles that are required to shade the gynoecium externally and to prevent direct irradiance into the centre of the trumpet (Fig. 6). If solar tracking was exact, the sun's rays would always enter the corolla tube and warm the gynoecium, a process which could be dangerous in a tropical climate. However, by adopting a certain angle away from the solar angle, this is prevented (Fig. 6). The trumpet shape of these flowers thus acts as a parasol shading the gynoecium at times of maximum solar radiation, and not allowing the rays to impinge on the gynoecium.

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References

Ehleringer JR, Forseth IN (1980) Solar tracking by plants. Science 210:1094–1098

Forseth IN, Ehleringer JR (1982) Ecophysiology of two solar tracking desert winter annuals. II. Leaf movements, water relations and microclimate. Oecologia 54:41–49

Hocking B (1968) Insect flower associations in the high arctic with special reference to nectar. Oikos 19:359–388

Hocking B, Sharplin D (1965) Flower basking by arctic insects. Nature 206:215

Kevan PG (1972) Heliotropism in some arctic flowers. Can Field Nat 86:41–44

Kevan PG (1975) Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science 189:723–726

Kevan PG (1989) Thermoregulation in arctic insects and flowers: adaptation and co-adaptation in behaviour, anatomy, and physiology. Proc Int Symp Thermal Physiol. Elsevier, Amsterdam, pp 747–753

Kjellberg B, Karlsson S, Kerstensson I (1982) Effects of heliotropic movements of flowers of *Dryas octopelata* L. on gynoecium temperature and seed development. Oecologia 54:10–13

Krannitz PG (1996) Reproductive ecology of *Dryas integrifolia* in the high Arctic semi- desert. Can J Bot 74:1451–1460

Kudo G (1995) Ecological significance of flower heliotropism in the spring ephemeral *Adonis ramosa* (Ranunculaceae). Oikos 72:14–20

Lang ARG, Begg JE (1979) Movements of *Helianthus annuus* leaves and heads. J Appl Ecol 16:299–305

Smith AP (1975) Insect pollination and heliotropism in *Oritrophium limnophilum* (Compositae) of the andean Páramo. Biotropica 7:284–286

Stanton ML, Galen C (1989) Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). Oecologia 78:477–485

Totland O (1996) Flower heliotropism in an alpine population of *Ranunculus acris* (Ranunculaceae): effects on flower temperature, insect visitation, and seed production. Am J Bot 83:452–458

Van Steenis CGGJ (1953) Convolvulaceae (van Ooststroom). Flora Malesiana 4:386–512

Wilson P (1994) The east-facing flowers of *Drosera tracyi*. Am Midl Nat 131:366–369