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FLOWERING PHENOLOGY, BREEDING SYSTEM AND POLLINATION OF FOUR CO-OCCURRING LEGUMINOUS SPECIES IN A BURNED ALEPPO PINE FOREST OF ATTICA, ONE YEAR AFTER FIRE

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SUMMARY

Four of the most abundant annual leguminous species (*Lathyrus aphaca*, *Scorpiurus muricatus*, *Lathyrus cicera*, *Vicia sativa*) were selected from the post fire flora of the investigated area. Their flowering and fruiting phenological patterns were studied at the individual and population level by measuring the number of flowers and fruits formed during the sampling period, in twenty tagged individuals of each species. Fruit to flower ratio was high, as expected and varied from 44.64% in *L. cicera* to 85.61% in *L. aphaca*. Two treatments were conducted on each species in order to define their pollination mode. Plants of each species were covered with fine mesh net so that floral visitors could be excluded and flowers of each species were bagged so that selfing rate could be estimated. Fruit to flower ratio from each treatment was calculated and compared with fruit to flower ratio under natural conditions, showing that all four species were self-pollinated and cross-pollinated at the same time. Insects visiting flowering individuals of each species were captured and identified. Although the flowers of the studied species are highly adapted to insect-pollination, our study revealed that these species did not rely on pollinators for high fruit-set.

INTRODUCTION

Leguminosae are considered to be a key plant group among the flora inhabiting the post-fire communities of Mediterranean ecosystems, mainly due to their remarkable abundance in the initial successional stages after fire (Naveh 1967, Papavassiliou & Arianoutsou 1992, Arianoutsou & Thanos 1996), and also because of their capacity to nodulate which is regarded as highly significant (Rundel 1983). Because of the uncertainty of the post-fire environment, the pioneer plant species consisting the community during the early stages of succession, should have a flexible way of reproduction, allowing them to reproduce with low energy consumption but, fast and with high reproductive outputs at the same time.

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

The zygomorphic pea flower is highly adapted to insect pollination (Faegri K. & L. van der Pijl 1979), even though in burned environments there is a lack of pollinators (Price & Jain 1981). *Lathyrus aphaca* L., *Lathyrus cicera* L., *Scorpiurus muricatus* L. and *Vicia sativa* L., were selected in order to investigate: flowering phenology, breeding system and pollination. Because of this importance, the study of their flowering phenology and reproductive biology was essential for the comprehension of their role as fire-followers.

MATERIALS AND METHODS

The study was conducted in Kapandriti ($38^{\circ}15'41''$ N; $23^{\circ}52'37''$ E, elevation 477 m), approximately 45 km from Athens, Attica, Greece. The fire event took place in a mature *Pinus halepensis* forest, with *Arbutus unedo*, *Quercus coccifera* and *Quercus pubescens*, being the dominant plant species of the understorey, in September 1992. The soil parent material is tertiary deposits and a thick ash-layer covered the soil surface. Observations and

experiments were conducted between April 1st and June 10th, 1993. The 1st of April was considered as day number 1 for all this study.

The species studied (*L. aphaca*, *L. cicera*, *S. muricatus*, *V. sativa*) were selected from other fire-following leguminous species, because of their abundance (Papavassiliou & Arianoutsou 1992) in the study area and their presence mainly the first years after fire (Kazanis & Arianoutsou 1996). Individual plants of each species (n=20) were marked *in situ* before the onset of flowering. Time and duration of flowering was estimated by counting flower numbers. Population curves were drawn by adding the number of flowers of all conspecific individuals used as sampling unit. A plant was considered at anthesis if it had opened at least one flower. Furthermore, the number of fruits of each individual was counted at every sampling date in order to have a complete picture of each species' reproductive effort.

In addition, a field experiment was designed in order to allow a comparison of pollination rates under natural conditions versus insect-free pollination. For this purpose individual plants of each species were covered with fine mesh transparent net to exclude pollinators. Pollen-proof plastic bags were also used on several flowers of each species, to check autogamy rates.

Finally, pollinators were collected, identified and their behavior was observed every three days from sunrise to dawn in order to investigate the composition and activity of the pollinating fauna.

RESULTS

Flowering times between individuals did not vary considerably even within species, and were less than eight weeks for *L. aphaca*, *L. cicera*, and *V. sativa* and less than nine weeks for *S. muricatus*. All the species had 'cornucopia' (Gentry 1974) flowering pattern, which means that they were in bloom with appreciable synchrony and producing one population flowering peak (Fig. 1)

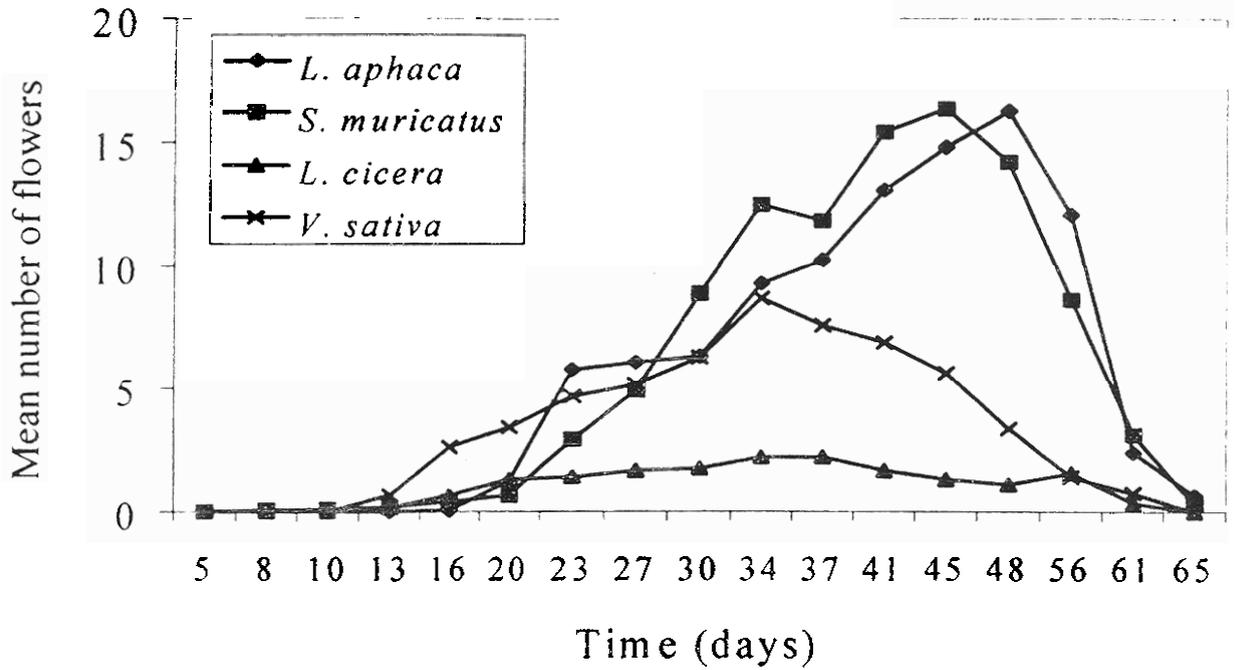


Fig.1. Flowering phenology of the species studied

Fruiting patterns within species were rather similar although the absolute number of fruits produced during the sampling period differed between the species studied (Fig.2).

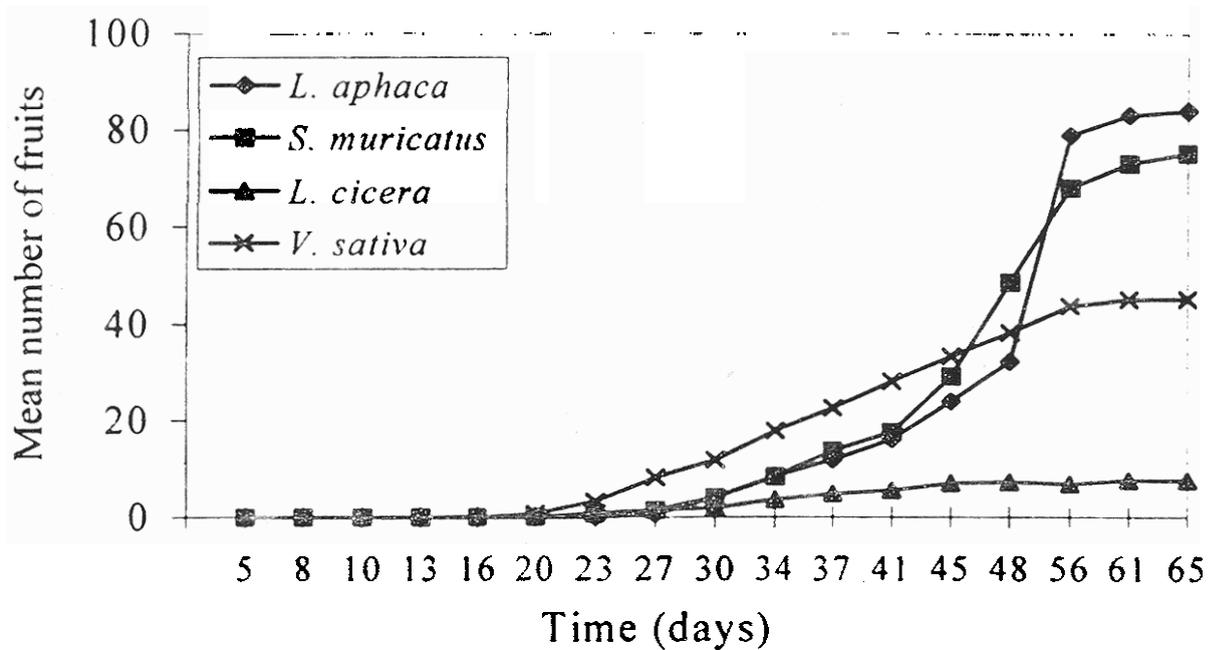


Fig.2. Fruiting phenology of the species studied.

There was not a great difference in fruit production between open-pollinated and self-pollinated individuals. However, there is a slight difference between the respective

percentages of fruit to flower ratio in the three treatments. The phenological parameters studied gave a similar phenological pattern in all the species.

The natural levels of fruit production was estimated from 20 individuals of each species and fruit to flower ratio was found to be 85.61% for *L. aphaca*, 77.01% for *S. muricatus*, 44.64% for *L. cicera* and 79.06% for *V. sativa*. In the first treatment, where pollinators were excluded, the percentages were 66.74%, 62.59%, 32.12%, 61.39% respectively. In the second treatment, the respective percentages for successful self-pollination per total number of treated flowers were 65.0%, 58.33%, 33.33% and 46.66% (Table 1).

The main pollinators were species of Hymenoptera, Thysanoptera (their role as pollinators is unknown) and Lepidoptera. The number of pollinators in the study area was very low and their foraging activity was rather insignificant. Their abundance was higher during the peak of the flowering period, without showing any special interaction with the species studied (Fig. 3). The only species, which visited constantly the flowers of *L. aphaca* and *S. muricatus*, was *Polyommatus icarus* and species of *Bombus* and *Eucera* for *V. sativa*. However, the insect species mentioned above were rather rare. The absence of *Apis mellifera* in the study area was really surprising.

Table 1. Fruit to flower ratio, for the three treatments.

	Open-pollinated	Covered plants	Bagged flowers
	Percentage of fruit to flower ratio	Percentage of fruit to flower ratio	Percentage of fruit to flower ratio
<i>L. aphaca</i>	85.61	66.74	65.0
<i>S. muricatus</i>	77.01	62.59	58.33
<i>L. cicera</i>	44.64	32.12	33.33
<i>V. sativa</i>	79.06	61.39	46.66

Table 2. Pollinators visiting the species studied

	<i>Lathyrus aphaca</i>	<i>Scorpiurus muricatus</i>	<i>Lathyrus cicera</i>	Vicia sativa
Hymenoptera	Sphecidae	-	-	Apoidae (<i>Eucera sp.</i> , <i>Bombus sp.</i>)
Diptera	(Species 1)	-	-	(Species 1)
Lepidoptera	Lycaenidae (<i>Polyommatus icarus</i>)	Lycaenidae (<i>Polyommatus icarus</i>)	-	-
Coleoptera	Cleridae (Species 1)	-	-	-
Thysanoptera	Thripidae (Species 1)	Thripidae (Species 1)	Thripidae (Species 1)	Thripidae (Species 1)

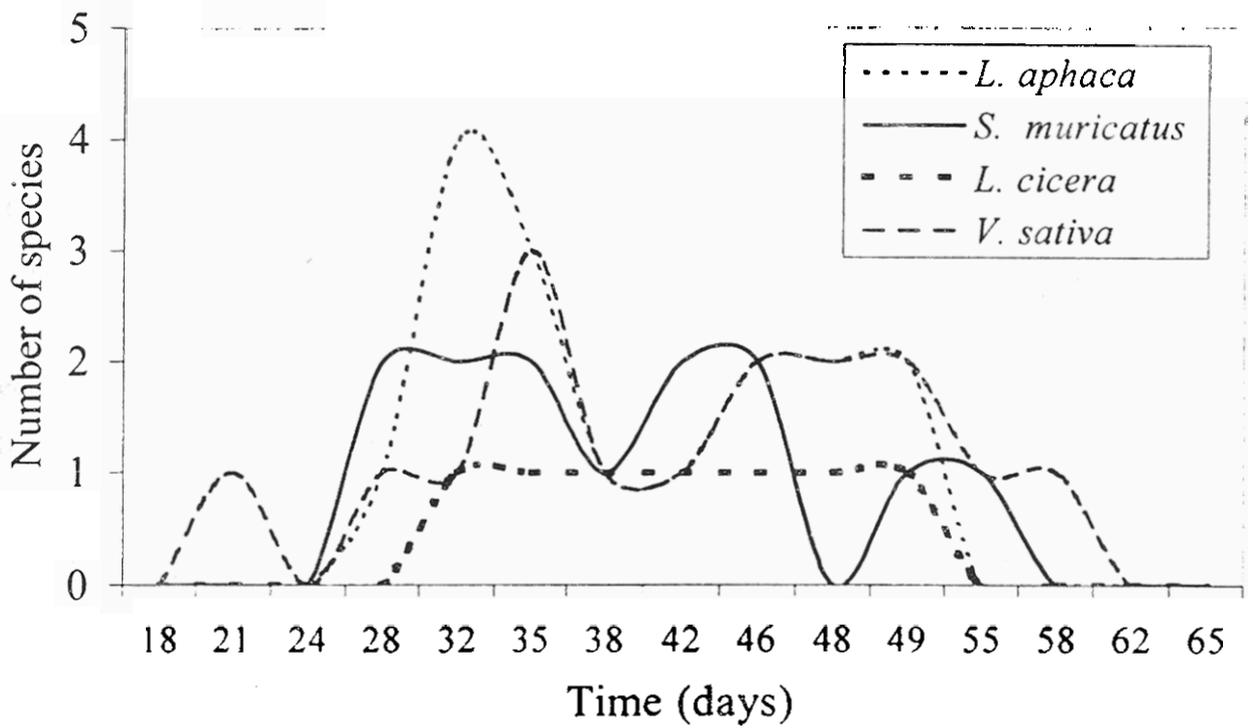


Fig.3. Daily insect species richness foraging on the plant species studied

DISCUSSION

It is remarkable that the mean numbers of flowers and fruits formed during the sampling period differ considerably within species. However, flowering and fruiting patterns are similar in the species studied, which suggest that annual legumes follow the same phenological pattern in burned environments.

As it is known, spring flowering taxa develop rapidly their fruits following a "spring quick ripening phenological strategy" (Herrera 1986, Dafni & O'Toole 1994). *L. aphaca*, *S. muricatus*, *L. cicera* and *Vicia sativa*, like other leguminous species, are hermaphrodites, following a spring flowering and quick ripening phenological strategy. On the other hand, selfing is predominant and cross-pollination is occasional, as it has also been observed in numerous other annual species (Levin 1972, Sutherland 1986, Zohary 1997).

A route for alleviating competition for pollinators is a shift from self-incompatibility to self-compatibility, in order to maximize the fitness of fire-following species (Levin 1970). We can assume therefore that the annual fire following obligate seeders do not rely on pollinators for high reproductive output after fire. The ideal strategy for the short-lived pioneer plant species, colonizing the early post-fire sites would be to encourage outbreeding and yet to be self-compatible to permit self-fertilization as it was proposed by Carpenter & Recher (1979) and Faegri & van der Pijl (1979).

During the first years following fire, the floristic richness is higher, but a great part of the colonizing species, mostly annuals, does not persist (Trabaud & Lepart 1980). Apart of their demands for high insolation, the species studied occur mainly the first two years after fire, producing large numbers of flowers and fruits mainly through self-pollination. Herbaceous plants, generally demonstrate a high reproductive effort during the first year of succession in old-field communities, as it was suggested by Newell (1978). The annual legumes of the post-fire flora allocate more of their resources in reproduction, in order to ensure their survival during the early post-fire years, and to form a new rich persistent soil seed bank.

Fire destroys the nests of pollinators and as a consequence their presence in the first post-fire year is very low. According to Petanidou & Ellis (1996), maximal bee diversity in phrygana occurred in 6-10 years after fire and not before or after. It is remarkable that the main insect species in the study area were bees and butterflies, which can cover long distances

coming from neighboring unburned areas. It is reasonable to suggest that under this lack of pollinators, annual plant species inhabiting the post-fire environments during the first years of succession should not rely on pollinators for their successful reproduction.

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