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Original article

The potential of marginal lands for bees and apiculture: nectar secretion in Mediterranean shrublands

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Summary — We studied the floral nectar production (volume, concentration, total sugar content) of 76 species of a phryganic community near Athens, Greece. The mean values per flower are 0.76 µl, 55.1% and 0.43 mg, respectively. The median date of flowering is not related to any of the nectar values measured. By contrast, family and life-form memberships, together with flower depth and shape, are related to nectar parameters. *Labiatae* are by far the most nectar-rewarding species of the community, contrasting mainly to *Compositae*. Therophytes produce significantly less nectar than herbaceous perennials. Species with flowers > 4 mm deep yield more nectar than those with shallow flowers. As a consequence, similar patterns are shown by the floral shapes. Nectar concentration is negatively correlated with flower depth. Our data allow us to estimate the apiculture potential of phrygana. A knowledge of this potential may lead to a better management of these areas, which may also benefit both the local flora and native pollinating fauna.

nectar production / flower characteristic / Mediterranean shrubland / bee / apiculture

INTRODUCTION

A considerable part of the Mediterranean region in the European Community is characterised by marginal lands, traditionally man-managed for goat and sheep grazing and kept for millennia. The tomillares (Spain), garrigue (France), gariga (Italy) and phrygana (Greece) are such ecosystems, restricted to the driest parts of the climatic gradient, and covering a considerable part of the territories. In Greece, for instance, phrygana occupy *ca* 13% of the total surface (Diamantopoulos, 1983). Throughout the Mediterranean region these areas suffer from continuous degradation due to overgrazing, frequent fires, change in land use (urbanisation, tourism), and general abandon. The latter is a very important feature of the Mediterranean regions nowadays, since it has had crucial consequences on the conservation of land, and thus on the ecosystem structure.The most important outcome is soil loss due to erosion following abandonment of terracing which retains the soil of hilly Mediterranean areas.

Mediterranean ecosystems are among the most poorly documented from the pollination point of view (Osborne *et al*, 1991). Nevertheless, they are characterised by a high number of flowering species (Petanidou and Vokou, 1990, 1993; Dafni and O'Toole, 1994; Petanidou *et al*, 1995), together with a striking number of bee species (Petanidou and Ellis, 1993). Moreover, there is a long-standing tradition of rural apiculture in these landscapes. This is important from the economic viewpoint, which has been noticed since classical times (Plato, Critias). A systematic exploitation of these marginal lands for apiculture might substantially contribute to the economic revival of these areas. On the other hand, a well-managed bee-keeping system may contribute to the ecological upgrading of these landscapes. This is very crucial from the nature conservation viewpoint, in particular because Mediterranean ecosystems are among the most important areas for wild bees (Osborne *et al,* 1991; Petanidou and Ellis, 1993; Petanidou, 1994). In the light of these conditions, and to attain the above-mentioned goals, we need more information concerning the nectar potential of Mediterranean areas at each different stage. Together with this, we certainly need an assessment of the impact of commercial bee-keeping on the native pollinating fauna.

Summer drought is a prominent characteristic of Mediterranean-type ecosystems (Aschmann, 1973) and is accompanied by a dominance of therophytes over perennials (Margaris, 1980). As a consequence of the drought, fire risks are dramatically increased and, despite all measures taken, fires are very frequent (Le Houérou, 1973; Arianoutsou-Faraggitaki, 1979). The early communities established after fire are particularly dominated by annuals (Arianoutsou-Faraggitaki and Margaris, 1981, and references therein). This implies that if the nectar production is different between these life forms, then the overall nectar potential of the system varies with its age and depending upon the fire frequency.

The majority of the species in the Mediterranean region flower early in the season and their bloom is spread over the first half of the year (Zohary, 1962; Auerbach and Shmida, 1987; Shmida and Dafni, 1989; Petanidou *et al,* 1995). This concentrated period of blooming would enable beekeepers to shift honeybee colonies to different crops in the second part of the year. The agricultural profits of this scheme may be considerable. A recent study on the economic contribution of honeybee pollination to the European Community agriculture showed that for 1989 the major insect-pollinated crops in the EC had a total annual market value of 65 billion ECU, to which pollination by insects contributed 5 billion ECU, and pollination by domesticated honeybees 4.25 billion ECU (Borneck and Merle, 1989; Corbet *et al,* 1991). The values for the USA and Canada are comparable (Robinson *et al,* 1989a,b; Winston and Scott, 1984; see also Richards, 1993).

A systematic study to assess the nectar potential of the Mediterranean shrublands at the ecosystem level is lacking. Herrera (1985) was the first to study the daily nectar secretion of several species at 6 localities distributed across Spain. Most other studies deal with the nectar production of Labiatae (Fahn, 1949; Dafni *et al*, 1988; Dafni, 1991). Petanidou and Vokou (1990) studied the energetics of pollen content in Mediterranean-type ecosystems, and argued that because of the limited availability of water and the unpredictability in precipitation between years in mediterranean [1] ecosystems, pollen is the main floral reward *vs* nectar (see also Herrera, 1985).

We studied the nectar potential of a phryganic community at its mature stage. The results contribute to the understanding of

[1] Note the difference between mediterranean = Mediterranean-type, and Mediterranean which refers to the Circum-Mediterranean Basin (*cf* di Castri and Money, 1973).

the energetics of the pollination system in the Mediterranean ecosystems. Moreover, they may be used to estimate benefits that could be drawn from such marginal lands, both in economic and in nature conservation contexts.

MATERIALS AND METHODS

Study site

The nectar measurements were carried out in a phryganic ecosystem, which had remained undisturbed for 15 years following a fire. It is situated at Daphni (38° 00' N, 23° 38' E), approximately 10 km west of the centre of Athens. The study area is a part of a natural reserve in the I and A Diomedes Botanical Garden of Athens University, situated on the slopes of Mt Aegaleo. Phrygana is the dominant ecosystem type of the reserve, covering 130 ha, with occasional occurrence of wild olive trees (*Olea europaea* var *sylvestris* L) and kermes oaks (*Quercus coccifera* L). A more detailed description of the site is available in Petanidou and Vokou (1990, 1993) and Petanidou and Ellis (1993). The substrate is calcareous and stony, typical for phrygana. The climate of the Athens area is mediterranean, according to Aschmann's criteria (1973). The annual long-term average for the rainfall is 370.0 mm, and for the temperature 22.3 °C (Maheras, 1983).

All measurements were carried out on a 30 ha section of the reserve, at a low altitude (135–215 m), with inclinations between 18° and 27°, exposed mostly to the N and E. Nectar production was measured mainly during 1992, continued in 1993, and in few cases in 1994.

Study species

The total number of entomophilous species that occurred in the area during the study period totalled *ca* 110 species. We measured the nectar of only 76 of them (table I), the rest being either non-nectariferous or very poor nectar producers (Petanidou, 1991).

Nectar collection

The amount of nectar was measured by inserting calibrated microcapillaries (Drummond) into the flower. Microcaps ranged from 0.1 to 10 µl, depending on the quantity of the nectar produced by the flowers of each species. Nectar concentration (expressed in % w/w sucrose) was measured with a pocket refractometer (Bellingham and Stanley, Tunbridge Wells, UK). Before opening, the flowers were marked and in the bud stage were covered with fine gauze to prevent insects from feeding on the nectar, and subsequently contaminating it. Nectar was collected the following day, always at noon to early afternoon (except for *Capparis ovata*, which was sampled at *ca* 9.30 h). As a standard procedure, at least 20 flowers were sampled at random for nectar volume and sugar concentration. In the cases where the use of a microcap was too difficult to accomplish, the nectar was collected on paper wicks for later analysis (see below). Because of the sampling method employed (*ie* destructive to flowers), the amount of nectar/sugar measured were underestimates of the per flower total production in the cases flower life exceeded the one-day span (table II). Total sugar weight was calculated on the basis of the above measured values (volume x concentration x nectar density), the latter taken from existing tables (Dafni, 1992).

In cases where it was likely to injure the floral tissue by microcap insertion (*eg*, *Muscari* spp), the presence of nectar was checked with the following method. The covered flowers were rinsed with a few millilitres of distilled water, with the aid of an automatic pipette. In 1 ml of the rinsate, a few drops of 5% phenol, then 1 ml concentrated H_2SO_4 were added. This solution becomes orange in the presence of sugars (Schemske *et al*, 1978). Nectar was collected for laboratory analysis (from covered flowers, as described above) on Whatman No 1 paper wicks prepared in advance and fixed on stainless steel pins that had been cleaned with acetone (McKenna and Thomson, 1988; Thomson *et al*, 1989; Harder and Cruzan, 1990). The paper wicks, placed on styrofoam blocks, were left to air-dry, and were stored in air-tight containers until analysis over silica gel. Analyses were made for each flower separately. Before analysis, the nectar content of each wick was dissolved in 1 ml of distilled water in a microcentrifuge tube by intermittent vortexing at room temperature for at least 1 h. Finally, the tubes were centrifuged to remove paper particles.

Sugar analysis

Sugar analysis was made directly on the diluted nectar (see above), by HPLC (Dionex, Sunny-

Table I. List of the phryganic species studied.

Plant code	*Collection date*	*Plant species*	*Plant family*	*Median date of flowering*
A. *Species for which the nectar was measured in the field*				
1. High nectar producers (> 0.5 μl/flower)				
1	12.6.93	*Alcea pallida* (Willd) Waldst & Kit	Malvaceae	160
2	6.4.92	*Asphodelus aestivus* Brot	Liliaceae	85
3	11.6.93	*Ballota acetabulosa* (L) Bentham	Labiatae	160
4	12–14.6.93	*Capparis ovata* Desf	Capparidaceae	188
5	10.7.92	*Delphinium peregrinum* L *	Ranunculaceae	185
6	3.6.92	*Echium angustifolium* Miller	Boraginaceae	178
7	13–15.5.93	*Phlomis fruticosa* L *	Labiatae	108
8	25–29.4.92	*Prasium majus* L	Labiatae	114
9	14.4.93	*Salvia triloba* L fil	Labiatae	94
10	2.6.92	*Stachys cretica* L subsp *cretica*	Labiatae	137
11	21.10.92	*Sternbergia lutea* subsp *sicula* (Tineo ex Guss) DA Webb	Amaryllidaceae	297
2. Low nectar producers (< 0.5 μl/flower)				
12	6–7.4.92	*Alkanna tinctoria* (L) Tausch	Boraginaceae	95
13	29–30.4.92	*Allium subhirsutum* L	Liliaceae	106
14	12.4.93	*Anchusa variegata* (L) Lehm	Boraginaceae	62
15	16–17.5.93	*Anthyllis hermanniae* L	Leguminosae	132
16	5–6.10.92	*Asparagus acutifolius* L	Liliaceae	268
17	8.4.92	*Astragalus monspessulanus* L	Leguminosae	102
18	13.4.93	*Calendula arvensis* L	Compositae	80
19	25.4.92	*Campanula drabifolia* Sibth & Sm subsp *drabifolia* *	Campanulaceae	118
20	9.8.92	*Carlina vulgaris* L subsp *vulgaris*	Compositae	215
21	14.6.93	*Centaurea orphanidea* Heldr & Sart ex Boiss subsp *orphanidea* *	Compositae	165
22	25–29.4.92	*Centaurea raphanina* subsp *mixta* (DC) Runemark	Compositae	117
23	3.5.92	*Chrysanthemum coronarium* L	Compositae	128
24	30.4.92	*Cistus parviflorus* Lam	Cistaceae	125
25	26.4–2.5.92	*Cistus salvifolius* L	Cistaceae	104
26	13.7.92	*Convolvulus arvensis* L	Convolvulaceae	170
27	8.7.92	*Convolvulus cantabrica* L	Convolvulaceae	169
28	17.11.92	*Crocus cancellatus* Herbert	Iridaceae	298
29	12–13.7.92	*Ecballium elaterium* (L) A Richard in Bory	Cucurbitaceae	214
30	12–13.7.92	*Echinops microcephalus* Sibth & Sm	Compositae	190
31	9.8.92	*Echinops spinosissimus* Turra subsp *bithynicus* (Boiss) Kozuharov	Compositae	220
32	20.11.92	*Erica manipuliflora* Salisb	Ericaceae	363
33	9.7.92	*Erodium cicutarium* (L) L'Her in Aiton subsp *cicutarium*	Geraniaceae	69
34	12–13.4.93	*Eruca vesicaria* subsp *sativa* (Miller) Thell in Hegi	Cruciferae	113
35	13–14.7.92	*Eryngium campestre* L *	Umbelliferae	193
36	5.3.94	*Fritillaria graeca* Boiss & Spruner in Boiss subsp *graeca*	Liliaceae	85

Table I. Continued

Plant code	*Collection date*	*Plant species*	*Plant family*	*Median date of flowering*
37	25.2.94	*Gagea granatelli* (Parl) Parl	Liliaceae	48
38	11.4.93	*Globularia alypum* L	Globulariaceae	77
39	11–14.7.92	*Heliotropium europaeum* L	Boraginaceae	276
40	11–14.7.92	*Heliotropium hirsutissimum* Grauer	Boraginaceae	277
41	28.4.92	*Hypochoeris achyrophorus* L	Compositae	114
42	26.2.94	*Lamium amplexicaule* L subsp *amplexicaule*	Labiatae	74
43	5.6.92	*Nigella arvensis* L *	Ranunculaceae	169
44	14.4.93	*Ornithogalum exscapum* Ten	Liliaceae	70
45	25–26.4.92	*Petrorhagia velutina* (Guss) PW Ball & Heywood	Caryophylaceae	106
46	29–30.4.92	*Psoralea bituminosa* L *	Leguminosae	135
47	5.6.92	*Pterocephalus papposus* (L) Coulter	Dipsacaceae	123
48	13.4.92	*Ranunculus spruneranus* Boiss	Ranunculaceae	98
49	28.4.92	*Reichardia picroides* (L) Roth	Compositae	107
50	16.5.93	*Reseda alba* L	Resedaceae	104
51	25.2.94	*Romulea linaresii* subsp *graeca* Beguinot *	Iridaceae	33
52	5.6.92	*Ruta graveolens* L *	Rutaceae	145
53	9.4.92	*Salvia verbenaca* L	Labiatae	85
54	3.6.92	*Satureja thymbra* L	Labiatae	137
55	12–15.5.93	*Scabiosa atropurpurea* L	Dipsacaceae	125
56	5.4.92	*Scandix australis* L subsp *australis*	Umbelliferae	73
57	20–21.10.92	*Scilla autumnalis* L	Liliaceae	290
58	8–9.4.92	*Silene colorata* Poiret	Caryophylaceae	95
59	2.5.92	*Sisymbrium orientale* L	Cruciferae	119
60	5.6.92	*Teucrium chamaedrys* L	Labiatae	135
61	4.6.92	*Teucrium polium* subsp *capitatum* (L) Arcangeli	Labiatae	156
62	4.6.92	*Thapsia garganica* L	Umbelliferae	136
63	27.2.93	*Thymelaea hirsuta* (L) Endl	Thymelaeaceae	25
64	8.7.92	*Thymus capitatus* (L) Hoffmanns & Link	Labiatae	171
65	9.4.92	*Tordylium apulum* L *	Umbelliferae	105
66	30.4–1.5.92	*Tragopogon porrifolius* L subsp *porrifolius* *	Compositae	110
67	27.4.92	*Tremastelma palaestinum* (L) Janchen	Dipsacaceae	116
68	8.4.92	*Trifolium stellatum* L	Leguminosae	98
B. *Species for which the nectar was measured in the laboratory*				
69	11.4.93	*Euphorbia acanthothamnos* Heldr & Sart ex Boiss	Euphorbiaceae	79
70	2.6.92	*Helichrysum stoechas* subsp barrelieri (Ten) Nyman	Compositae	136
71	17.4.93	*Hymenocarpos circinnatus* (L) Savi	Leguminosae	96
72	24.2.94	*Muscari commutatum* Guss	Liliaceae	54
73	24.2.94	*Muscari neglectum* Guss ex Ten	Liliaceae	39
74	12.5.93	*Pallenis spinosa* (L) Cass *	Compositae	144
75	1.5.92	*Phagnalon graecum* Boiss & Heldr	Compositae	125
76	6.9.92	*Urginea maritima* (L) Baker	Liliaceae	261

For each species, we give the plant and family names, the median date of flowering, as well as the date of nectar collection. Plant code corresponds to table II. Species marked with an asterisk were not visited by honeybees (after Petanidou, 1991). Median date of flowering is after Petanidou *et al* (1995).

Table II. Nectar volume, concentration, and sugar content for the phryganic species studied.

Plant code	Nectar							Species		Flower		
	Volume			Concentration			Sugar content sucrose (mg)	Flower abundance (x 1 000)	Life form	Depth (mm)	Shape	Life span
	Mean (µl)	SE	n	Mean (% w/w)	SE	n						
A. *Species for which the nectar was measured in the field*												
1. High nectar producers (> 0.5 µl/flower)												
1	1.76	0.302	22	71.76	0.55	18	1.701	1.5	h	0	d	
2	2.44	0.151	21	62.77	0.79	21	1.994	2 000	g	3.8	dt	+
3	4.42	0.711	44	49.17	2.29	36	2.655	210	h	8.6	g	+
4	15.21	1.940	12	65.49	1.94	12	13.075	12	w	6.2	br	+
5	0.52	0.053	24	42.31	1.47	23	0.261	3.2	t	16	t	
6	2.89	0.404	25	26.12	0.82	23	0.839	1 620	h	6.9	g	+
7	2.52	0.257	39	57.42	1.04	38	1.833	2 400	w	16.1	g	
8	7.48	0.653	11	31.79	3.83	11	2.685	156	w	9.8	g	
9	7.74	0.813	15	31.23	1.05	15	2.729	201.6	w	11.9	g	
10	0.59	0.085	53	51.94	2.37	49	0.378	630	h	7.4	g	
11	1.33	0.146	20	24.93	1.73	20	0.366	8.4	g	10.4	f	
2. Low nectar producers (< 0.5 µl=/flower)												
12	0.34	0.041	40	45.80	2.08	33	0.186	200	h	4.9	f	+
13	0.03	0.003	47	60.76	1.01	33	0.026	45	g	0	d	
14	0.45	0.099	20	43.82	2.64	18	0.234	20	t	6.2	g	
15	0.01	0.004	28	75.20	0.92	5	0.009	9 000	w	0	fl	
16	0.02	0.002	63	50.24	1.75	31	0.013	160	g	0	d	+
17	0.28	0.054	25	40.71	6.85	11	0.134	40	h	10.4	fl	+
18	0.01	0.003	12	56.00		1	0.004	720	t	3.6	h	+
19	0.03	0.006	14	63.38	1.25	4	0.025	4.5	t	6	b	
20	0.16	0.028	45	55.46	2.15	31	0.111	96	h	7.4	h	
21	0.01	0.002	20	65.17	3.39	13	0.011	800	t	11.2	h	+
22	0.21	0.041	17	52.08	3.49	16	0.138	40	h	21.6	h	
23	0.01	0.002	7	47.00	0.00	2	0.008	1 050	t	4.3	h	+
24	0.05	0.010	25	66.36	1.86	12	0.042	180	w	0	d	+
25	0.02	0.006	108	56.32	3.04	11	0.013	400	w	0	d	+
26	0.05	0.008	21	61.41	1.10	16	0.042	12	h	2.5	f	+
27	0.06	0.011	34	61.14	0.66	16	0.045	25	h	2.5	f	+
28	0.19	0.043	20	26.41	1.79	13	0.054	1.4	g	92	f	
29	0.03	0.009	49	58.34	2.63	13	0.021	15	h	0.7	f	
30	0.13	0.010	50	65.51	0.70	39	0.114	28.5	h	7.4	h	
31	0.16	0.023	24	64.23	1.75	21	0.137	18	h	6.5	h	
32	0.003	0.001	41	50.00	0.00	2	0.002	192	w	3.6	b	
33	0.01	0.002	4	75.00		1	0.011	120	t	0	d	+
34	0.13	0.041	20	52.89	3.21	8	0.084	40	t	9.2	dt	
35	0.004	0.001	52	66.16	0.76	7	0.004	50	h	1.9	h	
36	0.06	0.028	2	71.00	3.00	2	0.057	0.27	g	24.2	b	
37	0.03	0.015	3	66.50	0.50	2	0.029	6.9	g	0	d	
38	0.01	0.002	23	54.17	3.23	7	0.007	90	w	4.5	h	

Table II. Continued

39	0.05	0.006	52	32.43	2.02	28	0.018	300	t	2	f	
40	0.06	0.013	39	44.35	2.11	18	0.032	300	t	4.6	f	
41	0.01	0.001	27	31.00	1.00	2	0.002	420	t	3.5	h	+
42	0.20	0.021	12	21.48	1.24	12	0.047	10	t	14.6	g	
43	0.30	0.091	6	65.44	3.26	6	0.257	6	t	3.3	d	
44	0.05	0.009	20	46.29	3.65	15	0.029	24	g	0	d	
45	0.04	0.010	18	49.73	3.89	8	0.022	2	t	16	dt	
46	0.24	0.036	32	66.00	1.03	27	0.206	20	h	7.8	fl	
47	0.03	0.004	33	51.90	3.22	11	0.022	36	t	5.3	h	
48	0.08	0.013	16	58.46	1.82	13	0.063	4.8	g	1.4	d	
49	0.03	0.003	32	35.18	1.46	12	0.011	84	h	8.3	h	+
50	0.07	0.006	12	67.46	0.57	10	0.062	900	h	0	d	
51	0.07	0.022	4	51.63	3.02	4	0.042	0.2	g	5.7	f	
52	0.32	0.078	15	75.95	0.51	10	0.333	52	h	0	d	
53	0.33	0.034	46	41.57	2.12	26	0.160	5.6	t	7.1	g	
54	0.17	0.013	56	61.75	0.70	44	0.132	3 000	w	7.6	g	
55	0.01	0.003	21	64.70	4.83	11	0.012	456	t	4.5	h	
56	0.03	0.003	10	73.80		1	0.028	500	t	0	d	
57	0.01	0.002	34	49.33	2.05	12	0.008	45	g	0	d	+
58	0.06	0.008	34	52.02	2.15	11	0.038	15	t	5.9	dt	+
59	0.01	0.002	39	72.72	3.76	6	0.012	400	t	3.2	dt	
60	0.50	0.082	19	61.02	0.81	18	0.393	60	w	7.9	g	
61	0.06	0.006	43	69.57	0.84	29	0.059	180	w	4.2	g	+
62	0.02	0.005	9	75.50		1	0.018	480	h	0	d	
63	0.00003	0.000	20						w	2.9	dt	
64	0.10	0.005	53	58.13	0.97	45	0.072	14 000	w	5.4	g	
65	0.01	0.005	10	74.50	0.50	2	0.012	450	t	0	d	
66	0.01	0.002	44	57.21	3.04	7	0.010	12	t	7.7	h	+
67	0.05	0.005	23	59.37	3.04	15	0.037	36	t	5.7	h	
68	0.04	0.006	22	59.33	4.76	6	0.028	54	t	8.3	fl	

B. *Species for which the nectar was measured in the laboratory*

69	14	0.027	2 000	w	0	d	
70	40	0.028	2 800	w	4.4	h	+
71	13	0.021	1.76	t	1.9	fl	
72	15	0.022	100	g	5.5	b	
73	15	0.046	72	g	4.8	b	
74	10	0.129	180	t	2.2	h	+
75	12	0.022	1050	w	4.7	h	+
76	4	0.436	90	g	0	d	+

Values represent the amount of nectar per flower and day, and are accompanied by the number of flowers sampled *(n)* and the standard error (SE). For plant set **A**, we give the equivalent sucrose content, *ie* the sugar content calculated from volume and concentration of the nectar measured in the field. For set **B** the actual sugar content is given, *ie* resulted after laboratory analysis. We also give the flower abundance (in thousands of flowers per species population in the 30-ha study area), the plant life form, as well as the floral attributes depth and shape. Flower life span indicates the ephemerous flowers (*ie* if they span < 1.5 d on average). Abbreviations. Life forms: g: geophytes, h: herbaceous perennials, w: woody perennials, t: therophytes. Shape: b: bell, br: brush, d: disc, dt: disc-tube, f: funnel, fl: flag, g: gullet, h: head, t: tube. Plant life forms and flower life spans are from Petanidou *et al* (1995).

vale CA, USA) on a CarboPac PA1 anion-exchange column and quantified by a pulsed amperometric detector. The flow rate was 1 ml min^{-1}. The elution conditions were 100 mM NaOH for 4 min, a linear gradient from 0 to 30 mM Na-acetate in 100 mM NaOH over a 16 min period, a linear gradient of 30 to 100 mM Na-acetate in 100 mM NaOH over 30 min, and finally 300 mM NaOH for 10 min. The column was regenerated with 1 M NaOH for 10 min and equilibrated for 20 min with starting buffer after every run. Quantification was performed on the peak areas with the external standards method.

Flower abundance

The flower abundance of each species was estimated on the basis of their population size and the average number of flowers per individual (floral stems x number of flowers per stem). These 2 values were estimated on the basis of 20 counts made on 20 different individual plants selected at random. The population size was estimated over the whole study site.

Depth

Depth was measured with the aid of the Drummond capillaries, also used to measure nectar volume. Flowers were grouped into 4 categories: i) shallow (0 mm), ii) relatively shallow (<4 mm), iii) relatively deep (4–10 mm), iv) and deep (>10 mm).

Shape

The determination of the floral shape was based on Faegri and van der Pijl (1979) and Barth (1985). Nine shapes were identified: bell, brush, disc (dish, or bowl), disc-tube (stalked-plate), gullet, flag (butterfly), funnel, head, and tube.

Analysis of data

As only a few parameters were normally distributed, we adopted non-parametric tests for all sets of data. In the *post hoc* comparisons following Kruskal–Wallis anova, we applied the ultra-conservative Bonferoni correction (Pagano and Gouvreau, 1993).

RESULTS

Table I contains the list of the 76 phryganic species studied, plant family and median date of flowering, together with the dates of nectar collection. The nomenclature follows Tutin *et al* (1964–1980). Table II contains nectar production (volume, concentration, and total sugar content) of the species. For 68 species in which it was possible to measure nectar volume and concentration per flower, these values are given, together with the total sugar amount expressed in sucrose equivalent (except for *Thymelaea hirsuta,* where only volume is given). The other 8 species contained too little or too viscous nectar to be directly measured in the field. For these species only the total sugar content per flower was made available through laboratory analysis (see *Materials and methods*). Along with the above measurements in the table II, we give the population, plant, and floral parameters studied, *viz* the estimated flower abundance *(ie* total number of flowers per species population), the plant life form, the floral depth, shape, and life span.

Per species flower, the average nectar volume in the community is 0.77 ± 0.279 µl, $n = 68$), the mean nectar concentration $55.1 \pm 1.69\%$ w/w ($n = 67$), and the mean sugar content 0.44 ± 0.185 mg ($n = 75$). None of these 3 nectar attributes is correlated with the median date of flowering of the species as listed in table I. There is a negative correlation between flower depth and nectar concentration ($R = -0.381$, $P = 0.001$).

We tried to explore to what extent the 3 nectar attributes measured are related to phylogeny (*viz* family), to plant life form, as well as to floral depth and shape (table II). It appears that all these parameters play a discriminatory role as to the nectar production. The results are summarised in table III, along with the results of the comparisons after application of the Bonferoni correction.

DISCUSSION

Total nectar potential of phrygana

As clearly shown in the table II, out of all 76 species studied only 9 produced more than 1 µl of nectar and, only 11 produced more than 0.5 µl. It is noteworthy that the species that yields the most nectar of the community is *Capparis ovata*, a nocturnally flowering species. The low nectar production of the rest of the phrygana is comparable to the Spanish scrub studied by Herrera (1985). The values for both systems are very low compared with those of other regions. In Central and North America for instance, in a complex of localities and ecosystem types, Cruden *et al* (1983) found an average of 2.10 ± 0.67 µl nectar volume produced per flower of exclusively bee-visited species (n = 12). Opler (1983) in a study of nectar production of tropical systems, distinguished between high-rewarding, large-bee pollinated species that produce 9.75 ± 4.350 µl of nectar (n = 19), and low-rewarding, small bee/wasp pollinated species with only 0.63 ± 0.182 µl (n = 14) per flower.

On the other hand, nectar concentration in phrygana is very high, reaching a maximum of 76%. It should be born in mind that this value represents the average concentration per species; individual flowers exceeded 80%, while in other cases concentration was so high that nectar could not be sampled by a regular microcap (*viz*

Table III. Summary statistics for 4 plant and floral attributes (see tables I and II) for their difference in volume, concentration, and sugar content of the nectar produced per flower.

	df	H	P		Post hoc *comparisons*
Plant family					
Volume	5, 42	20.693	0.0009	***	Labiatae-Compositae *
Concentration	5, 41	16.430	0.0057	**	–
Sugar content	5, 48	18.277	0.0026	**	Labiatae-Compositae*
Plant life form					
Volume	3, 69	7.443	0.0591	NS	Herbaceous perennials-therophytes *
Concentration	3, 67	1.835	0.6070	NS	–
Sugar content	3, 75	8.489	0.0369	*	Herbaceous perennials-therophytes *
Flower depth class					
Volume	3, 69	16.417	0.0009	***	1–3*, 1–4*, 2–3*, 2–4*
Concentration	3, 67	16.219	0.0010	***	1–3**,1–4**
Sugar content	3, 75	8.811	0.0319	*	-
Flower shape					
Volume	6, 67	26.098	0.0002	***	g–d**, g–h**
Concentration	6, 65	17.627	0.0072	**	d–g*
Sugar content	6, 73	23.713	0.0006	***	g–b*, g–d *, g–f *, g–h**

The attributes tested are plant family, plant life form, flower depth, and flower shape. In the case of plant family and flower shape only the major categories were tested, *ie* those comprising > 5 species (*viz* Boraginaceae, Compositae, Labiatae, Liliaceae, Leguminosae, Umbelliferae, and b, d, dt, g, f, fl, h, respectively). For abbreviations see table II and *Materials and methods*. Given are the degrees of freedom, the Kruskal–Wallis H value, the significance, as well as the results of the comparisons (Mann–Whitney U test) after the Bonferoni correction has been applied. The groups appear in order of magnitude as a result of these comparisons.* $P < 0.05$, ** $P < 0.01$, $P < 0.001$.

Urginea maritima). Beutler (1930) found that flower nectars of 18 flowers visited by honeybees ranged between 10 and 70%. Von Frisch (1967) examined 65 species and found a similar range. The concentration found by Cruden *et al* (1983) was 32.5 ± 2.46 (n = 12). The same author found that the sugars contained in the same floral nectars he studied amounted to 0.761 ± 0.271 mg per flower. This value is comparable to that of the phrygana despite differences in nectar volume. The low nectar quantity of phrygana together with its high energetic content must certainly be related to the water limitations in the Mediterranean ecosystems. This is also reflected in the type of the pollinators involved. A large number of insects rely upon the floral resources in the Mediterranean communities, dominated by bees and flies (Petanidou and Ellis, 1993). These species are able to feed on very concentrated nectar by licking it, although the nectar concentrations that are preferred by large bees range between 20 and 50% (Eickwort and Ginsberg, 1980; Petanidou, 1993).

The estimated nectar sugar production of phrygana over all 76 plant species is 455 g per hectare, and 307 g when only the honeybee-visited species are taken into account. If we consider that nectar is concentrated up to 85% (80–90% according Maurizio and Grafl, 1982) to reach honey levels, we conclude that the above values roughly correspond to *ca* 535 and 360 g of honey, respectively. This is an underestimate, as already mentioned, since the nonephemerous flowers may produce nectar amounts that can reach the double of the amounts measured during anthesis. Nevertheless, this value allows us to make a conservative estimation of the honey production potential of an area. In Greece, for instance, with 13% of the territory covered by phrygana, the annual gross productivity of honey may exceed 600 metric tons.

Nectar production and floral attributes

Labiatae are by far the most nectar rewarding species in the phrygana, both in volume and sugar content (table III; see Herrera, 1985). This implies that the total honey production is strongly dependent upon their abundance, which is lower during the first years after fire compared with the immature phase of the phryganic ecosystem (see Arianoutsou-Faraggitaki and Margaris, 1981, and references therein; Petanidou, unpublished data).

Life form is also linked with nectar production. When only simple parametric methods are employed (*viz* Mann-Whitney *U* tests) nectar yield seems to be higher in woody perennials, decreasing gradually to herbaceous perennials, geophytes, and is the lowest in therophytes. However, by using the conservative Bonferoni correction in the subsequent tests, only herbaceous perennials are clearly differentiated from annuals. These findings show that the species-rich annuals, which are particularly abundant during the first post-fire years are the poorest nectar producers in phrygana. This finding indicates the significance of the perennial plants in the pollination web of these systems, and, as a consequence, their importance for the native insects. Ellis and Ellis-Adam (1993) in a review study on 29 000 plant–pollinator relationships of NW Europe, found that it is the perennials, again, that are particularly serviced by many pollinators *(ie* they are 'cornucopian').

As expected, deep flowers yield much more than shallow ones (> 4 and ≤ 4 mm, respectively), while there is an opposite trend as to their nectar concentration. Nectar differences observed in respect to floral shape are most probably due to a combination of depth and family membership (table III).

Conclusions for management

The nectar production pattern of phrygana is important in exploiting the system for apiculture and managing these areas to conserve them. The finding that therophytes are poorer nectar producers in both volume and sugars indicates that nectar production is higher in mature Mediterranean systems when perennials have been established and come into bloom, compared with the first post-fire years. These are exactly the years of establishment of a very diversified pollinating fauna, which is lower during the first years after fire compared with unburnt communities (Moldenke, 1979; Petanidou, 1991; Petanidou and Ellis, 1993). Since solitary bees, the main native pollinators of the Mediterranean ecosystems, are relatively inferior competitors, they risk a possible extinction because of the foraging overcompetence of honeybees (Roubik, 1978, 1988; Eickwort and Ginsberg, 1980; Paton, 1993; Dafni and O'Toole, 1994). Therefore, exploitation of these ecosystems by apiculture should be done with caution during the first post-fire years, when nectar production is lower compared to the mature stage.

These results suggest that phrygana may offer a substantial commercial honey crop. For optimal exploitation of the ecosystem, it would have to be maintained in its original, semi-natural state, with sustained but extensive grazing, and protected from excessive burning. This would (1) give an economic incentive for the preservation of this landscape for the time being either abandoned or misused, and (2) control and diminish the detrimental effects of the present regime of overgrazing. Apiculture may be the best guarantee for the maintenance of such marginal areas. Because intensive apiculture may influence the diversity of the native pollinator fauna, we feel that apicultural schemes should be sustained so that exploiting these areas by apiculture may also benefit the local anthophilous fauna.

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Résumé — Importance des terres incultes pour les abeilles et l'apiculture : la sécrétion nectarifère dans une formation arbustive méditerranéenne. De 1992 à 1994 nous avons étudié la sécrétion nectarifère (volume, concentration, teneur en sucres) des fleurs de 76 espèces nectarifères d'une communauté végétale de type garrigue («phrygana») située près d'Athènes, Grèce. Ces valeurs ont été mises en relation avec le nombre de plantes en fleurs et les caractéristiques de la fleur, données mesurées au champ ou tirées de la littérature. Toutes les mesures et les valeurs calculées sont données dans les tableaux I et II. On a prélevé le nectar de fleurs encagées de 1 j à l'aide de microcapillaires de 0,1-10 µl pour en déterminer le volume et mesuré la concentration en sucres avec un réfractomètre à main. Les valeurs moyennes ont été respectivement de 0,77 µl et 55,1% (en rapport de poids). À partir de ces valeurs on a calculé la teneur absolue en sucres par fleur. Pour un petit nombre d'espèces qui fournissaient très peu de nectar, cette valeur a été obtenue par une analyse des sucres par chromatographie liquide à haute pression (HPLC) au laboratoire ; pour ce faire, le nectar floral a été récolté au champ sur des mèches de papier, qui ont été séchées et conservées jusqu'au moment de l'analyse. La teneur moyenne en sucres par fleur des 76 espèces a été de 0,44 mg. La date moyenne de floraison n'est corrélée

avec aucune des 3 caractéristiques du nectar. Une corrélation négative a été trouvée entre la profondeur de la fleur et la concentration en nectar. Il existe des différences en fonction de la famille botanique, de l'appartenance à une forme de vie (géophyte, herbacée pérenne, ligneuse pérenne thérophyte), de la profondeur ou de la forme de la fleur. Le tableau III donne les résultats de l'ANOVA pour ces 4 paramètres, ainsi que les tests *a posteriori* faisant intervenir la «correction de Bonferoni» : les Labiées sont de loin les espèces de la communauté les plus riches en nectar, à la fois en volume et en teneur en sucres. Elles se distinguent significativement des Composées. Les thérophytes produisent significativement moins de nectar et/ou de sucre que les plantes herbacées pérennes. Les espèces dont les fleurs ont une profondeur > 4 mm produisent plus de nectar que les fleurs peu profondes, mais cela ne conduit pas à une plus forte teneur en sucres à cause de leur concentration significativement plus faible. En ce qui concerne la forme, les fleurs en forme de sac sont de loin les meilleures productrices de nectar et/ou sucre, bien qu'ayant une concentration moindre que les fleurs en forme de disque, mais ceci est probablement une conséquence de leur position taxonomique. Les données mentionnées ci-dessus nous permettent d'estimer le potentiel mellifère de la «phrygana» aussi bien que d'autres formations végétales méditerranéennes de même type. Le potentiel mellifère par ha de la communauté étudiée a été estimé à 455 g de sucres ($n = 76$), ou 307 g si l'on ne prend en compte que les plantes visitées par les abeilles mellifères, ce qui correspond en gros à 535 et 360 g de miel respectivement. Mais ces valeurs sont certainement sous-estimées en raison de la méthode employée. Nous espérons que ces résultats contribueront à la sauvegarde de la faune pollinisatrice indigène et à un meilleur aménagement des régions concernées. De ce point de vue nous insistons particulièrement sur le fait que ces écosystèmes devraient être exploités avec précaution au cours des années qui suivent les incendies, puisque la production de nectar est alors plus faible que celle d'un système pleinement développé. Dans les cas où le nectar est en quantité limitée, les abeilles solitaires, qui sont les pollinisateurs indigènes de ce système, pourraient être menacées d'extinction par l'efficacité de butinage et les meilleurs performances de l'abeille domestique.

secrétion nectarifère / apiculture / Apoidea / garrigue / région méditerranéenne / caractéristique florale

Zusammenfassung — Mögliche Bedeutung von Brachland für die Bienenhaltung: Nektarsekretion in einer mediterranen Buschvegetation. In den Jahren 1992–1994 untersuchten wir die florale Nektarproduktion (Volumen, Konzentration, absoluten Zuckergehalt) von 76 nektarerzeugenden Arten in einer Pflanzengesellschaft der Felsenheide (Phrygana) in der Nähe von Athen, Griechenland. Die Werte wurden zu der Anzahl der blühenden Pflanzen und den Blüteneigenschaften in Beziehung gesetzt, die entweder im Feldversuch gemessen oder der Literatur entnommen wurden. Alle Meßdaten und berechneten Werte sind in den Tabellen I und II wiedergeben. Der Nektar von eintägigen, mit Gaze umhüllten Blüten wurde mit einer 10 µl Mikrokapillare aufgenommen und das Volumen bestimmt. Mit einem Taschenrefraktometer wurde die Zuckerkonzentration gemessen. Die Mittelwerte lagen bei 0,77 µl bzw 55,1% Gewichtsprozent (w/w). Aus diesen Werten von Volumen und Zuckerkonzentration wurde der absolute Zuckergehalt pro Blüte berechnet. Bei einer geringen Anzahl von Arten, die sehr wenig Nektar erzeugten, wurde eine Zuckeranalyse im HPLC (Hochdruckflüssigchromatographie) im Labor durchgeführt. Dazu wurde der Blütennektar im Feld mit Papierdochten auf-

gesaugt, getrocknet und bis zur Analyse aufbewahrt. Der mittlere Zuckergehalt von allen 76 Arten betrug 0,44 mg pro Blüte. Der mittlere Blühtermin korrelierte mit keinem der 3 Nektarwerte Volumen, Konzentration und absolutem Zuckergehalt. Es wurde eine negative Korrelation zwischen Blütentiefe und Nektarkonzentration gefunden. Farbe, Größe, Länge oder Grad der Verwachsung der Blütenblätter hatte keinen Einfluß auf die drei Eigenschaften des Nektars. Dagegen bestanden Unterschiede in Bezug auf die Familie oder die Zugehörigkeit der Lebensform, sowie auf die Tiefe und Form der Blüte. Tabelle III zeigt die Anova Ergebnisse für diese 4 Parameter, zusammen mit *a Posteriori* Tests, unter Anwendung der 'ultra conservativen Bonferoni Korrektur': die Lippenblütler (Labiatae) sind mit Abstand die Arten der Pflanzengesellschaft, die die lohnensten Nektarerzeuger sind, sowohl in Hinsicht auf Volumen als auch auf den Zuckergehalt. Sie unterscheiden sich signifikant von den Korbblütlern (Compositae). Therophyten erzeugen signifikant weniger Nektar/ Zucker als winterharte, mehrjährige Kräuter. Pflanzen, deren Blüten tiefer als 4 mm sind, haben mehr Nektar als flache Blüten, aber sie enthalten nicht mehr Zucker, weil die Konzentration signifikant niedriger ist. In Bezug auf die Form sind die röhrenförmigen Blüten die bei weitem am meistem Nektar / Zucker erzeugenden Typen, trotz der geringeren Zuckerkonzentration im Vergleich zu den scheibenförmigen Blüten, aber das ist wahrscheinlich eine Folge der taxonomischen Position. Die oben angegebenen Daten erlauben uns, die Bedeutung sowohl der Phrygana als auch ähnlicher mediterraner Gebiete für die Imkerei abzuschätzen. Die Möglichkeiten für den Honigertrag dieser Pflanzengesellschaft liegen bei 455 g Zucker pro Hektar (n = 76) oder 307 g, wenn man nur die Arten berücksichtigt, die von Honigbienen besucht werden. Diese Werte entsprechen annähernd 535 bzw 360 g Honig, und sie wurden mit der hier angewandten Methode sicher eher unterschätzt. Wir hoffen, daß unsere Ergebnisse zu einer Erhaltung der hier natürlicherweise bestäubenden Fauna und zu einer besseren Pflege dieses Ökosystems führen. In Bezug auf die natürliche Fauna möchten wir besonders darauf hinweisen, daß die Nutzung dieser Ökosysteme im ersten Jahr nach einem Feuer vorsichtig erfolgen soll, denn die Nektarerzeugung ist dann verglichen mit einem voll entwickelten Gebiet sehr niedrig. In solchen Fällen, in denen es wenig Nektar gibt, besteht die Gefahr, daß solitäre Bienen, die natürlichen Bestäuber dieses Systems, durch die Sammeleffizienz und Leistungsfähigkeit der Honigbienen vernichtet werden könnten.

Nektarproduktion / Eigenschaften der Blüten / mediterranes Ökosystem / Bienen / Imkerei

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