

CONSTRAINTS ON FLOWERING PHENOLOGY IN A PHRYGANIC (EAST MEDITERRANEAN SHRUB) COMMUNITY¹

THEODORA PETANIDOU,^{2,5} WILLEM N. ELLIS,³
NIKOS S. MARGARIS,⁴ AND DESPINA VOKOU²

² Department of Ecology, School of Biology, Aristotle University, 540 06 Thessaloniki, Greece;

³ Institute of Systematics and Population Biology, Department of Entomology,
University of Amsterdam, Plantage Middenlaan 64, 1018 DH Amsterdam, The Netherlands; and

⁴ Department of Environmental Studies, Aegean University,
Kavetsou 12–14, 811 00 Mytilini, Greece

The phenological pattern of flowering at the community level was studied in a Greek phryganic ecosystem near Athens for 4 consecutive years. Flowering is strongly seasonal: 80% of the insect-pollinated flora, which consists of 133 species, blooms between February and June. There is a variably expressed secondary flowering period in autumn. The pollinating fauna follows a strongly correlated pattern of abundance. Two types of plants were distinguished: pauciflorous species bearing <10 flowers that are large compared to the plant body, and multiflorous species with many small flowers. Pauciflorous species flower in the winter half of the year, while multiflorous species flower mainly in the summer half. The mean flower life spans are 9 and 3 days, respectively. The duration of flowering (DF) for each species is 55 days on average, which is long compared to other communities. The DF shows year-to-year variations, concomitant with the vicissitudes of the climate. The start of flowering of a species is statistically correlated with the temperature in the previous month, not with rainfall; its end date of flowering only partly compensates for the time gained or lost. DF is maximal in winter. The average flower life span of species flowering at any given date varies strongly and independently of the average DF. We tested the hypothesis that flowering phenology is set by phylogenetic and life form constraints. This could not be corroborated for phylogeny, evidently because of the overriding influence of the mediterranean climate, and probably also for biogeographical reasons. In contrast, life forms and multiflorous and pauciflorous species show strong differences. Many (51) of the species are therophytes; we tested the hypothesis that because of their annual habit they would be more dependent on pollination than perennials. Thus we anticipated that therophytic species would be differentiated from perennials in their flowering phenologies. This is not corroborated. We therefore conclude that the seed bank plays a role that is analogous to that of a perennial plant body.

The evolution of the timing of flowering in animal-pollinated plants has been the subject of several studies, recently reviewed by Bawa (1983), Rathcke (1983), Waser (1983), Rathcke and Lacey (1985), Kochmer and Handel (1986), and van Schaik, Terborgh, and Wright (1993). The general opinion is that the optimal time of flowering is determined by the balance between a multitude of factors, both intrinsic (e.g., constrained by phylogeny) and extrinsic, like pollinator availability (Waser, 1979), interspecific competition (Rathcke, 1983; Bawa, 1983; Waser, 1983), moisture availability (Bell and Stephens, 1984; Zimmerman, Roubik, and Ackerman, 1989; Friedel et al., 1993), rainfall seasonality (Johnson, 1993), conditions for seed germination and seedling establishment (Burt, 1970; Pierce, 1984), and seed dispersal (Wheelwright, 1985). In particular, competition of co-flowering plants for pollinators has attracted much attention, not in the

least because the staggered blooming of species in a community has been interpreted as a response to competition (Mosquin, 1971; Pojar, 1974; Reader, 1975; Heinrich, 1976; Stiles, 1979; Pleasants, 1983). This view has been criticized (Poole and Rathcke, 1979; Rathcke and Lacey, 1985; but see Cole, 1981). On the other hand, there is evidence that flowering time is governed by intrinsic, conservative factors, reflecting shared phylogenetic constraints (Bell and Stephens, 1984; Kochmer and Handel, 1986; Zimmerman, Roubik, and Ackerman, 1989; Johnson, 1993; see also McKittrick, 1993).

In this study we examine the flowering pattern of a Mediterranean shrub community in relation to phylogenetic affinities and to the strong constraints imposed by the mediterranean climate, in particular the severe summer drought. (Note the difference between "Mediterranean," which refers to the circummediterranean basin, and "mediterranean," which refers to all regions of the world with a Mediterranean-type climate, in accordance with di Castri and Mooney, 1973.) Phrygana, i.e., the garrigue of the East Mediterranean region (comparable to the Californian chaparral), is one of the most common ecosystems of Greece. It covers ca. 13% of the Greek territory, occupying the driest parts of the country (Diamantopoulos, 1983; Petanidou and Vokou, 1990, 1993). Although its physiognomy is determined by woody plants, therophytes are the most species-rich life form (45% of its flora; Margaris, 1980). The therophytic life form is generally considered an adaptation to the prolonged and severe summer drought. In fact, it is this summer drought

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⁵ Author for correspondence, current address: Catholic University of Leuven, Botanical Institute, Laboratory of Systematics, Kardinaal Mercierlaan 92, 3001 Heverlee, Belgium.

that, combined with the relatively mild and wet winter, characterizes the mediterranean climate (Aschmann, 1973). In addition to strong seasonality, the mediterranean climate is unpredictable, both within and between years. Unlike temperate systems, for instance, flowering in mediterranean ecosystems occurs before the critical season, i.e., the summer (Zohary, 1962; Mooney, Parsons, and Kummerow, 1974; Moldenke, 1979; Diamantopoulos and Margaris, 1981; Auerbach and Shmida, 1987; Shmida and Dafni, 1989; but see Johnson, 1993). The majority of phryganic plants are dependent on pollination by insects (Margaris, 1984; Herrera, 1987), which themselves occur mostly in the short, favorable period between winter and the onset of summer (Petanidou, 1991a).

In terms of entomophilous plant species, phrygana is one of the most species-rich communities studied outside of the tropics, comparable to those reported from similar ecosystem types in California and Chile (i.e., >100 species; cf. Moldenke, 1975, 1979). The enhanced plant diversity of phrygana may be linked to: 1) the prolonged length of the growing season in this ecosystem, extending from September to April (Moldenke, 1975; Margaris, 1976; Pleasants, 1983); and 2) the great environmental stress (nutrient-poor, dry soils, frequent fires, heavy grazing) and resulting reduced competition for space.

Little is known of flowering at the community level in phrygana, as compared to tropical ecosystems (Frankie, Baker, and Opler, 1974; Stiles, 1975, 1979; Opler, Frankie, and Baker, 1980; reviews by Bawa, 1983, 1990) or temperate ones (Pojar, 1974; Moldenke, 1975; Heinrich, 1976; Ostler and Harper, 1978; Parrish and Bazzaz, 1979; Lack, 1982; Motten, 1986; Rathcke, 1988). Most information on mediterranean ecosystems comes from the Californian and Chilean chaparral (Moldenke, 1975). Struck (1992) studied the flowering phenology of 20 woody perennials in the northwest Cape of South Africa, while Johnson (1993) did the same for the Cape flora, based on a literature search. In the Mediterranean Basin, Herrera (1986) studied the flowering phenology of a shrub community in Spain, limiting himself to 30 species. Arroyo (1990) followed the woody flora of several plots in southern Spain.

Our study is based on the complete entomophilous flora of a phryganic ecosystem. We investigate to what extent phenological characteristics (timing of bloom, duration of flowering, and flower life span) are governed by climatic or phylogenetic constraints. Kochmer and Handel (1986) formulated three predictions in a comparison between the floras of North Carolina and temperate Japan: 1) families should generally differ in flowering time; 2) a family's total range of flowering time should be a positive function of the number of included species, but this total range should be significantly shorter than the flowering period of the whole flora; and 3) families in different regions should have similar phenologies. Because the ecological and biogeographical gap between the Mediterranean region and North America or Japan is much wider than the gap between the latter two (cf. Moldenke, 1976; Pielou, 1979; Herrera, 1985; Petanidou and Vokou, 1990, 1993), our test is more exacting.

Kochmer and Handel (1986) predicted that life form constraints are effective. In their words, "a pure life history constraints hypothesis would predict that species of dif-

ferent life forms should differ significantly in mean flowering times, regardless of family membership." In fact, because life forms are groupings that summarize the way a species passes the most difficult season rather than entities that necessarily share a common history, life form constraints to flowering can be no more than correlates (cf. also McKittrick, 1993). Yet such correlations might exist, and we test them as well.

The large number of therophytes is one of the most characteristic aspects of floras like the phrygana with an extended dry period. In our study site all therophytes are dependent on insect pollination. One could expect a priori that these annual plants, which require a yearly crop of seeds in order to persist, are more strongly dependent on pollination than perennials. Perennials may, after all, survive the loss of a year's seed crop without serious risk of local extinction. We therefore tested the hypothesis that therophytes would form a distinct group, as far as antheological traits are concerned, when compared to perennial species.

MATERIALS AND METHODS

Study site—The study was carried out from 1983 to 1987 at Daphni (38°00'N–23°38'E), situated approximately 10 km west of the center of Athens. The study area is a part of the Diomedes Botanical Garden of Athens University nature reserve, situated on the slopes of Mt. Aegaleo. The dominant ecosystem type in the reserve is phrygana, covering 130 ha, with occasional wild olive trees (*Olea europaea* var. *sylvestris* L.) and kermes oaks (*Quercus coccifera* L.). A great part of the area was burnt in 1977; since then, it has been protected from both fire and grazing. The substrate is typical for phrygana; calcareous and stony. The study site is a 30-ha section of the reserve, at a low altitude (135–215 m), with slopes of between 18° and 27°, exposed mostly to the north and east. The climate of the Athens area is mediterranean, according to Aschmann's criteria (1973). The area has the most severe yearly drought stress recorded in Greece, but comparatively little winter cold stress (Mittrakos, 1980). Detailed rainfall data for the observation period were taken from the nearest national meteorological station (Eleusis) (Fig. 1). Annual totals were 350.4, 394.6, 307.6, and 254.5 mm/year for the years 1983 through 1986, respectively; the long-term average for rainfall is 370.0 mm (Maheras, 1983). Monthly maximal and minimal temperatures were taken on the spot (Fig. 1); in 1985 the temperature reached –1 C, while for the rest of the monitoring period it did not drop below 3 C. The long-term average is 22.3 C.

Field studies—All angiosperm species encountered in the study site that exhibited a biotic pollination syndrome (Faegri and van der Pijl, 1979) were included in the study. Nomenclature follows Tutin et al. (1964–1980). Voucher specimens of plants are deposited in the Herbarium of the Institute of Systematic Botany and Phytogeography of the University of Thessaloniki (TAU). All fieldwork was done by the first author.

In order to study the flowering phenology of the community, each species was monitored weekly from February through July and biweekly in the remaining part of

the year. Field observations were made systematically throughout the year, from March 1983 until September 1986, and additional data were collected until May 1987.

Time and duration of flowering (DF) were monitored over 2 or 3 years for most of the species (39 and 56 species, respectively). Twenty species were followed during all 4 years, the remaining 18 in only 1 year. For each species two to six plots were chosen at the most densely populated spots of the study area. In these the number of flowers or flowering stems were counted. Blooming time was estimated on the basis of the grand total over all plots. Totals <2% of the maximal values were treated as sporadic flowering, and the corresponding dates were not analyzed. The DF of a species is defined as the difference between the start and the end dates of flowering.

The flower life span of the species was measured from May 1985 to May 1987. For each species, a number of flowers (≥ 15) was followed from bud to wilting. The flower life span was expressed in days as the average over all flowers studied. Flower life spans are based on individual florets in all species, except for *Euphorbia acanthothamnus*, where the cyathium was treated as a unit.

Species were assigned to life forms based mainly on the Flora Europaea (Tutin et al., 1964–1980). For some dubious cases (e.g., *Anemone* spp., *Asparagus acutifolius*, *Ecballium elaterium*, *Medicago lupulina*, *Salvia verbenaca*), or where information was not available, the life form of the species was checked in the field. Plants were classified as therophytes, herbaceous perennials, woody perennials, or geophytes.

We divided the species into two other categories on the basis of their total number of flowers produced: pauciflorous species produce a very limited (<10) number of flowers that are large in comparison with the plant body, while multiflorous species produce >10 flowers. *Crocus* is an example of a pauciflorous genus.

We also monitored the phenology of the flower-visiting insects (Petanidou, 1991a; Petanidou and Ellis, 1993). The period of activity of each insect species is based on the first and last observations in any year of fieldwork. This approach was taken because the numbers of observations per species in a year are generally low and tend to underestimate the period of activity. In this paper we will discuss the entomological results only to the extent that they contribute to a better understanding of the flowering patterns.

Analysis of data, definitions—The daily number of plant species in flower (DNP) was obtained from the phenological data (start and end date) for all species. For some graphs, values are smoothed by calculating the running average over 15 days. All calculations were done with an ad hoc computer program. The average DNP was calculated using the average start and end dates of the species, rather than the year-to-year actual dates. The daily number of visiting insect species (DNI) was calculated in a similar way, always based on averaged data.

As will be explained in the Results section, there are two dates on which the number of species in flower reached a local maximum. The first and higher peak occurs in spring; the second in autumn. The intervals when the DNP $\geq 50\%$ of its local maximum will be called the main and secondary flowering periods, respectively. We will

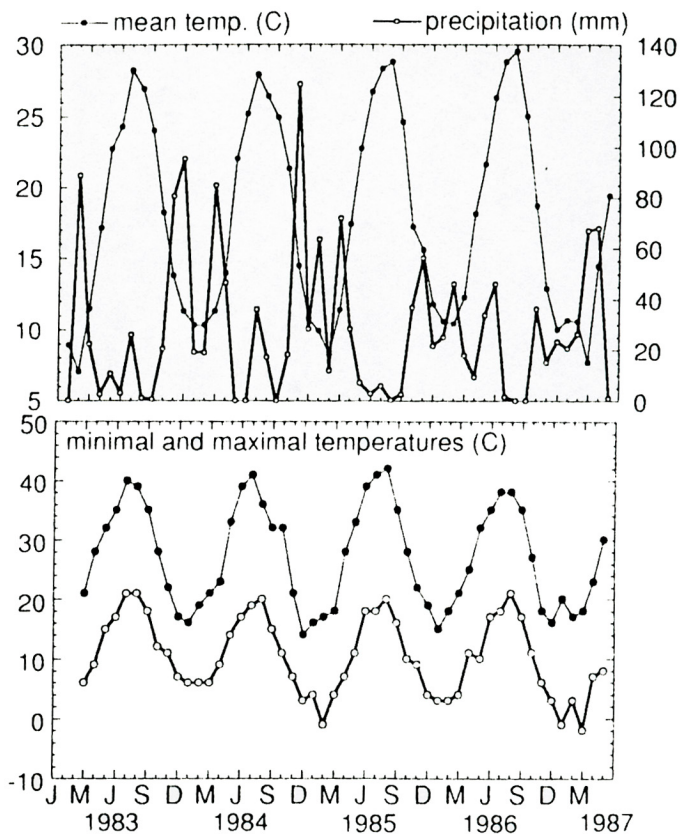


Fig. 1. Climatic data on a monthly basis, over the 4 years of study. Top: mean temperature and precipitation (Eleusis meteorological station). Bottom: absolute maximal and minimal temperatures taken at the study site.

refer to the species having their midpoint of flowering in the period between the main and secondary period as “summer species,” and to those between the secondary and main flowering period as “winter species.”

The average value of the DF (or comparable parameter) of all species flowering on a given calendar day is referred to hereafter as the average daily DF; these values always are based on averaged start and end dates of the individual species. Calculations based on the mean daily DF may give results that differ from the results obtained from raw data. The “daily-average” method is more appropriate to describe the community structure through time, while the raw, per-species values tell more about a plant’s adaptations. The midpoint for a species is halfway through its DF (cf. Anderson and Hubricht, 1940; Kochmer and Handel, 1986). A species is assigned to a particular flowering period using its midpoint.

The distributions of flowering over time of different ecological and systematic groups were compared on the basis of the average DNP over 10-day periods (thus, 36 values over the year, for almost 4 years). For comparisons between taxonomic groups, statistical analyses were limited to the four families with the highest number of species ($N \geq 10$). The resulting distributions were analyzed with an $R \times C$ test of independence, using the G -statistic (Sokal and Rohlf, 1981). Because of the large number of data rows, the Williams’ correction is unusually large; therefore

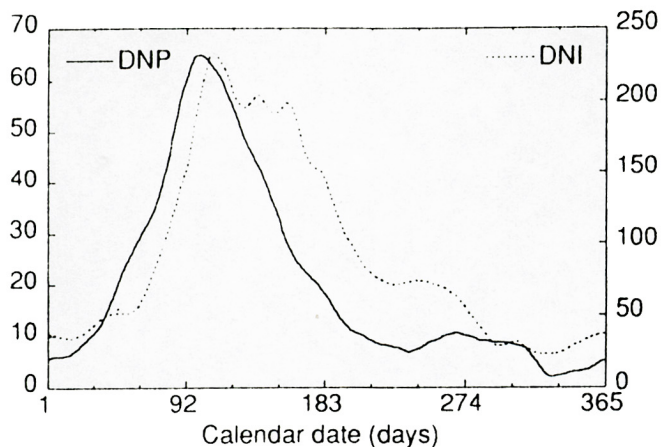


Fig. 2. Distribution of the average daily number of plant species in flower (DNP) and insect species (DNI) over the year (running averages).

G-scores with and without this correction are presented. This approach differs from that adopted by Kochmer and Handel (1986), who used Kruskal-Wallis tests to compare phenological patterns.

Estimation of the year-to-year variation of flowering time is based on the shift of the starting date of flowering of each species, compared with its mean starting date over the years the species was monitored (shift = actual minus mean). A monthly mean temperature surplus was calculated as the actual monthly mean minus the long-range monthly average, as obtained from Maheras (1983). Similarly, a monthly rain surplus was calculated as the actual monthly total rainfall minus the average over the period 1951–1985 (records from the Eleusis National Meteorological Station). To estimate the influence of climate on flowering phenology, we performed multiple stepwise regression analyses.

To compare the phenological pattern of the largest families found by us with that published by Kochmer and Handel (1986) for the same families in North Carolina, we extracted monthly numbers of flowering species from their histograms. Then we compared, for each family separately, the number of species flowering per month in the two regions. Months in which no species in either region bloomed were excluded from analysis. Significance was assessed using the *G*-statistic (Sokal and Rohlf, 1981).

In most cases the data were not normally distributed, and nonparametric tests were used, although the large number of values makes this a somewhat conservative approach. Statistical analyses were run with Statistica/Mac (*G*-tests with a program written by WNE). In a posteriori comparisons the Bonferroni correction was applied (Pagano and Gouvreau, 1993); the corrected probability will be referred to as *P*.

RESULTS

Insect visitors—Data on the pollinating fauna of the community are given in Petanidou (1991a, b) and Petanidou and Ellis (1993). The total anthophilous fauna amounted to 666 species. Figure 2 shows the temporal

distribution of the DNI (averaged over the whole study period), with the distribution of the DNP. The general congruity of the graphs is apparent ($R = 0.835$, $P < 0.000$), but there is a noteworthy lag in both the rise and the decline of the visiting fauna. As noted above, our estimates of the period of activity of insects are probably underestimates, which may account for the later peak of the DNI.

Reproductive characteristics of the flowering plants—

The number of plant species studied totaled 133 (purple and red-flowered forms of *Anemone coronaria* are treated as separate forms). Each species, along with its life form, family, flower life span, and average DF is listed in Appendix 1. Of the 51 species of therophytes, all are annuals except one semelparous biennial.

All species are chasmogamous. With the exception of *Capparis ovata*, all have diurnal flowers. All species but five have monoclinal flowers. The exceptions are *Euphorbia acanthothamnus*, *Ecballium elaterium* and *Sarcopoterium spinosum* (monoecious), *Osyris alba* (dioecious), and *Asparagus acutifolius* (trioecious).

Only 13 species were pauciflorous. They are, in order of their appearance: *Cyclamen graecum*, *Sternbergia lutea*, *Crocus cancellatus*, *C. laevigatus*, *Anemone pavonina*, *Arisarum vulgare*, *Anemone coronaria* (purple), *Gagea granatelli*, *Romulea linaresii*, *Ornithogalum exscapum*, *Iris pumila*, *Fritillaria graeca*, and *Anemone coronaria* (red). All are geophytes.

The entomophilous character of the species, suggested by their biotic pollination syndrome (Faegri and van der Pijl, 1979), was confirmed by field observations. All species were observed to be visited by insects except for *Romulea linaresii*. Only *Sarcopoterium spinosum* was found to be substantially wind-pollinated (Petanidou, unpublished data). Some species are described as partly anemophilous in the literature, but we did not verify this in the field. These are *Plantago lagopus* (cf. Stelleman and Meeuse, 1976), *Cyclamen graecum* (Petanidou and Vokou, 1990; Kugler, 1977), *Urginea maritima* (Dafni and Dukas, 1986), and *Anemone* spp. (Horovitz, 1991).

Almost all species have a single yearly flowering period. *Taraxacum officinale* is exceptional, blooming in spring and again in autumn. As its flower abundance was much higher in autumn than in spring, only its autumnal flowering is considered below.

Timing of flowering—The number of species in flower rises steeply from mid-January to early April (Fig. 2); the cumulative maximum is 67 species, which is reached on day 102. The main flowering period is between calendar days 70 and 151 (inclusive). After that, the DNP declines less steeply to mid-July, thereafter remaining at a low, more or less constant level, until early November. The lowest values of the DNP occur on days 324 through 336. The midpoints of 107 species occur in February–June, 88 of these within the main flowering period. The secondary flowering period is from days 241 to 320, with highest number of species (11) on days 262–275. Consequently, the winter species, defined above, have their midpoints in the interval 321–69.

Figure 3 shows the distribution of the DNP for the last 3 years of the study. Flowering in these years peaked

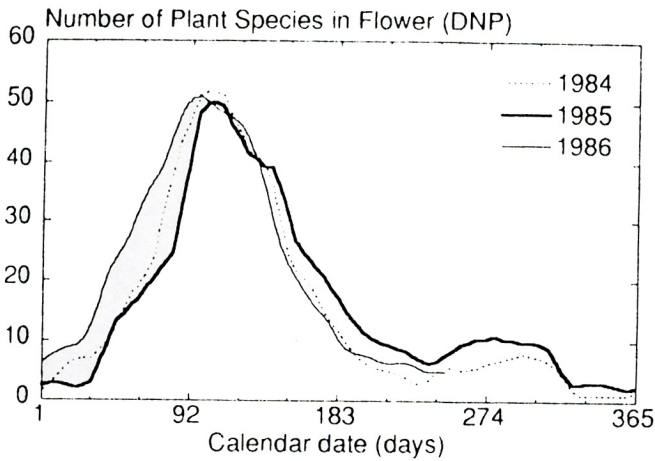


Fig. 3. Distribution of DNP over the period January 1984–September 1986 (running averages).

around a value of 50–56 species on days 95–110. The lower number of species at the peak date in the separate years is an artifact of the fact that we lack dates for some species for some years (see Materials and Methods).

Of the pauciflorous species, six are winter species and seven are nonwinter species (i.e., the first three and the last four listed in the previous section). Out of the 120 multiflorous species, only nine are winter species (in order of appearance, *Thymelaea hirsuta*, *Erica manipuliflora*, *Muscari neglectum*, *Erodium cicutarium*, *Muscari commutatum*, *Bellis annua*, *Senecio vulgaris*, *Thymelaea tartonraira*, and *Anchusa variegata*).

All four life forms peak in the main flowering period (Fig. 4). However, their patterns of flowering (based on the 10-day averages of the DNP over 1983–1986) are strongly differentiated (Table 1). A post hoc comparison showed that in all combinations the life forms are distinct ($P < 0.002$), except for the pairs woody perennials—therophytes, and woody—herbaceous perennials. Multiflorous and pauciflorous species are also distinct. Between the main families and between annuals and perennials there are no differences.

Shift in flowering time—The 4 years differ significantly in the magnitude of the shift in the time when species

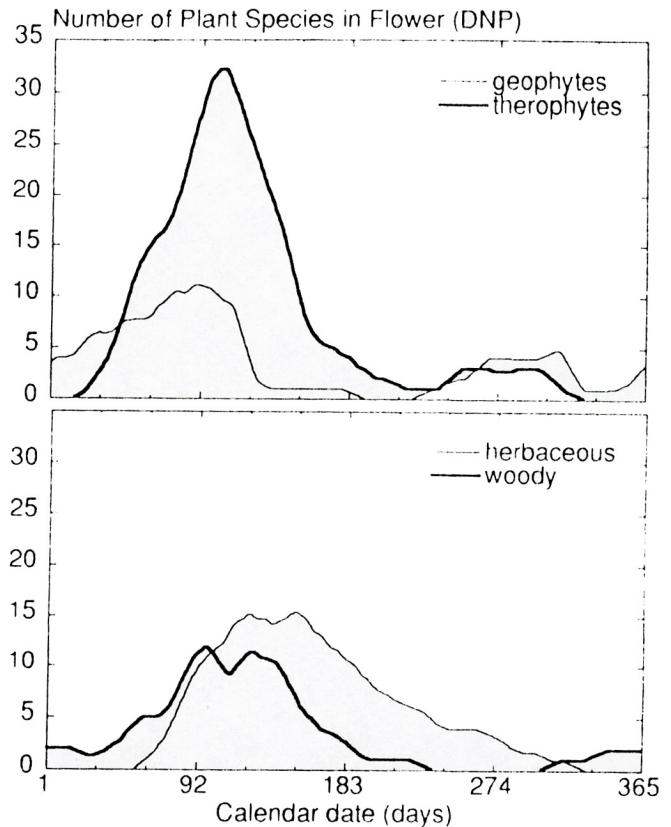


Fig. 4. Distribution of average DNP for the life forms over the years 1984–1986 (running averages).

begin to flower (Kruskal-Wallis $H_{(3, 344)} = 97.282$, $P < 0.000$). Most species came into flower relatively early in 1986, relatively late in 1985, and close to their average in 1984 (Fig. 5). All taxonomic and life form categories show between-year differences in the shift of their start date of flowering (Table 2).

Over 1984–1986, the species were significantly correlated in the shift of their start of flowering (Kendall's concordance_(2, 86) = 0.430, $P < 0.000$). Neither the life forms nor the four main plant families differed in the absolute magnitude of the shift of their start dates over

TABLE 1. Difference between plant groups, as to four time parameters.

	Flowering time				Amount of shift ^c				Duration of flowering (DF)				Flower life span			
	Test ^d	Value	df	Sig. ^e	Test ^d	Value	N1/N2	Sig.	Test	Value	N1/N2	Sig.	Test	Value	N1/N2	Sig.
Families ^a	<i>G</i>	314.789	294	—	<i>H</i>	2.176	3/145	—	<i>H</i>	10.057	3/145	*	<i>H</i>	13.973	3/55	**
	<i>Gadj</i>	195.187	294	—												
Life forms ^b	<i>G</i>	903.607	405	***	<i>H</i>	1.671	3/344	—	<i>H</i>	2.031	3/344	—	<i>H</i>	22.764	3/133	***
	<i>Gadj</i>	696.874	405	***												
Annuals-Perennials	<i>G</i>	132.787	135	—	<i>U</i>	13,442.5	139/205	—	<i>U</i>	13,479.5	139/205	—	<i>U</i>	1,759.0	51/82	—
	<i>Gadj</i>	98.376	135	—												
Multi-Pauciflorous	<i>G</i>	353.483	107	***	<i>U</i>	3,089.0	313/31	***	<i>U</i>	4,354.5	313/31	—	<i>U</i>	109.5	13/120	***
	<i>Gadj</i>	269.958	107	***												

^a Compositae, Labiatae, Leguminosae, Liliaceae.

^b Geophytes, herbaceous and woody perennials, therophytes.

^c Absolute value of shift of start date of flowering.

^d *G*-test (*G*), *G*-test with Williams' correction (*Gadj*), Kruskal-Wallis (*H*) and Mann-Whitney (*U*).

^e * 0.05 > *P* > 0.01; ** 0.01 > *P* > 0.001; *** 0.001 > *P*.

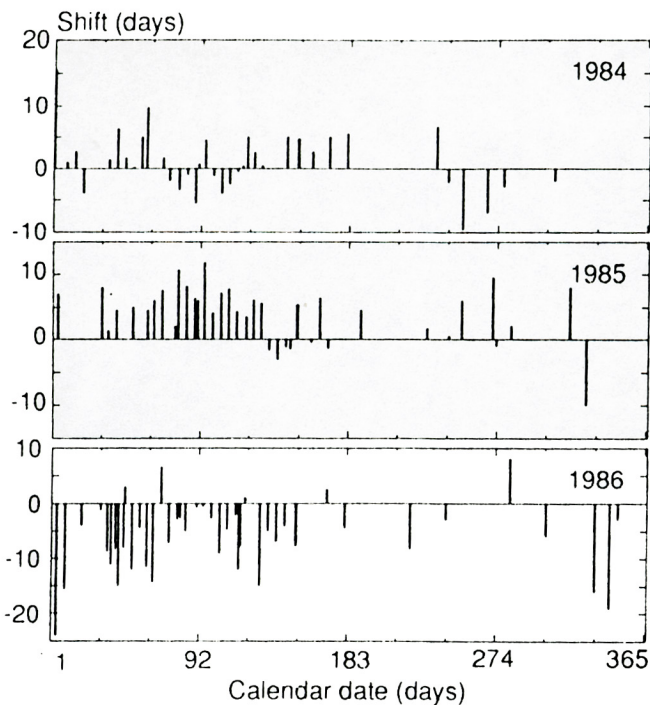


Fig. 5. Shift of the start dates of flowering in the years 1984–1986. The vertical axis gives the shift (in days), i.e., the actual date minus the average for that species over all the years of observation. Each bar signifies the average shift for those species that started flowering on a particular date.

the 4 years of the study (Table 1). In other words, within both groupings all members are similarly responsive to yearly climatic variations. The multiflorous and pauciflorous species do, however, differ in this respect, shifting 5.4 ± 0.25 and 8.6 ± 0.58 days, respectively. The mean value of the absolute shift of start of winter species is 9.9 ± 1.15 days, and that of nonwinter species is 5.6 ± 0.24 (Mann-Whitney $U = 2,668$, $P = 0.001$).

The effects of rainfall and temperature on the start and end of flowering are summarized in Table 3. They were studied as follows. In a first (forward) stepwise multiple regression analysis, the shift of the start date of flowering was used as the dependent variable, and the temperature and rainfall surpluses of both the present and the previous month as independent variables. In the second regression the shift in the end date of flowering was the dependent variable, and the four climatic variables just mentioned,

TABLE 2. Kruskal-Wallis tests of between-years differences in the shift of the start date of flowering.

	<i>H</i>	<i>df</i>	<i>P</i>
Geophytes	13.260	2/54	***
Therophytes	52.161	3/139	***
Perennials	47.454	3/205	***
Multiflorous	89.105	3/313	***
Pauciflorous	8.315	2/31	**
Compositae	19.691	3/64	***
Labiatae	14.010	3/32	**
Leguminosae	18.528	3/26	***
Liliaceae	9.917	2/23	**

TABLE 3. Results of two stepwise multiple regression analyses of the shift in the start and end dates of flowering, as affected by four climate parameters (listed in the order of entry in the regression).

	Start of flowering		End of flowering	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
Previous month temperature ^a	0.251	0.000	0.490	0.181
Month rain ^b	0.269	0.066	0.493	0.254
Previous month rain ^c	0.281	0.117	0.493	0.771
Month temperature ^d	0.285	0.356	0.493	0.786
Shift in start date ^e	—	—	0.485	0.000

^a Temperature surplus of the previous month.

^b Monthly rainfall surplus.

^c Rainfall surplus of the previous month.

^d Monthly temperature surplus.

^e For the end of flowering, the shift in the start of flowering was used as a fifth independent variable.

plus the shift in the start of flowering, were independent. The main results are that the start of flowering is primarily influenced by the previous month's temperature (warmer → earlier flowering) and to a lesser, nonsignificant degree by the amount of rain in the current month (drier → earlier). The previous month's precipitation has no significant effect. The shift at the end of flowering is not significantly correlated with climatic data (Table 3).

The average of the absolute magnitude of shift in the end date of flowering (5.7 ± 0.25 days, $N = 344$) is approximately equal to that of the starting date (5.3 ± 0.28 days, $N = 344$). The shifts in start and end, over all species and years, are significantly correlated: $R = 0.497$, $N = 344$, $P < 0.001$.

At the specific level, the strongest shifters in flowering time (manifesting a shift of the absolute magnitude of approximately 1 month between 2 years) are those flowering in late winter–early spring. These are *Capsella bursa-pastoris*, *Senecio vulgaris*, *Bellis annua*, *Sherardia arvensis*, *Trifolium stellatum*, *Plantago lagopus*, and *Silene colorata* among the therophytes, and *Gagea granatelli*, *Romulea linairesii*, *Ornithogalum* spp., *Anemone pavonina*, and *Arisarum vulgare* from the geophytes. There are only a few strong shifters among the perennials, i.e., *Fumaria arabica* and *Cistus salvifolius* (woody), and *Reichardia picroides* (herbaceous).

For the 115 species whose starting date has been recorded in at least 2 years, the absolute values of the shift of their start of flowering were normally distributed (Kolmogorov-Smirnov $d = 0.100$, $P < 0.20$), although the distribution is somewhat leptokurtic (kurtosis = 0.588). This means that there is no excess of close-to-zero shift values, which could suggest photoperiodic control of the onset of flowering.

DF—Figure 6 shows the distribution of the average DF of multiflorous and pauciflorous species over the year (cf. Appendix 1 and Table 4). In the course of the year, the average daily DF is negatively correlated with the DNP and DNI ($R = -0.677$, $P < 0.000$ and $R = -0.359$, $P < 0.000$, respectively; cf. also Table 5). The average DF of all species is 55.1 ± 2.23 days.

The average DF for the winter species is 66.4 ± 8.09 , and for the nonwinter species 53.7 ± 2.29 (Mann-Whitney $U = 598$, $P = 0.041$). Species having their midpoint in

TABLE 4. Summarized data on duration of flowering (DF) and flower life span, broken down by phenological groups, life forms, and main families.

	N	DF		Flower life span	
		Mean (days)	SE	Mean (days)	SE
All species	133	55.1	2.25	3.5	0.30
Main flowering period	88	51.5	2.11	3.2	0.30
Between main and secondary	20	66.6	8.92	2.6	0.52
Secondary flowering period	10	46.9	6.79	2.7	0.61
Winter	15	66.4	8.10	7.1	1.60
Geophytes	27	49.9	4.05	7.0	5.59
Therophytes	51	54.5	2.95	2.6	0.23
Herbaceous perennials	33	59.7	5.74	2.5	0.32
Woody perennials	22	56.1	29.78	2.9	0.49
Multiflorous	120	55.9	2.42	2.9	0.24
Pauciflorous	13	48.0	5.42	8.6	1.54
Compositae	23	54.6	5.38	1.5	0.14
Labiatae	10	45.2	4.64	2.3	0.19
Leguminosae	10	38.9	3.91	2.9	0.28
Liliaceae	12	49.6	6.05	3.7	0.87

the main and secondary flowering period do not differ from those that have their midpoint outside of these periods (Mann-Whitney $U = 1,359$, $P = 0.069$; averages are 51.0 ± 2.01 , and 66.5 ± 6.08 , respectively).

The DF does not differ among the life forms (Table 1). Neither is there a significant difference between therophytes and perennials nor between pauciflorous and multiflorous species. The four main families do differ (Table 1); values are given in Table 4. In a posthoc comparison only the difference between Compositae and Leguminosae is significant ($P' = 0.020$).

Table 5 shows that for multiflorous species the daily averages of DF and both DNI and DNP are negatively correlated, except in the secondary period of flowering. Pauciflorous species show a negative correlation in the main flowering period and a positive correlation in the secondary flowering period and winter.

The total range of a family's flowering time is a positive function of the number of species in the family (correlation, over the 38 families, average values of DF, $R = 0.640$, $P < 0.000$). The ranges for the four main families are: Compositae 28–323 (295 days), Labiatae 43–285 (142

days), Leguminosae 76–165 (89 days), and Liliaceae 244–185 (306 days).

Flower life span—The average daily flower life span for multiflorous and pauciflorous species is presented in Fig. 6. The main families show significant differences in flower life span (Table 1). Summarized data for life forms and the major families are given in Table 4 (cf. Appendix 1). Significant differences exist between Compositae and Labiatae ($P' = 0.021$) and Compositae and Leguminosae ($P' = 0.006$). Also, the life forms differ significantly in flower life span, but this significance is a consequence of a greater flower life span of pauciflorous species, which in majority are composed of geophytes. In fact, only the three a posteriori comparisons involving geophytes are significant ($P' < 0.005$). The average flower life span for the winter species is 7.1 ± 1.60 , and for the nonwinter species 3.0 ± 0.24 (Mann-Whitney $U = 481.0$, $P = 0.004$). Species with long-lived flowers (flower life span > 4 days) are not equally distributed over the year ($G_{adj(3)} = 16.587$, $P = 0.001$), but are concentrated in winter ($P' < 0.000$).

The daily average of the flower life span is negatively correlated with the DNP and DNI ($R = -0.402$, $P < 0.000$ and $R = -0.581$, $P < 0.000$, respectively). For multiflorous species it is negatively correlated with the DNI in winter and main flowering period, but positively in between. For pauciflorous species this correlation, when relevant, is always positive (Table 5).

Table 6 shows the pattern of correlation between average daily DF and flower life span. In general the correlation is positive, except for the period between main and secondary peaks. This is caused mainly by the flowering in this period of some species with a very long DF, in particular the two *Chondrilla* species, *Echium angustifolium*, and *Capparis ovata* (cf. also Fig. 6).

The North Carolina flora—We reanalyzed the difference in time of flowering of the 24 main families from North Carolina, and found this to be highly significant ($G_{adj(183)} = 837.047$, $P < 0.000$). We also compared the phenological pattern of the four major families (using the averaged dates) with those obtained for the same families by Kochmer and Handel (1986). We used their method of attributing species to a month on the basis of its midpoint of flowering. Because there are large climatological

TABLE 5. Spearman's rank correlation of daily averages of the DF and of the flower life span with DNI and DNP (broken down into multiflorous and pauciflorous species) in the four flowering periods.

Days	Period	Duration of flowering (DF)				Flower life span			
		Multiflorous		Pauciflorous		Multiflorous		Pauciflorous	
		R	P	R	P	R	P	R	P
Average daily number of insect species (DNI)									
70–151	Main	-0.798	***	-0.016	—	-0.525	***	0.560	***
152–240	Between	-0.967	***			0.555	***		
241–320	Secondary	0.877	***	0.800	***	0.434	***	0.816	***
321–69	Winter	-0.860	***	0.849	***	-0.781	***	0.318	***
Average daily number of plant species (DNP)									
70–151	Main	-0.267	—	-0.277	0.057	0.148	—	0.260	0.074
152–240	Between	-0.996	***			0.526	***		
241–320	Secondary	0.215	0.056	0.415	***	-0.324	**	0.490	***
321–69	Winter	-0.926	***	0.830	***	-0.910	***	0.219	*

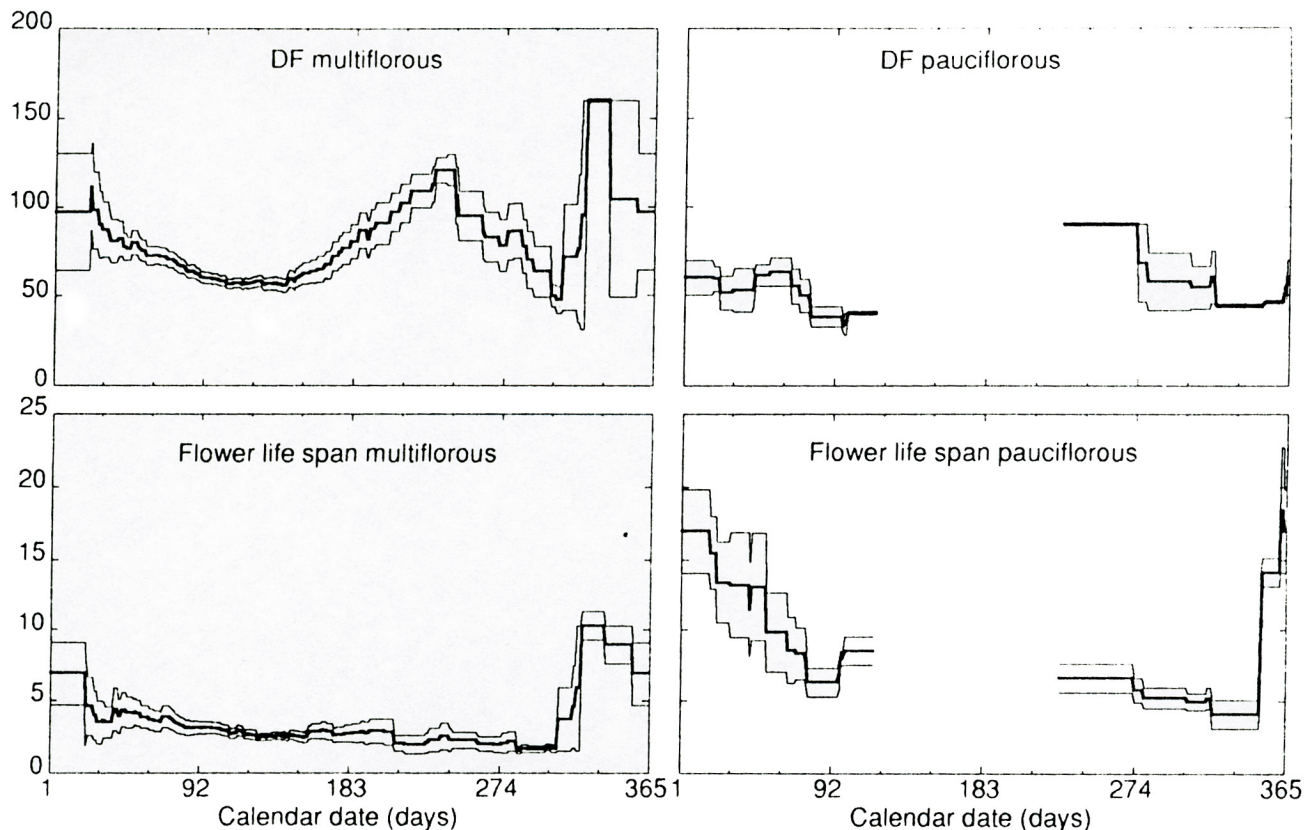


Fig. 6. Distribution of the average daily duration of flowering (DF) and average flower life span of the species in bloom over the year (\pm SE, thin lines), for multiflorous and pauciflorous species separately.

differences between the regions compared, matching the two phenological patterns presented a problem. We therefore shifted one pattern relative to the other and selected the shift that gave maximal congruence. Table 7 presents the comparison when there is no shift (January matches January) and when January in NC matches April in Greece. In the latter analysis the distributions of Labiatae, Liliaceae, and perhaps Leguminosae, are not distinct. Those of Compositae differ significantly, and the overall difference in distribution of flowering still is highly significant.

DISCUSSION

Phylogenetic constraints—The four largest plant families do not differ significantly in flowering times (Table 1). This is at variance with the prediction of Kochmer

and Handel (1986) that phylogenetic constraints are effective. According to their second prediction, a family's total range of flowering should be positively correlated with the number of species; moreover this total range should be significantly shorter than the flowering range of the whole flora. Indeed, we find a positive correlation between the size and the range of a family, but this is to be expected. On the other hand, because Liliaceae and Compositae have ranges of 306 and 295 days, respectively, close to what is maximally possible, we conclude that the second prediction is not strongly supported. The third prediction, that of the global property of phenologies, cannot be fully corroborated either; the four main families do seem to flower in the same order both in Greece and Carolina (as far as "order" can be applied to this type of data). However, the times of flowering of at

TABLE 6. Spearman's rank correlation between the average daily DF and flower life span in the four flowering periods for multiflorous and pauciflorous species. All-year and all-species values are given as well.

Days	Period	Multiflorous		Pauciflorous		All	
		R	P	R	P	R	P
Average daily values of DF and flower life span							
70–151	Main	0.738	***	0.720	***	0.697	***
152–240	Between	–0.536	***			–0.046	—
241–320	Secondary	0.600	***	0.971	***	–0.478	***
321–69	Winter	0.910	***	0.456	***	0.406	***
1–365	Whole year	0.278	***	0.182	**	0.037	—

least the Compositae and perhaps the Leguminosae differ between the two regions (Table 7). Contrary to the conclusions of Kochmer and Handel (1986), we therefore conclude that, along with possible phylogenetic constraints, regional differences (either ecological or biogeographical) play a decisive role in determining flowering time.

The discrepancy between the results of Kochmer and Handel and ours is not really surprising. Kochmer and Handel based their conclusions largely on a comparison of two floras that share a very comparable climate and common biogeographical history (e.g., Pielou, 1979). That the four main families of the phrygana did not differ in flowering time, contrary to the situation in North Carolina, might be an artifact of our small sample, but is more probably connected with the short favorable period for blooming.

Life history constraints—The finding that there are significant differences in flowering phenology among the life forms (Table 1; Fig. 4) means that how a plant species overcomes the most critical period of the year is correlated somehow with its flowering phenology. This is surprising, because in mediterranean systems flowering is ruled by factors such as climate and probably competition for pollination, while life forms express the ability of the plant to overcome the dry summer, during which flowering is very scarce (Moldenke, 1976, 1979; Johnson, 1993). As Fig. 4 shows, the total flowering span of each of the life forms covers most of the year, which refutes the second prediction of Kochmer and Handel. It was not possible to compare the phenologies of life forms between North Carolina and our study site to test the third prediction, since life form data for North Carolina could not be derived from their paper.

The prediction that therophytes, being annuals, are more strongly dependent upon pollinators than perennials, and therefore should be the most strongly differentiated in time of flowering, is refuted (Tables 1, 4). We hypothesize, therefore, that annuals compensate for their short life cycle by having long-lived seeds (Harper, 1977). The importance of the seed bank in phrygana becomes vividly apparent after a fire (Arianoutsou-Faraggitaki and Margaris, 1981). It is possible, however, that therophytes have a competitive edge over other species due to their high population densities, and concomitant flower abundance.

Multiflorous and pauciflorous species—Pauciflorous species are well differentiated from the multiflorous species in the greater unpredictability of their start date of flowering and relatively long duration of their flowers and their time of flowering (Tables 1, 4, 5, 7; Fig. 6).

The pauciflorous habit is not exclusive to the Mediterranean region, or even the mediterranean climate (Dafni, Shmida, and Avishai, 1981; Shmida and Dafni, 1989; Cohen and Shmida, 1993). Genera like *Colchicum*, *Narcissus*, *Galanthus*, *Trillium*, and *Arum* occur in temperate climates as well. Nevertheless, *Crocus*, *Tulipa*, *Scilla*, *Colchicum*, and *Cyclamen* are much more speciose in the Mediterranean region. This is generally explained by their geophytic habit, but we feel that the pauciflorous habit provides these species with an additional adaptation.

TABLE 7. Test of the difference in distribution over time of the four main families in Daphni and North Carolina, both "as is," and shifted to match Greek January with American April. (Note that the test statistic for the overall significance is *G*, rather than *Gadj*, which is not additive.)

	Amount of shift					
	January–January			January–April		
	<i>Gadj</i>	df	<i>P</i>	<i>Gadj</i>	df	<i>P</i>
Compositae	41.455	9	0.000	20.010	9	0.018
Labiatae	24.355	7	0.001	2.956	7	0.814
Leguminosae	32.246	5	0.000	9.863	5	0.079
Liliaceae	26.763	9	0.002	11.754	9	0.302
Total <i>G</i>	176.23	30	0.000	73.34	30	0.000

Probably, the adaptation is not the long flower life span, but the large flower size. This, we assume, limits the number of flowers that can be produced and in turn forces the species to display their flowers over a flowering period that cannot be reduced in time (compared to the multiflorous species), because of the unpredictable weather and low number of flower visitors. It is harder to speculate on the advantage of large flowers. We tentatively suggest that it is important to maximize visual attraction in the face of low visitor density and small plant size; fragrance is probably an inefficient attractant in the relatively cold and windy autumn and spring. The absence of insect visitation to *Romulea linarsisii*, a pauciflorous species flowering at this time (end January–mid-February), may be attributed to its small population (30 individuals).

Because pauciflorous species mainly flower in autumn and early spring in temperate regions as well, we do not believe that their time of flowering in the Mediterranean should be interpreted as the result of a shift in time of flowering, allegedly to avoid competition with multiflorous species as has been hypothesized by Dafni and Dukas (1986), and Dafni and Werker (1982) for some geophytes. Rather, it seems that a preadaptation enabled these genera to flourish and diversify after the time the local summer-rain climate changed into the present winter-rain climate, approximately 3.2 million years before Present (BP) (Suc. 1984).

Mediterranean climate constraints—Seasonality—Phrygana, like all mediterranean ecosystems, is very seasonal, predominantly characterized by a wet, mild winter and a hot, dry summer (Aschmann, 1973). Both the phenologies of plants and their visitors are very seasonal here (Fig. 2). Flowering starts by late winter and ends in July. From February to June, 80% of the insect-pollinated species flower; the midpoint of the flowering period of 66% of the species lies in the main flowering period (mid-March through May). The maximum DNP is in April, which is similar to Zohary's (1962) description of comparable Mediterranean ecosystems in Israel. The flowering of a mediterranean chaparral in California has a seasonal pattern that is similar to that of the Greek phrygana; its main flowering season is from mid-February to mid-July, with a peak in May (Mooney, Parsons, and Kummerow, 1974; Moldenke, 1979). Moldenke likewise reported that flowering in Chilean mediterranean scrub communities is limited in time.

Unlike the above results, which suggest a strong seasonality of flowering, Herrera (1986) found that flowering in a comparable Spanish shrub community is rather continuous throughout the year. He attributed this to the high "ecophysiological heterogeneity" of the species he studied. Likewise, the low-altitude plots that Arroyo (1990) followed in southern Spain show a rather less seasonal distribution in the flowering of their shrub flora, although, here too, is a clear peak in April–May. Similarly, Johnson (1993), in a study of the flowering phenology of the winter rainfall part of Cape region, concluded that at least 20% of the flora is in flower at any time of the year. In phrygana, the corresponding value is only 1.5%. We assume that this may be connected to the relatively high summer rainfall that prevails in the mediterranean climate Cape (> 50 mm/month).

Two-seasoned flowering phenology—Neither the phenology of the entire plant spectrum nor that of any of the plant groups (ecological or taxonomic) is strongly bimodal. This is in agreement with Johnson (1993) and differs from the situation that is normal in temperate floras (Kochmer and Handel, 1986 and literature cited therein). Nonetheless, geophytes and therophytes have a secondary, autumnal flowering period (Fig. 4). It is unlikely, however, that the seemingly analogous flowering strategies in the mediterranean and temperate ecosystems are ecologically convergent. Bimodality in the case of temperate ecosystems is attributed to the heterogeneity of the sample, either by being composed of species from different habitat types, or, more probably, different day-length regimes (Anderson and Hubricht, 1940; Jackson, 1966). As regards the phrygana, there is little reason to adopt the first explanation. As we demonstrated, it is not likely that photoperiodic response plays a role in the phryganic flora; this is not surprising, given the latitude of Greece.

Inconstancy of the flowering time—Flowering time of the individual plant species appears to vary between years (Figs. 3, 5; Table 2). This is an element of the generally strong year-to-year variations of Mediterranean communities (O'Toole and Raw, 1991; Petanidou and Ellis, 1993). On a shorter time scale there are additional fluctuations, which are most strongly correlated with the temperature of the previous month (Table 3). It is interesting to note that temperature, rather than amount of precipitation, seems to trigger flowering; perhaps temperature is a more reliable predictor of the progression of the season.

The shift of the start of flowering is independent of either phylogenetic or life history affiliations, implying that as to their starting, all species respond similarly to climatic variations. The shift appears to be particularly pronounced in the case of the species flowering in late winter–early spring; this apparently is a response to the greater unpredictability of the weather in winter time.

DF—The average DF over the whole year is 55 days, and Herrera (1986) found a value of 75 days for a Spanish shrubland. These values are high when compared with results obtained either from temperate or tropical communities. Pojar (1974) found a mean DF of 46 days in a salt marsh, 27 days and 32 days in two *Sphagnum* bogs,

and 23 days in a subalpine meadow in British Columbia. According to data presented by Lack (1982), the ten main insect-pollinated species in a British chalk grassland have a mean DF of 42 days. In lowland Costa Rica, Frankie, Baker, and Opler (1974) found a mean DF of 38–39 days. In two other studies, based on pooled community data, the results point in the same direction: Heinrich (1976) found values between 18 and 32 for undisturbed North American bog and woodland habitats (although native and exotic plants of disturbed habitats flowered much longer, i.e., 43 and 57 days, respectively). Parrish and Bazzaz (1979) found DF values ranging from 31 to 52 days in successional prairie communities. The long DF in the phrygana could be related to year-to-year unpredictability in severity of the drought stress.

The DNP rises steeply to a maximum in mid-April (Fig. 2). This coincides with a decline in the DF. This general result is in agreement with Pojar (1974), who studied temperate communities in North America. In this period, when most of the coexisting species are blooming, it must be of great advantage for a species to flower synchronously and briefly, in order to enhance the number of flowers. This maximizes its ability to compete for pollinators. Generally, the daily average DF correlates negatively with the average DNI and the average DNP. However, the correlation between DNI and both average daily DF and flower life span becomes positive in the secondary flowering period (for multiflorous and pauciflorous species; Table 5). We have no data to prove it, but our field experience is that at this time the density of visitors is low, although the taxonomic diversity still is appreciable. Plants would be expected to respond to this pollinator shortage by extending their DF and flower life span.

Flower life span—The average flower life span is 3.4 days. This value is intermediate between the relatively high values known for temperate forests and prairies, and the lowest values, which come from tropical forests (Primack, 1985). Primack hypothesized that plants in dry, hot environments are expected to have short-lived flowers in order to reduce drought stress. This implies that species with ephemeral flowers mainly flower in the driest season. Our data do not support this prediction. The highest values of flower life span, both for multiflorous and pauciflorous species, occur in winter, confirming Kerner von Marilaun's (1891) old hypothesis that a long flower life span should coincide with relatively unpredictable weather conditions. Kerner von Marilaun also pointed out the relatively long flower life spans in species with very limited number of flowers.

At the community level, DF and flower life span are positively correlated in winter and the main flowering period, but negatively in the secondary period. However, when multiflorous and pauciflorous species are separated, strong positive correlations emerge in almost all periods, including the secondary peak. It appears that multiflorous and pauciflorous species have different trends that, when pooled, result in a diminished overall correlation, even leading to a negative one in the secondary period. Our explanation is that although the DF of multiflorous and pauciflorous species do not differ, the flower life span in pauciflorous species is almost twice as high. This produces a negative correlation.

At the level of individual species, there is a negative correlation between DF and flower life span in the main flowering period and a positive one in the secondary flowering period. It may be hypothesized that there is a trade-off between the DF and the flower life span in order to achieve a certain degree of reproductive success. This simple rule would be broken in the secondary flowering period when the low number of pollinators forces species to extend the life of flowers, even at the expense of additional risk of predation and of transpiration loss.

Competition for pollination—Raynal and Bazzaz (1975) and Parrish and Bazzaz (1979) found that the flowering time of individual plant species is largely determined by intrinsic factors. However, it is widely held that the flowering time that maximizes the chance for pollination is determined extrinsically, by the presence of their pollinators and competing plant species (Bawa, 1983; Waser, 1983). Bawa (1983) sums up several reasons why it is advantageous to have a long DF: it allows a better distribution of investment over flowers and fruits, increases the degree of outcrossing while reducing the degree of geitonogamy, and spreads the risks of flowering over time. There is one main force that counters the selection pressure to extended flowering, i.e., competition. We believe that concentrated flowering during the main flowering period must indeed entail at least some competition; in fact it is in this period that the average daily DF is conspicuously low. The coincidence of the maximal DNP with the maximum of nectar supply (Petanidou, 1991a; Petanidou and Vokou, 1993) supports this assertion.

Other correlations are more ambiguous. The close correlation between DNP and DNI together with the well-marked peaks of both values suggest that competition is unavoidable in the peak period; yet it is not possible to decide which factor is causal (Fig. 2). Moreover, the peaks coincide with the narrow climatic window that acts as the driving variable. Staggered flowering in a community was hypothesized in a series of studies to have evolved under the selective pressure of competition for pollination with co-flowering species (Mosquin, 1971; Pojar, 1974; Heinrich, 1976; Stiles, 1977; Parrish and Bazzaz, 1979; Lack, 1982; Bawa, 1983; Petanidou and Vokou, 1993). Yet it is hardly possible to disentangle this signal from stochastic effects (Rabinowitz et al., 1981; Rathcke and Lacey, 1985). Finally, models of staggering necessarily assume a more or less aseasonal climate.

The visiting fauna of this study site is, with 666 species, the richest recorded so far (Petanidou and Ellis, 1993). The large majority of this diversity is squeezed, like that of the plants, in the main flowering period. It does not seem probable, therefore, that plants have to compete for pollinator visits per se at this time. Their main problem could be a high level of improper pollen transfer (Rathcke, 1983). It therefore is relevant that 262 of the visiting species are bees, which generally show a relatively high degree of fidelity (Linsley, 1958; Moldenke and Lincoln, 1979).

Conclusion—In the phrygana the balance between phylogenetic constraints and the exigencies of climate appears to be strongly shifted toward the latter. It seems that the flora is composed of two fundamentally different ele-

ments: multiflorous species that flower in a short favorable period and then meet a concentrated array of visitors, and pauciflorous species that flower in the winter, thereby evading both the summer drought and the overwhelming majority of the multiflorous species.

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APPENDIX 1. The 133 plant species occurring in the study site of Daphni. Family, life form, flower life span, and average first and last day of flowering are given following the species' names.

Abbreviations of life forms and families are as follows. g: geophytes; h: herbaceous perennials; t: therophytes; w: woody perennials; Ac: Acanthaceae; Am: Amaryllidaceae; Ar: Araceae; B: Boraginaceae; C: Cistaceae; Cc: Cucurbitaceae; Cm: Campanulaceae; Cn: Convolvulaceae; Co: Compositae; Cp: Capparidaceae; Cr: Caryophyllaceae; Cu: Cruciferae; D: Dipsacaceae; Er: Ericaceae; Eu: Euphorbiaceae; Ge: Geraniaceae; Gl: Globulariaceae; Gu: Guttiferae; I: Iridaceae; La: Labiatae; Le: Leguminosae; Li: Liliaceae; Ln: Linaceae; M: Malvaceae; Or: Orchidaceae; Ox: Oxalidaceae; Pa: Papaveraceae; Pl: Plantaginaceae; Pr: Primulaceae; Ra: Ranunculaceae; Rb: Rubiaceae; Re: Resedaceae; Ro: Rosaceae; Rt: Rutaceae; Sa: Santalaceae; Sc: Scrophulariaceae; Th: Thymelaeaceae; U: Umbelliferae.

Plant species	Family	Life form	Flower life span	First date	Last date
<i>Acanthus spinosus</i> L.	Ac	h	5.0	129	155
<i>Alcea pallida</i> (Willd.) Waldst. & Kit.	M	h	3.5	145	175
<i>Alkanna tinctoria</i> (L.) Tausch	B	h	1.0	62	129
<i>Allium neapolitanum</i> Cyr.	Li	g	2.6	104	185
<i>Allium subhirsutum</i> L.	Li	g	3.9	90	122
<i>Anagallis arvensis</i> L.	Pr	t	1.2	83	134
<i>Anchusa undulata</i> L.	B	h	1.0	87	166
<i>Anchusa variegata</i> (L.) Lehm.	B	t	2.5	35	88
<i>Anemone coronaria</i> L. (purple color)	Ra	g	14.0	364	77
<i>Anemone coronaria</i> L. (red color)	Ra	g	8.5	77	117
<i>Anemone pavonina</i> Lam.	Ra	g	14.1	350	30
<i>Anthyllis hermannaiae</i> L.	Le	w	3.8	117	147
<i>Arisarum vulgare</i> Targ.-Tozz.	Ar	g	22.7	362	52
<i>Asparagus acutifolius</i> L.	Li	g	1.0	262	274
<i>Asphodelus aestivus</i> Brot.	Li	g	1.0	57	114
<i>Astragalus monspessulanus</i> L.	Le	h	1.0	81	124
<i>Ballota acetabulosa</i> (L.) Bentham	La	h	1.4	145	175
<i>Bellardia trixago</i> (L.) All.	Sc	t	1.7	104	147
<i>Bellis annua</i> L.	Co	t	1.4	28	85
<i>Biscutella didyma</i> L.	Cu	t	2.3	57	102
<i>Calendula arvensis</i> L.	Co	t	1.4	45	115
<i>Campanula drabifolia</i> Sibth. & Sm. subsp. <i>drabifolia</i>	Cm	t	3.0	102	134
<i>Capparis ovata</i> Desf.	Cp	w	1.0	147	229
<i>Capsella bursa-pastoris</i> (L.) Medicus	Cu	t	2.5	52	97
<i>Cardaria draba</i> (L.) Desv.	Cu	h	3.0	88	132
<i>Carduus pycnocephalus</i> L. subsp. <i>albidus</i> (Bieb.) Kazmi	Co	t	2.7	100	148
<i>Centaurea orphanidea</i> Heldr. & Sart. ex Boiss. subsp. <i>orphanidea</i>	Co	t	1.1	150	180
<i>Centaurea raphanina</i> Sibth. & Sm. subsp. <i>mixta</i> (DC.) Runemark	Co	h	3.0	92	142
<i>Chamomilla recutita</i> (L.) Rauschert	Co	t	1.2	89	137
<i>Chondrilla juncea</i> L.	Co	h	1.0	170	287
<i>Chondrilla ramosissima</i> Sibth. & Sm.	Co	h	1.0	170	302
<i>Chrysanthemum coronarium</i> L.	Co	t	1.0	100	156
<i>Cistus parviflorus</i> Lam.	C	w	1.0	94	156
<i>Cistus salvifolius</i> L.	C	w	1.0	84	124
<i>Convolvulus althaeoides</i> L. subsp. <i>tenuisimus</i> (Sibth. & Sm.) Stace	Cn	h	1.0	108	169

APPENDIX 1. Continued.

Plant species	Family	Life form	Flower life span	First date	Last date
<i>Convolvulus arvensis</i> L.	Cn	h	1.0	144	195
<i>Convolvulus cantabrica</i> L.	Cn	h	1.0	146	192
<i>Crocus cancellatus</i> Herbert	I	g	4.2	280	317
<i>Crocus laevigatus</i> Bory & Chaub. in Bory	I	g	4.1	306	350
<i>Crupina crupinastrum</i> (Moris) Vis.	Co	t	1.5	119	149
<i>Cyclamen graecum</i> Link	Pr	g	6.6	229	320
<i>Daucus guttatus</i> Sibth. & Sm.	U	t	3.0	122	180
<i>Delphinium peregrinum</i> L.	Ra	t	9.7	159	210
<i>Dittrichia graveolens</i> (L.) W. Greuter	Co	t	2.0	280	320
<i>Ebenus sibiricus</i> DC.	Le	h	3.1	115	168
<i>Echallium elaterium</i> (L.) A. Richard in Bory	Cc	h	6.0	144	284
<i>Echinops microcephalus</i> Sibth. & Sm.	Co	h	3.5	176	204
<i>Echium angustifolium</i> Miller	B	h	1.0	117	238
<i>Erica manipuliiflora</i> Salisb.	Er	w	7.6	338	22
<i>Erodium cicutarium</i> (L.) L' Hér. in Aiton subsp. <i>ciutarium</i>	Ge	t	1.0	23	114
<i>Erodium malacoides</i> (L.) L' Hér. in Aiton	Ge	t	1.0	40	136
<i>Eruca vesicaria</i> (L.) Cav. subsp. <i>sativa</i> (Miller) Thell. in Hegi	Cu	t	3.5	83	144
<i>Eryngium campestre</i> L.	U	h	2.8	170	216
<i>Euphorbia acanthothamnus</i> Heldr. & Sart. ex Boiss.	Eu	w	2.0	54	104
<i>Fritillaria graeca</i> Boiss. & Spruner in Boiss. subsp. <i>graeca</i>	Li	g	7.4	71	99
<i>Fumana arabica</i> (L.) Spach	C	w	1.0	78	146
<i>Fumana thymifolia</i> (L.) Spach ex Webb	C	w	1.0	84	190
<i>Fumaria amarysia</i> Boiss. & Heldr. in Boiss.	Pa	t	3.0	86	122
<i>Gagea granatelli</i> (Parl.) Parl.	Li	g	11.0	19	76
<i>Geranium rotundifolium</i> L.	Ge	t	1.0	65	119
<i>Globularia alypum</i> L.	Gl	w	2.6	45	108
<i>Helichrysum stoechas</i> (L.) Moench subsp. <i>barrelieri</i> (Ten.) Nyman	Co	w	1.0	112	160
<i>Heliotropium dolosum</i> De Not.	B	t	2.3	186	275
<i>Heliotropium europaeum</i> L.	B	t	2.2	246	305
<i>Heliotropium hirsutissimum</i> Grauer	B	t	2.2	246	309
<i>Hirschfeldia incana</i> (L.) Lagreze-Fossat	Cu	t	3.0	90	149
<i>Hymenocarpus circinnatus</i> (L.) Savi	Le	t	3.0	82	109
<i>Hypericum empetrifolium</i> Willd.	Gu	w	2.0	119	147
<i>Hypericum triquetrifolium</i> Turra	Gu	h	1.0	165	231
<i>Hypochoeris achyrophorus</i> L.	Co	t	1.0	80	147
<i>Iris pumila</i> L. subsp. <i>attica</i> (Boiss. & Heldr.) Hayek	I	g	4.7	66	97
<i>Lamium amplexicaule</i> L. subsp. <i>amplexicaule</i>	La	t	2.2	43	104
<i>Lathyrus cicera</i> L.	Le	t	4.0	97	117
<i>Linum strictum</i> L. subsp. <i>strictum</i>	Ln	t	4.0	127	149
<i>Malcolmia chia</i> (L.) DC.	Cu	t	6.6	53	124
<i>Malva sylvestris</i> L.	M	h	4.0	93	142
<i>Medicago lupulina</i> L.	Le	h	2.3	81	118
<i>Muscari commutatum</i> Guss.	Li	g	4.3	24	83
<i>Muscari comosum</i> (L.) Miller	Li	g	3.3	78	119
<i>Muscari neglectum</i> Guss. ex Ten.	Li	g	2.8	355	73
<i>Nigella arvensis</i> L.	Ra	t	6.5	147	192
<i>Ononis ornithopodioides</i> L.	Le	t	3.5	116	158
<i>Ophrys lutea</i> (Gouan) Cav. subsp. <i>lutea</i>	Or	g	15.0	40	119
<i>Ophrys sphegodes</i> Miller subsp. <i>sphegodes</i>	Or	g	15.0	45	127
<i>Ophrys tenthredinifera</i> Willd.	Or	g	15.0	70	110
<i>Ornithogalum exscapum</i> Ten. & O. <i>gracicum</i> Zahariadi	Li	g	4.5	43	96
<i>Osyris alba</i> L.	Sa	w	2.5	118	151
<i>Oxalis pes-caprae</i> L.	Ox	g	6.0	90	119
<i>Pallenis spinosa</i> (L.) Cass.	Co	t	1.0	125	164
<i>Papaver rhoas</i> L.	Pa	t	1.1	79	158
<i>Petrorhagia velutina</i> (Guss.) P. W. Ball & Heywood	Cr	t	4.0	87	126
<i>Phagnalon graecum</i> Boiss. & Heldr.	Co	w	1.6	103	147

APPENDIX 1. Continued.

Plant species	Family	Life form	Flower life span	First date	Last date
<i>Phlomis fruticosa</i> L.	La	w	3.1	82	134
<i>Plantago lagopus</i> L.	Pl	t	1.0	77	143
<i>Prasium majus</i> L.	La	w	2.8	88	141
<i>Psoralea bituminosa</i> L.	Le	h	2.9	104	165
<i>Pterocephalus papposus</i> (L.) Coulter	D	t	4.0	95	152
<i>Ranunculus spruneranus</i> Boiss.	Ra	g	4.2	80	116
<i>Reichardia picroides</i> (L.) Roth	Co	h	1.4	75	139
<i>Reseda alba</i> L.	Re	h	2.1	62	146
<i>Romulea linaresii</i> Parl. subsp. <i>graeca</i> Be- guinot	I	g	5.0	23	43
<i>Ruta graveolens</i> L.	Rt	h	9.8	116	173
<i>Salvia triloba</i> L. fil.	La	w	2.6	76	112
<i>Salvia verbenaca</i> L.	La	t	2.3	48	122
<i>Sarcopoterium spinosum</i> (L.) Spach	Ro	w	4.5	52	104
<i>Satureja thymbra</i> L.	La	w	2.4	115	160
<i>Scabiosa atropurpurea</i> L.	D	t	3.4	99	151
<i>Scaligeria cretica</i> (Miller) Boiss.	U	t	3.0	101	129
<i>Scandix australis</i> L. subsp. <i>australis</i>	U	t	3.1	43	102
<i>Scilla autumnalis</i> L.	Li	g	1.0	262	318
<i>Scolymus hispanicus</i> L.	Co	h	1.7	147	185
<i>Scorzonera cana</i> (C. A. Meyer) O. Hoffm.	Co	h	1.1	78	139
<i>Scorzonera lanata</i> (L.) Hoffm.	Co	h	1.1	74	120
<i>Senecio vulgaris</i> L.	Co	t	1.0	30	104
<i>Sherardia arvensis</i> L.	Rb	t	2.6	57	112

APPENDIX 1. Continued.

Plant species	Family	Life form	Flower life span	First date	Last date
<i>Silene colorata</i> Poiret	C	t	1.0	69	121
<i>Sisymbrium orientale</i> L.	Cu	t	3.0	48	190
<i>Stachys cretica</i> L. subsp. <i>cretica</i>	La	h	2.7	118	156
<i>Sternbergia lutea</i> (L.) Ker-Gawler ex Sprengel subsp. <i>sicula</i> (Tineo ex Guss.) D. A. Webb	Am	g	4.9	274	320
<i>Taraxacum officinale</i> Weber	Co	h	1.5	292	323
<i>Teucrium polium</i> L. subsp. <i>capitatum</i> (L.) Arcangeli	La	w	1.2	139	173
<i>Thapsia garganica</i> L.	U	h	4.0	128	144
<i>Thymelaea hirsuta</i> (L.) Endl.	Th	w	10.3	310	105
<i>Thymelaea tartonraira</i> (L.) All. subsp. <i>tartonraira</i>	Th	w	4.5	34	104
<i>Thymus capitatus</i> (L.) Hoffmanns. & Link	La	w	2.7	156	185
<i>Tordylium apulum</i> L.	U	t	3.0	87	124
<i>Tragopogon porrifolius</i> L. subsp. <i>porrifol-</i> <i>ius</i>	Co	t	1.1	90	129
<i>Tremastelma palaestinum</i> (L.) Janchen	D	t	4.0	90	142
<i>Trifolium repens</i> L. subsp. <i>orphanideum</i> (Boiss.) D. E. Coombe	Le	h	3.2	134	165
<i>Trifolium stellatum</i> L.	Le	t	2.0	76	120
<i>Urginea maritima</i> (L.) Baker	Li	g	1.0	244	279
<i>Verbascum undulatum</i> Lam.	Sc	h	2.3	143	270
<i>Veronica persica</i> Poiret	Sc	t	1.3	43	112