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Structural and functional divergence of *Campanula spatulata* subspecies on Mt Olympos (Greece)

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Abstract. *Campanula spatulata* is represented on Mt Olympos (2917 m) by two subspecies: the lowland *spruneriana*, from 400 to 1100 m, and the upland *spatulata*, from 1700 m to 2500 m. *Spatulata* populations significantly differed from those of *spruneriana* in the following features: (i) they consisted of shorter individuals with smaller flowers and lower flower production, (ii) they allocated more energy and resources below ground, (iii) they flowered much later in the year, had longer duration of flowering, and longer flower life span, (iv) they produced smaller fruits with fewer but heavier seeds, (v) they received lower numbers of insect visits for fewer hours per day, and (iv) they were pollinated by smaller insects. Between and within subspecies comparisons showed that in most cases the patterns of character change were neither gradual nor monotonous all along the elevation gradient. The differences in phenological characters are in agreement with patterns associated so far with elevation change. The taxonomic and biometric differences of the insect pollinators as well as the temporal separation of the flowering periods provide substantial evidence of reproductive isolation of the two *C. spatulata* subspecies on Mt Olympos.

Key words: *Campanula spatulata*, elevation gradient, phenology, morphology, pollination, reproduction.

Campanula spatulata Sibth. & Sm. is a perennial protandrous species. It has a globose or napiform tuber, one to several stems, and a bluish-violet corolla. It is endemic in the southern part of the Balkan Peninsula. In Greece, it has been collected from a large number of localities. Three subspecies have been recognised: (i) the lowland ssp. *spruneriana* (Hampe) Hayek, found throughout the range of the species, except in Kriti, (ii) ssp. *filicaulis* (Halácsy) Phitos, the Cretan endemic occurring on calcareous screes of Mt Dhikti, and (iii) the very variable *spatulata*, found in mountain grasslands of Greece and neighbouring countries (Fedorov and Kovanda 1976, Hartvig 1991). *C. spatulata* has a wide altitudinal range on Mt Olympos (2917 m), the highest mountain of Greece, represented by two subspecies, altitudinally distinct: *spruneriana*, occurring within the range 400–1100 m and *spatulata* occurring within the range 1700–2000 m (Strid 1980).

Works conducted at the community level have shown remarkable differences between lowland and upland plant species in a number of characters, such as resource allocation, seed number and weight, flowering time and duration of the flowering period, floral longevity, pollinator visitation rates, composition of pollinators. Grime (1979) argued that in unfavourable environments, such as arctic or alpine, perennials with short stature and high

partitioning to below ground structures dominate. It has been suggested that the declining length of the growing season associated with increasing elevation have repercussions on reproductive output; Baker (1972) provided results from plants on Californian mountains indicating a trend of decreasing seed weight with increasing elevation. Onset of flowering was found to be delayed (Waser 1983, Reader 1984) and duration of flowering and floral longevity were found to increase (Arroyo et al. 1981, Primack 1985) at high altitudes. The composition of the pollinating fauna differs between lowland and upland species (Arroyo et al. 1982, Primack 1985, Warren et al. 1988, Totland 1993, Körner 1999). Also, pollinator visitation rates are lower at high altitudes (Arroyo et al. 1985, Totland 1993, Bingham and Orthner 1998).

Works exploring patterns of plant performance along elevation gradients at the species level are usually confined within a rather narrow elevation range (Vasek and Sauer 1971, Sawada et al. 1994, Bingham and Orthner 1998). The reasons are obvious; a species can seldom tolerate such a wide variety of environmental conditions prevailing from the foot to the top of a high mountain.

The wide elevation distribution of *C. spatulata* on Mt Olympos offered a unique opportunity to study how large elevation differences affect plant performance at the species level. Further to that and given the representation of *C. spatulata* on the mountain by two subspecies, we wanted to explore the extent to which they are reproductively isolated and have an insight on the processes that induced divergence of their morphological characters.

The specific aims of this paper were to examine (i) whether the differences between the two *C. spatulata* subspecies could be explained on accounts of the altitudinal dimension of their habitat, (ii) whether apart from altitude, the soil factor played a role in their distinct distribution on the mountain, and (iii) whether there are characters that clearly separate the two subspecies on Mt Olympos, particularly because their distinction is considered rather arbitrary (Hartvig 1991).

Materials and methods

Our study was conducted in 1993 and 1994 on the northeastern slopes of Mt Olympos (40°4′N, 22°27′E). Five populations were examined, at 400 m, 900 m, 1100 m, 1850 m and 2200 m. The first three correspond to ssp. *spruneriana* and the latter two to ssp. *spatulata*; an additional population at 650 m (*spruneriana*) was examined only for reproductive characters. Table 1 gives information on the characteristics of the sites where each population occurs, the traits examined in each one, and the year(s) of study of every particular trait.

There is no meteorological station in Mt Olympos National Park. To have some estimation of the climatic variability within the study area, we kept daily records of rainfall at 350 m and 2750 m, and of temperature at 850 m, 2100 m, and 2750 m, during July, August, and September of 1993 and 1994. We also used climatic data from two lowland stations located in the surrounding area, within a radius of 20 km from the Park: Katerini, at 31 m above sea level, and Vrondou, at 182 m.

We collected soil samples from the A-horizon of the study sites by use of 100 cm^3 sampling tubes. The small soil core method (Cassel and Nielsen 1986) was used to estimate field capacity (at 10 kPa). Porosity and bulk density were estimated by using formulas which take account of the mass of dry and wet soil samples (Blake and Hartge 1986). Soil pH and particle size were also estimated (Day 1965).

Two permanent plots, 5 × 5 m each, were set in the study sites. All individuals within these plots were mapped in 1993 and 1994. Densities of individuals and clumps as well as clump size (number of individuals per clump) were estimated. Two-way analysis of variance was used to examine the effect of year and subspecies on density attributes. Wherever the subspecies effect were significant, two-way analysis of variance was run separately for each subspecies, with year and population as factors.

Measurements of the morphological characters, plant height and number of stems and flowers produced per individual, were conducted *in situ* on ten individuals from each population.