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Sequences of phenological phases as adaptation to Mediterranean climate in a metal-tolerant serpentine ecosystem

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Summary: The objective of this work is to obtain the annual phenophasic characterisation of Mediterranean serpentine vegetation and its comparison with other studied Mediterranean-type ecosystems. The study was conducted in the serpentine ecosystem of Sierra Bermeja (Spain), where two plots were established (low and high plot) at different altitudinal levels and two endemic scrubland associations (*Staehelino baeticae-Ulicion baetici* alliance) were studied. A phenophasic study was carried out in both plots regarding vegetative and reproductive phenophases. APC index was calculated for the studied plots to obtain the time course of the phenophasic activity of the vegetation through the whole year.

The annual sequence of the phenophases showed that the two associations follow a similar phenophasic pattern, especially regarding vegetative phenophases. An advance of the reproductive phenophases was observed in the low plot and a delay (of one month) in the flowering time compared to other Mediterranean ecosystems in the high plot. The APC index showed a period of strong decrease in phenophasic activity up to 30%, which can serve to differentiate the serpentine ecosystem from other Mediterranean ecosystems, where the APC is higher. No significant differences were obtained neither due to altitude nor to vegetation type.

Keywords: Mediterranean basin, phenology, serpentine vegetation, adaptation, bioclimate

Phenological studies constitute an important part of research on ecosystems (Schwartz 2003). Phenology is one of the main components of the adaptations ('fitness') of plants to the environment (O'Neill 1997; Michelaki et al. 2019). Variations in phenology may cause vulnerability to extreme changes in climatic conditions and changes in latitudinal and altitudinal distribution (Templ et al. 2017) and can modify the composition and structure of plant communities (Bertin 2008; Morecroft & Sally 2016).

Knowledge of the phenology of plant communities can have many implications for knowledge of its structure, dynamics, functions and capacity for regeneration (Floret et al. 1987, 1990). As interest in global change studies increases, a precise knowledge of the phenological cycles of plant communities worldwide is necessary, since they allow monitoring the current climate and predicting the general behaviour of vegetation (White et al. 1997; Menzel et al. 2006; Cleland et al. 2007; Zhao et al. 2016).

The methodology of phenological studies (Orshan 1989) at the community level has been applied to various regions with Mediterranean climate in different parts of the planet including Australia (Pate et al. 1984), Chile (Orshan et al. 1984; Montenegro et al. 1989), France (Floret et al. 1987, 1990; Romane 1987), Israel (Danin & Orshan 1990; Keshet et al. 1990), South Africa (Le Roux et al. 1989) and Spain (Cabezudo et al. 1992, 1993; Caritat et al. 1997; Navarro & Cabezudo 1998; Guàrdia Rúbies et al. 1998; Castro Díez & Montserrat-Martí 1998; Pérez Latorre & Cabezudo 2002, 2006; Pérez Latorre et al. 1996, 2007, 2009; Milla et al. 2009).

At the phenological level, the Mediterranean ecosystems studied so far are generally scrub-like and show certain spatio-temporal patterns (Herrera 1986, 1987, 1992; Arroyo 1990; Aronne & Wilcock 1997; Guàrdia Rúbies et al. 1998; Pérez Latorre & Cabezudo 2002; Tébar et al. 2004; Pérez Latorre et al. 2007). A fairly obvious feature in all of them is the harshness of the summer and its influence on phenology (Mooney & Kummerow 1981). Most of the phenophases, especially those of growth (Arroyo 1990), avoid this season. Furthermore, Mediterranean species shed a large number of leaves in response to summer aridity (Martín & Escarre 1980; Hoffman & Walker 1980; Montenegro 1987; Pereira et al. 1987; Navarro & Cabezudo 1998; Pérez Latorre & Cabezudo 2002; Pérez Latorre et al. 2007), following the semi-deciduous summer strategy (Navarro & Cabezudo 1998). However, these general patterns can be modified, contributing to a high phenological variety, coinciding with a high diversity of growth forms among the species (Kummerow 1983; Orshan 1989; Montserrat-Martí et al. 2004; Pérez Latorre et al. 2009).

So far, a phenological-functional study of Mediterranean scrub-like plant communities on ultramafic rocks (peridotites, serpentines) has not been carried out; these have only been studied at the taxon level (Hidalgo-Triana & Pérez-Latorre 2018a). Serpentine ecosystems are very scarce worldwide and are concentrated only in certain areas of the planet (Roberts & Proctor 1992). It is a type of vegetation of great ecological interest since it must harbour both functional characteristics derived from the adaptation to the special features of serpentine soils (high Fe and Mg content and the deficient nutrient concentrations (N, P and K) and especially the high concentrations of toxic heavy metals (Brooks 1987)) and the adaptation to the Mediterranean climate (Rune 1953; Kruckeberg 1954, 2002; Whittaker 1954; Ornduff 1974; Proctor & Woodell 1975; Brooks 1987; Roberts & Proctor 1992; Baker et al. 1992). The serpentine scrublands in the south of the Iberian Peninsula belong to an endemic phytosociological alliance (*Staehelino baeticae-Ulicion baetici* Rivas Goday and Rivas-Martínez 1969). There are two scrub plant communities, the 'jaguarzales' of *Digitali laciniatae-Halimietum atriplicifolii* Rivas Goday and Rivas Martínez 1967 in the thermo-Mediterranean bioclimatic belt and the 'jaral-brezales' of *Genisto lanuginosae-Cistetum populifolii* Asensi and Díez Garretas 1988 in the meso-Mediterranean belt (Pérez Latorre et al. 1997; Mota et al. 2017). Both types have a high amount of serpentinophytes (Pérez Latorre et al. 2013, 2018) and they are protected in the ultramafic outcrops by the European Directive 92/43UE (Natura 2000 net of protected spaces) (Gómez Zotano et al. 2014).

Among the functional characters related to phenology that are evidenced in the evolution of serpentinophytes (plants linked exclusively to serpentinized soils), changes can be found in time of flowering (phenological divergence). On a taxon level this is translated into a delay due to population isolation (Macnair & Gardner 1998; Hidalgo-Triana & Pérez Latorre 2018a).

The first objective of this article is to obtain the annual phenophasic characterisation of the Mediterranean serpentine vegetation, taking as a model the scrublands of the ultramafic outcrops in the south of the Iberian Peninsula. And the second objective is to check if there are phenophasic differences due to different types of scrub and altitude. Thirdly, similarities or differences of serpentine scrubland phenology with respect to other plant communities in the western Mediterranean are contextualized.

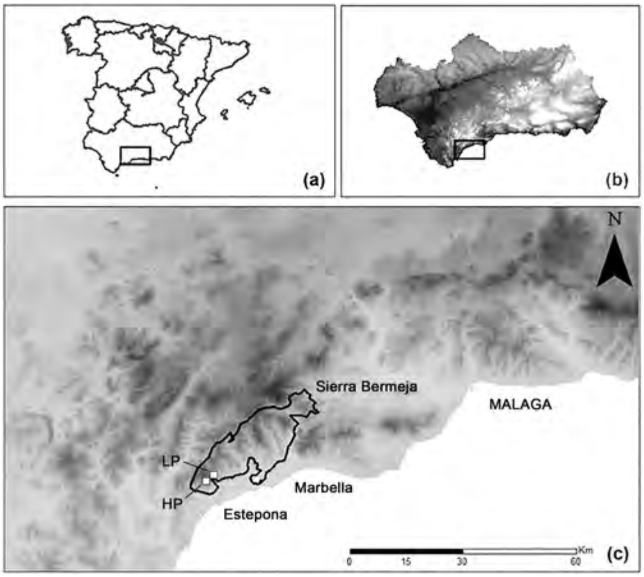


Figure 1. Location of the plots in the Iberian Peninsula (Spain) (a), Andalusia (b) and in the ultramafic outcrop of Sierra Bermeja (Estepona, Malaga province) (c). LP = low plot, HP = high plot.

Materials and methods

Study area

The study was conducted in the serpentine ecosystem of Sierra Bermeja (municipality of Estepona, Malaga, Andalusia, Spain; Fig. 1). It is the largest ultramaphic (serpentine) outcrop in the western Mediterranean with more than 300 km^2 and presents altitudes between 200 m and 1511 m with two bioclimatic belts: thermo-Mediterranean and meso-Mediterranean (Rivas Martínez 2007; Gómez-Zotano et al. 2014). Its landscape consists of *Pinus pinaster* forests, but successional vegetation dynamics as fire or grazing generates scrublands like the *Halimium* plant community (*Digitali laciniatae-Halimietum atriplicifolii*) and the *Cistus populifolius* plant community (*Genisto lanuginosae-Cistetum populifolii*) (Pérez Latorre et al. 1997). Regarding biogeography, Sierra Bermeja is located in the Holarctic Western Mediterranean subregion, Atlantic-Aljibic-Tingitanean superprovince, Baetic ranges province, Bermejense sector (Pérez Latorre & Cabezudo 2002). In this outcrop, two plots were established to study the two types of existing scrubs that also coincide with the two types of bioclimatic belts due to the altitude range of the outcrop. Each plot was located in the centre of a one hectare area covered by each studied plant community. The area for each selected plot was 400 m^2, which was sufficient to include the whole plant diversity of scrub species there, using the minimum area method (Braun-Blanquet 1979; Sawyer et al. 2009; Hidalgo-Triana 2016). The sample area was chosen considering the presence of the characteristic scrub species belonging to the selected scrubland in a phytosociological sense (Boulangeat et al. 2012). In order to gather vegetation data, two selective plant inventories (Appendix 1 and Appendix 2) were made following Braun-Blanquet (1979), including environmental data, presence and cover of plant species. For identification of the taxa, both the Vascular Flora of Eastern Andalusia (Blanca et al. 2011) and the Iberian Flora (Castroviejo et al. 1986–2019) were used. Herbarium sheets were collected for each of the species studied. Once identified and properly labelled and treated, they were deposited in the

Herbarium of the University of Malaga [MGC] and are accessible through the Global Biodiversity Information Facility (GBIF).

Diagnosis of the two plots

Lower plot (LP, Fig. 1). UTM Coordinates (ETRS89): 30S304.507.65 / 4.039.560.77. Altitude: 590 m. Facing slope: SE. Bioclimatology: upper thermo-Mediterranean bioclimatic belt, lower sub-humid ombrotype, type of soil (USDA): entisol. Vegetation: *Digitali laciniatae-Halimietum atriplicifolii* association according to Appendix 1.

Higher plot (HP, Fig. 1). UTM Coordinates (ETRS89): 30S302.870.59 / 4.039.286.46. Altitude: 1270 m. Facing slope: SE. Bioclimatology: upper meso-Mediterranean bioclimatic belt and lower humid ombrotype, type of soil (USDA): lithosol. Vegetation: *Genisto lanuginosae-Cistetum populifolii* according to Appendix 2.

Experimental design

Phenological characterisation. The phenophasic study was carried out according to the methodology proposed by Orshan (1989) with modifications and additions (Pérez Latorre & Cabezudo 2002; Hidalgo-Triana & Pérez Latorre 2018a). Arid-active species in the sense of Evenari et al. (1975), which show a photosynthetic aerial active part during the unfavourable period of summer, were selected and studied during two climatic annual cycles (from October 2011 to September 2013). The presence/absence of each of the phenophases in each species was studied during 24 monthly visits to the plots (around the middle of each month). The studied phenophases were divided into vegetative ones as dolichoblast growth (DVG), brachyblast growth (BVG), leaf shedding of both dolichoblast and brachyblast (LSD and LSB) and dead matter on the plant (DM), and reproductive ones as flower bud formation (FBF), flowering (F), fruit setting (FS) and seed dispersal (SD). A phenophase was considered to be active in the population, when it was observed in at least 5% of the crown and in a minimum of 10% of the studied and marked individuals of the species and was otherwise recorded as an ‘infrequent event’ or absent (Castro-Díez & Montserrat-Martí 1998). Seasons were set as follows: spring (March, April and May), summer (June, July and August), autumn (September, October and November) and winter (December, January and February) (Orshan 1989).

To establish the phenophasic calendar of the two plant communities studied in each year, for each month and for each phenophase, the presence of each phenophase in each species was calculated for each month, obtaining two tables (one for each plot) of species / monthly occurrence of phenophases. From these tables, the annual sequence of each phenophase over the two annual cycles studied was also calculated by obtaining the percentages of presence of each phenophase.

The APC index or ‘active phenophasic period of the plant community’ was calculated (Pérez Latorre & Cabezudo 2002), which represents the percentage of species that show activity in each month with respect to the phenological phases that need favourable conditions for their development and expenditure of resources, similar to the APS for species (Pérez Latorre & Cabezudo 2002). This is a monthly index that can vary from the total number of species (when all species are active) to zero (when none are active).

Comparison with other Mediterranean vegetation types. The phenophasic results obtained in the southern Iberian Mediterranean serpentine scrublands have been compared with those shown

Table 1. List of works on phenology of plant communities studied in the south of the Iberian Peninsula used for the discussion of this work.

Publication	Studied vegetation	Studied area
Cabezudo et al. 1992, 1993	*Cistus* species and *Quercus suber* forests	Baetic ranges
Navarro et al. 1993	Vegetation of bad-lands	Arid south-eastern Iberian Peninsula
Navarro & Cabezudo 1998	Dolomitic shrublands	Baetic ranges
Pérez Latorre & Cabezudo 2002	*Cistus* shrublands	Baetic ranges
Pérez Latorre et al. 2007	Heathlands	Strait of Gibraltar area
Pérez Latorre et al. 2009	*Maytenus* semi-arid shrublands	Semi-arid Andalusian coastal area
Rodríguez-Gallego & Navarro 2015	Dune shrub ecosystems	South-Iberian coasts

by other types of plant communities in the Western Mediterranean, which will allow them to be placed in a more general phenological context within the Mediterranean Basin. Data from the works presented in Table 1 were used.

Results

Phenophasic calendars of plant communities. Appendix 3 and Appendix 4 show the annual phenophasic results for each constituent species of each studied plant community (plot).

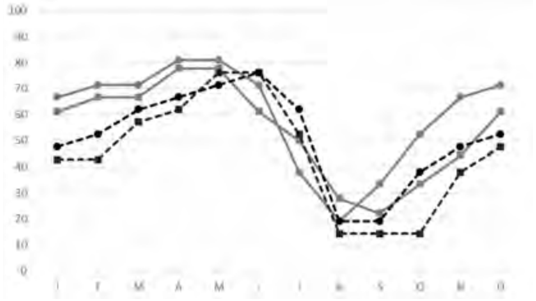
Annual sequence of the phenophases. The phenophase charts represent the sequence of the different phenophases throughout each year in the communities (plots) studied. Figures 2 and 3 correspond to vegetative phenophases, Figs 4 and 5 represent the reproductive phenophases. In general, the phenological patterns ocurring in both plots (Figs 2–5) are very similar, although a certain advance of the reproductive phenophases in the LP with respect to the HP is observed.

Vegetative phenophases: dolichoblast and brachyblast vegetative growth and leaf shedding. In the studied communities dolichoblasts were active (vegetative growth) during almost the whole year, except for the summer decrease, where it falls to approximately 20% (DVG, Fig. 2a). The vegetative growth of the dolichoblast (Fig. 2a) has its maximum during April and May in the LP with 80%, while there is a delay in the upper plot (May to June, 75%) (Fig. 2a).

The minimum of vegetative activity takes place from August to September (activity below 30%), coinciding with the maximum leaf fall of both dolichoblasts and brachyblasts (Fig. 3a–b). There is a small second decrease in the middle of winter, especially in LP (January to February; Fig. 2a–b).

Brachyblast growth (BVG, Fig. 2b) showed differences between the plots: a peak in May (90%) in the upper plot that remains above 70% from December to April (4 months) and a plateau from February to May (greater than 80%) in the lower plot that extends even from December to January with more than 70%. The growth minima occurred in August and September (20% in LP and less than 30% in HP).

The percentage of species with growth of their brachyblasts (BVG, Fig. 2b) is always slightly higher than the percentage of species with growth in the dolichoblast (DVG, Fig. 2a).



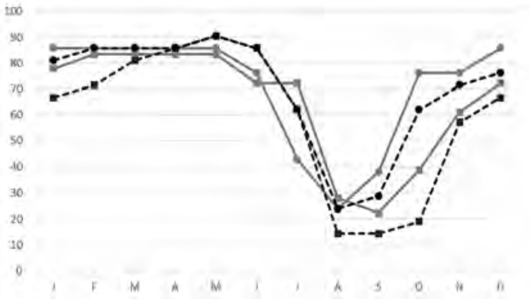


Figure 2a. Monthly percentage of species showing dolichoblast vegetative growth for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle=% taxa year 2, HP.

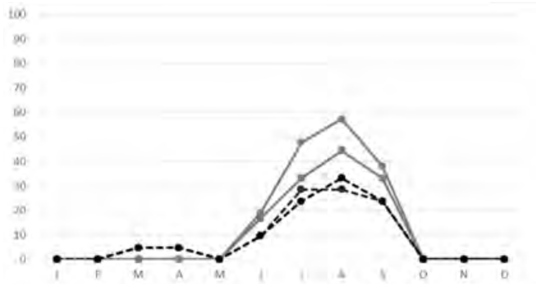
Figure 2b. Monthly percentage of species showing brachyblast vegetative growth for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

The studied plant communities tend to experience a maximum leaf drop in the months of August and September for both dolichoblasts and brachyblasts (LSD and LSB, Fig. 3a–b), coinciding with the sharp decrease in vegetative growth of both types of branches (DVG and BVG, Fig. 2a–b). There is a slight advance to July at the peak of dolichoblast leaf fall in the upper plot. Note that the percentages of species that shed their brachyblast leaves (40–60%) are slightly higher than those of dolichoblasts (30–55%). The brachyblasts practically do not lose leaves (<5–10%) in both plant communities for 8 months (October to May).

Dead matter on the plant body. The presence of dead matter on the individuals of the communities was quite high throughout the year, ranging between 90 and 100% of the species.

Reproductive phenophases. The communities of both plots formed their flower buds in spring (FBF, Fig. 4a), with a maximum peak in the month of May for both plots, but the HP peak was slightly more pronounced (65–80%) than that of LP (60–70%). The minimum occurs in both plots from July to January with less than 20%.

Flowering in both plots was bi-seasonal (F, Fig. 4b), since it took place mainly between the months of May (spring) to June (summer), although the peak in LP took place in May and is slightly



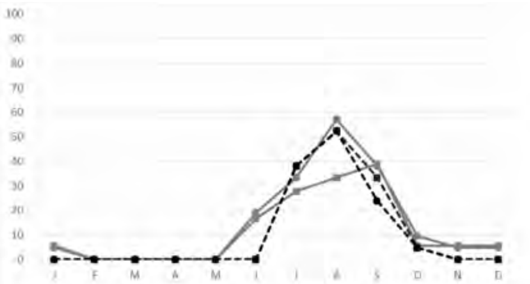
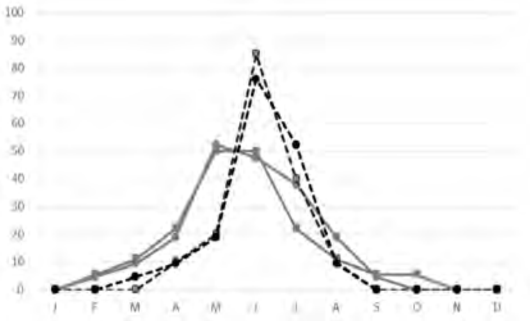


Figure 3a. Monthly percentage of species showing leaf shedding dolichoblast for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

Figure 3b. Monthly percentage of species showing leaf shedding brachyblast for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.



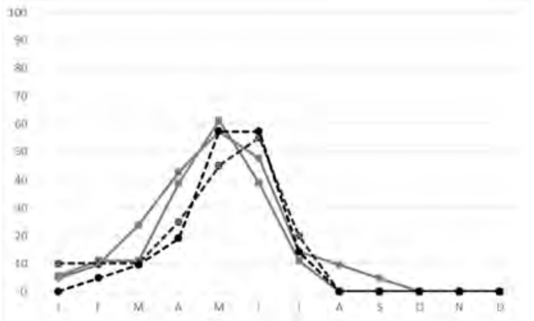


Figure 4a. Monthly percentage of species showing flower buds formation for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

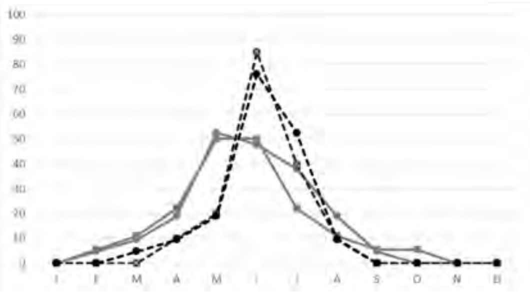
Figure 4b. Monthly percentage of species showing flowering for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

higher (60%) than in HP (55%), which is delayed to May–June. In LP, flowering is null only for 3 months (October to December), while in HP it is for almost half a year (August to December).

The community fructified mainly at the beginning of the summer season (FS, Fig. 5a), predominantly in the month of June in both plots with an early peak for the LP in May. It is noteworthy that the peak of FS in HP (80%) is produced by a percentage of species much higher than that of LP (50%).

Both communities begin the dispersal of their fruits and seeds in the summer, extending to a lesser extent towards the autumn with small differences (SD, Fig. 5b). This phenophase contradicts the general advance shown by the lower plot, since in HP the peak is in July (70%), while in LP it is in August (60%).

Phenophasic Activity Index (APC). The APC index (Fig. 6a) showed that the two communities studied were active throughout the year, although there was a considerable decrease in activity from the end of summer to the beginning of autumn, during August and September, with 30–40% of activity in LP and 20–30% in HP. The APC of the LP was slightly higher than that



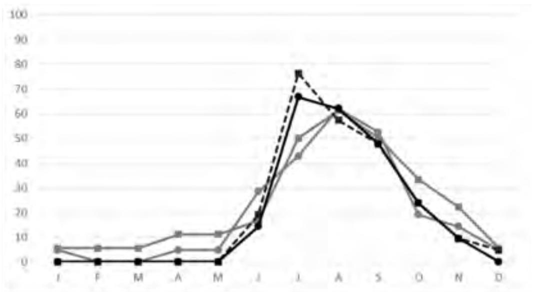
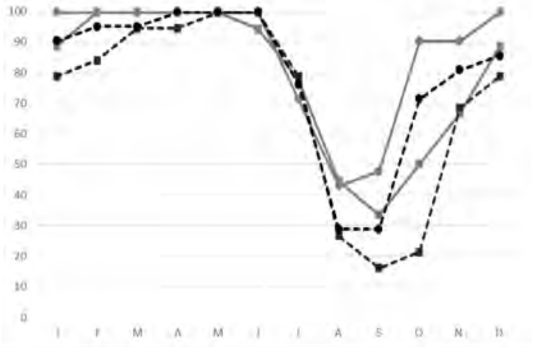


Figure 5a. Monthly percentage of species showing fruit setting for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

Figure 5b. Monthly percentage of species showing seed dispersal for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.



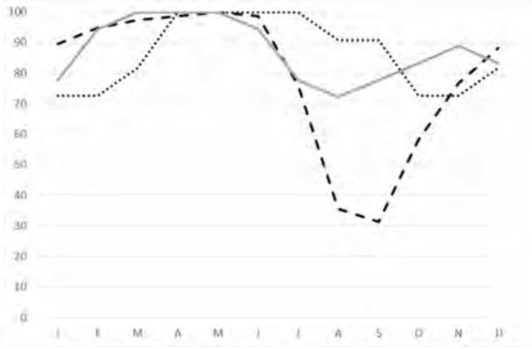


Figure 6a. Annual evolution of the APC index (monthly percentage of species showing phenophase activity) for each community (plot, LP, HP) and year (1 or 2). Grey square = % taxa year 1, LP. Grey circle = % taxa year 2, LP. Black square = % taxa year 1, HP. Black circle = % taxa year 2, HP.

Figure 6b. APC index (monthly percentage of species showing phenophase activity) throughout an annual cycle for different plant communities of Mediterranean scrubs. Dotted line = *Cistus ladanifer* shrublands (data from Pérez Latorre & Cabezudo 2002), grey line = *Erica umbellata* and *Stauracanthus boivinii* heathlands (data from Pérez Latorre et al. 2007) and dashed line = serpentine shrublands (average of the two years of study and of the two plots).

of the HP during the period from December to April-May (about 6 months). The maximum in both plots (above 90%) occured between March and June and even reached more than 80% during December and February, which means more than 80% activity for more than half a year. The maxima in the LP (above 90%) began earlier and were observed from December to the end of June, whereas in the HP these maxima (greater than 90%) occurred from spring (March) to early summer (June). The lowest APC values (close to 30–60%) were concentrated at the same time for both study plots in August and September. These minima were slightly more pronounced for HP (values close to 20% of species).

Comparison with other Mediterranean vegetation types. Figure 6b shows the APC values for the plant communities studied in this work along with the APC values for other types of scrubs such as *Cistus* communities (Pérez Latorre & Cabezudo 2002) and heathlands (Pérez Latorre et al. 2007). In all the Mediterranean scrub ecosystems studied so far, there is a very favourable period of the year with APC above 70% and reaches 100% during the months of November to July (9 months). On the other hand, in all the types of vegetation studied there is a strong decrease in phenological activity in summer. It is also observed that in the serpentine ecosystems, the summer minima (July to August) and early autumn minima (September to October) with APC less than 40% (up to 31%) are much more pronounced than those of the other two types of scrublands that maintain APC always above 70%. In addition, the *Cistus* community only show a small decrease in summer activity and their minima occur in autumn to winter, while the heathland presents its minimum in summer (August). The maxima in most of the ecosystems studied so far coincide with the spring months (May with APC of 100% for the three types of vegetation and above 90% in April and June).

Discussion

Phenophasic results obtained in this study are discussed in relation with altitude (LP and HP) and the type of scrubs in the studied plots and compared with those obtained in other types of scrubs and vegetation distributed in the westernmost Mediterranean basin.

Vegetative phenophases

Dolichoblast and brachyblast vegetative growth. The lag in the DVG peaks of LP and HP shows the existence of a slight delay of one month in HP. In turn, decreases in DVG in LP coincide with increases in HP, especially in the months of transition from spring to summer, which could be due to the fact that the climatic conditions become arid earlier in the LP. However, during 6 months of winter and spring (December to May), the DVG in the HP is 10–20% lower, which could indicate better general climatic conditions in the LP or, what is the same, less benignity in HP. Compared with other Mediterranean ecosystems, it is observed that in both scrubs (Navarro & Cabezudo 1998) and *Cistus* communities (Pérez Latorre & Cabezudo 2002) increases in BVG occur before increases in DVG, but the percentages of DVG achieved in these ecosystems are greater than the percentages of BVG, unlike in the serpentine scrubs, probably because the annual elongations are less due to the smaller size that the plants reach in serpentine ecosystems (Hidalgo-Triana & Pérez Latorre 2018a). In Mediterranean heathlands (Pérez Latorre et al. 2007), the peak of increase of DVG occurs before that of BVG (resembling the serpentine scrubs), but the percentage of DVG is greater than that of BVG (resembling the *Cistus* community and to the dolomite scrubland). The peaks of BVG being earlier (February to May) than the DVG (May to June) of the serpentine ecosystem may be due to the fact that many of the plants in this ecosystem flower on brachyblast branches, or dolichoblasts are formed from brachyblasts, and therefore BVG has to be produced before DVG. Furthermore, it has been proven that BVG responds more quickly than DVG to growth events associated with environmental changes (Puntieri et al. 2002).

Dolichoblast and brachyblast leaf shedding. Leaf fall occurs mostly in the summer season for both types of branches, coinciding with the patterns observed in other Mediterranean ecosystems (Navarro & Cabezudo 1998; Pérez Latorre & Cabezudo 2002; Pérez Latorre et al. 2007). The percentages of species that show shedding of brachyblast leaves are slightly higher than those that show shedding of dolichoblast leaves, which could be explained by the fact that, in general, the species form more brachyblasts than dolichoblasts since the presence of species with brachyblasts (which also may show flowering) is higher in the community (Hidalgo-Triana & Pérez Latorre 2018a). These plants are going to spend the summer with their active brachyblasts, so it should be more profitable for their water balance to have a smaller breathable surface in their brachyblasts and to shed their leaves (Orshan 1989; Palacio & Montserrat-Martí 2006).

Dead matter on the plants. The fact that the content in dead matter of these communities is very high throughout the year coincides with what occurs in the ecosystems of Mediterranean heathlands (Pérez Latorre et al. 2007), where 80% of the species maintain dead matter throughout the year increasing to 95% in August to September and falling to 70% in October to November and June. The same occurred in the *Maytenus senegalensis* communities (Pérez Latorre et al. 2009). These high contents in dead matter could have very negative repercussions in the face of flammability and the expansion of possible fires (Montserrat-Martí et al. 2004; Hidalgo-Triana & Perez Latorre 2018b). It should be noted that the amount of dead matter that these plants retain, at the individual level, is low due to the low biomass content of their reduced structures as they are serpentinophytes (Pichi-Sermolli 1948). The plants detach from all that dead biomass just before summer, due to the fact that they are semi-deciduous in summer and due to the basipetal shedding of branches, accumulating in the soil and therefore increasing the flammability of the ecosystem (Hidalgo-Triana 2016; Hidalgo-Triana & Pérez Latorre 2018b).

Reproductive phenophases

Flower bud formation. The larger and faster pre-flowering of HP in relation to LP, could show that the conditions of the HP are more hostile (more rigorous winter and summer stress starting the same as in the LP despite the lower altitude) and that is why the vegetation is forced to flower during shorter time before the summer. In benign climates, phenophases can extend over a longer time (Mooney & Dunn 1970; Di Castri et al. 1981; Kummerow 1983).

Flowering. The later peak of flowering (as occurring with the pre-flowering period) in the HP, with a slightly smaller peak and much shorter lasting, could indicate again that the conditions of the HP are more hostile, with the flowering compressed for a winter more rigorous (Vera 1995) and summer stress starting at the same time as in the LP despite the altitudinal difference. If we compare the flowering peaks in the two study plots (between 50–60%) with those of other Mediterranean ecosystems, they all occur in spring and the percentages are similar: in the *Cistus* community, approximately 40–50% (Pérez Latorre & Cabezudo 2002) and 30–40% in Mediterranean dolomite scrublands (Navarro & Cabezudo 1998); it was in the heathlands, where the highest percentage was given with 70% (Pérez Latorre et al. 2007) in the same way as in relict communities of *Maytenus senegalensis* (Pérez Latorre et al. 2009). This similarity in the number of species at the flowering peak could be explained by the fact that all the communities studied are biogeographically considered as Mediterranean and therefore behave in the same way. However, there are differences in the seasonal time, when the peak of flowering occurs, since in the Mediterranean heathlands it is in May and in the other communities it is in April. On the contrary, in serpentine vegetation, flowering is bi-seasonal, extending until May or June, which supposes a certain delay compared to other studied plant communities, probably produced by the typical isolation of serpentine ecosystems (Macnair & Gardner 1998; Wright et al. 2006) and whose adaptive meaning could be related to greater reproductive success (Hidalgo-Triana & Pérez Latorre 2018a). This delay has also been detected at the species level (Hidalgo-Triana & Pérez Latorre 2018a) and by other authors in gypsum ecosystems, which are also quite hostile soils for plants (Escudero et al. 2015). Regardless of the plot, the group of serpentinophytes show flowering later than that of widely distributed species, which could have reproductive significance and also be phenologically dependent on strong and/or abrupt changes in the bioclimatic conditions (precipitation and/or temperature) (Hidalgo & Pérez Latorre 2018a).

Fruiting. The peak of fruiting is in early summer and presents a quite significant asymmetry, since in the HP it reaches almost 80% in June, while the LP only reaches 50% in May to June. This peak of flowering in early summer coincides with that observed in other scrublands and there is no prolongation of fruiting during the rest of the summer and even in early autumn as in forests (Pérez Latorre & Cabezudo 2002). In the heathlands (Pérez Latorre et al. 2007), the peak of fruiting occurs in May like in the LP.

Seed dispersal. The asynchrony detected in the dispersion peak (July in the HP and August in the LP) implies in both cases that the dispersion occurs in the summer season, as in other similar scrub communities with a peak in September (Navarro & Cabezudo 1998) or late summer

(August) in *Cistus* scrublands (Pérez Latorre & Cabezudo 2002). In heathlands, the main peak occurs in July just like in HP.

Phenological comparison between plots. At the level of phenophases in each of the plant communities studied (LP and HP), some differences have been observed: (1) one month of delay in the flowering phenophase of HP compared to LP. (2) In HP, there is no winter flowering. (3) Vegetative and reproductive phenophases are shorter in HP. Despite the facts that the plant communities are phytosociologically different and there are important differences at the bioclimatic level between the plots, the differences detected and indicated are not very noticeable. This lack of differences in functional patterns between physiognomically similar, but floristically different associations has already been highlighted by Pérez Latorre et al. (2001) between two types of *Quercus suber* forests with different distribution.

Active phenophasic period of the plant communities (APC). Since in the LP the maxima of APC are about six months above those of the HP, this may indicate the greater benignity of the ecological conditions in the LP (lower altitude) compared to the HP (higher altitude). Besides that, although the minimum values occur at the same time in both plots, the lower APC values in the HP compared to the LP, could be due to the fact that in the HP the amount of edaphic relative humidity is always lower, since the soils are shallower and more rocky (lithosols).

The most relevant result is that the drop in summer of the APC index is much more pronounced (falls up to 30–35%) in the serpentine ecosystems than in the other represented Mediterranean scrub ecosystems (in which it only falls to values close to 70%). This could be explained by the water stress caused by the low water retention capacity of serpentine soils and in combination with the physiological aridity caused by the special mineralogical composition and heavy metals (Brady et al. 2005), since the effect of the Mediterranean climate (strong summer drought) is the same for all types of compared scrubs. Thus, it could be deduced that the serpentine habitat is the most hostile of all the scrubs studied so far.

Conclusions

The general phenophasic characterization of the South Iberian serpentine scrublands is similar in the two plots studied and also to the general model of the Mediterranean scrubs previously studied, although there are slight differences, also between the two types of serpentine scrubs.

The most notable phenophasic differences between the two types of serpentine scrubs consist of: an advance of reproductive phenophases in the LP, a shorter duration of flowering and no winter flowering in the HP, a notable asynchrony in the fruiting peak and a delay in the DVG in the HP. Finally, both vegetative and reproductive phenophases are shorter in HP. All these differences are possibly related to the altitude and bioclimatic differences.

The APC phenophasic index shows a period of strong decrease in phenophasic activity (leaf fall and vegetative growth) up to 30%, which coincides with the most unfavourable period in the Mediterranean bioclimatic type (summer) and can extend even in early autumn. This sharp drop in phenophasic activity could serve to differentiate the studied serpentine scrubs from other types of Mediterranean scrubs, which do not descend from an APC of around 70%.

Growth and flowering trends can be modified due to the adaptation of the plants to the serpentine substrate, especially in the case of flowering and pollination (Macnair & Gardner 1998; O'Neill

1997). In our study, these phenophasic events have presented few differences between the two plant communities studied: flowering begins in late spring and occurs mostly in the summer season, indicating that there is a certain delay (of one month) compared to other Mediterranean ecosystems studied in the south of the Iberian Peninsula; for example, heathlands with flowering in May and a notable fall in June (Pérez Latorre et al. 2007) and scrublands of dolomites with a flowering peak in April (Navarro & Cabezudo 1998) that show spring flowering. This delay in the flowering of serpentine communities (even sharper in groups of serpentinophytes; Hidalgo & Pérez Latorre 2018a) does not coincide with the fact of the lower general water availability, and even more in summer, in ultramafic xeric soils, which should theoretically advance the flowering due to its consumption of resources and water, which opens a field of research to search for answers to this phenological event.

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Appendix 1. Phytosociological inventory of the lower plot. UTM: 304509/4039557; Orientation: SE; Inclination: 30°; Cover: 80%; Altitude: 590 m; Lithology: peridotite (dunites); Area: 120 m^2; Vegetation height: 100 cm; Date: 17/4/2012.

Association characteristics (*Digitali laciniatae-Halimietum atriplicifolii*)	
Halimium atriplicifolium subsp. *atriplicifolium*	*4*
Digitalis obscura subsp. *laciniata*	+
Alliance characteristics (*Staehelino-Ulicion*)	
Ulex borgiae	*3*
Staehelina baetica	*1*
Genista hirsuta subsp. *lanuginosa*	+
Teucrium haenseleri	+
Class characteristics (*Cisto-Lavanduletea*)	
Cistus salviifolius	*1*
Glandora prostrata susbp. *lusitanica*	+
Companion	
Brachypodium retusum	*3*
Erica scoparia	*2*
Carex distachya	*1*
Elaeoselinum asclepium subsp. *millefolium*	*1*
Phlomis purpurea	*1*
Bellis pappulosa	+
Daphne gnidium	+
Galium boissieranum	+
Linum narbonense	+
Quercus coccifera	+
Sanguisorba verrucosa	+
Scilla maritima	+
Smilax aspera	+

Appendix 2. Phytosociological inventory of the upper plot. UTM: 30S 302.870.59/4.039.286.46 m. Orientation: SE. Inclination: 20°. Cover: 80%. Altitude: 1250 m. Lithology: peridotite (lherzolites). Area: 125 m^2. Vegetation height: 40 cm. Date: 13/6/2012.

Association characteristics (*Genisto lanuginosae-Cistetum populifolii*)	
Genista hirsuta subsp. *lanuginosa*	*2*
Cistus populifolius subsp. *major*	*1*
Genista triacanthos	*1*
Alliance characteristics (*Staehelino-Ulicion*)	
Halimium atriplicifolium susbp. *atriplicifolium*	*3*
Staehelina baetica	*2*
Ulex baeticus subsp. *baeticus*	*2*
Alyssum serpyllifolium subsp. *malacitanum*	+
Class characteristics (*Cisto-Lavanduletea*)	
Glandora prostrata subsp. *lusitanica*	*1*
Cistus salviifolius	+
Companion	
Brachypodium retusum	*2*
Erica scoparia	*1*
Anthyllis vulneraria	+
Aphyllantes monspeliensis	+
Asphodelus albus	+
Carlina hispanica	+
Coris monspeliensis	+
Juniperus oxycedrus	+
Linum carratracense	+
Sesamoides canescens	+
Thymus baeticus	+

Appendix 3. Monthly presence of phenological phases for each species in the thermo-Mediterranean plot (LP). Serpentine scrubland of *Digitali laciniatae-Halimietum atriplicifolii*. Year of study: 1 = 2011–2012; 2 = 2012–2013. FBF: flower bud formation; F: flowering; FS: fruit setting; SD: seed dispersal; DVG: dolichoblast growth; LSD: leaf shedding of dolichoblast; LSB: leaf shedding of brachyblast; BVG: brachyblast growth; DM: dead matter on the plant; APS: active phenophasic period of the plant (monthly).

Taxon	Year of study	Reproductive Phenological Phases				Vegetative Phenological Phases					Phenological Index
		FBF	F	FS	SD	DVG	LSD	BVG	LSB	DM	APS
Arenaria montana subsp. *intricata*	2	Apr	Apr	May	Jun	Sep–Jun	Jul–Sep	Sep–Jul	Jul–Sep	All year	Sep–Jul
Brachypodium retusum subsp. *retusum*	1	Jun	Jun	Jun	Jul	Apr–May	none	Dec–Jul	none	All year	Dec–Jul
	2	Jun	Jun	Jun–Jul	Aug	Apr–May	none	Oct–Jun	none	All year	Oct–Jun
Bupleurum acutifolium	2	Apr–Aug	Jun–Aug	Jul–Aug	Sep–Oct	Dec–Jun	Jul–Sep	Oct–Jun	Aug–Sep	All year	Oct–Aug
Bupleurum rigidum subsp. *rigidum*	1	Jul	Jul	Aug–Oct	Aug–Nov	none	none	Feb–Jul	Sep–Jan	Aug–Jan	Feb–Oct
	2	Jul–Aug	Jul–Sep	Aug–Sep	Aug–Sep	none	none	Dec–Jun	Aug–Jan	Aug–Jan	Dec–Sep
Carex distachya	1	Apr	Apr–May	Apr–May	Jun–Ago	none	none	Dec–Jun	none	All year	Dec–Jun
	2	Mar	Mar–May	Apr–May	Jun–Ago	none	none	Oct–Jul	none	All year	Oct–Jul
Cistus salviifolius	1	Feb–Apr	Apr	Apr–May	Oct	Oct–Jul	Jun	Nov–Jul	Jun–Jul	All year	Oct–Jul
	2	Feb–Mar	Mar–Apr	Apr–May	Nov	Oct–Jul	Jun–Jul	Sep–Jul	Jun–Jul	All year	Sep–Jul
Digitalis obscura subsp. *laciniata*	1	Apr–Jun	May–Jun	Jun–Jul	Oct–Nov	Nov–Jan and Apr–May	Aug–Sep	Oct–Jul	Sep	All year	Oct–Jul
	2	Apr–May	May	Jul	Oct–Jan	Nov–Jan and Apr–Jun	Aug–Sep	Oct–Jul	Sep–Oct	All year	Oct–Jul
Erica scoparia subsp. *scoparia*	1	Jul–Sep	None	None	Nov–May	Feb–Jul and Dec	Jun–Jul	None	None	All year	Feb–Sep and Dec
	2	Oct–May	May–Jun	Jun–Aug	Aug–Sep	Sep–Dec and Feb–Jul	Jun–Jul	None	None	All year	All Year
Euphorbia flavicoma subsp. *bermejense*	2	May	May–Jun	May–Jun	Jun	Sep–May	Jun–Sep	Sep–May	Jun–Aug	All Year	Sep–Jun

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Euphorbia flavicoma subsp. *flavicoma*	1	May	Nay–Jun	Jun	Jul	Dec–Jul	Jul–Sep	Nov–Jul	Aug–Sep	All year	Nov–Jul
	2	May	May–Jun	Jun	Jul	Nov–Jul	Jul–Sep	Sep–Jun	Aug–Sep	All year	Sep–Jul
Genista hirsuta subsp. *lanuginosa*	1	Apr–May	May	Jun	Jul–Sep	None	None	Jan–May	Jun–Jul	All year	Jan–Jun
	2	Apr–May	May	Jun	Jun–Sep	None	None	Dec–May	Jun–Aug	All year	Dec–Jun
Galium boissieranum	1	May–Jun	Jun	Jul–Aug	Aug–Sep	Jan–Jun	Aug–Sep	Oct–Jun	Aug–Sep	All year	Oct–Aug
	2	May–Jun	Jun	Jul–Aug	Jul–Sep	Nov–Jun	Aug–Sep	Oct–Jun	Aug–Sep	All year	Oct–Aug
Glandora prostrata subsp. *lusitanica*	1	Jan–Apr	Feb–May	Mar–May	Apr–May	All Year	None	All Year	None	All Year	All Year
	2	Jan–Mar	Feb–Apr	Mar–May	Apr–May	All Year	None	All Year	None	All Year	All Year
Halimium atriplicifolium subsp. *atriplicifolium*	1	Apr–Jun	May–Jul	Jun–Jul	Jul–Nov	Nov–Jul	Jul–Aug	Nov–Jul	Jul–Aug	All Year	Nov–Jul
	2	Apr–Jun	May–Jul	Jun–Jul	Jul–Nov	Oct–Jun	Jul–Aug	Oct–Jun	Jul–Aug	All Year	Oct–Jul
Lavandula stoechas	1	Jan–May	Apr–May	May–Jun	Aug–Oct	All Year	Aug–Sep	All Year	Aug–Sep	All Year	All Year
	2	Jan–Jun	Mar–Jun	May–Jul	Aug–Sep	All Year	Aug–Sep	All Year	Aug–Sep	All Year	All Year
Linum narbonense	1	Apr–May	Apr–May	May–Jun	Jul–Sep	Dec–Jun	Jul–Aug	None	None	Dec–Sep	Dec–Jun
	2	Apr–May	Apr–May	May–Jun	Jul–Sep	Oct–Jun	Jul–Aug	None	None	All Year	Oct–Jun
Phlomis purpurea	1	Mar–May	May	May–Jun	Aug–Sep	Oct–Aug	Jun–Jul	OctvAug	Jun–Jul	All Year	Oct–Aug
	2	Feb–May	Apr–May	May–Jun	Aug–Sep	Oct–Jul	Jun–Aug	Oct–Aug	Jun–Aug	All Year	Oct–Aug
Sanguisorba verrucosa	1	Apr–May	Apr–Jun	May–Jun	Jun–Jul	None	Jul–Sep	Nov–Jul	Jul–Sep	All Year	Nov–Jul
	2	Apr–May	Apr–Jun	May–Jun	Jun–Jul	None	Jul–Aug	Oct–Jun	Jul–Aug	All Year	Oct–Jun
Staehelina baetica	1	May–Jun	May	May	Jul–Oct	All Year	None	All Year	None	All Year	All Year
	2	May–Jun	May	May	Jul–Oct	All Year	None	All Year	None	All Year	All Year
Teucrium haenseleri	1	May–Jun	Jun	Jul	Aug–Sep	All Year	Aug–Sep	All Year	Aug–Sep	All Year	All Year
	2	May–Jun	Jun	Jul	Aug–Sep	All Year	Aug–Sep	All Year	Aug–Sep	All Year	All Year
Ulex borgiae	1	Nov–Mar	Jan–Apr	Feb–May	Jun–Aug	Feb–May	None	None	None	All Year	Nov–May
	2	Oct–Apr	Jan–Apr	Feb–May	Jun–Aug	Feb–Jun	None	None	None	All Year	Oct–Jun

Appendix 4. Monthly presence of phenological phases in the species of the meso-Mediterranean plot (HP). Serpentine scrubland of *Genisto lanuginosae-Cistetum populifolii*. Year of study: 1 = 2011–2012; 2 = 2012–2013. FBF: flower bud formation; F: flowering; FS: fruit setting; SD: seed dispersal; DVG: dolichoblast growth; LSD: leaf shedding of dolichoblast; LSB: leaf shedding of brachyblast; BVG: brachyblast growth; DM: dead matter on the plant; APS: active phenophasic period of the plant (monthly).

Taxon	Year of study	Reproductive Phases				Vegetative Phases					Phenological Index
		FBF	F	FS	SD	DVG	LSD	BVG	LSB	DM	APS
Alyssum serpyllifolium subsp. *malacitanum*	1	Apr–Jun	May–Jun	Jun–Jul	Aug–Oct	All year	Mar–Apr	All year	Aug–Sep	All year	All year (12)
	2	Apr–Jun	May–Jun	Jun–Jul	Aug–Oct	All year	Mar–Apr	All year	Jul–Sep	All year	All year
Armeria colorata	1	Apr–Jun	May–Jul	Jun–Jul	Jul–Oct	–	–	Nov–May	Sep–Oct	All year	Nov–Jul
	2	Apr–Jun	May–Jun	Jun	Jul–Oct	–	–	Sep–May	Sep–Oct	All year	Sep–Jun
Brachypodium retusum subsp. *retusum*	1	Jun	Jul	Jul	Jul–Aug	May–Jun	–	Jan–Jul	–	All year	Jan–Jul
	2	Jun	Jun–Jul	Jul–Aug	Jul–Aug	May–Jun	–	Oct–Jun	–	All year	Oct–Jun
Carex distachya	1	Apr–May	Apr	May–Jun	Jun–Jul	–	–	Dec–Jun	–	All year	Dec–Jun
	2	Apr	Apr	May–Jun	Jul	–	–	Oct–Jun	–	All year	Oct–Jun
Centaurea haenseleri	1	May–Jun	Jun	Jun	Jul	–	–	Apr–Jul	Aug	Jun–Sep	–
	2	May–Jun	Jun–Jul	Jul	Jul	–	–	Oct–Jul	Aug	Jun–Sep	Oct–Jul
Cistus populifolius subsp. *major*	1	May	May	Jun	Sep–Nov	May–Jul	Jul	May–Jul	Jul	All year	May–Jul
	2	Apr–May	May	Jun	Sep–Nov	Jun–Jul	Jul	May–Aug	Jul	All year	Apr–Aug
Cistus salviifolius	1	Mar–May	May	Jun	Oct	Nov–Jul	Jul	Nov–Jul	Jul	All year	Nov–Jul
	2	Mar–May	May	Jun	Oct–Nov	Oct–Jul	Jul–Ago	Oct–Jul	Jul	All year	Oct–Jul
Erica scoparia subsp. *scoparia*	1	Jul–Sep	–	–	Oct–Dic	Nov–Dec and May–Jul	Jun–Jul	–	–	All year	–
	2	Nov–May	May–Jun	Jun–Aug	Jul–Sep	Oct–Dec and Apr–Jul	Jun–Jul	–	–	All year	Oct–Aug
Euphorbia flavicoma subsp. *flavicoma*	1	May	May–Jun	Jun	Jul	Jan–Jun	Aug–Sep	Oct–Jun	Jul–Aug	All year	Oct–Jun
	2	May	Jun	Jun	Jul	Oct–Jul	Aug–Sep	Oct–Jun	Aug	All year	Oct–Jun

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Fumana thymifolia	1	Mar–Jun	May–Jun	Jun	Jun–Aug	Mar–Jul	Aug–Sep	Nov–Jul	Aug–Sep	All year	Nov–Jul
	2	Apr–May	May–Jun	Jun	Jun–Jul	Feb–Jul	Aug–Sep	Oct–Jul	Jul–Aug	All year	Oct–Jul
Galium boissieranum	1	May–Jun	Jun	Jul–Aug	Jul–Sep	Mar–Jun	Aug–Sep	Mar–Jun	Aug–Sep	All year	Mar–Aug
	2	Jun	Jun	Jul	Jul–Aug	Mar–Jun	Aug–Sep	Feb–Jun	Aug–Sep	All year	Feb–Jul
Genista hirsuta subsp. *lanuginosa*	1	Jun	Jun	Jun–Jul	Aug–Sep	–	–	Feb–Jun	Jul–Aug	All year	Feb–Jul
	2	May–Jun	Jun	Jun–Jul	Aug–Sep	–	–	Jan–Jun	Jul–Aug	All year	Jan–Jul
Genista triacanthos	1	Apr–May	Apr–May	Jun	Jul	Dec–Jul	Aug–Sep	Dec–Jul	Aug–Sep	All year	Dec–Jul
	2	Apr–May	Apr–May	Jun–Jul	Jul–Aug	Nov–Jul	Aug–Sep	Nov–Jul	Aug–Sep	All year	Nov–Jul
Glandora prostrata subsp. *lusitanica*	1	Jan–May	Jan–Apr	Apr–Jun	Jun–Jul	All year	–	All year	–	All year	All year
	2	Jan–Apr	Feb–May	Apr–Jun	Jun–Jul	All year	–	All year	–	All year	All year
Halimium atriplicifolium subsp. *atriplicifolium*	1	May–Jul	Jun–Jul	Jun–Aug	Jul–Sep	Dec–Jul	Jul–Aug	Nov–Jul	Jul–Aug	All year	Nov–Aug
	2	May–Jun	Jun	Jun–Jul	Aug–Oct	Dec–Jul	Jul–Aug	Dec–Jul	Jul–Aug	All year	Dec–Jul
Lavandula stoechas	1	Jan–May	Jan–Apr	May–Jun	Jul–Sep	All year	Jul–Sep	All year	Jul–Sep	All year	All year
	2	Jan–Apr	May	May–Jun	Aug–Sep	All year	Aug–Sep	All year	Aug–Sep	All year	All year
Linum carratracense	1	May–Jun	Jun	Jun–Jul	Jul–Sep	Nov–Jul	–	Nov–Jul	–	All year	Nov–Jul
	2	May–Jun	Jun	Jun–Jul	Aug–Sep	Nov–Jul	–	Nov–Jul	–	All year	Nov–Jul
Sanguisorba verrucosa	1	Apr–May	May	Jun	Jul	–	–	Nov–Jul	Jul–Sep	All year	Nov–Jul
	2	May	May	Jun	Jul	–	–	Sep–Jul	Jul–Aug	All year	Sep–Jul
Staehelina baetica	1	May–Jul	Jun–Jul	Jul	Jul–Sep	Nov–Jul	–	Nov–Jul	–	All year	Nov–Jul
	2	Jun–Jul	Jul	Jul	Jul–Sep	All year	–	All year	–	All year	All year
Thymus baeticus	1	May–Jun	Jun	Jun	Jul–Sep	Nov–Dec/ Mar–Jun	Jun–Jul	Nov–Dec/ Mar–Jun	Jul–Aug	All year	Nov–Dec/ Mar–Jun
	2	May	May–Jun	Jun–Jul	Jul–Sep	Oct–Jul	Jun–Jul	Oct–Jul	Jul–Aug	All year	Oct–Jul
Ulex baeticus subsp. *baeticus*	1	Jan–Apr	Apr–May	Apr–Jun	Jun–Aug	Apr–Jun	–	–	–	All year	Nov–Jun
	2	Oct–Apr	Mar–May	Mar–May	Jun–Aug	Mar–Jun	–	–	–	All year	Oct–Jun

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