Flowering and fruiting phenology of four herbaceous species of Leguminosae in a burned *Pinus halepensis* forest of Attica, Greece

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Abstract

Flowering and fruiting phenological patterns of four annual leguminous species (*Lathyrus aphaca* L., *Lathynrs cicera L.,* *Scorpiurus muricatus* L., *Vicia sativa* L.) were studied at the individual and population level to elucidate their strategies. The study took place in a burned Aleppo pine (*Pinus halepensis* Mill.) forest of Attica, central Greece, during the first post-fire year Statistical analysis of the mean number of buds, flowers and fruits per plant and sampling day, indicated that all four species present the same flowering and fruiting pattern, although the absolute numbers of the reproductive units produced per plant were notably different. A spring flowering and quick-ripening phenological strategy was followed by all the species studied. Fruit to flower ratios were found to be high. The numbers of seeds per pod were also high for all species studied. The investigation of their breeding system revealed that for the legume species studied self-pollination was predominant whereas cross-pollination might be occasional. The plant species demonstrated the pattern which most pioneer species do; i.e. they follow an opportunistic way of resource allocation, a strategy revealed by their phenological pattern and way of reproduction. Such a way of reproduction results in a high reproductive output in the ephemeral post-fire environment

Introduction

The mediterranean vegetation of the World evolved under the influence of recurrent fires (Naveh, 1975; Rundel, 1981; Specht, 1981; Kruger, 1983; Arianoutsou, 1998). Approximately 24 % of the areas burned each year in Greece are *Pinus halepensis* Mill. and *Pinus brutia* Ter. forests (Kailidis, 1992). These Mediterranean pine forests cover 8.7% of the country's forested area (Ministry of Agriculture, 1992). Provided that no secondary disturbance occurs at the burned sites, succession proceeds. In this autosuccesional process Leguminosae, one of the richest plant families of the World's mediterranean environments, play an important role (Arianoutsou & Margaris, 1981; Papavassiliou & Arianoutsou, 1993; Cocks, 1994; Arianoutsou & Thanos, 1996; Kazanis & Arianoutsou, 1996).

It is well known that legumes form a permanent soil seed bank (Bewley & Black, 1982) in most of the environments in which they grow. Additionally, because most of the Leguminosae are annual taxa, seed production after fire is their only mean of regeneration (Papavassiliou & Arianoutsou, 1993; Martinez-Sanchez *et al.,* 1994; Kazanis &

Arianoutsou, 1996). Their prolific occurrence in the early post-fire successional stages of Mediterranean ecosystems (Arianoutsou & Thanos, 1996) is explained by the massive germination of their seeds, the dormancy of which is broken by the fire-induced heat shock (Doussi & Thanos, 1994). These plant species apparently exhibit a reproductive strategy which will ensure their persistence through time, indicated by the fact that this abundance is characteristic of the early post-fire successional stages only (Arianoutsou & Margaris, 1981; Kutiel, 1994; Kazanis & Arianoutsou, 1996).

Spatial and temporal patterns of flowering and fruiting in plant populations influence many aspects of their reproductive biology, including pollinator attraction and visitation, reproductive success and gene exchange (Carthew, 1993). In particular, plant species which colonize rapidly changing habitats are expected not to rely upon pollinators to facilitate fruit-set (Price & Jain, 1981) and as suggested by Harper (1967), to allocate more of their resources to reproduction. Fruit to flower ratios are also expected to be higher in these plant species than in species from more stable habitats (Gross, 1993).

Despite the post-fire abundance of Leguminosae, no study dealing with their flowering phenology and

breeding system, as major components of the above mentioned adaptation, has been reported so far. The objective of this study is to investigate the flowering phenology and breeding system of pioneer leguminous annuals aiming to reveal their patterns of behaviour in the early post-fire environment. Four species *(Lathyrus aphaca* L., *Lathyrus cicera* L., *Scorpiurus muricatus* L. and *Vicia sativn* L.) were selected among the annual legume taxa, due to their presence in large numbers only during the first few years after fire (Kazanis & Arianoutsou, 1996). The four species flower simultaneously, develop single flowers, which have a vertical position relative to the plant axis. *L. aphaca* and *S. muricatus* have yellow flowers, L. *cicera* red and *V. sativa* purple-red flowers. Details of general floral structure and function in the Papilionoideae can be found in Faegri & van der Pijl (1979). They are all annual plants and their flowering and fsuit formation are judged as critical for the reason mentioned above.

Materials and methods

The study was conducted in Kapandriti (38°15' 41" N, 23°52'37" E, 477 m a.s.l.), approximately 45 km from Athens, in the prefecture of Attica,

Greece. The fire event took place in a mature *Pinus halepensis* forest with an understorey dominated by *Arbutus unedo* and *Quercus coccifera,* in September 1992. The soil parent material was tertiary deposits, while a thick ash-layer covered the soil surface for at least 10 months after the fire. Observations and experiments were conducted between April 1, (day # 1 for the study), and June 10, 1993. Meteorological data were obtained from the National Meteorological Service from the nearest available weather station of Tatoi (237 m a.s.l.), situated at a distance of 18 km from the study site (Fig. 1).

Twenty individuals of each species, were randomly selected and marked *in situ* before the onset of flowering. The flowering phenology was described by using two variables:
a) the number of open flowers per individual plant on each sampling date
b) the duration of flowering for each individual (number of days the plant had at least one flower open)
Each species' phenological parameters were recorded every 1-5 days. A plant was considered in anthesis if it had opened at least one flower. Mean number of flowers per sampling day was estimated by adding the number of flowers of all conspecific
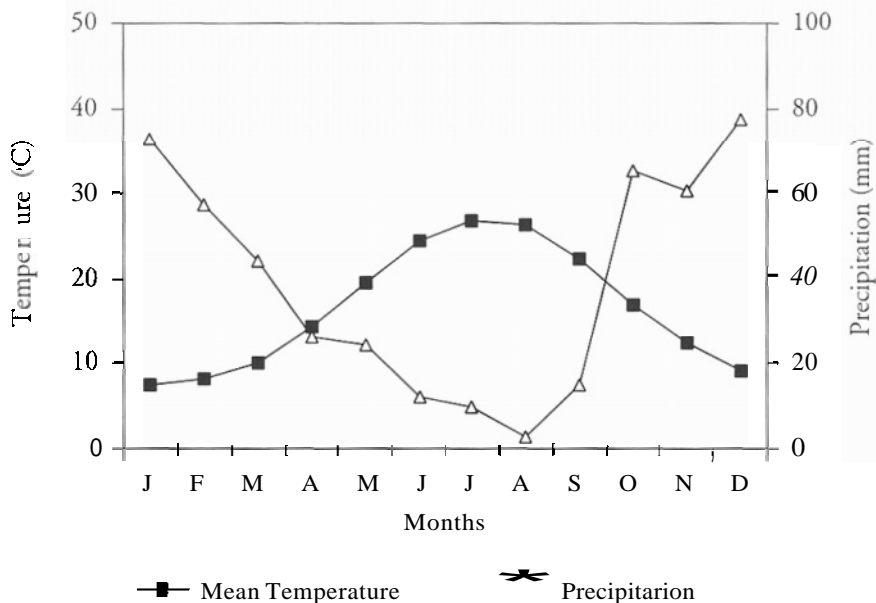
1. Climatological diagram of the Meteorological Station in Tatoi for the years 1951-1989.

individuals used as sampling units and was depicted in the same diagram for all species studied.

Furthermore, the number of buds and fruits of each individual was counted at every sampling date in order to have a complete picture of each species' reproductive effort. In order to avoid recounting, buds, flowers and fruits were marked with colored (green) threads. Flower life span was estimated over 50 marked flowers of each studied species observed every day.

A field experiment was designed in order to allow a comparison between fruit production under natural conditions and that under insect-free pollination. For this purpose individual plants (n=12 for L. *aphaca,* n=11 for L. *cicera,* n=7 for *S. muricatus,* n=10 for *V. sativa)* were covered with fine-mesh transparent net to exclude pollinators (from now on these plants will be called "covered"). Thus, by using this method all other modes of pollination were free to operate. Non-dehisced pods from all "covered" plants (n=67 for L. *aphaca,* n=25 for *L. cicera,* n=50 for *S. muricatus,* n=15 for *Ysativa)* were collected at the end of the flowering season in order to estimate seed production.

The second field treatment dealt with spontaneous self-pollination in particular. Pollen-proof bags were put on flowers (n=20 for L. *aphaca,* n=24 for *L. cicera,* n=12 for *S. muricatus,* n=15 for *V. sativa)* of each species (from now on these flowers will be called "bagged). Pods (n=13 for L. *aphaca,* n=8 for *L. cicera,* n=7 for *S. muricatus,* n=7 for *V. sativa)* formed during the study period were collected from these flowers at the end of the flowering season in order to estimate seed production. All modes of pollination other than spontaneous self-pollination were excluded. Fruit production at the plant level could not be estimated in the second field treatment because only individual flowers were bagged and not whole plants.

As control data for seed production in both treatments, 50 open-pollinated pods from L. *aphaca, L. cicera, S. muricatus,* and 12 open-pollinated pods from *V. sativa* were collected from the 20 initially marked individuals of each species.

In order to test for concordance of the temporal distributions of mean number of flowers, buds, and mean cumulative number of fruits on each sampling date among the four studied species, Kendall's coefficient of concordance (W) was applied for each of the above mentioned parameters. Mann-Whitney (U-test) was applied for the comparison of the mean number of pods per plant between "open-pollinated" and "covered" plants. The same statistical approach was used for the comparison of the mean number of seeds per pod between "open-pollinated", "covered and "bagged flowers. For all statistical analyses performed the software package STATISTICA 4.3 was used.

The species under study were observed for pollinators visiting their flowers during the whole flowering period and the number of visits was recorded every three days. Insects that visited the species studied were captured and "identified".

Plant nomenclature follows Flora Europaea (Tutin *et al.,* 1968-1980).

Results

Flowering and fruiting patterns

Flowering duration of individuals did not vary considerably even among different species, being less than eight weeks for L. *aphaca,* L. *cicera* and *V. sativa* and less than nine weeks for *S. muricatus* (Table 1). All the species had similar flowering pattern, which means that they were in bloom with appreciable synchrony (Table 1 and Fig. 2) and appeared one flowering peak (Fig. 2).

Table I. Phenological parameters of the species studied. Mean flowering duration= the mean flowering duration of the sample (n= 20 plants); flower life span= the mean number of days each flower remained open (n=50 flowers); numbers in brackets are the standard errors of the mean.

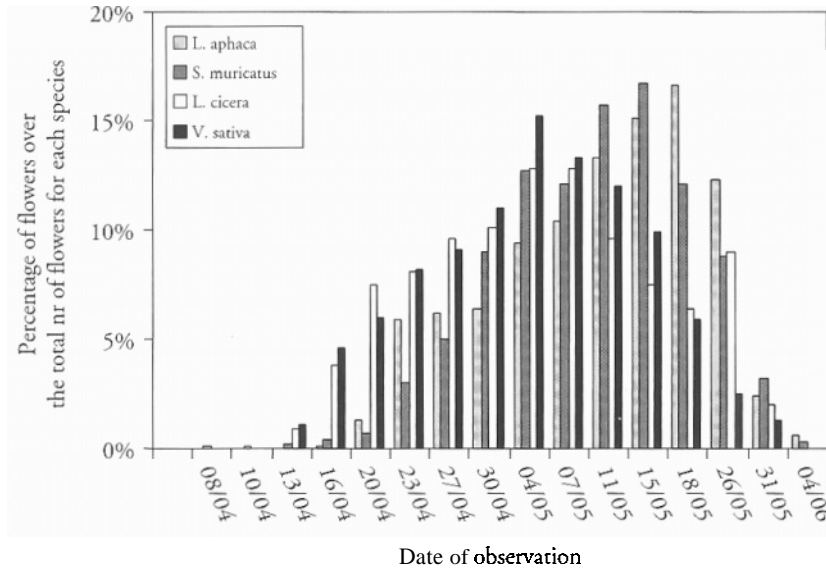| Phenological parameters	L. *aphaca*	S. *muricatus*	L. *cicera*	V. *sativa*	
Mean flowering duration (in days)	42.3 (6.4) n= 20	46.8 (5.9) n= 20	34.2 (7.8) n= 20	42.4 (8.5) n= 20	
Flower life span (in days)	4.2 (0.3) n= 50	4.6 (0.2) n= 50	2.0 (0.0) n= 50	1.4 (0.2) n= 50	

Fig 2. Percentage of flowers on each sampling date over the total number of flowers produced during the whole flowering period for the species studied.
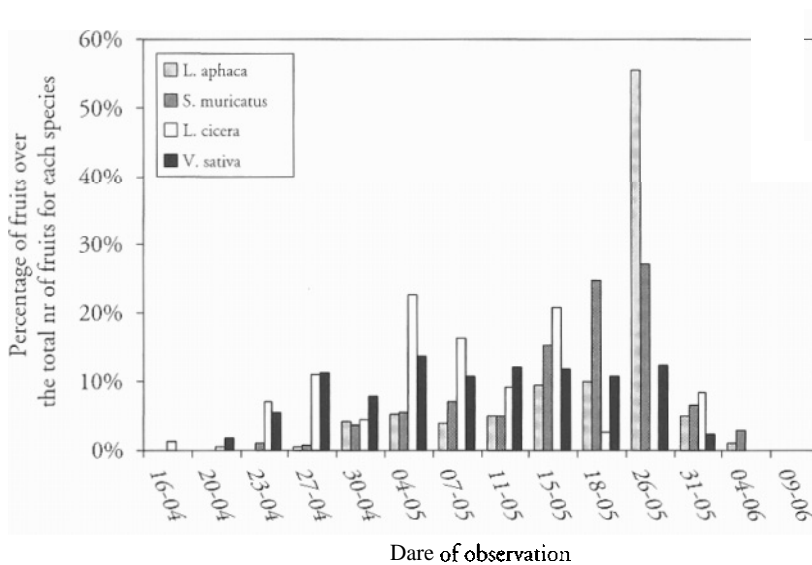

Fig 3. Percentage of fruits on each sampling date over the total number of fruits produced during the whole sampling period for the species studied.

A significant concordance in the temporal pattern of bud formation, flowering and fruiting among the species studied (buds: W=0.405, p<0.001, flowers: W=0.533, p<0.001, fruits: W=0.244, p<0.006, respectively) was statistically revealed.

An increase of the pod formation rate occurred for L. aphaca and *S. muricatus* at the end of the flowering season (Fig. 3) while *V. sativa* showed a peak of newly formed fruits at the beginning of flowering, thus having a more regular rate of fruit formation (Fig. 3). On the other hand L. *cicera*

showed a rather erratic pod formation rate. In all species studied fruit maturation was taking place while plants were still in bloom. Seed dispersal was observed within 10 days after the completion of flowering, late in June (pers. obs.). Each species produced different numbers of buds, flowers, fruits and their flower to bud ratio was also different (Table 2).

Breeding Systems

The levels of fruit production in the field were estimated from the 20 marked individuals of each species. Fruit to flower ratio was found to be 85.6% for L. *aphaca,* 44.6% for L. *cicera,* 77.0% for *S. muricatus* and 79.1% for *V. sativa.* In the first field treatment, where pollinators were excluded, the percentages were 66.7%, 32.1%, 62.6%, 61.4%, respectively. In the second field treatment, where allogamy was excluded, the respective percentages for spontaneous self-polli-

nation per total number of treated flowers were 65.0%, 33.3%, 58.3% and 46.7%. Although in the first treatment the mean numbers of fruits per plant were found to decrease compared to the "open-pollinated" plants (Table **3),** the statistical analysis revealed that the difference between open-pollinated (A) and covered (B) plants' fruit production in all studied species was not significant (Table 3).

The mean numbers of seeds per pod in both treatments was found to decrease compared to "open-pollinated" plants (Table 4) and the statistical analysis showed significant difference among open-pollinated (A), covered (R) and bagged (C) flowers' seed production. Statistical analysis also showed that there was no significant difference between the mean numbers of seeds per pod of B plants' flowers and C flowers. The only exception was that of *S. muricatus,* where seed production differed significantly between B and C flowers (Table 5).

Table 2. Mean number of buds, flowers and fruits formed during the sampling **period** for **the** species studied (n=20 in **all** cases); numbers in brackets are the standard errors of the mean.

	Buds	Flowers	Fruits	Flower to bud ratio
L. aphaca	179.1 (15.8)	98.0 (9.8)	83.9 (8.2)	54.7%
S. muricatus	158.3 (22.5)	97.9 (15.5)	75.4 (12.3)	61.8%
L. cicera	57.4 (6.9)	17.2 (2.0)	7.7 (1.1)	30.0%
V. sativa	176.0 (39.2)	56.8 (13.0)	44.9 (10.4)	32.2%

Table 3. Mean number of pods formed for open-pollinated (A) and covered (B) plants (The numbers in brackets correspond to the standard error the first and to the size of the sample for each case the second; U= results of the Mann-Whitney test obtained after the comparison of the number of pods per plant collected after each treatment, significant p< 0.05).

	A	B	Nr. of pods A-Nr. of pods B	
	Mean nr. of pods/plant	Mean nr. of pods/plant	U	p
L. aphaca	83.9 (8.2) (20)	65.4 (9.2) (12)	81.0	0.1290
S. muricatus	75.4 (12.3) (20)	61.3 (5.0) (7)	69.5	0.9779
L. cicera	7.7 (1.1) (20)	5.5 (0.9) (11)	90.0	0.4090
V. sativa	44.9 (10.4) (20)	34.9 (5.2) (10)	96.0	0.8603

Table 4. Mean number of seeds for all the species studied after each treatment (A= open-pollinated flowers, B=covered flowers, C= bagged flowers. The numbers in brackets correspond to the standard error the first and to the size of the sample for each case the second).

	A	B	C
	Mean nr. of seedstpod	Mean nr. of seeds/pod	Mean nr. of seedstpod
L. uphaca	5.70 (0.1) (50)	4.02 (0.15) (67)	3.61 (0.37) (13)
S. muricatus	8.92 (0.17) (50)	7.63 (0.19) (50)	6.43 (0.48) (7)
L. cicera	8.70 (0.21) (50)	6.60 (0.28) (25)	5.75 (0.65) (8)
V. sativa	8.00 (0.40) (12)	5.53 (0.51) (15)	4.43 (0.68) (7)

Table 5. Comparison of the number of seeds per pod collected after each treatment (A= open-pollinated flowers, B=covered flowers, C= bagged flowers; U= Results of the Mann-Whitney test; significant p< 0.05).

	A-B	A-C	B-C
L. aphaca	U= 421.0 p= 0.000000	U= 55.5 p= 000000	U= 361.0 p= 0.33125
S. muricatus	U= 605.0 p= 0.00000	U= 27.0 p= 0.00032	U= 85.0 p= 0.02866
L. cicera	U= 239.5 p= 0.00001	U= 42.0 p= 0.00037	U= 61.5 p= 0.10582
V. saliva	U= 33.0 p= 0.00542	U= 3.5 p= 0.00114	U= 39.0 p= 0.34129

The main pollinator of L. *aphaca,* S. *muricatus* and *Vsativa* was the butterfly *Polyommatus icarus* (Lycaenidae). It was observed to visit the above mentioned plants between May 12th and May 25th. The mean time spent by an individual of P *icarus* at a flower was 15.2 ± 0.4 s (n=5). A further 8 hours of observations at marked flowers revealed that, on average, a flower of L. *aphaca* received one visit from *P. icarus* while *S. muricatus* and *Vsativa* did not receive any visit from *P. icarus* in 8 hours. No pollinators were observed on flowers of L. *cicera.* Other taxa that visited the studied plants were a species of *Eucera* (Apidae) on *V. sativa,* a species of *Bombus* (Apidae) on *V. sativa* and a species of Diptera on L. *aphaca* and *V. sativa.* The above-mentioned insect taxa were very rare (less than one visit per observation day, per flower) and visited the plants without touching the stigma or the anthers. Consequently, the only true pollinator was *P. icarus.* It was remarkable that *Apis mellifera* was never observed on the species studied.

Discussion

In the process of post-fire succession, a great portion of the early colonizing species, the majority being annual plants, does not persist (Trabaud & Lepart, 1980; Kazanis & Arianoutsou, 1996). The four species studied occur in large numbers only during the first few years after fire (Kazanis & Arianoutsou, 1996).Their massive seed germination is induced both by the high temperatures of a wildfire and by the high insolation (Bazzaz, 1996) prevailing in the open space of the early successional stages.

In order to ensure their persistence through the early post-fire years, under the unpredictability of the Mediterranean climate, annual legumes adopt a strategy of mixed growth and reproduction (Waller, 1988). Their reproductive output, enumerating thousands of seeds per unit area, leads to the formation of a seed bank which will persist in the following years (Papavassiliou *et al.,* 1994).

Despite the fact that in the four species studied the mean numbers of buds, flowers and fruits formed during the flowering period differ considerably, flowering and fruiting patterns are similar. This suggests that they follow the same phenological pattern in the burned habitats of the Mediterranean where they are encountered in large numbers as opposed to the unburned ones in which they exhibit limited representation. Additionally, like other spring flowering taxa (Herrera, 1986; Dafni & O'Toole, 1994), the four species rapidly develop their fruits, following a so-called "spring quick ripening phenological strategy".

Noteworthy is the fact that most of the buds do not develop into flowers, an indication that the plants allocate part of their energy to reproductive units, which do not produce a successful offspring. In contrast to the low flower-to-bud ratios of the four species, the fruit-to-flower ratios were found to be high, especially for *L. aphaca* and *S. muricatus*. We can, therefore, assume that successful fruit-set in the annual legumes of the post-fire communities is mostly dependent on the bud and not on the flower stage while a great number of buds abort as it is also mentioned by Siemens (1994) for *Cercidium microphyllum.*

The fact that only *Polyommatus icarus* visited the three species, denotes that these species compete for the same pollinator. According to Petanidon (1991) L. *cicera* in a phryganic ecosystem of Attica was visited by seven species of Hymenoptera while in the study area was not visited by any species. The route undertaken by a pioneer species to alleviate competition for pollinators is through a shift from self-incompatibility to self-compatibility, in order to maximize its fitness (Levin, 1970; Carpenter & Recher, 1979; Faegri & van der Pijl, 1979). In our study, the successful self-fertilization of the "bagged flowers" indicates that all four species are self-compatible. Moreover, the high fruit-to-flower ratios of the species studied are a common phenomenon among self-compatible annuals, as shown by Sutherland (1986) in a comparison of fruit-set among self-compatible and self-incompatible annuals.

Fruit production in the species studied is not significantly different between "open-pollinated" and "covered" plants as it was revealed by the relevant statistical analysis. This evidence implics that fruit production is not affected by the presence of pollinators. On the other hand, the significant difference in seed production among "open-polli-

nated", "covered" and "bagged flowers" implies the importance of pollinators to the formation of the final number of seeds produced per pod.

We can assume, therefore, that the annual fire-following obligate seeders do not rely on pollinators for their successful reproduction after fire, whereas seed production increases with their contribution. Hence, we can assume that selfing is predominant and cross-pollination might be occasional, as it has also been observed in numerous other annual species (Levin, 1972; Sutherland, 1986; Zohary, 1997). The ideal strategy for the short-living pioneer plant species colonizing the early post-fire sites would be to encourage outbreeding and still to be self-compatible to permit self-fertilization. As it is mentioned above, in the studied species self- and cross-pollination coexist but there is difference in seed production behveen selfed and open-pollinated plants which might lead to the reduction of their fitness when they are exclusively self-pollinated.

This work showed that the annual species studied have a spring flowering and quick ripening phenological strategy, producing large numbers of fruits and seeds mainly through self-pollination. The phenological strategy and the breeding system adopted by the leguminous species studied give them the ability to reproduce with flexibility in the post-fire environment, independently of the presence of pollinators and through the seed bank to persist the long time intervals between two fires. However, further research is needed on the reproductive biology and phenology of the pioneer plant species –perennials and annuals- in order to comprehend their adaptations in the post-fire environment.

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