# Flowering phenology of *Campanula* on Mt Olympos, Greece

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We studied the flowering phenology of the genus *Campanula* (represented by nine species) along the elevation gradient of Mt Olympos (Greece) in order to assess whether there are elevation patterns at the genus level and whether these relate to patterns previously observed along such gradients at the community level. The traits examined were time and duration of the flowering period, flower life span, and duration of male and female flower phases. Floral attributes, such as number of flowers per plant, flower biomass, flower size, were also studied in order to examine whether they change with elevation or influence flower phenology. Flowering of *Campanula* species started in mid-May and ended in late September. The average duration of flowering of the genus was ca 27 d and the average floral longevity 4 d. In all but one species, the female phase lasted longer than the male. *Campanula versicolor* differed remarkably from all others in flower phenology and other floral traits. Nearly all *Campanula* populations studied had right or positively skewed flowering distributions indicating that flowering begins more abruptly than it ends. At the genus level, the time of flowering increased with elevation by 2–3 d for every 100 m. Floral longevity also increased with elevation, by 0.2 d for every 100 m. Neither duration of flowering nor duration of the flower phases showed any consistent change with elevation. The same is true of the non-phenological floral traits examined. No trade-off between duration of flowering and flower life span or between structure and maintenance of flowers was apparent. The pattern of increasing floral longevity along the elevation gradient suggests a mechanism of compensation for reduced pollinator availability.

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Phenology of flowering has been found to vary at all spatial scales, associated in part with climatic differences. Phenology varies among microsites within the same area (Jackson 1966), with latitude (Panje and Srinivasan 1959, Kalisz and Wardle 1994, Jonas and Geber 1999), and with elevation.

Phenological shifts as a function of elevation have been reported for time and length of flowering, floral longevity, and stigma receptivity. At the community level, Reader (1984) reported that at high altitudes in the mediterranean climate zone, flowering peaks at the warmest part of the summer, whereas at lower elevations it occurs throughout the year but peaks in late spring, before the summer drought begins. Arroyo et al. (1981) observed an increase of the duration of flowering

and of floral longevity with elevation in the Chilean Andes. However, this pattern held only for north-facing slopes; the situation on south-facing slopes was less clearly defined. Primack (1985) reported a similar but not significant trend for floral longevity in New Zealand communities. At the species level, Vasek and Sauer (1970) reported the existence of early flowering ecotypes at low elevations and later flowering ecotypes at higher elevations for *Clarkia unguiculata*. In the case of *Campanula* species, Bingham and Orthner (1998) showed that the period of stigma receptivity in *C. rotundifolia* increased with elevation. Such phenological shifts have been interpreted as a response of plants to differing climatic conditions and/or different pollinator distribution and abundance (Körner 1999).

Studies at the community level revealing phenological patterns suffer from an inherent drawback in that they deal with differing assemblages of plant species. Phylogenetic or life-form constraints that influence the evolution of flowering phenology in animal-pollinated plants (Kochmer and Handel 1986) may confound the emerging patterns. On the other hand, studies at the species level are by necessity confined within a relatively small elevation range, as the habitat of a single species rarely extends from the foot to the top of a high mountain.

To overcome the methodological limitations of studies either at species or community level, we decided to examine a model system consisting of congeneric species along an elevation gradient. Mt Olympos was selected as our study area as it is the highest mountain of Greece (2917 m). After a preliminary investigation, the genus *Campanula* was chosen for analysis since it is represented by numerous species all along this elevation gradient corresponding to a progression from mediterranean to alpine environments. Nine *Campanula* species occur on Mt Olympos, ranging from local endemic to cosmopolitan (Strid 1980). They are all herbaceous and seven of them have the same life form (hemicryptophytes). One of these, *C. versicolor*, differs from all others in floral morphology and composition of pollinating fauna (Blionis and Vokou 2001).

The aim of our work is to explore patterns of flower traits along an elevation gradient at the genus level and compare them to those reported at the community and species level. The particular questions that we ask are: does *Campanula* flower phenology change with elevation in a predictable way in response to climatic conditions and pollinator availability? Do floral display characteristics, other than phenological ones, exhibit elevation patterns? Is there a trade-off between floral display characters? And, finally, does the phenology of *C. versicolor* show the same remarkable divergence from other *Campanula* species as do its floral morphology and pollinating fauna?

## Materials and methods

### Data collection

The study was conducted on the northeastern slopes of Mt Olympos (40°4′N, 22°27′E), within Mt Olympos National Park. *Campanula* species are given in Table 1 along with data on geographical distribution, altitudinal distribution on Mt Olympos and life form (Fedorov and Kovanda 1976, Strid 1980). *Campanula spatulata* is represented by two subspecies, *spatulata* and *spruneriana*. The habitat of *C. versicolor* at 300 m differed from all others in that it was man-made; the species occured on walls in the village of Litochoro, at the foot of the mountain. Altitudinally different populations of *Campanula* species were chosen (Table 2). Initial sampling and measurements took place during the summer (May–September) of 1992, while the main study period included summers of 1993 and 1994.

There is no meteorological station within Mt Olympos National Park. In order to estimate climatic variability, we kept daily records of rainfall and temperature at three elevations (850 m, 2100 m, 2750 m) during July, August, and September of 1993 and 1994.

Two permanent quadrats, $5 \times 5$ m, were set within each population under study. *Campanula* individuals inside the quadrats were mapped and the population density (plants m$^{-2}$) estimated. At regular intervals during the flowering period, we counted the total num-

Table 1. *Campanula* species occurring on Mt Olympos (life form and distribution features).

| Species | Life form | Geographical distribution | Altitudinal distribution on Mt Olympos (m) |
|---|---|---|---|
| *C. lingulata* Waldst. & Kit. | Hemicryptophyte (Hbienn)[1] | Balkans, SW Romania, S Italy | 200–1700 |
| *C. versicolor* Andrews | Hemicryptophyte (Hscap)[2] | Balkans, SE Italy | 250–1200 |
| *C. spatulata* Sibth. & Sm. | Geophyte (Gbulb)[3] | Balkan endemic | 400–2500 |
|   a) ssp. *spruneriana* | | (Al, Bu, Gr, Ju) | 400–1100 |
|   b) ssp. *spatulata* | | | 1700–2500 |
| *C. sparsa* Friv. (*C. patula* sensu lato) | Therophyte (annual) | Balkan endemic (Al, Bu, Gr, Ju, Rm, Tu) | 500–1900 |
| *C. trachelium* L. | Hemicryptophyte (Hscap)[2] | Europe, Caucasus, W Siberia | 600–1600 |
| *C. persicifolia* L. | Hemicryptophyte (Hscap)[2] | Europe | 600–2000 |
| *C. glomerata* L. | Hemicryptophyte (Hscap)[2] | Europe, central Asia | 1200–2100 |
| *C. rotundifolia* L. (syn.: *C. albanica* Witasek) | Hemicryptophyte (Hscap)[2] | Europe, NE Africa, N Asia, N America | 1200–2700 |
| *C. oreadum* Boiss. & Heldr. | Hemicryptophyte (Hscap)[2] | Olympos endemic | 1900–2900 |

[1] = Biennial hemicryptophyte, [2] = Scaposus hemicryptophyte ( = with a flower stalk growing directly from the ground), [3] = Bulbosus geophyte ( = bearing bulbs).

Table 2. Study sites and year(s) of study of plant traits examined.

| Species | Elevation (m) | Plant density | Biomass | Per-plant flower size and number | Mean time and duration of flowering | | | Floral longevity and sexual phases | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Year of study of each parameter | | | | | |
| | | 1993 | 1993 | 1993 | 1992 | 1993 | 1994 | 1993 | 1994 |
| C. lingulata | 450 | * | * | * | * | * | * | * | * |
| | 850 | * | * | * | * | * | * | * | * |
| | 1300 | * | * | * | * | * | | * | * |
| | 1700 | * | | * | | * | * | * | |
| C. versicolor | 300 | * | * | * | | * | * | * | * |
| | 900 | * | * | * | | * | * | * | * |
| C. spatulata | 400 | * | * | * | | * | * | * | |
| | 900 | * | * | * | * | * | * | * | * |
| | 1100 | * | * | * | | | | | |
| | 1850 | * | * | * | | | * | | * |
| | 2200 | | * | * | | | * | | |
| C. sparsa | 600 | * | | | * | * | | * | |
| | 1300 | | * | * | | | | * | |
| | 1400 | * | * | | | * | | * | |
| | 1800 | * | * | * | * | * | | | |
| C. trachelium | 600 | * | | * | * | | | * | * |
| | 1100 | | * | | | | | | |
| C. persicifolia | 900 | * | * | * | | * | * | * | * |
| | 1300 | | | * | | | | * | * |
| | 1500 | | * | | | | | | |
| C. glomerata | 1500 | | * | | | | | | |
| | 1850 | * | * | * | | | * | | * |
| C. rotundifolia | 1500 | * | * | * | * | * | * | | * |
| | 2100 | * | * | * | | * | * | | |
| | 2700 | * | * | * | | * | * | * | * |
| C. oreadum | 2100 | * | * | * | | * | * | | |
| | 2300 | * | * | * | | | * | | |
| | 2500 | * | * | * | * | * | * | * | * |

ber of flowers on all individual plants found inside these quadrats. This number was expressed as a percentage of the total number of flowers recorded over the whole flowering period and was plotted against calendar day. Since the exact dates of the beginning and end of flowering periods were not known, we defined these respectively to be the 2.5th and 97.5th percentiles (expressed in calendar days) of a normal distribution having the same mean and variance as the observed sample. The duration of the flowering period was defined as the difference between these percentiles.

*Campanula* species are dichogamous, i.e. they have temporal separation between the male and female flower phases. In order to estimate floral longevity and duration of the different flower phases, we marked 10 to 30 randomly chosen buds in most populations (Table 2), and examined these flowers at regular intervals. Subsequently, the duration of phases was expressed as a percentage of the total flower life span. Flower phases were determined after Faegri and van der Pijl's (1979) description of *Campanula* development stages.

In ten individuals of the populations under study (Table 2), we recorded in situ the number of flowers produced. In ca 30 randomly selected flowers of these

individuals, corolla length and width were measured; their volume was estimated by the use of the formula for a cylinder.

To study the biomass allocation patterns of *Campanula* species, keeping destructive sampling to a minimum, we collected five plants from each of the populations examined (Table 2). We separated them into different parts (roots, stems, leaves, and flowers), left them at 70°C for two days to dry, and weighed them.

## Statistical analysis

Four flowering phenology attributes were analysed (mean time and duration of population flowering, floral longevity, and relative duration of the male phase) using analysis of covariance (ANCOVA). In each, species and year were fixed factors and elevation a covariate. We also considered interactions between fixed factors and covariate. In order to have a balanced set, some data had to be omitted from this part of the analysis. This included the year 1992 as well as those species for which there were data for either only one population or for only one year (Table 2). Where the

ANCOVA detected no significant differences between years, it was repeated with species only as a factor.

Using the full set of species, we investigated the effect of elevation, at the genus level, using linear regression analysis. We tested for a linear relationship with elevation for each flowering attribute, both phenological and non-phenological. To examine whether there is any relationship between phenological and non-phenological floral traits, correlation analyses were carried out between floral longevity and 1) flower biomass per plant, 2) flower number per plant, and 3) flower size. We also tested for correlation between duration of flowering and 1) plant density, 2) flower number per plant, and 3) flower biomass per plant. We examined whether the floral phenology attributes, floral longevity, duration of the male phase and duration of flowering are interrelated.

For three phenological attributes (time of flowering, flower life span, relative male phase duration) it was possible to carry out a linear regression for each species separately. We analysed flower life span and relative male phase duration as a function of elevation using individual flowers. The procedure for the time of population flowering was similar, except we did not use all flowers counted, but randomly chose 100 observations from each population. This eliminated the excessive weighting of those populations with larger samples. Each observation represented a single flower on a single calendar day. Normality of samples was checked by observing the linearity of the residuals on a normal scores plot. Bonferroni's correction was used to avoid inflation of type I errors (Wright 1992) in all species-level regressions.

Statistical procedures were carried out in MINITAB and SPSS.

## Results

Temperature data at three elevations of Mt Olympos are given in Fig. 1. The difference of average monthly temperatures from the base to the summit may exceed 13°C.

Flowering of *Campanula* species on Mt Olympos starts in mid-May and ends in late September. Lowland species tend to flower earlier than upland species; an exception to this is the lowland *C. versicolor*, which is the last to flower, between August and September. The duration of flowering differs largely among species, from ca 10 d for *C. persicifolia* and *C. spatulata* ssp. *spruneriana* to > 50 d for *C. oreadum* and *C. lingulata*. Summary descriptions of the flowering distributions of each *Campanula* population at different elevations and years are given in Fig. 2a–g. The distributions of flowering are in general close to normal but are characterized by a small but persistent positive skewness (Fig.

3). Positively skewed flowering distributions have been observed for many other species (Rabinowitz et al. 1981, Schmitt 1983, Rathcke and Lacey 1985).

A clear trend of flowering to occur later, as elevation increases, is visible for most species in Fig. 2. ANCOVA (Table 3) revealed the year effect to be entirely insignificant. Therefore, the year factor was omitted and the analysis repeated; it revealed significant elevation and species effects. The strong interaction term reflects the powerful difference in the behaviour of *C. versicolor* compared to the other species. This interaction effect became insignificant when *C. versicolor* was omitted from the analysis. In the regression analysis at the genus level that followed, data from both years were pooled. The relationship with elevation was highly significant (mean time of population flowering = 169.559 + 0.0174 × elevation, r = 0.44, p = 0.0084, n = 34). When the anomalous *C. versicolor* was excluded from the analysis, the relationship was even stronger, with the mean time of population flowering (calendar day) increasing with elevation, by ca 3 d for every 100 m (Fig. 4). At the level of individual species, delays of flowering, where they occurred, ranged from 0.7 to 6.7 d 100 m$^{-1}$ (Table 4). *Campanula versicolor* diverged again from this pattern in both years of study, showing the opposite trend (Figs 2f, 4, Table 4).

The average duration of flowering of the genus was 26.6 ± 1.9 d. ANCOVA (Table 3) revealed a significant year (1993 and 1994) effect but no elevation or species effects. At the species level, there was no consistent pattern of change with elevation (Fig. 5). For example, duration of flowering decreased with elevation in *C. versicolor*, increased in *C. spatulata*, and exhibited a
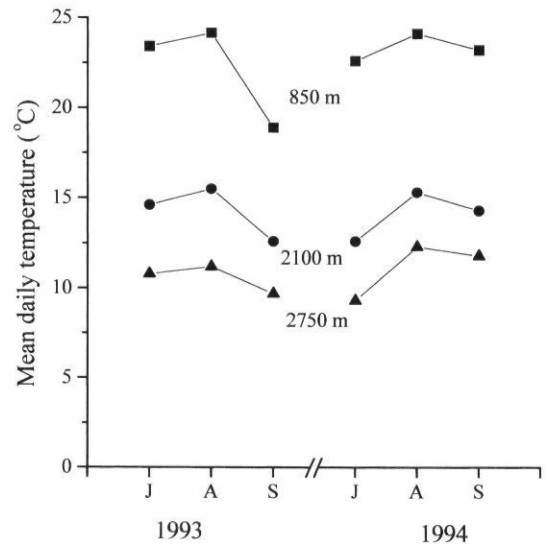


Fig. 1. Mean daily temperatures recorded in July, August and September 1993 and 1994 at the old monastery of St Dionysios (850 m a.s.l.) (squares), Refuge A (2100 m) (circles) and Refuge S.E.O. (2750 m) (triangles), on Mt Olympos.
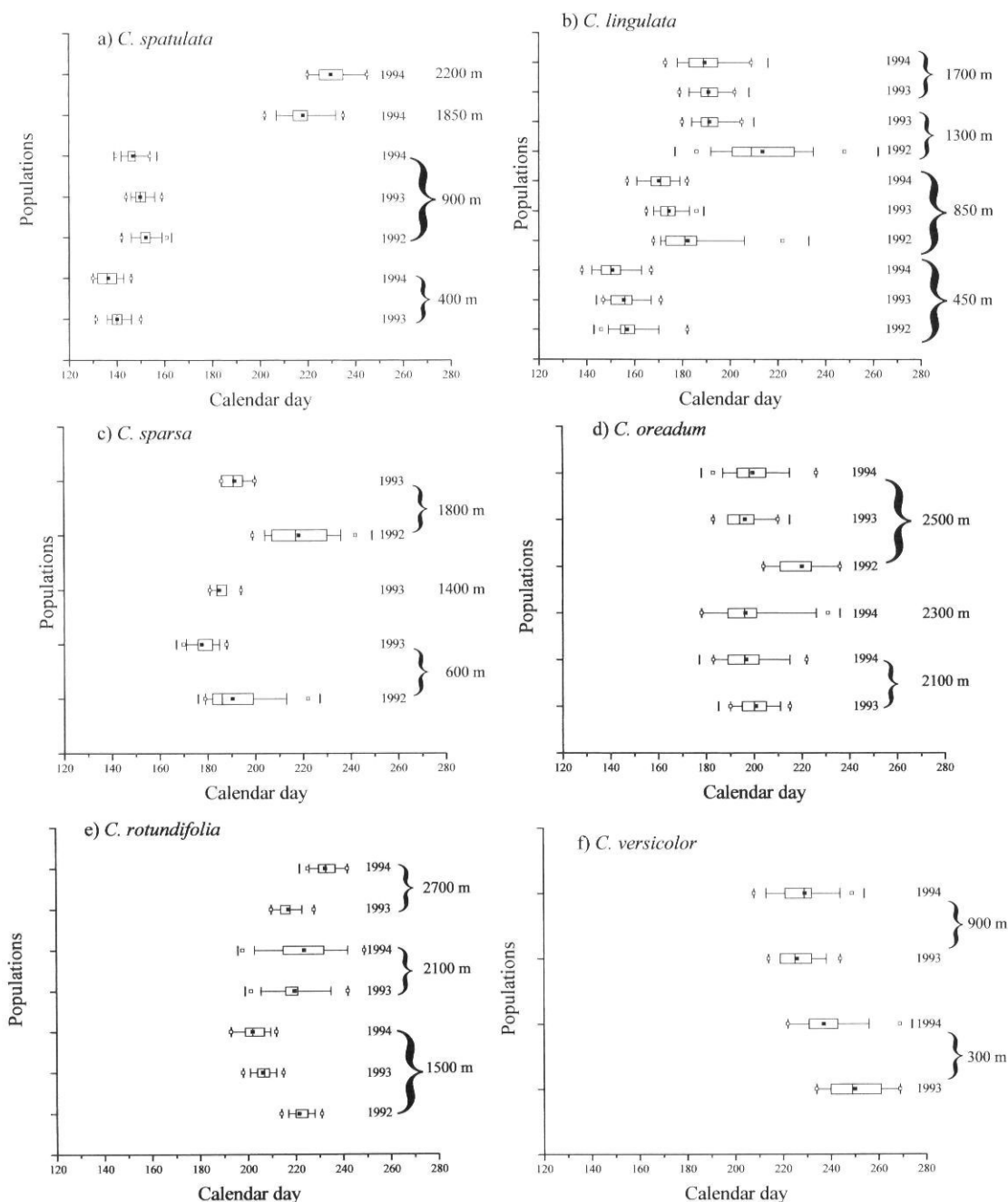
Fig. 2. Flowering curves of *Campanula* species on Mt Olympos at different elevations and for different years. Note that calendar day 121 correspond to 1 May. Each box defines the 25th and 75th percentiles and the whiskers the 5th and 95th percentiles, with the bar inside the box representing the median. Also shown are the extremes (lone bars), the mean (filled box) and the 1st and 99th percentiles (open boxes).

mid-altitude peak in the case of *C. rotundifolia*. This explains why no significant elevation effect was found at the genus level. Figure 5 underlines the primacy of yearly variability over elevation and species effects, suggesting that if sufficient data had been collected in 1992, to allow a balanced design for ANCOVA, an even more significant overall year effect would have

been observed. The duration of flowering in 1992 of those species for which data were available (*C. lingulata* and *C. sparsa*) differed remarkably from that of the other two years. The year 1992 was the coldest and wettest of the three, according to data from lowland meteorological stations within a radius of 25 km from our study area (Terzidis and Babatzimopoulos 1995).

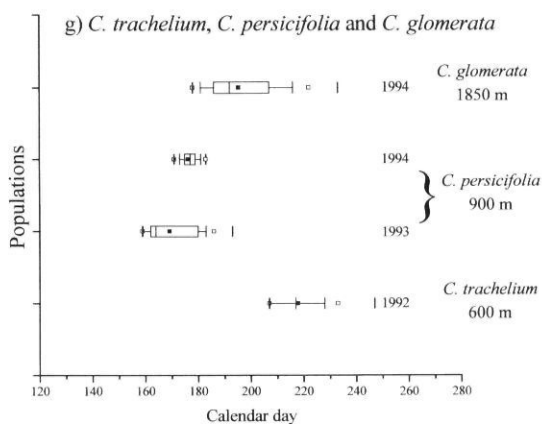g) *C. trachelium*, *C. persicifolia* and *C. glomerata*



Fig. 2, Cont.

The flower life span of *Campanula* species ranged from 1.95 to 9.85 d (corresponding to *C. spatulata* ssp. *spruneriana* and *C. oreadum*, respectively). Average floral longevity of the genus was $4.11 \pm 0.09$ d. The balanced ANCOVA with species and year as factors, that was only possible with three species, showed no significant year effect (Table 3). This gave us good grounds for pooling years 1993 and 1994 (in order to have more species included in the analysis) and carrying out a balanced, one-factor ANCOVA, which revealed a significant elevation effect plus significant species and interaction effects (Table 3). Regression analysis at the genus level (Fig. 6) revealed a significant positive trend (floral longevity $= 2.309 + 0.0015 \times$ elevation, $r = 0.54$, $p = 0.0021$, $n = 30$). However, at the level of individual species, flower life span increased with elevation only for some of the species (Table 5). Hence, the large interaction term between elevation and species. Here, too, the behaviour of *C. versicolor* was atypical in that it exhibited a considerably larger elevation trend than the other species. Nevertheless, even when *C. versicolor* was omitted from the analysis, the relationship with elevation at the genus level continued to be positive and significant (floral longevity $= 1.846 + 0.0017 \times$ elevation, $r = 0.62$, $p = 0.0008$, $n = 26$).

In eight out of the nine species studied, the duration of the female phase far exceeded that of the male phase. In *C. lingulata* and *C. persicifolia*, the percent duration of the male phase could be as low as 8–9% of the total flower life span (Table 6). Only in *C. versicolor* did the male phase last as long as the female phase. As in the case of floral longevity, a balanced ANCOVA with species and year as factors was only possible with three species. No elevation effect was found although there were significant species and year effects (Table 3).

The distribution of individual flower life span and relative male phase duration were in some cases highly skewed, while the logarithms of these quantities were close to normal. Therefore, all analyses for these at-

tributes were repeated using the logarithms. The differences between the results of the logarithmic and linear analyses at the genus level were negligible. At the species level, some of the differences were substantial but always retained the essential features found in the linear analysis (Table 5).

The average flower size, number of flowers produced per plant, flower biomass (in absolute values and as percent of the total plant biomass), and densities of the populations under study are given in Table 6. *Campanula versicolor* at 300 m diverged greatly from all other populations regarding number of flowers produced. This population, found on walls in the village of Litochoro, at the foot of the mountain, is subject to fertilizer run-off leading to excessive growth and concomitantly high flower production.
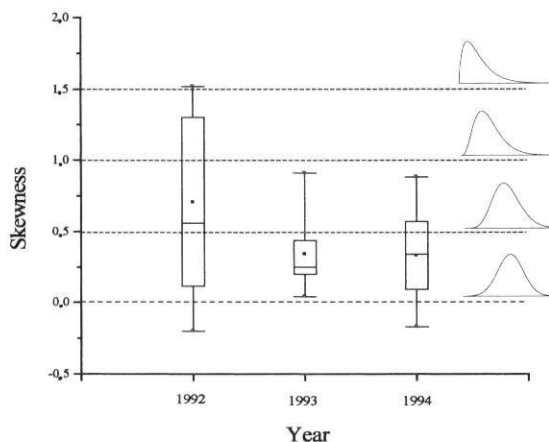


Fig. 3. Skewness of the flowering curves for three years. All sampled populations are included for each year. The symbols have the same meaning as in Fig. 2. The inset figures are normal and gamma distributions with skewness 0, 0.5, 1 and 1.5, displayed for comparison just above each of the corresponding levels on the diagram. These may be regarded as "typical" examples of such levels of skew.

Table 3. Results of covariance analysis for mean flowering date, duration of flowering, floral longevity, and relative duration of male phase. Given are the p-values for the effects of species, year, elevation and the interaction between species and elevation. None of the other interaction effects were significant in any of the analyses and are, therefore, not included in the table.

| Source | Mean flowering date | DF | Duration of flowering | DF | Floral longevity | DF | Relative male phase duration | DF |
|---|---|---|---|---|---|---|---|---|
| Species | 0.000 | 4 | 0.168 | 4 | 0.121 | 2 | 0.007 | 2 |
| Year | 0.424 | 1 | 0.030 | 1 | 0.451 | 1 | 0.013 | 1 |
| Elevation | 0.091 | | 0.739 | | 0.030 | | 0.306 | |
| Species × elevation | 0.001 | | 0.583 | | 0.009 | | 0.069 | |
| Results of analyses of covariance in cases of no significant year effect | | | | | | | | |
| Species | 0.000 | 5 | – | | 0.034 | 7 | – | |
| Elevation | 0.033 | 1 | – | | 0.005 | 1 | – | |
| Species × elevation | 0.001 | | – | | 0.002 | | – | |

The number of flowers produced per plant and the flower biomass per plant decreased with elevation [log(no. flowers) = 1.8440 − 0.0005 × elevation, r = −0.50, p = 0.016, n = 24; log(flower biomass) = −0.1009 − 0.0005 × elevation, r = −0.45, p = 0.03, n = 24] but the same did not hold true for proportional flower biomass. When the corresponding exceptional values of C. versicolor at 300 m were omitted, there was no significant trend in any of these attributes. No relationship was found either between flower size and elevation. Floral longevity was not related with flower size, flower biomass per plant, number of flowers per plant or duration of the male phase. Duration of flowering was not significantly correlated with population density, number of flowers per plant, flower biomass per plant. It was not significantly correlated to floral longevity either. However, when the values for the exceptional C. versicolor population at 300 m were omitted a significant positive relation was found between these two flower phenology attributes.

## Discussion

We found a number of phenological attributes of Campanula to be strongly correlated with elevation. Altitudinal changes of floral attributes seem to respond to changes of environmental factors. Temperature, considered to be the major cue that initiates the onset of flowering (Rathcke and Lacey 1985, Petanidou et al. 1995), changes drastically from the foot to the peak of the mountain (Fig. 1). The distribution and abundance of pollinators, considered to be the most important selective agents in the evolution of floral traits, also change with elevation. It was found that pollination visitation rates to Campanula flowers on Mt Olympos decreased drastically with elevation (Blionis and Vokou 2001). Also, the composition of the pollinating fauna differed between lowland and upland species. For example, Melittidae and bumblebees that were dominant pollinators of upland Campanula species were not

recorded as pollinators of the lowland species (Blionis and Vokou 2001).

At the genus level, the time of flowering increased with elevation by 2–3 d for every 100 m. Of the species studied, all but two (C. versicolor, C. oreadum) showed a significant delay of flowering as elevation increased. In the case of C. versicolor, in particular, a significant opposite trend was observed in both years of study. Earlier blooming at higher elevations was not the only peculiarity of C. versicolor. Though a lowland species, it flowers later than all others, starting in August, the warmest month.

According to Waser (1983), patterns that do not follow elevation gradients are suggestive of evolutionary divergence to reduce competition for pollination. The flat flower shape of C. versicolor (in contrast to the typical for the genus bell shape) gives the opportunity to non-specialist insect-pollinators to have access to
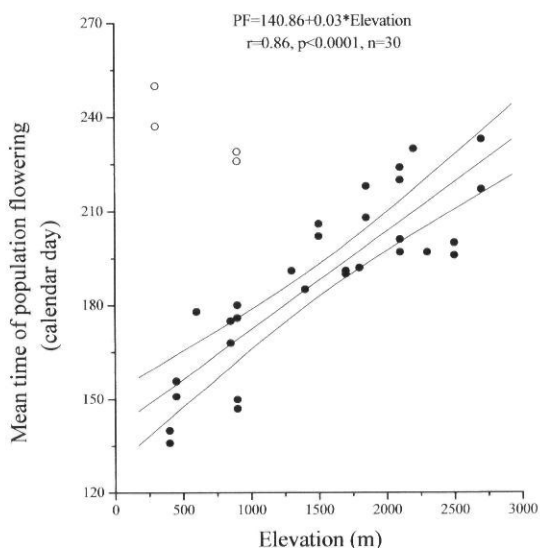


Fig. 4. Mean day of flowering of Campanula representatives on Mt Olympos vs elevation for 1993–1994. The late-flowering C. versicolor (open circles) has not been included in the regression.

Table 4. The slope of the linear relationships between flowering time and elevation of the different *Campanula* species on Mt Oympos observed for three different years (NS means $p > 0.05$, ** means $p < 0.01$); the units of slope are given in days 100 m$^{-1}$. All significance levels include the Bonferroni correction.

| Species | 1992 | 1993 | 1994 | All years |
|---|---|---|---|---|
| C. lingulata | 6.7** | 2.9** | 3.0** | 3.4** |
| C. oreadum | | −1.1** | 0.7 NS | −0.2 NS |
| C. rotundifolia | | 0.9** | 2.5** | 1.7** |
| C. sparsa | 2.3** | 1.1** | | 1.6** |
| C. spatulata | | 2.0** | 5.7** | 5.5** |
| C. versicolor | | −4.0** | −1.3** | −2.7** |

floral rewards. Generalists rather than specialists are more likely to act as selective agents promoting floral character/reward differentiation or shift of flowering times or both (Heinrich 1976, Waser 1983) and it is possible that they have played a role on *C. versicolor* flower phenology. Flowering in the Mediterranean climatic zone is very seasonal (Zohary 1962, Mooney et al. 1974, Moldenke 1979). Petanidou et al. (1995) found that 66% of the insect pollinated flora of a mediterranean ecosystem of Greece were in flower from mid-March through May. If this strong seasonality held also in the case of the low Olympos community, we might expect vigorous competition for insect-pollinators. Particularly for a species with non-specialized flowers, competition might substantially decrease if it flowered later in the year, when only a few other species are in bloom.

Nearly all *Campanula* flowering curves were positively skewed (Figs 2 and 3), which means that flowering begins more abruptly than it tails off. Many species
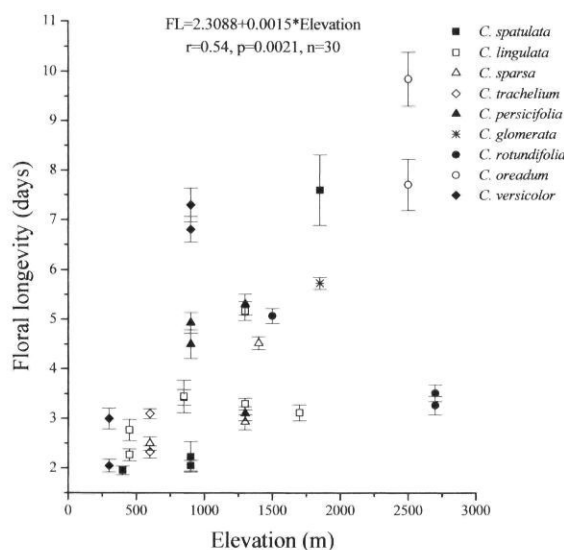


Fig. 6. Floral longevity (FL) of populations of *Campanula* representatives on Mt Olympos vs elevation (mean ± SE) for 1993–1994.

have been observed to have right- or positively skewed flowering distributions (Rathcke and Lacey 1985). Thomson (1980) argued that right-skewness could increase detectability and attractiveness to pollinators, which would continue to visit these known plants even as flowering declined. Nevertheless, this cannot explain why both wind-pollinated (Rabinowitz et al. 1981) and autogamous species (Schmitt 1983) present the same pattern. According to Rathcke and Lacey (1985), sudden, synchronous onset of flowering could reflect similar responses to a uniform and unambiguous environmental cue. However, we note that positive skewness might arise in a purely geometric way. The flower curve is a convolution (Spiegel 1968) of two curves: the distribution of flower opening times and the floral longevity curve. The floral longevity curve is the probability that a flower is still surviving a specified time after opening. Any flower that has survived for $x$ days after opening has already survived for $x - 1$ d, $x - 2$ d, and so on, so the probability of surviving for a small number of days is always greater than the probability for surviving for a larger number of days. Therefore, the floral longevity curve is a decreasing function of time (over its entire range) and by necessity positively skewed. On the other hand, it is reasonable to hypothesise that the distribution of flower opening times is symmetric (on average). The convolution of a symmetric with a positively skewed curve is itself positively skewed (a property of convolution via Fourier analysis: see Platt and Denman 1975 or Mallat 1998, for discussions of Fourier analysis). As a result, the flowering curve will itself be positively skewed (on average).
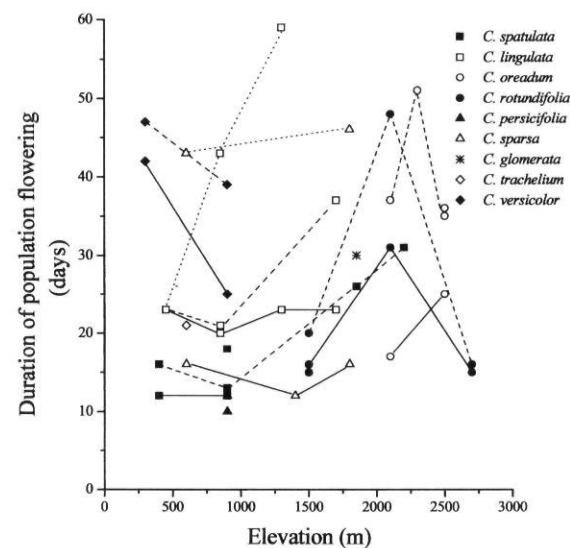


Fig. 5. Duration of flowering of altitudinally different populations of *Campanula* species on Mt Olympos, in 1992 (dotted lines), 1993 (solid lines) and 1994 (dashed lines).

The average flowering period of *Campanula* on Mt Olympos is ca 27 d. There exist only three other representatives of Campanulaceae (*Trachelium jacquinii*, *Asyneuma limonifolium*, *Edraianthus graminifolius*) on the mountain and, therefore, we can argue that this number approximates the average flowering period of the whole family on Mt Olympos. This duration is much less than that estimated for the families of Lamiaceae, Asteraceae, Fabaceae and Liliaceae, in a Mediterranean ecosystem, which are 45, 55, 39 and 50 d, respectively (Petanidou et al. 1995). It is, however, very close to that estimated for a subalpine meadow in British Columbia (23 d) (Pojar 1974) and for undisturbed North American woodland habitats (18–32 d) (Heinrich 1976), i.e. habitats that are similar to those of the *Campanula* species that we studied.

At the genus level, we found no significant relationship between duration of flowering and elevation. This result is not in agreement with Arroyo et al. (1981), who observed longer flowering periods at higher altitudes at the community level, although, as they state, this pattern held only for north-facing slopes. The length of the flowering period of each *Campanula* species did not change with elevation in a consistent way and varied considerably within populations from year to year. This agrees with the results of Price and Waser (1998): experimental warming of a subalpine meadow influenced the mean timing of plant reproduction but there was no detectable effect on the duration of flowering. The crucial importance of yearly variability is also supported by the results of Tepedino and Stanton (1980). They found considerable changes in duration of flowering of shortgrass prairie species in different years and, reviewing the literature, they suggested that they are related to the climatic patterns of the years in question. Our results suggest that there is no uniform pattern of change for the duration of the flowering period in response to changes of elevation, and that even differences between species may be insignificant by comparison with yearly variability.

The average floral longevity of the genus is 4.1 d. This value is very close to that reported by Primack (1985) for montane species in the Chilean Andes (4.2 d), less than that of subalpine species (6.9 d), and

longer than that of species in a Mediterranean ecosystem (3.5 d) (Petanidou et al. 1995). We found that floral longevity at the genus level increased with elevation. It is the first time that this pattern, though well documented for communities, has been reported for a genus.

With experimental manipulations, we found that floral longevity of *Campanula* species increased dramatically under pollinator exclusion conditions (Blionis and Vokou 2001). This gave us good reasons to expect increased floral longevity in cases of reduced pollinator availability. The results we report in this paper further support this hypothesis. The decreasing insect visitation rates to *Campanula* flowers with elevation (Blionis and Vokou 2001) is paralleled by increase of their floral longevity. Therefore, we can argue that this phenological pattern constitutes a compensatory mechanism of *Campanula* species to balance the low availability of pollinators.

The female phase of *Campanula* flowers lasted longer than the male in eight of the nine species studied (in *C. versicolor*, the two phases were about equal). This supports Primack's (1985) postulate that male flowers (or male phases of flowers, in our case) are shorter-lived than female flowers. In general, male flowers allocate more resources than females to floral structures and products (e.g. petals, nectar, odour) to increase their attractiveness to pollinators. Within hermaphroditic, dichogamy-exhibiting species (like *Campanula* species), pollinators have often been reported to prefer to visit flowers during the relatively more rewarding male phase (Delph and Lively 1992). However, in three *Campanula* species studied, viz. *C. rotundifolia* (Cresswell and Robertson 1994), *C. spatulata* ssp. *spruneriana* and *C. lingulata* (Blionis and Vokou unpubl.), nectar was found to be produced only during the female phase. Therefore, whereas female phase flowers offer both nectar and pollen, male phase flowers offer only pollen. Although pollen availability is relatively higher during the male phase, it is arguable whether it is more rewarding than the female phase. Experimental manipulations have shown that the duration of either phase of *Campanula* flowers decreases with increasing pollinator service (see Richardson and Stephenson 1989, for hand pollination effects on both sexual phases of *C.*

Table 5. Linear relationships between floral longevity and elevation for *Campanula* species for two years. The slope of the linear relationship (longevity = A × elevation + B) is given in days 100 m$^{-1}$. The corresponding results for the logarithmic analysis are given in brackets. The fitted curve [log(longevity) = C × elevation + D] is close to a straight line over the relevant range of elevations for each species, so the figure given is the slope of this curve at the middle of this range. All significance levels (NS means $p > 0.05$, * means $p < 0.05$, ** means $p < 0.01$) include the Bonferroni correction.

| Species | 1993 | | 1994 | | Both years | |
|---|---|---|---|---|---|---|
| *C. lingulata* | 0.11** | (0.11**) | 0.0 NS | (0.07 NS) | 0.10** | (0.10**) |
| *C. persicifolia* | −0.35** | (−0.31**) | 0.01** | (0.10 NS) | −0.22** | (−0.24*) |
| *C. rotundifolia* | | | −0.15** | (−0.15**) | | |
| *C. sparsa* | 0.25** | (0.25**) | | | | |
| *C. spatulata* | 0.02 NS | (0.02 NS) | 0.39** | (0.27**) | 0.34** | (0.20**) |
| *C. versicolor* | 0.88** | (0.83**) | 0.64** | (0.68**) | 0.78** | (0.80**) |

Table 6. Population density, flower number per plant, floral biomass (absolute and as a percent over the total plant biomass), flower volume (observations and measurements carried out in 1993) and relative duration of the male phase (pooled data for 1993 and 1994) of *Campanula* species on Mt Olympos.

| Species | Elevation (m) | Population density (individuals m$^{-2}$) | Flower no. per plant | Flower biomass (g) | Flower biomass (%) | Corolla volume (mm$^3$) | Duration of the male phase (%) |
|---|---|---|---|---|---|---|---|
| *C. spatulata* | 400 | 1.64 ± 0.20 | 7.0 ± 1.7 | 0.082 ± 0.028 | 9.7 | 1281.4 ± 145.2 | 29.6 ± 3.6 |
| | 900 | 0.78 ± 0.14 | 14.4 ± 2.8 | 0.066 ± 0.021 | 7.6 | 1760.2 ± 155.5 | 23.5 ± 1.5 |
| | 1100 | 2.04 ± 0.64 | 13.6 ± 2.0 | 0.193 ± 0.042 | 10.3 | 1991.4 ± 272.4 | – |
| | 1850 | 1.20 ± 0.04 | 2.2 ± 0.4 | 0.013 ± 0.003 | 6.2 | 1246.1 ± 104.5 | 34.5 ± 1.9 |
| | 2200 | 1.08 ± 0.16 | 2.4 ± 0.4 | 0.021 ± 0.007 | 4.1 | 890.6 ± 138.9 | – |
| *C. lingulata* | 450 | 1.16 ± 0.37 | 52.0 ± 11.4 | 1.238 ± 0.276 | 21.6 | 524.0 ± 40.5 | 20.8 ± 2.3 |
| | 850 | 1.04 ± 0.12 | 30.2 ± 6.7 | 1.556 ± 0.436 | 25.2 | 460.4 ± 28.9 | 11.2 ± 1.1 |
| | 1300 | 0.12 ± 0.00 | 102.7 ± 14.8 | 2.802 ± 0.533 | 25.7 | 594.8 ± 33.6 | 9.2 ± 0.7 |
| | 1700 | 0.56 ± 0.25 | 26.5 ± 5.3 | – | – | 458.6 ± 29.5 | 14.5 ± 1.8 |
| *C. sparsa* | 600 | 0.72 ± 0.06 | – | – | – | – | 45.7 ± 1.8 |
| | 1300 | – | 61.6 ± 11.4 | 0.362 ± 0.121 | 15.9 | 378.4 ± 34.9 | 30.2 ± 2.5 |
| | 1400 | 2.06 ± 0.13 | – | 0.245 ± 0.036 | 22.7 | – | 15.2 ± 3.6 |
| | 1800 | 1.70 ± 0.50 | 13.7 ± 1.8 | 0.310 ± 0.139 | 19.5 | 603.3 ± 48.0 | – |
| *C. trachelium* | 600 | 0.38 ± 0.01 | 51.9 ± 12.8 | – | – | 1200.2 ± 207.6 | 39.7 ± 4.1 |
| *C. persicifolia* | 900 | 0.64 ± 0.25 | 3.0 ± 0.4 | 0.310 ± 0.088 | 16.5 | 10 298.0 ± 950.2 | 8.3 ± 0.8 |
| | 1300 | – | 8.3 ± 2.5 | – | – | 11 947.4 ± 782.8 | 15.7 ± 1.8 |
| *C. glomerata* | 1850 | 1.56 ± 0.08 | 10.6 ± 2.0 | 0.163 ± 0.017 | 27.5 | 944.1 ± 99.3 | 21.3 ± 1.6 |
| *C. rotundifolia* | 1500 | 0.68 ± 0.20 | 1.2 ± 0.1 | 0.016 ± 0.004 | 9.0 | 306.3 ± 36.9 | 42.8 ± 3.9 |
| | 2100 | 1.08 ± 0.08 | 3.4 ± 0.5 | 0.030 ± 0.005 | 14.1 | 1269.8 ± 87.5 | – |
| | 2700 | 1.84 ± 0.45 | 3.4 ± 1.0 | 0.016 ± 0.002 | 18.0 | 1648.7 ± 121.0 | 34.4 ± 1.4 |
| *C. oreadum* | 2100 | 1.54 ± 0.06 | 6.8 ± 1.5 | 0.086 ± 0.057 | 6.4 | 1964.7 ± 185.3 | – |
| | 2300 | 1.82 ± 0.10 | 20.9 ± 9.5 | 0.170 ± 0.100 | 10.0 | 3801.3 ± 322.0 | – |
| | 2500 | 1.32 ± 0.44 | 22.0 ± 9.2 | 0.594 ± 0.167 | 5.2 | 2276.0 ± 137.6 | 34.3 ± 2.9 |
| *C. versicolor* | 300 | 0.20 ± 0.08 | 1323.2 ± 291.0 | 0.483 ± 0.061 | 6.3 | – | 43.6 ± 3.7 |
| | 900 | 0.28 ± 0.04 | 31.3 ± 16.3 | 0.145 ± 0.009 | 8.0 | – | 47.2 ± 1.9 |

*rapunculoides* flowers, and Nyman 1993, for tactile stimulation of pollen collecting hairs and its effect on male phase of *C. rotundifolia* flowers). Our findings of a shorter male phase for *Campanula* flowers suggest that pollinators favour the male phase more than the female. However, data on the reward availability, in both qualitative and quantitative terms, and visitation rates associated with each particular phase would be needed for all *Campanula* species in order to prove it.

None of the non-phenological floral traits that we studied exhibited any significant elevation pattern (the trends observed of reduced floral biomass and number with elevation did not hold up when the exceptional *C. versicolor* population at 300 m was omitted). Floral investment can be divided into structural and functional parts representing the costs of constructing and maintaining flowers, respectively. None of the parameters related to flower construction that we examined was significantly correlated with floral longevity or duration of flowering (flower maintenance). This suggests absence of a trade-off between structural and temporal floral traits and reflects the fact that individual *Campanula* species allocate differently their resources. Whereas some seem to balance a long flower life span with a low number of flowers, others are well able to invest in both large numbers of flowers and relatively long flower life span. In addition, like we found at the genus level, Petanidou et al. (1995) found at the community level that duration of flowering and flower life span were positively correlated.

In conclusion, the temporal (yearly) and spatial (elevation) variation of environmental factors induced substantial variation in *Campanula* flower phenology traits. In some cases, this variation of floral traits followed a predictable elevation pattern at the genus level (e.g. time of flowering, floral longevity). At the species level, though, there were exceptions, mostly manifested by *C. versicolor*, which diverged remarkably from all other species. In some other cases (e.g. duration of flowering, duration of flower phases), the year or species effect dominated and no elevation effect was detectable. For plants to achieve a certain degree of reproductive success, no trade-off between duration of flowering and flower life span or between structure and maintenance of flowers is necessarily required. The pattern of increasing floral longevity coupled with a decrease of pollinator visitation rates (Blionis and Vokou 2001) along the elevation gradient indicates the operation of a mechanism of compensation for reduced pollinator availability. Further research on the reproductive output of *Campanula* species will be needed in order to show that this mechanism is really effective, and thus to prove that upland species are not pollination limited.

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