

**FIRE, BEES, AND SEED PRODUCTION IN A MEDITERRANEAN KEY SPECIES
SALVIA FRUTICOSA MILLER (LAMIACEAE)**

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ABSTRACT

The typical Mediterranean phrygana has a very rich biodiversity of plants and of solitary bees. Fire may kill the brood of soil-nesting and other solitary bees and may affect pollen and nectar sources. Such changes would be expected to influence seed production in populations of post-fire obligate seeder species and thus also their population dynamics. We compared nectar standing crop, flower visitation rate of bumble bees and solitary bees, and consequent seed production in a typical Mediterranean shrub (*Salvia fruticosa* Miller) growing in unburned east Mediterranean phrygana vegetation and in an adjacent burned area. The volume of nectar standing crop in the burned area was higher than in the unburned area, while the nectar concentration showed the opposite trend. The mean frequency of *Bombus*' visits was higher in the burned area, while solitary bees visited flowers only in the unburned habitats. The seed production of *S. fruticosa* was significantly lower in the burned area. This reduction might have a long-term effect on post-fire species composition and abundance due to the fact that this species is an obligate post-fire seeder. The present evidence indicates that the bee-dependent pollination environment was not re-balanced even six years after fire. This situation has important implications concerning plant species and their bee pollinator diversity.

INTRODUCTION

Wildfires are an extreme disturbance in forest ecosystems, causing extensive destruction of the aboveground plant biomass, and affecting seeds and organs located in the upper layers of the soil. Fire is a dominant factor in Mediterranean-type ecosystems (Biswell, 1974; Navéh, 1990; Trabaud, 1990), and as a result most of these ecosystems are resilient to fire (Westman, 1986; Navéh, 1990). Under the prevailing circumstances of frequent man-made fires, there is always a continuum among recently burned areas and various stages of post-fire vegetation succession. The early stage in this recovery process is a phrygana plant formation dominated by dwarf shrubs, especially *Cistus* spp., *Salvia fruticosa*, *Satureja thymbra*, *Majorana syriaca*, *Phlomis viscosa*,

annual legumes, and many other species (Lahav, 1988; Navéh, 1990; Ne'eman, 1997). Three to five years after fire, a shrubby vegetation densely covers the area and there is a quick reduction in coverage and diversity of the annual species (Schiller et al., 1997). Most of the phrygana species are insect-pollinated (Dafni and O'Toole, 1994; Petandou and Ellis, 1996). The full recovery of the woody elements of the Mediterranean maquis takes about 30 to 50 years (Moravec, 1990; Schiller et al., 1997). In contrast to the annual and shrubby species, most of the dominant tree species are wind-pollinated (Aronne and Wilcock, 1994; Dafni and O'Toole, 1994).

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sistant to fire (Naveh, 1973; Lahav, 1988). However, many shrubs, including *Cistus* spp. and *Salvia fruticosa*, are obligate seeders that are completely dependent on their soil-stored seed bank. In this type of species, the death of mature plants, as a result of fire, is followed by a pulse of seedling recruitment (Naveh, 1973; Ari-anoutsou and Margaris, 1981; Trabaud et al., 1985; Trabaud, 1987; Lahav, 1988; Trabaud and Oustric, 1989; Moravec, 1990; Saracino and Leone, 1993; Keeley, 1994; Thanos et al., 1996). All the obligate seeders, except *Pinus halepensis* are entomophyllous, and thus depend on the services of insects, mainly solitary bees (Aronne and Wilcock, 1994; Petanidou and Ellis, 1993) which proliferate in open Mediterranean plant communities (O'Toole and Raw, 1991). In case of repeated fires, the regeneration ability of obligate seeders is mostly dependent on post-fire seed production and thus pollination could be a limiting factor in their reproduction.

The typical Mediterranean phrygana has a very rich plant biodiversity with a dominant contribution of annual species (Zohary, 1962; Shmida and Wilson, 1985; Grueter, 1991). This biome is also very rich in species of solitary bees (Mitchner, 1979; O'Toole and Raw, 1991; Petanidou and Vokou, 1993; Petanidou and Ellis, 1996). Fire may kill the brood of soil-nesting and other solitary bees. Post-fire changes in physical properties of the upper soil layers and in vegetation cover may cause scarcity of bees' nesting sites. *Cistus* spp. shrubs are dominant in the first years after fire in Mediterranean biomes. *Cistus* spp. have pollen-rich but nectar-poor flowers; this may cause a shortage of nectar sources in burned areas. All these changes would be expected to strongly influence seed production in populations of post-fire obligate seeder species.

Salvia fruticosa Miller (Lamiaceae) is a leading species of the Mediterranean phrygana. The plants do not survive fires but the population regenerates after fire by seed germination. This heliophilic species is typical to the early post-fire period. Therefore, it was chosen as an indicator for the evaluation of fire's effect in this fire-prone habitat.

Fire has an influence on biodiversity via its effect on plant species richness (Naveh, 1990) and solitary bee species richness (O'Toole and Raw, 1991; Petanidou and Ellis, 1996). Therefore, fire is also important from the point of view of nature conservation (Given, 1994).

As far as we are aware, almost no studies of the influence of fire on pollination systems were published (but see Carpenter and Recher, 1979). Our present study aims to examine the effects of fire on bee species com-

The study was carried out on Mount Carmel, 3–7 km east of Haifa, Israel. The elevation is about 300 m and the distance from the Mediterranean Sea, 5–10 km. The climate is typical Mediterranean with an annual average precipitation of 600 mm. Study sites were established in open unburned garigue and phrygana vegetation, and in an adjacent burned area (fire in September 1989). Both areas were of similar slope, aspect, and on the same soil type (Rendzina).

The burned area was previously an open mixed *Pinus halepensis* Miller forest, and at the time of this study (5–7 years post-fire) was dominated by *Cistus salviifolius* and *C. creticus* shrubs (65% cover) and young pine trees (15% cover) (Schiller et al., 1997). *Salvia fruticosa* plants were highly dispersed among the *Cistus* spp. shrubs and pine seedlings. The examined plants in the burned area were located about 1000 m from the fire's border.

The unburned area, which was located about 1 km from the burned area, consisted of typical *Sarcopoterium spinosum* phrygana (40% cover) with many other perennial species (e.g., *Salvia fruticosa*, *Satureja thymbra*, *Majorana syriaca*, *Phlomis viscosa*) and about 150 annual species.

Salvia fruticosa (Labiatae) is a typical east Mediterranean shrub which is a key species as a nectar source for most medium and large bees (Kasher, 1991); it also subsidizes the pollination of deceptive orchids (Dafni, 1983). Its flowering season is March–April and coincides with the peak of the Mediterranean flowering season (Shmida and Dafni, 1989; Zohary, 1962; Petanidou et al., 1995). The shrubs in both areas were about 1 m high and at least 10 m from each other.

FLOWER VISITORS, NECTAR MEASUREMENTS, AND SEED PRODUCTION

The study was carried out in spring 1995. Flower visitors were observed during 10 days (from 30 March to 26 April) at the peak flowering season in the burned and unburned areas. Each day another shrub was randomly chosen for observation. Shrubs were not observed twice. Pollinator activity was mainly from 07:00 to 18:00, when temperatures are above 15 °C. We counted all the individual insects that visited the flowers of each plant for periods of 10 min in each hour (12 times a day). Since the insects were not marked, a visitor was counted regardless of whether or not it had visited a flower of the same individual plant before. Visit frequency of bees to flowers was calculated as number of visits per flower per minute. Bee species were identified

Nectar standing crop (NSC) volume, and sucrose equivalent concentration (%) were measured (six flowers for each measurement), parallel to the counts of visitors during one day (26 April). Two persons carried out observations in parallel in the burned and the unburned areas. Nectar volume was measured with calibrated 1 μl capillaries. Nectar concentration was determined by Bellingham and Stanley refractometer adjusted for small samples. Temperatures and relative humidity were recorded during the same day, as closely as possible to the flowers, about 1 m above the ground, with a digital thermo-hygrometer (Fig. 1).

Fruit-set was counted in 6 terminal inflorescences of 10 randomly selected individual plants in each habitat. Fruits were counted at the end of the flowering season and before seed dispersal. Percentage fruit-set was calculated for each individual plant. Each *Salvia* flower can potentially produce 4 nutlets; thus, percentage of fruit-set for each branch was calculated as % fruit-set = 25 \times number of nutlets/number of flowers.

Plant nomenclature follows Feinbrun-Dothan and Danin (1991).

DATA ANALYSES

Bee visitation frequency to flowers was calculated as the number of visits per flower per minute. We used ANOVA to analyze the effect of date and hour on visit frequencies to flowers. We used *t*-tests for comparisons between variables of the burned and the unburned sites. Data that are proportions were arcsin square root transformed before being submitted to statistical test. Pearson correlation coefficients for visit frequencies and nectar standing crop were calculated for solitary and bumble bees.

All statistical analyses were performed by SYSTAT (Wilkinson et al., 1992).

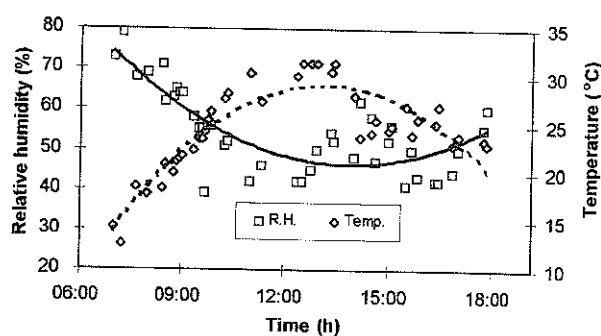


Fig. 1. Typical daily changes in temperature ($^{\circ}\text{C}$) and relative humidity (%) in unburned area on Mt. Carmel (26.4.95).

RESULTS

NECTAR STANDING CROP

The daily mean volume of nectar standing crop in flowers of plants growing in the unburned area was almost half of that in flowers of plants in the burned area (Table 1) and this difference was significant ($t_{55} = -2.709$, $p = 0.009$). The daily mean concentration (equivalent to % sucrose) of nectar in flowers of plants growing in the unburned area was significantly greater ($t_{55} = 3.393$, $p = 0.001$) than that in flowers of plants in the unburned area (Table 1).

There was no clear daily pattern of fluctuation in sugar concentrations or nectar volume in flowers in both areas (Fig. 2A,B), despite the considerable variation in temperatures and relative humidity through the day (Fig. 1). No significant correlation was found between the concentration and the volume of nectar in the flowers of unburned and burned areas ($r = -0.356$, $p = 0.176$, and $r = 0.271$, $p = 0.086$, respectively).

Table 1

Average (\pm SD) nectar volume and concentration (equivalent of % sucrose) in *Salvia fruticosa* growing in burned and unburned areas

	n	Volume (μl)	Concentration (%)
Unburned	16	0.15 ± 0.11	29.9 ± 5.5
Burned	40	0.28 ± 0.19	24.8 ± 5.0

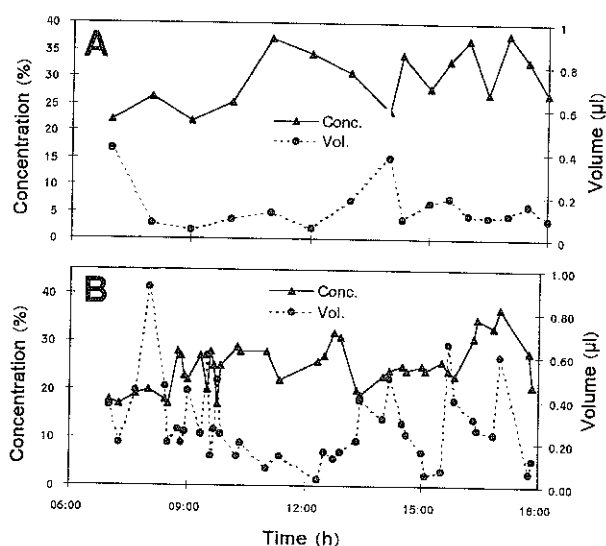


Fig. 2. Typical daily (26.4.95) changes in nectar volume (μl) and concentration (equivalent to % sucrose), in unburned (A) and burned (B) areas.

FLOWER VISITORS

The bumble bees were almost the only visitors in the burned area, while both bumble bees and solitary bees were observed in the unburned area (Fig. 3). The most common solitary bees in our unburned and burned areas were *Synhalonia grandis*, *Anthophora dispar*, *A. biciliata*, *A. dufourii*, *A. nigriceps*, *A. plumipes*, *Ceratina cucurbitina*, *Eucera clypeata*, *E. dalmatica*, *E. nigrifacies*, and *Habropoda tarsata*. In addition, several genera (*Ceratina*, *Halictus*, *Lasioglossum*, *Melecta*, *Nomada*, and *Osmia*) of small to medium solitary bees visited flowers but collected only pollen and seemed to be pollen thieves more than pollinators.

The date and hour of observation did not affect significantly the visit frequency (per flower per hour) of bumble bees ($F_{9,37} = 0.88, p = 0.552$ and $F_{11,35} = 0.647, p = 0.776$, respectively), nor of solitary bees ($F_{9,37} = 0.421, p = 0.915$ and $F_{11,35} = 0.843, p = 0.601$, respectively), in both areas. We calculated the daily average visit frequencies and used them for a comparison between the burned and unburned areas. The average visit frequency of bumble bees was higher in the burned area than that in the unburned area (Fig. 3), but the difference was not significant ($t_{13} = -1.06, p = 0.309$). Solitary bees were observed almost exclusively in the unburned area and thus their visit frequency was significantly higher in this habitat (Fig. 3; $t_7 = 3.676, p < 0.008$).

The changes in visit frequencies of solitary and bumble bees to flowers in the burned and unburned areas broadly matched the changes in nectar standing crop (Fig. 4). In the unburned area, bee activity was high at 07:00–09:00, which may be a response to the initially high standing crop of nectar, and decreased during the rest of the day, as nectar standing crop decreased (Fig. 4A,B). The pattern of bumble bee visits in the burned area is more complex, and it seems to follow the changes in the nectar standing crop with a time lag (Fig. 4B). However, the calculated Pearson correlation

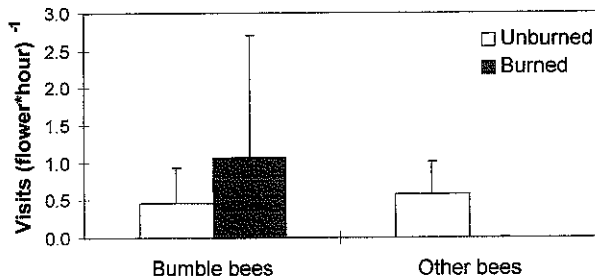


Fig. 3. Mean visit frequencies (visits per flower per hour) of bumble bees and other bees, in burned and unburned sites. Error bars represent one SD.

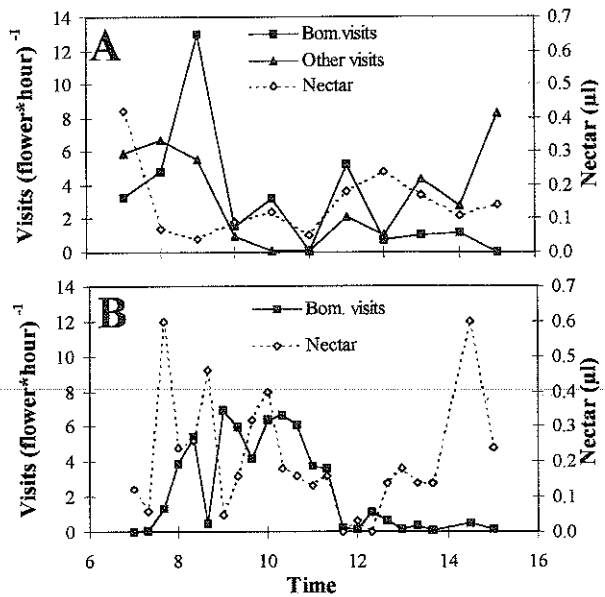


Fig. 4. Typical daily (26.4.95) changes in nectar standing crop (μl) and mean visit frequencies (visits per flower per hour) of bumble bees (Bom.) and other (Other) bees in unburned (A) and burned (B) areas. Since solitary bees were almost absent from the burned area, they are not presented in Fig. 4B. Time scale as for Fig. 1.

coefficients between the visit frequencies of solitary bees, bumble bees, and nectar standing crop in the unburned and burned area were all not significant ($p > 0.05$) (Table 2).

FRUIT SET

The average percentage fruit-set in the unburned areas was 19.9 ± 8.4 and in the burned areas 11.0 ± 3.8 ; this difference was significant ($t_{31.5} = -4.079, p < 0.001$).

DISCUSSION

NECTAR AND BEES' VISITS

Nectar standing crop (NSC) volume is an outcome of the nectar production rate, nectar consumption by visi-

Table 2
Pearson correlation coefficient (probability in parenthesis) for visit frequencies of bumble bees and solitary bees with nectar standing crop in unburned (A) and burned areas (B)

A. Unburned	Bumble bees	Solitary bees
Solitary bees	0.256 (0.448)	
Nectar standing crop	-0.214 (0.527)	0.16 (0.638)
B. Burned	Bumble bees	
Nectar standing crop	0.025 (0.91)	

tors, as well as possible volume loss due to microclimatic conditions inside the flower (Zimmerman and Pyke, 1988; Corbet, 1990) and reabsorption.

In the present paper we studied the course of NSC volume in *S. fruticosa* at the burned vs. unburned habitats at the same date in order to minimize the possible influence of weather. This procedure enabled us to evaluate the effect of pollinators on the NSC volume. Kasher (1991) has already found that nectar production rate in *S. fruticosa* was subject to weather conditions as well as to individual plant variation, but the NSC volume was negatively correlated to the visitors' activity. We found similar ranges of nectar concentration in the unburned (20–37%) and the burned (16–36%) areas, which are also similar to the concentrations recorded by Kasher (1991).

The average NSC volume in the burned area was significantly higher in comparison to the unburned area while the nectar concentration showed the opposite significant trend. The mean frequency of *Bombus*' visits per flower per hour, was higher at the burned area. *Bombus* make a far better nectar exploiter than most of the solitary bees because their proboscis is longer (Knuth, 1906–1909) and their nectar imbibing rate is higher (Roubik, 1989). This may explain why *B. terrestris* visited flowers mainly in the burned area where NSC volume was higher. However, it can not explain why solitary bees visited flowers only in the unburned habitats.

Frequent short-term temporal fluctuations of NSC volume and bees' activity (Figs. 3,4) were observed. The changes in bees' activity matched the changes in nectar quantity with a time lag of 10–20 min; therefore, no direct correlation was found between these two parameters. The "near-far" search model of bee foraging (Motro and Shmida, 1995) may explain the rapid fluctuations in NSC volume. In a nectar-rich plant (after the accumulation of enough nectar), the bees tend to fly short distances and visit flowers on the same plant (near search) till the depletion of the nectar below a certain threshold level, when they make long jumps to other plants (far search) (Bertch, 1987). Very few visits were recorded when the NSC volume was below 0.05 μ l, favoring a "far search" type to another plant; this resulted in low bee frequency till the re-accumulation of nectar for a new wave of short-range visits (Figs. 3,4). This interpretation is in accordance with several authors who have shown less visits in nectar-poor patches which were followed by longer interplant flights in honey bees (Waddington and Holden, 1979), bumble bees (Heinrich 1979; Pyke, 1987), and solitary bees (Kadmon, 1992).

Kasher (1991) found in *S. fruticosa* that NSC was correlated negatively with temperature but positively

with humidity; however, nectar concentration was correlated only with temperature. We have no explanation for the observed difference in nectar concentrations between the burned and unburned habitats, unless one may assume individual differences among plants in nectar production rates, as was found in *S. fruticosa* by Kasher (1991) and in other species (Hodges, 1993).

FIRE, BEES, AND CONSERVATION

Three fire-related factors may affect the populations of solitary bees: (1) The direct thermal effect of fire destroys nests of solitary bees located in plant cavities (Megachilidae) and near the soil surface (O'Toole, pers. comm.). (2) The dense shrub vegetation of *Cistus* spp. that follows fire disturbance (Lahav, 1988; Schiller et al., 1997) several years after the fire may prevent the recolonization by bees via the elimination of the available exposed sites suitable for ground, cavity nesting, and carpenter bees (O'Toole and Dafni, 1994). (3) The dense perennial vegetation, several years after fire, reduces the abundance of nectariferous annual plants (Lahav, 1988), which may be exploited by bees.

All these factors led to a situation in which small to medium-sized solitary bees were unable to penetrate the shrubby vegetation to reach the isolated patches of *S. fruticosa* in the burned area. These bees have a relatively short flight range; access to the nectar they need for refueling is relatively rare in the burned area due to the scarcity of nectariferous plants (Dafni and O'Toole, 1994).

Large bees have a long flight range; thus they are able to cross a long non-rewarding gap on their way to rich nectariferous patches inside the burned area. In our case, the only such bee was *B. terrestris*. Pollen load analyses of *B. terrestris* showed their ability to fly for several kilometers in search of nectar sources on Mt. Carmel (Dafni and Shmida, 1996; Dafni and Ne'eman, unpublished data). The ultimate result was that *B. terrestris* was almost the only visitor of *S. fruticosa* in the burned area.

The seed production of *S. fruticosa* was significantly lower in the burned area, as was found also for several other perennial nectariferous species (Dafni and Ne'eman, unpublished data). This reduction might have a long-term effect on post-fire species composition and abundance due to the fact that this species is an obligate post-fire seeder (Keeley, 1994).

S. fruticosa is visited by many species of solitary bees. Kasher (1991) found about 45 bee species visiting the flowers on the Judean Mountains, Israel. We recorded 20 species on Mt. Carmel. The post-fire pollination environment appears to be unbalanced due to the scarcity of the solitary bees and the dominance of *B. terrestris*, a new invader in Mt. Carmel (Dafni and

Shmida, 1996). It seems that *B. terrestris* faces competition with solitary bees at the unburned area, as can be inferred from its lower visit frequency, in comparison to the burned area where it is the only visitor.

S. fruticosa is a heliophilic species which invades recently disturbed or burned habitats (Keeley, 1994). Its relative rarity, several years after fire, may be explained by the low abundance of efficient pollinators, medium- to large-sized bees, as suggested by the lower fruit-set in the burned area. This is in contrast to the dominant *Cistus* spp. which are pollinated by a large array of various unrelated insects, mainly small bees and beetles (Bosch, 1992).

The present evidence indicates that in the phrygana, a bee-dependent pollination environment (Petanidou and Ellis, 1996), the post-fire recovery of solitary bee populations seems to take longer than six years, resulting in lower seed-set. Such a situation may pose a threat to entomophilous post-fire obligate seeder species, such as *S. fruticosa*. The problem could be even more acute in areas under frequent fire regime, which could cause extinction of local bee and plant populations.

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