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## Phenological pattern of fifteen Mediterranean phanaerophytes from *Quercus ilex* communities of NE-Spain

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Key words: Annual cycle, Bud type, Mediterranean shrublands, Phenophase sequence index

### Abstract

The phenological pattern of fifteen Mediterranean phanaerophytes has been studied in several sites per species, by visiting the populations on a monthly basis over a one year period. Studied phenophases were dolichoblast vegetative growth (DVG), flower bud formation (FBF), flowering (F), fruit setting (FS), seed dispersal (SD), and leaf shedding of dolichoblasts (LSD). Considering the whole set of species, DVG, FBF and F took place mainly in spring, FS in summer, SD in autumn and LSD in summer and in autumn. Interspecific comparisons showed a wide variety of phenological patterns, which have been sorted according to the 'phenophase sequence index' (PSI). This index quantified the degree of superposition between DVG, FBF and F, and it constituted the basis for a functional classification of phenological patterns. Two groups were established. The 'type I' group was characterised by the concentration of phenophases in a short time in spring, while the 'type II' by the protraction and sequential arrangement of phenophases. Type I species performed most of their functions during a resource surplus period, but they have to face an intraplant competition between vegetative and reproductive demands. Type II species avoided intraplant competition but had to develop part of DVG, FBF and F during sub-optimal periods. It is hypothesised that type I species possess deeper roots, rely on predictable water sources and occupy mature stages of succession. Type II species, on the contrary, are expected to depend on more unpredictable water sources, to possess shallower root systems and to colonise earlier stages of succession. Intraspecific variability of phenology was found to be low among populations of the same species. Bud structure, which is a phylogenetic trait, may exert important constraints on plant phenology.

Nomenclature: Flora Iberica - Castroviejo et al. 1986-1997, Flora Europaea - Tutin et al. 1964-1980.

### Introduction

Plants perform different functions throughout the year in order to persist in their habitats. These functions are maintenance of their biomass, vegetative growth and reproduction. All of them demand resources that must be supplied by their environment. The timing of life cycle events through the year is a decisive feature determining the plant's adaptation to seasonally changing environments (Orshan 1989a), phenology being the discipline which deals with its study (Rathcke & Lacey 1983). Phenophases are the life cycle events, and their distribution through the year constitutes the plant phenological pattern.

Plants living in Mediterranean-type climates often have to stand freezing temperatures in winter and hot and dry summers (Nahal 1981; De Lillis & Fontanella 1992), the favourable period for plant photosynthetic activity being split up into spring and autumn (Mitrakos 1980; Terradas & Savé 1992). Under these conditions, plant communities reach a maximum of growth and flowering in spring, sometimes with a smaller peak in autumn (Floret et al. 1989, Orshan 1989b; Navarro et al. 1993; Cabezudo et al. 1993). Plant phenological patterns in (semi-)arid regions have been related to the seasonality of the climate, mainly the distribution of rainfall (Beatley 1974, Cabezudo et al. 1993; Friedel et al. 1993). However, individual species growing under the same climate may differ widely in the arrangement of their phenophases (for example, see Mooney et al. 1974; Orshan 1989a; Navarro et al. 1993; Cabezudo et al. 1993). This variety may respond to interspecific differences in plant traits, such as morphology, anatomy or physiology, which affect the phenological pattern (Rathcke & Lacey 1983, De Lillis & Fontanella 1992; Wang et al. 1992; Lechowicz 1995). Some attempts have been made to classify life cycles of plants into ecologically meaningful groups. Evenari et al. (1975) considered the persistence of the green shoot during the arid period as a criterion to classify dessert plants. However, this is not suited for Mediterranean woody plants, as most of them exhibit a persistent shoot. Baker et al. (1982) defined three models of phenology in chaparral shrubs based on the duration and overlapping of phenophases, but they referred only to three species. Orshan (1989a) described several patterns of arrangement of vegetative growth vs flowering. We considered that competition between vegetative and reproductive demands for resources may have been a major force governing the evolution of life cycles. Therefore the relative timing of growth and reproduction is considered the main basis for a phenological pattern classification.

The phenological pattern of 15 Mediterranean phanaerophytes common in the NE Spain sclerophyll communities is explored. The main objective is to define a few main types of phenophase arrangement, discuss their ecological meaning in the context of the Mediterranean climate, and explore how the phenological pattern is influenced by plant structural features (bud type, growth form, root depth). Another objective is to analyse the average phenological pattern of the whole set of species in relation to the climate and to compare it with those described for other Mediterranean communities.

### Methods

The study area is located in NE Spain. It extends through an altitudinal range, from the Middle Ebro Basin, in Zaragoza province (300 m of altitude) to the Prepyrenean Range in the province of Huesca (up to 870 m) (Figure 1). The climate varies from

Table 1. Sampling sites with their geographic and climatic characteristics.

Sampling sites (province)*	Altitude	P (mm)	<i>Т</i> (°С)
<ol> <li>Peñaflor (Z)</li> <li>Sierra de Alcubierre (Hu)</li> <li>Murillo de Gállego (Z)</li> <li>Agüero (Hu)</li> <li>Olvena (Hu)</li> </ol>	300–380	371	14.5
	600–685	452	14.2
	455	586	14.2
	800–870	681	14.2
	380–400	587	13.2

\*Abbreviation of the site province: Hu = Huesca, Z = Zaragoza

the semiarid Mediterranean type of the former to the sub-mediterranean of the latter. The distribution of precipitation is similar through all the range, with maxima in spring and autumn and a clear minimum in summer. Maximum summer temperatures are around 40 °C in the lower sites and decrease with increasing altitude. Winters are fresh through all the range, with several days of frost (Table 1). Climatic data were obtained from the closest weather station of the National Meteorological service.

The landscape through this area is dominated by forests or shrublands of sclerophyll communities presided by *Quercus ilex* susbp. *ballota* (*Q. rotundifolia*). The study species were selected among the most typical phanaerophytes of the *Q. ilex* communities of the area (Castro-Díez 1996) so as to have a representation of different plant growth forms, leaf habits and families (Table 2).

Each species was studied at 1-4 different localities (Table 2). In each site a mature population per species was selected, avoiding the limits of the species distribution area. One adult and healthy plant was marked in each population as a reference point. The field work was conducted between September 1992 and December 1993. The timing of phenological events was established following Orshan's pheno-morphological method (Orshan 1989a). Every month we visited the population to examine the marked plant plus its closest neighbours, up to a minimum of 10 plants. We recorded the presence or absence of six phenological events or phenophases: dolichoblast vegetative growth (DVG), flower bud formation (FBF), flowering (F), fruit setting (FS), seed dispersal (SD) and leaf shedding of dolichoblasts (LSD). A phenophase was considered to be active in the population just when it was observed in at least 5% of the crown in a minimum of 20% of the studied plants, otherwise being recorded as 'infrequent event' or absent. Brachyblasts were not



Figure 1. Provinces of Huesca and Zaragoza (NE Spain). Numbers indicate the sampling points (see Table 1 for site names).

considered due to their low incidence in the selected species (Floret et al. 1989). Additionally, representative branches of phenological stages were collected on each visit to make up a phenological herbarium.

Phenophase calendars (excluding infrequent events) of every natural population were averaged for each species and represented in diagrams. For the whole set of species, the frequency of phenophase occurrence in each month was calculated. Plant phenological patterns were classified according to the duration and the overlapping between vegetative and reproductive growth, as both functions may compete for the same pull of resources. A 'phenophase sequence index' (PSI) has been developed to quantify how sequential the arrangement of DVG, FBF and F is:

$$PSI = \frac{t(DVG + FBF + F)}{t(DVG) + t(FBF) + t(F)}$$

*t* being the number of months required to complete the phenophase/s represented in parenthesis beside it

*Table 2.* Studied species, their abbreviation, sampling sites (like Table 1) and some of their features. Growth form: SS–small shrub, S–shrub, ST–small tree, T–tree and C–climber. Leaf habit: E–evergreen and D–deciduous. Type of buds depending on the kind of branches they produce: V–vegetative, R– reproductive, V–R mixed (see material and methods).

Species	Sampling	ampling Abbrev. Family		Growth	Leaf	Type of buds		
	site			form	habit	V	R	V–R
Acer monspessulanum	2	Am	Aceraceae	Т	D	х		x
Arbutus unedo	4	Au	Ericaceae	S/T	Е	х	х	
Buxus sempervirens	4, 5	Bs	Buxaceae	S	Е	х	х	
Celtis australis	5	Ca	Ulmaceae	Т	D	х		х
Cistus albidus	2	Csa	Cistaceae	SS	Е	х	х	
Daphne gnidium	5	Dg	Thymelaeaceae	SS	Е	х	х	
Lonicera implexa	4	Li	Caprifoliaceae	С	Е	х	х	
Pistacia lentiscus	1, 2, 3, 4, 5	Pl	Anacardiaceae	S	Е	х	х	
Pistacia terebinthus	5	Pt	Anacardiaceae	S	D	х	х	
Quercus coccifera	1, 2, 4, 5	Qc	Fagaceae	S	Е	х		х
Quercus faginea	2,4	Qf	Fagaceae	Т	D	х		х
Quercus ilex subsp. ballota	1, 2, 4, 5	Qi	Fagaceae	Т	Е	х		х
Rhamnus alaternus	2, 5	Ra	Rhamnaceae	S	Е	х	х	
Rosmarinus officinalis	1, 3	Ro	Labiatae	SS	Е	x	х	
Viburnum tinus	4, 5	Vt	Caprifoliaceae	S	Е	x	х	

(infrequent events excluded). Index values close to zero indicate that phenophases are highly overlapped, while index values close to one indicate a sequential arrangement of phenophases.

Plant buds were classified following Kozlowski (1971) in vegetative (V), reproductive (R) and mixed (V–R) according to the vegetative or reproductive nature of their content. The former type produces only leafy shoots, the second produces just reproductive branches, which at their time bear the flower buds, and the latter produces both shoot types. The term 'bud' is considered here in its broader sense in order to allow interspecific comparison. It includes meristems protected by bud scales, as all V and V–R buds, but also meristems which did not exhibit an evident dormant stage, as in the case of some R buds. The fate of the studied plant's buds was carefully followed to determine which type was present in each species.

### Results

Plant phenology has been examined first considering the 15 species all together. There was one peak of plant activity in spring which affects mainly DVG and F. FBF exhibited a small maximum in spring and a small minimum at the beginning of summer, being evenly



*Figure 2.* Percentage of species presenting each phenophase throught the year. DVG – dolichoblast vegetative growth, FBF – flower bud formation, F – flowering, FS – fruit setting, SD – seed dispersal, LSD – leaf shedding of dolichoblasts.

distributed through the rest of the year. FS started in spring and extended to summer and the beginning of autumn. SD clearly peaked in autumn while LSD exhibited two maxima, one in summer and the other in autumn (Figure 2).

All the studied species grew in spring. Although many of them resumed DVG in summer or autumn, this event was only frequent in Cistus albidus (Figure 3, Table 3). Most of the species flowered from late winter to early summer, except Arbutus unedo, Daphne gnidium and Rosmarinus officinalis which did so in autumn, summer-autumn, and from autumn to spring, respectively. Flower buds were conspicuous just before flowering in Acer monspessulanus, Celtis australis and Quercus spp., while in Buxus sempervirens, Rhamnus alaternus, R. officinalis and Viburnum tinus they could be observed several months before the F season. F was usually completed in a short time (1-2.5 months), although in some species it was much longer, like in D. gnidium (4 months) and R. officinalis (5.5 months). In most of the species FS took place between spring and autumn, most of this period being the arid season. The duration of FS varied from 3 months in Lonicera implexa to 12.5 and 17 months in A. unedo and Quercus coccifera, respectively. SD showed its maximum in autumn and winter, although in some species it occurred in spring (R. officinalis) or summer (B. sempervirens and R. alaternus). SD duration was usually around 2 months, although in Pistacia lentiscus it took 4 months. The two peaks of LSD corresponded to the two leaf habit types, deciduous plants shedding leaves in a short time during the autumn and evergreens doing so between spring and summer, at the end of DVG (Figures 2 and 3).

Plant PSI values varied between 0.3 and 0.9. No plant appeared between 0.5 and 0.6 PSI interval, therefore we established 0.6 as a threshold to separate two groups of species (Figure 4): Type I (PSI < 0.6). DVG, FBF and F were completed in less than 2.5 months, being highly overlapped. This group included all the winter deciduous plants (*A. monspessulanum, C. australis, Quercus faginea* and *Pistacia terebinthus*) and two evergreen (*Q. ilex* subsp. *ballota* and *Q. coccifera*). Most of them were trees and exhibited V–R buds, except *P. terebinthus* (Table 2).

Type II (PSI > 0.6). They needed more than 2.5 months to complete the above phenophases, minimising superposition between them. This group included the rest of evergreen species, these being (small-) shrubs (*B. sempervirens, Cistus albidus, D. gnidium, P. lentiscus, R. alaternus, R. officinalis* and *V. tinus*), climbers (*L. implexa*) or small trees (*A. unedo*). All of them possessed R and V buds (Table 2). The phenology of this group seemed to be more flexible, as most of these species were able to start these phenophases at

any time of the year when conditions were favourable (see Table 3).

PSI values did not vary too much among different populations of the same species (Figure 4). The analysis of the plant bud's fate revealed two groups of species. *Quercus* spp., *C. australis* and *A. monspessulanum* possessed V and V–R buds which produced, respectively, leafy, and reproductive plus leafy branches at budburst. The rest of the species exhibited R and V buds, therefore reproductive and leafy branches were never produced at the same point (Table 2).

### Discussion

### Seasonality of phenophases

Although the studied species were not selected according to a quantitative sampling, their average phenological pattern may be indicative of the community trends. The concentration of growth and flowering in spring coincided with patterns described in some Mediterranean communities (Floret et al. 1989; Cabezudo et al. 1992; Cabezudo et al. 1993), although others from drier and warmer regions start DVG in winter (Orshan 1989b; Navarro et al. 1993). The peaks of F and DVG coincided with the increase of temperature and a maximum of precipitation. Although some species resumed growth or even flowering in autumn, in most cases less than 20% of the crowns were affected. Therefore, our phenological diagrams contrast with others which also included infrequent events (for example Floret et al. 1989, Cabezudo et al. 1993).

FBF was concentrated in a short period of spring in some species, while in others it started in the previous or the following summer and took several months before budburst. Therefore, when the whole species set was considered together, FBF appeared quite evenly distributed through the annual cycle. This contrasts with other communities where FBF was concentrated in spring, due to the predominance of the former FBF calendar among their species (Navarro et al. 1993; Cabezudo et al. 1993).

FS took place from spring to autumn. Many Mediterranean species decrease their stomatal conductivity in summer to save water (Rhizopulou et al. 1991; Duhme & Hinckley 1992; Tretiach 1993). Therefore, part of the FS demands are expected to be supplied by carbon reserves stored in more favourable seasons (Mooney & Hays 1973; Bloom et al. 1985). In *A. unedo* and *Q. coccifera* FS took longer than one year



*Figure 3.* Phenological diagrams of the studied species. Dark grey bars indicate average duration of phenophases over the populations. Pale grey bars indicate the whole period where phenophases have been detected. Numbers in parenthesis beside the species names are the number of considered populations. (Infrequent events were not included.)

(12.5 and 17 months, respectively). The protraction of FS has been related to scarcity or unpredictability of resources needed for fruit development (Rathcke & Lacey 1985). In *A. unedo* FS started in winter. The plant assimilation rate during this season is low in temperate climates (Larcher 1995), spring resources may be preferentially delivered to DVG (Kozlowski 1992), and summer is a water shortage period. Therefore FS cannot be completed until the following autumn. In contrast, *Q. coccifera* initiated FS in spring, at the

same time as the other two *Quercus* species, but kept the incipient fruits without noticeable changes of size until the beginning of the following spring. This strategy allowed *Q. coccifera* to start a quick feeding of its fruits at the very beginning of spring, while this process cannot start until the end of the current F in *Q. ilex* and *Q. faginea*. The reason for FS differences between the three *Quercus* species may be the occurrence of *Q. coccifera* in poorer soils (Braun-Blanquet & Bolòs 1957), which would enhance the effect of the

### Pistacia terebinthus (1)



### Quercus coccifera (4)

Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec



### Quercus ilex subsp. ballota (4)

Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec



### Rosmarinus officinalis (2)



					DVG
	l				FBF
		1	 		F
		1			FS
					SD
					LSD

Figure 3. Continued.

arid period and decrease the chances of a successful fructification in a single season.

### Types of phenology and ecological implications

PSI values represent the position of each plant along a continuum between two extreme phenological patterns. However, the lack of species with values between 0.5 and 0.6 allowed us to distinguish two species groups. The first one, represented by type I species, exhibited short phenophases concentrated in spring, therefore avoiding their young tissues to be exposed to low temperature in winter and to water deficit in summer. They grew and flowered when resources were abundant and remained with low phenological activity the rest of the year. However, their vegetative and reproductive demands had to be supplied almost simultaneously, establishing a competition for resources (Mooney 1983). In the other group, type II species minimised intraplant competition by developing their phenophases sequentially, at the expense of doing so in periods of resource shortage. Type I species must have accumulated enough resources

*Table 3.* Phenology of the studied populations. Numbers of sites like in Table 1. Phenophases are represented in different columns and the numbers indicate the interval of months of the year when they occur (1–January, 2– February, etc.). Periods in parenthesis indicate infrequent events (see text). A double hyphen between the beginning and the end of a period indicates that there is a one-year interval between the indicated months. DVG = dolichoblast vegetative growth, FBF = flower bud formation, F = flowering, FS = fruit setting, SD = seed dispersal, LSD = leaf shedding of dolichoblasts.

Species	Site	DVG	FBF	F	FS	SD	LSD
Acer monspessulanum	2	3–4	3–4	4	4-8	8–10	(9) 10 (11)
Arbutus unedo	4	4–6	7–10	10-12	10=10	11–12	5-7 (8-9)
Buxus sempervirens	4	3-6 (7-12)	7–3	3–4	4–7	7–8	6-8 (9-11)
Buxus sempervirens	5	2-6 (10-11)	7–3	2-3 (10-11)	3-6 (10-12)	6–7	5–7
Celtis australis	5	3–5	3–4	3–4	3-11	11-12	10-12
Cistus albidus	2	4-6/10-11	1–4	4–5	5–7	8-11 (12-1)	5-8
Daphne gnidium	5	3–6	6–9	7–10	8-11	10-12	5-11
Lonicera implexa	5	2-7 (10-1)	5-6 (12-4)	(1-5) 6-7	7–9	9–10	5-11
Pistacia lentiscus	1	5-6 (8-10)	3–4	4–5	5-11 (12-1)	10-1 (2-3)	5-7 (8)
Pistacia lentiscus	2	5–7	3–4	4–5	5-11 (12-1)	10-1 (2-4)	6–8
Pistacia lentiscus	3	5-7 (8-10)	3–4	4-5	5-11 (12-1)	10-1 (2-3)	-
Pistacia lentiscus	5	4-7 (8-9)	3–4	4–5	5-12(1)	10-1 (2-3)	5-8
Pistacia terebinthus	5	4–6	4	4–5	5–9	9–12	(9) 10–12
Quercus coccifera	1	4–5	4–5	5	5=10	10-11	5-6 (7-9)
Quercus coccifera	2	4–5	4	4	5=10	10-11	4-6 (7-9)
Quercus coccifera	4	4–5	4	5	5=10	10-11	5-6 (7-9)
Quercus coccifera	5	4-5 (9-10)	4 (9–10)	5 (10)	5=10	10-11	5-6 (7-9)
Quercus faginea	2	4	4	4	4–10	10-11	11-12 (1-3)
Quercus faginea	4	4-5 (7-8)	4	4-5	5-10	10-11	(10) 11–12 (1–3)
Quercus ilex subsp.	1	3–5	4–5	4–5	4–10	(9) 10–11	5-7 (10-12)
ballota	2	3–5	4–5	4–5	4-10 (11)	(10) 11 (12)	5-7 (8)
Quercus ilex subsp.	4	4–5	5	5	5-11	10-11	5-8 (9-10)
ballota	5	4–5	4–5	4–5	4-11	10-11	5-7 (8-12)
Rhamnus alaternus	2	(3) 4–6 (7/10–11)	10–3	(2) 3–4	4–7	7-8 (9)	5-8
Rhamnus alaternus	5	2-6 (7/10-11)	11–3	3–4	4–7 (8)	7–9 (10)	6–8
Rosmarinus officinalis	1	3–6	10–2	11-4	(12–1) 2–5	4–6	(4) 5–7
Rosmarinus officinalis	3	2–7	9–1	(10-11) 12-4	2–5	5-6(7)	6–7 (8)
Viburnum tinus	4	4-7 (9-12)	9–3	(1) 2–4	4–10	10-12	7-8 (9-3)
Viburnum tinus	5	2–7	9–3	2–4	4–10	10-12	6–8



*Figure 4.* PSI values of the species in every studied populations. Species names are abbreviated like in Table 2 and populations are represented by different symbols. Species have been divided into type I and II depending on their PSI value (see text).

before initiating all the phenophases to assure their quick fulfilment. Therefore this strategy is probably more efficient to exploit environments where resources are abundant and temporally predictable, as with the mature stages of succession. On the contrary, the protraction of life cycle events in type II species allow them to accumulate resources through the period of phenophase development. This would make type II species more suitable for environments where resources are either scarse or temporally unpredictable (Rathcke & Lacey, 1985), as is the case of the early successional stages. The fact that among the studied species all trees belonged to type I and most of the shrubs to type II could be in accordance with this hypothesis.

A question which arises in every classification is whether the same species belongs to the same group when growing under different conditions. The present data have shown little PSI variation among populations of the same species. The remaining question is the extent to which the PSI of a population may vary over several years of contrasting climatic conditions.

### Root depth as related to phenology

Some authors have shown a relation between plant phenology and the depth of the root system (Kummerow 1981; Bertiller et al. 1991). This is related to the different water availability through the annual cycle across the soil profile. In the studied region the deeper layers (those exploited by deep roots) are refilled after long rainfall periods (spring and autumn), while uneven and short rainfall just humidify the shallower layers. This water is efficiently exploited by shallow and laterally extended root systems. The concentration of growth and flowering in spring exhibited by type I species suggests a reliance on the predictable water sources of the deeper layers, and therefore the possession of deep roots. On the contrary, the phenophase protraction of type II species suggests a higher contribution of erratic rainfall to the total annual water uptake, and the possession of superficial root systems. Although further evidences would be necessary to test this hypothesis, we have found in literature that roots of some type I species (Q. ilex, Q. coccifera) are deeper than 5 m, while those of some type II species are shallower (A. unedo 2-5 m, R. alaternus 1-2 m, R. officinalis and L. implexa <1 m, Specht 1988). The only exception among the available data was P. lentiscus, which possesses roots deeper than 5 m (Oppenheimer 1957) but phenological pattern type II.

### Bud nature as related to phenology

The timing of vegetative growth as related to flowering depends to a great extent on the nature of buds (Kummerow 1983). The possession of V–R buds which produce leafy branches and inflorescences at budburst, causes the plant to start DVG and FBF almost simultaneously. In consequence, all the studied species with V–R buds exhibited a type I phenology. On the other hand, species with V and R buds may open them simultaneously (*P. terebinthus*), or sequentially (R first, like in *P. lentiscus*, or V first, like in *A. unedo*, *D*.

*gnidium* and *L. implexa*). Therefore they may be more flexible in the arrangement of their phenophases.

There is evidence for the genetic basis of the phenological pattern (see Rathcke & Lacey 1985), but the effect of plant phylogeny may be also indirect if other selected traits constrain the life cycle of plants. In this study the phenological pattern of the three Quercus species was very similar, maybe due to the similarity of plant structure, like the type and location of buds. However, the phenology of the two Pistacia species differed more in spite of their similar plant structure. This may be due to the possession of V and R buds, which allow the adoption of different phenological patterns. Therefore, the effect of phylogeny on the species' phenology may be stronger in some groups than in others, depending on how much the plant traits shared by the phyletic group constrain the temporal arrangement of phenophases.

In conclusion, phenological patterns of the phanaerophytes which constitute *Q. ilex* communities in NE Spain, may be classified in two main types on the basis of the degree of overlapping between DVG, FBF and F. Each type faces the limitations imposed by the Mediterranean climate with different strategy, therefore, playing different functional roles in the community. The phenological pattern adopted by each species can be constrained by structural features such as the nature of buds. However some plant structures may constrain the phenological pattern more than others.

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