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Does temperature stress induce nectar secretion in Mediterranean plants?

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SUMMARY

We studied the effect of temperature on nectar secretion in *Thymus capitatus*, a typical labiate of phrygana (i.e. the garrigue of the East Mediterranean Basin). Experiments were carried out at controlled temperatures in a climatic chamber. We measured the nectar standing crop of the flowers at the end of the first day of their anthesis. All nectar values (i.e. volume per flower, sugar content and concentration) increased with temperature up to 38 °C, as long as the plants were not water stressed. However, in the open and under normal temperate conditions (i.e. at relatively low temperatures) nectar secretion depended more on changes in solar irradiance than on temperature.

Under the same conditions, nectar secretion in *Ballota acetabulosa*, a species that is sympatric and coflowering with *T. capitatus*, was affected neither by light nor temperature. Since in the wild these two species are found in different microhabitats (full sun and shade, for *T. capitatus* and *B. acetabulosa*, respectively), we attribute the differences we observed to the differential natural adaptation of the plants to these factors. We conclude that *T. capitatus* is very well adapted to the Mediterranean conditions. By performing optimally as a nectar source at high temperatures, it can support a very large insect fauna that visits its flowers for nectar. It is in fact a temperature-induced cornucopian species.

Key words: Nectar secretion, temperature effect, *Thymus capitatus*, *Ballota acetabulosa*, Mediterranean plants.

INTRODUCTION

Nectar secretion rate is temperature dependent (Fahn, 1949; Shuel, 1952; Huber, 1956; Corbet, 1978, 1990; Jakobsen & Kristjánsson, 1994). In most of the cases studied, nectar secretion rate decreases at low temperatures (but see Kropácová & Haslbachová, 1970, where the nectar secretion rate of *Trifolium repens* correlates negatively with temperature). Normally, the highest nectar yield is secreted at a particular temperature, that differs from species to species. For *Oenothera biennis* (Onagraceae) this temperature is 24 °C, whereas for *Borago officinalis* (Boraginaceae) it is *c.* 23·5 °C (Huber, 1956). Jakobsen & Kristjánsson (1994) found that the temperature for optimum yield can differ even between clones of the same species, e.g. between 10 and 18 °C for *Trifolium repens* (cf. also Shuel, 1952). It is worth mentioning that most studies in the literature have focused on species of temperate systems, where temperatures rarely exceed 28 °C. Thus the effects of higher temperatures on nectar secretion are largely unknown. High temperatures during flowering are very common in arid ecosystems such as the mediterranean. (Note the distinction between mediterranean = Mediterranean climate type, and Mediterranean referring to the Circum-Mediterranean Basin; see di Castri & Mooney, 1973.)

Mediterranean climate is characterized by mild winters and very hot summers, with a high water deficit during summer (Aschmann, 1973; Maheras, 1983). In such a climate many plant species flower relatively early, before high summer (Petanidou *et al.*, 1995). As a consequence, in the mediterranean areas, pollen is the major reward for pollinators, and rates of nectar production are low (Herrera, 1985; Petanidou & Vokou, 1990, 1993; Petanidou & Smets, 1995). Since high temperatures are a feature of the mediterranean climate, we hypothesize that the nectar secretion of species highly adapted to mediterranean conditions will not be suppressed at high temperatures, as long as the plants are not water stressed. Therefore, we expect that the temperature of optimal nectar yield will be much higher than 24 °C, as found by Huber (1956). We asked two principal questions: (1) Is nectar secretion influenced by high temperature? (2) What is the relative role of temperature vs. light in influencing nectar secretion? We tested our hypotheses primarily on *Thymus capitatus* Hoffmans. et Link (Labiatae), but also studied *Ballota acetabulosa* (L.) Bentham. These two

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Table 1. *Nectar production of* Thymus capitatus *under controlled temperature conditions in climatic chambers, expressed as the mean volume and concentration per flower during the first day of anthesis (nectar standing crop at the end of a 14 h day): the number of nectar-empty flowers is also noted*

Date (July 1993)	Group of plants	Temperature (°C)	Mean volume			Mean concentration			*n* Blank flowers
			(μl)	SE	*n*	(% w/w)	SE	*n*	
8	A	28·0	0·10	0·02	19	62·2	1·72	15	
9	A	28·0	0·10	0·01	24	60·6	1·29	24	
10	A	25·0	0·11	0·03	8	53·8	3·34	7	
11	A	19·0	0·08	0·01	9	39·3	1·92	9	
12	A	19·0	0·09	0·02	12	38·2	3·59	12	
13	A	22·7	0·08	0·01	16	43·1	2·79	15	1
14	A	25·0	0·12	0·02	19	53·0	2·77	19	
15	A	28·0	0·09	0·02	25	55·8	1·92	22	1
16	A	30·5	0·19	0·02	18	56·2	1·86	18	
17	A	33·8	0·22	0·02	11	56·8	2·79	11	
18	A	36·7	0·20	0·03	12	58·2	1·91	12	
19	A	38·7	0·06	0·01	15	63·2	1·46	14	
13	B	22·7	0·11	0·03	5	51·6	1·55	5	
14	B	25·0	0·10	0·02	12	64·7	1·37	11	
15	B	28·0	0·10	0·01	12	62·0	0·89	12	
16	B	30·5	0·13	0·01	7	60·8	0·83	7	
17	B	33·8	0·13	0·00	3	65·7	1·85	3	
18	B	36·7	0·13	0·02	5	64·6	1·26	5	
19	B	38·7	0·06	0·01	8	69·6	1·67	8	
20	A+B	40·0	0·06	0·01	21	59·1	1·46	19	
21	A+B	38·0	0·06	0·01	15	64·7	1·24	11	2
22	A+B	38·0	0·14	0·02	10	56·1	3·90	10	
23	A+B	39·7	0·11	0·02	31	53·7	2·90	26	3
24	A+B	39·2	0·09	0·04	5	50·3	7·65	4	1
25	A+B	38·3	0·15	0·03	15	48·0	4·90	12	2
26	A+B	41·8	0·13	0·04	12	56·2	4·80	9	2
27	A+B	45·2	0·23	0·07	11	47·7	6·17	9	2
28	A+B	43·5	0·10	0·02	14	56·3	3·16	11	3
29	A+B	45·5	0·06	0·03	6	44·1	11·22	3	3
30	A+B	39·0	0·11	0·03	13	33·8	5·63	11	2

labiate species are both found in the Mediterranean region. If our hypothesis is correct, we expect that high temperatures of mediterranean magnitude (i.e. > 30 °C) may induce nectar secretion.

MATERIALS AND METHODS

The species studied

T. capitatus and *B. acetabulosa* are typical species of phrygana, the vegetation type that occupies the driest parts of the East Mediterranean area. Both species flower in June, i.e. late in the flowering season. The flowers of both species are pink, of gullet type. Those of *T. capitatus* are deeper and larger (see Petanidou & Vokou, 1993, for descriptions). The two species differ in habit: *T. capitatus* is a woody perennial characterized by seasonal dimorphism and small, dark green leaves, whereas *B. acetabulosa* is an herbaceous perennial with relatively large, soft, non-aromatic leaves. In the wild they occupy different habitats: *T. capitatus* grows in places which are very dry and sunny, whereas *B. acetabulosa* is always part of the understorey vegetation, often in stands of *Pinus halepensis* Miller.

For each species *c.* 25 plants were selected at random in the wild (from the Nature Reserve of I. and A. Diomedes Botanical Garden of the University of Athens, Athens, Greece). The site is described in Petanidou & Vokou (1993), Petanidou & Ellis (1993), and Petanidou *et al.* (1995). Plants were grown in the National Botanical Garden of Belgium from January 1992. During the winter they were grown under glass in a heated glasshouse, and then in the summer they were moved out of doors and watered regularly. Preliminary observations in 1992 allowed us to pinpoint the exact time of the flowering peak, which was during July. The experiments and observations reported in this paper were made in July 1993.

The experiments

Experiments were carried out both indoors and outdoors. In the indoor experiments (conducted in climatic chambers) we tested the effect of high day temperatures on nectar secretion of *T. capitatus*. The outdoor experiments enabled us to estimate the relative effects of temperature and light on the nectar secretion of the two species.

Table 2. *Temperature dependence of the nectar secretion of* Thymus capitatus

Parameters tested	*R*	*P*
All temperatures		
Volume	0·137	n.s.
Concentration	0·155	n.s.
Sugar content	0·020	n.s.
Temperatures ⩽ 40 °C		
Volume	0·087	n.s.
Concentration	0·335	n.s.
Sugar content	0·070	n.s.
Temperatures ⩽ 39 °C		
Volume	0·217	n.s.
Concentration	0·395	0·062
Sugar content	0·182	n.s.
Temperatures ⩽ 38 °C		
Volume	0·462	*
Concentration	0·710	***
Sugar content	0·619	**
Temperatures ⩽ 37 °C		
Volume	0·709	**
Concentration	0·750	***
Sugar content	0·862	***

Coefficients (R) and significance (P) of the regressions between temperature and the nectar parameters (values from Table 1). * $P < 0{\cdot}05$; ** $0{\cdot}05 < P < 0{\cdot}01$; *** $0{\cdot}01 < P < 0{\cdot}001$.

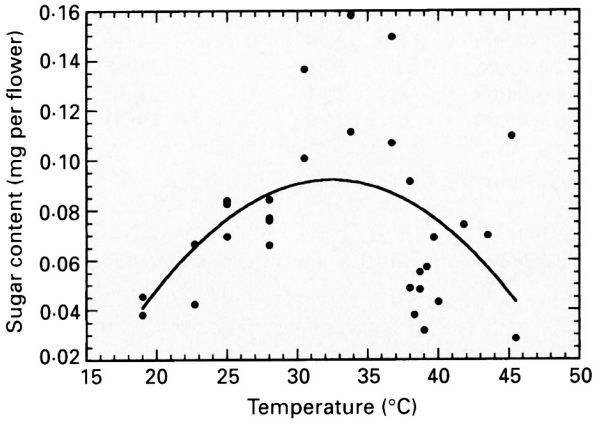

Figure 1. Sugar content at the end of the first day of anthesis of flowers of *Thymus capitatus* grown in climatic chambers at different temperatures.

Outdoor experiments

For the outdoor experiments we used eight and four potted plants of *T. capitatus* and *B. acetabulosa*, respectively. All plants were in full bloom during the experiments. Flowers were marked, and covered in the bud stage with fine gauze, to prevent insects from feeding on the nectar. Nectar was collected the following day between 1630 and 1700 hours. Thus, we measured the nectar standing crop of the flowers at the end of the first day of anthesis. The amount of nectar was measured by inserting 0·5 μl and 5 μl calibrated microcapillaries (Drummond) into each flower separately. Because a destructive method was employed, both in the indoor and outdoor experiments only the first-day yield was measured. Nectar concentration (almost entirely due to sugars) was measured immediately after collection, separately for each flower, with a pocket refractometer (Bellingham and Stanley, Tunbridge Wells). It was expressed as $^{0}_{0}$ (w/w) sucrose. We calculated total sugar content of each flower sampled (in mg of equivalent sucrose) as volume × concentration/100 × nectar density. Nectar density was determined from published tables (Dafni, 1992). In the very few cases where a concentration value could not be estimated owing to the presence of an extremely small quantity of nectar, we used the mean concentration of the whole group. Light (solar irradiance in MJ m^{-2} d^{-1}) and shade temperature (°C) were measured *c.* 200 m and 45 m from the plants, respectively (solarimeter CM5, Kipp & Zonen, Delft, The Netherlands; temperature sensor Pt 100, Jumo; convertor GTU461, METRAWATT; recorder GTA601, METRAWATT).

Indoor experiment

The experiment was carried out on 16 potted plants in a temperature-controlled climate chamber at the Botanical Institute of the Catholic University of Leuven (Stephens Electro N.V.). Observations were made on 10 plants in full bloom (group A in Table 1). Later, a second group of six later-flowering individuals (B) was also studied. To avoid drought stress during the experiment the plants were watered modestly. Thus, while temperature was controlled, humidity was allowed to fluctuate. The photoperiod was adjusted to simulate mediterranean conditions during flowering time, i.e. 14 h daylight. Night temperature was kept at 18 °C. Illumination rate was constant at *c.* 36000 lux. The nectar volume of each flower was measured with the aid of 0·2 μl Drummond Microcaps® just before the end of the 14 h day. Flowers were sampled at random from the available open flowers. Measurements of nectar were carried out using the methods outlined above.

Data analysis

Throughout the paper we refer to the nectar standing crop of the flowers at the end of their first day of anthesis. We were unable to determine a rate of secretion because the exact initiation of nectar secretion is not known; nevertheless, in what follows, we assume that the nectar standing crop is proportional to the rate of secretion.

Mean values and standard errors (SE) were calculated for all sample sets on the basis of the individual flower samples. Multiple regressions were calculated to determine the relationship between two independent variables (air temperature and solar irradiance) and a dependent variable (nectar value:

volume, concentration, and sugar content per flower). The unique contributions of each independent variable to the prediction of the dependent variable were estimated by computing the partial correlation coefficients (STATISTICA/MAC, 1986–1991). All the other statistical tests were made using the same package. The line in Figure 1 was fitted by using polynomial regression (KALEIDAGRAPH/Mac).

RESULTS

Nectar volume and concentration in *T. capitatus* increased with temperature, but not over the whole range of the temperatures we applied (Table 1). This may be partly attributed to a number of non-producers (nectar-blank flowers) that were found at high temperatures. Only temperatures up to 38 °C induced nectar secretion and clearly favoured higher concentrations (Table 2). Accordingly, sugar content of nectar increased with equally high temperatures (i.e. up to 38 °C). After applying polynomial regression we found that the optimal temperature for nectar secretion in *T. capitatus* was 32·5 °C (Fig. 1).

The daily nectar volume, concentration, and sugar content (per flower secretion during the first day of anthesis) of *T. capitatus* and *B. acetabulosa* flowering in the open under different temperate conditions of temperature and light are given in Tables 3 and 4. The per flower volume, concentration, and sugar content of nectar of *T. capitatus* were light-dependent, whilst in *B. acetabulosa* only the

Table 3. *Nectar standing crop of first-day flowers of potted plants of* Thymus capitatus (*outdoors, in the National Botanical Garden of Belgium*)

Date (1993)	Volume (Mean ± SE) (μl)	*n*	Concentration (Mean ± SE) (% w/w)	*n*	Sugar content (Mean ± SE) (mg per flower)	*n*	Temperature (°C)	Solar irradiance (MJ m^{-2} d^{-1})
June								
28	0·03 ± 0·01	7	40·0 ± 3·51	3	0·014 ± 0·004	7	14·5	11·26
29	0·14 ± 0·04	7	54·9 ± 2·85	7	0·100 ± 0·030	7	16·2	26·62
30	0·11 ± 0·01	5	57·3 ± 1·95	5	0·078 ± 0·004	5	22·2	25·10
July								
1	0·17 ± 0·02	11	55·5 ± 1·89	11	0·113 ± 0·006	11	22·4	24·04
2	0·14 ± 0·01	10	54·7 ± 1·36	10	0·092 ± 0·006	10	19·5	21·94
3	0·09 ± 0·01	8	53·9 ± 0·87	8	0·064 ± 0·008	8	20·4	21·32
4	0·11 ± 0·02	6	49·3 ± 3·04	6	0·066 ± 0·009	6	21·9	19·70

Shade temperature is the mean of the median values taken each hour for 24 h period.

Table 4. *Nectar standing crop of first-day flowers of potted plants of* Ballota acetabulosa (*outdoors, in the National Botanical Garden of Belgium*)

Date (1993)	Volume (Mean ± SE) (μl)	*n*	Concentration (Mean ± SE) (% w/w)	*n*	Sugar content (Mean ± SE) (mg per flower)	*n*	Temperature (°C)	Solar irradiance (MJ m^{-2} d^{-1})
June								
9	0·50 ± 0·18	3	44·5 ± 4·22	3	0·246 ± 0·059	3	23·6	23·95
22	0·70 ± 0·27	6	36·2 ± 2·95	6	0·267 ± 0·097	6	16·3	18·08
23	0·83 ± 0·19	8	37·3 ± 3·35	8	0·314 ± 0·063	8	15·7	14·03
24	0·48 ± 0·09	11	56·4 ± 3·36	11	0·315 ± 0·041	11	14·6	21·97
25	0·77 ± 0·16	10	44·7 ± 2·94	10	0·371 ± 0·056	10	15·3	20·38
26	0·89 ± 0·33	13	30·4 ± 1·59	9	0·275 ± 0·095	13	17·1	11·23
27	0·52 ± 0·16	9	41·5 ± 4·49	7	0·218 ± 0·055	9	17·5	24·68
28	0·86 ± 0·24	7	26·5 ± 0·52	7	0·248 ± 0·064	7	14·5	11·26
29	1·24 ± 0·29	8	51·9 ± 3·31	8	0·705 ± 0·107	8	16·2	26·62
30	0·79 ± 0·15	14	51·6 ± 1·98	14	0·462 ± 0·071	14	22·2	25·10
July								
1	0·99 ± 0·19	15	49·9 ± 1·88	15	0·550 ± 0·077	15	22·4	24·04
2	1·26 ± 0·28	12	38·5 ± 1·45	12	0·536 ± 0·114	12	19·5	21·94
3	1·11 ± 0·29	4	40·9 ± 1·77	4	0·521 ± 0·120	4	20·4	21·32
4	2·44 ± 0·31	11	28·1 ± 1·03	11	0·747 ± 0·088	11	21·9	19·70
5	1·98 ± 0·30	7	19·0 ± 1·13	7	0·420 ± 0·072	7	17·0	4·91

Shade temperature is the mean of the median values taken each hour for 24 h period.

Table 5. *Relationship of volume, concentration, and sugar content of nectar of* Thymus capitatus *and* Ballota acetabulosa *to light and temperature (cf. Tables 3, 4)*

			Partial regression coefficients			
			Temperature		Solar irradiance	
Tested attributes	*R*	*P*	*R*	*P*	*R*	*P*
Thymus capitatus						
Volume	0·859	0·069	0·230	n.s.	0·799	*
Concentration	0·971	**	0·610	n.s.	0·952	**
Nectar sugars	0·902	*	0·166	n.s.	0·865	*
Ballota acetabulosa						
Volume	0·510	n.s.	0·416	n.s.	−0·474	n.s.
Concentration	0·874	***	−0·260	n.s.	0·955	***
Nectar sugars	0·416	n.s.	0·286	n.s.	0·179	n.s.

The coefficients of multiple regressions together with those of the partial correlations (R) and their significances (P). *$P < 0{\cdot}05$, **$0{\cdot}05 < P < 0{\cdot}01$, ***$0{\cdot}01 < P < 0{\cdot}001$.

concentration was light-dependent. In all cases the influence of temperature was not significant ($P > 0{\cdot}05$; Table 5).

DISCUSSION

Effect of temperature

Our experimental results show that, as a nectar source, *T. capitatus* performs better at high temperatures. In fact, the best results were obtained between 30 and 38 °C vs. < 25 °C, with optimal yield at 32·5 °C. Increasing the temperature beyond 38 °C resulted in some flowers producing abundant quantities of nectar, and some others producing none at all (Table 1). We attribute this phenomenon to high temperatures stress rather than to the off-peak flowering, since all plants employed in the experiment were in full bloom.

These findings point to the adaptation and success of *T. capitatus* to the Mediterranean conditions. Indeed, the fact that nectar secretion rate of *T. capitatus* peaks at very high temperatures allows this species to be a major nectar source even in very hot, sunny weather, and it is visited by the large array of insects active in such conditions (Petanidou & Ellis, 1996). For instance, in the Athens reserve (see 'Materials and Methods'), 123 insect species visited *T. capitatus*, which was the highest figure observed in the whole community (Petanidou, 1991; Petanidou & Vokou, 1993).

Effect of light

When grown at lower temperatures (in Belgium), light but not temperature had a significant effect on nectar secretion rate in *T. capitatus* (Table 5). These results indicate that the temperatures expressed in the experiment might have been too low to have a significant impact on nectar secretion rate. By contrast, in *B. acetabulosa* neither light nor temperature affected nectar secretion rate. It is suggested that sunlight might have another effect, but only on *T. capitatus*. In nature, solar radiation will influence the temperature of a sunlit flower (Corbet *et al.*, 1993; Corbet, personal communication). Therefore, in the wild, the actual flower temperature is likely to be higher in *T. capitatus*, in the sun, than in *B. acetabulosa*, which grows in shade. In our outdoor experiments in Belgium, both species were exposed to the same microenvironmental conditions. If nectar secretion rate depended on flower temperature equally in both species, it should be correlated with solar irradiance in the sunlit flower (*T. capitatus*) and with temperature in the shaded flower (*B. acetabulosa*). Because these predictions were only confirmed for *T. capitatus*, we conclude that the two species differ in the ways that flower temperature influences nectar secretion rates.

Water stress

Temperature stress is likely to increase the nectar secretion rate in *T. capitatus*, but water could be a limiting factor, and the best nectar yields could occur in the years of the highest precipitation. Although we have no experimental results, there is some support for this hypothesis from observations made in the wild in Athens, for the years 1992–1994. The mean nectar standing crop of 1-d flowers of *T. capitatus* was then 0·10, 0·03 and 0·15 μl, respectively, in response to precipitation of 340, 237 and 456 mm during the rainfall period October–June in the three years (Die Grosswetterlagen Europas (1991–1994); Petanidou unpublished). Investigations by

Petanidou, Van Laere & Smets (1996) have also revealed that nectar secretion in *Capparis spinosa* L. depends on precipitation.

Concluding remarks

From our results we conclude that increase in temperature can induce a greater nectar secretion rate in *T. capitatus* than in *B. acetabulosa*. This is very important for the apiculture potential of the phrygana, since *T. capitatus* is widespread and abundant throughout the Mediterranean region. In this area, *T. capitatus*, a cornucopian species, constitutes the most important food source for wild bees and honeybees (Petanidou & Smets, 1995; Petanidou & Ellis, 1996), whereas *B. acetabulosa* is visited by a smaller array of wild bees and only very occasionally by honey bees (Petanidou, 1991; Petanidou & Vokou, 1993).

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