Bulbous and tuberous plants (geophytes) feature as one of the most prominent life forms in Mediterranean type ecosystems. As currently registered in the Flora Hellenica Database there are 5661 species of native and fully naturalised species of vascular plants in Greece. 535 of these (9.5%) have distinctly swollen underground storage organs and can thus be classified as geophytes in the strict sense. Approximately 80% of these belong to four major monocot families – Amaryllidaceae, Iridaceae, Liliaceae s.lat. and Orchidaceae; the rest are distributed amongst 17 families.

The geophytic life form is an adaptation to the Mediterranean climate with water stress during the hottest months of the year and relatively mild, wet winters. The plants respond by becoming dormant in the summer and producing vegetative growth in winter. A similar pattern can be observed in other warm, seasonal and somewhat unpredictable climates, e.g., in steppic areas. Most of the species flower in the spring, produce seed rapidly, and lie dormant during the long, hot summer before producing new vegetative growth in the autumn and winter. A smaller group of geophytes flower in the autumn and produce slowly ripening fruits and seed during the winter and spring before becoming dormant in summer. The spring-flowering species are generally synanthous, i.e., with flowers and leaves developing simultaneously, whereas the autumn-flowering ones are often hysteranthous, i.e., with flowers and leaves developing in different seasons (cf. Dafni & al. 1981; Strid 1988).

When scored for 500 m intervals of altitude, the highest percentage of geophytes in the Greek flora (10.6%) is found at low to moderate altitudes (500-1000 m) and the lowest (6.9%) among high mountain species (>2000 m). Although few in number of species, the geophytes may be prominent by snowpatches at alpine levels where they are generally
represented by species of Crocus, Scilla and Corydalis. Autumn-flowering, hysteranthous species are usually confined to low altitudes with a typical Mediterranean climate.

Three different themes are briefly considered in this article:

**Perennial weeds of arable land**

A fair number of bulbous and tuberous species have become adapted to agricultural habitats and are sometimes restricted to arable land subject to annual tilling by traditional methods. It must be assumed that they have evolved with agriculture, having originated from ancestral forms of the same species growing in steppe-like habitats further east. As a consequence of deep-ploughing and use of herbicides some species are now threatened with extinction, e.g., Tulipa undulatifolia, Leontice leontopetalum, Bongardia chrysogonum, Allium nigrum and Bellevalia ciliata. Others are more resilient and able to survive at the edge of fields or in semi-natural habitats, e.g., Gladiolus italicus, Bellevalia dubia, Muscari comosum and Ornithogalum nutans.

Tulipa undulatifolia is now a rare plant in Greece, having formerly occurred in large quantity in ploughed fields, e.g., in the vicinity of Athens. It persists in a few places, notably near the village of Didima in NE Peloponnese where it is protected by the villagers and used for decoration in homes and churches notably on National Day (March 25). It is occasionally found in semi-natural habitats in the surrounding area. Leontice leontopetalum, a herbaceous member of the Berberidaceae with a deep-seated tuber, is fast-disappearing in most of Greece, but still occurs in large quantity locally in C and NE Peloponnese and on some of the Aegean islands. The related Bongardia chrysogonum may now be extinct in Greece (and Europe), having been discovered in two small populations in the N and C Peloponnese. Its distribution ranges from central Anatolia to Pakistan where at least some forms of it grow in semi-natural, steppe-like vegetation.

Geophytes of agricultural habitats generally flower in the early spring (mid-March to mid-April) and have produced ripe seed by the time of harvest. The dried-up stems and infructescences of Leontice leontopetalum are distributed as tumbleweeds. The inflated, bladder-like fruits have no dispersal mechanism but with mechanical thrashing, the thin wall ruptures and the seeds fall out. Similarly, in Bellevalia ciliata the fruiting pedicels become hardened, elongated, and patent to erecto-patent; the infructescence is broken off and blown along until the ripe seeds are shaken out of the capsule.

More successful and resilient perennial weeds of arable land are those with more efficient vegetative reproduction by means of bulblets or other propagules. Geranium tuberosum, some Ornithogalum species and certain forms of Muscari comosum fall into this category. An extreme example is the introduced Oxalis pes-caprae which spreads aggressively by means of bulb-like propagules and is now a troublesome weed of fields and olive groves in southern Greece, flowering in the winter and early spring.

**Endemism**

The incidence of endemism in the Greek flora is high by European standards, c. 13% at the species level (cf. Kit Tan & al. 2001). For mountain taxa the percentage of endemism
Fig. 1. Distribution of four endemc species of *Fritillaria* in Greece. Dots: *F. epirotica* Rix, squares: *F. euboeica* Rix, diamonds: *F. obliqua* Ker-Gawler (also on the Aegean islands of Kithnos, Giaros and Serifos), stars: *F. rhodocanakis* Baker (also on the adjacent islands of Itra, Poros and Spetse). *Fritillaria* has 20-22 species in Greece, c. half are endemic.
clearly increases in a southerly direction and is highest in Crete (Strid 1993); no less than 42% of the species occurring at upper montane and alpine levels in the White Mountains (Levka Ori) of western Crete are endemic to Greece or a smaller area. A similar trend can be observed for lowland taxa, although no precise figures are available.

Local and regional endemism is pronounced in some of the major geophyte genera in Greece, e.g., Allium, Colchicum, Crocus, Fritillaria and Ophrys. To take an example, Fritillaria has one of its centres of diversity in Greece with 20-22 species, c. half of which are endemic to the country (Kamari 1991). Four taxa are mapped in figure 1. Although ecologically very different these species are confined to small geographical areas. F. epirotonica is a species of serpentine screes at subalpine and alpine levels. F. rhodocanakis and F. obliqua occur in phrygana on rocky limestone hills at low altitudes, the former also in cultivated fields, whereas F. euboeica is a species of stony hillslopes at moderate altitudes.

The largest geophyte genus in Greece is Allium with a total of c. 75 species, several of which are endemic and several of which have been only recently recognized. Colchicum has c. 35 species, and the taxonomy especially of the hysteranthous species is complicated by the fact that both flowers, leaves and fruits are frequently needed for positive identification. Some species, including some very distinct ones, have been only recently described (cf. Persson 1999). The genus Crocus has c. 22 species and an additional 9 subspecies in Greece, and the incidence of endemism is high (Mathew 1982). The orchids, especially Ophrys and Dactylorhiza, have recently been subjected to excessive taxonomic splitting, inflating the number of local species; in reality, the incidence of endemism is probably lower than in Allium, Colchicum and Crocus.

Flowering time

The annual life cycle for most geophytes involves flowering in the spring, for lowland species from mid-March to the beginning of May. Seed is produced rapidly, and aerial parts die back so that the plants are dormant during the hot, dry summer. New leaves are produced in response to the autumn rains, and vegetative growth continues throughout the mild winter, with new flowers appearing again in the spring. However, in several taxonomic groups, mostly among the monocotyledons (Biarum, Colchicum, Crocus, Galanthus, Narcissus, Scilla, Sternbergia, Urginea), but including also a few dicotyledonous genera (Cyclamen, Ranunculus), certain species have reversed this pattern. They flower in the autumn (September to early December), often without leaves. Vegetative growth and seed maturation is slow during the winter and spring, and the plants remain dormant throughout the summer. In some genera such as Galanthus and Ranunculus, autumn-flowering is rather an exception (G. reginae-olgae, R. bullatus), in others (e.g., Crocus) it is common, and in a few such as Colchicum and Sternbergia it has become the dominant pattern. There are approximately seven times as many spring-flowering as autumn-flowering species. Only a few, 5-10% of the total, can be classified as summer- or winter-flowering (cf. Fig. 2).

The genus Crocus, generally considered a spring-flowering genus, has in fact almost as many autumn-flowering as spring-flowering taxa worldwide (Fig. 3). Among the latter are some interesting and beautiful endemics of southern Greece, e.g., C. boryi, C. goulmenyi and C. niveus.
Fig. 2. Bulbous and tuberous plants of Greece: Number of species collected or reported at any given month of the year. The vast majority of records refer to flowering material. There is a pronounced peak of flowering in the spring (March to mid-June) with a secondary, much smaller peak in the autumn (mid-September to mid-November). Data from *Flora Hellenica Database*.

Fig. 3. The genus *Crocus* worldwide: Number of taxa (species and subspecies) flowering at any given month of the year. Spring-flowering taxa only slightly outnumber the autumn-flowering ones. A fair number of taxa, mostly from the Mediterranean lowland, flower in winter (December to February), very few, usually alpine, flower in mid-summer (July and August). Data from Mathew (1982), with some amendments.
In some groups, e.g., the *Crocus biflorus* complex, the *Galanthus vernus* complex (incl. *G. reginae-olgae* and *G. peshmenii*) and *Biarum tenuifolium* s.lat. there are closely related spring-flowering and autumn-flowering taxa. They may have evolved from winter-flowering ancestors through the process of disruptive selection as winters became colder or the plants migrated to higher altitudes or latitudes.

References


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