

The effect of management treatments on pheno-morphological traits of *Phillyrea latifolia* L.

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ABSTRACT: Vegetative growth, blooming and fruiting of *Phillyrea latifolia* L. were monitored through 5 years under different management regimes in a Mediterranean garrigue in Israel. Vegetative growth and blooming occurred constantly and massively each spring, with slight inter-annual temporal fluctuations, probably controlled by water availability. Frequency, rate and intensity of vegetative growth were also constant and massive. Reproductive performance was very irregular and variable, both at population and individual levels. Management treatments had no effect on the timing of the phenological events, but caused massive growth of elongated shoots accompanied by decrease of leaf sclerophylly. Management intervention enhanced blooming and fruit production. The adaptive significance of the phenological pattern and the short-term modifications by management is discussed.

1 INTRODUCTION

Mediterranean ecosystems have been shaped by a variety of anthropogenic disturbances, such as wild fire, wood cutting and livestock grazing. At present, these human interventions are used frequently as management tools of natural areas, aimed to achieve the goals of biodiversity maintenance, reclamation of natural ecosystems, prevention of fire and for recreation purposes. The effects of management interventions are studied mostly at the ecosystem and the community levels or at the population level in terms of abundance parameters of particular species. In this study, some aspects of the effects of management treatments were investigated in one species, at the population and individual levels.

The phenological pattern of a certain plant species is considered as an adaptation to its environment (Mooney and Kummerow, 1981). Phenological processes, like vegetative growth, blooming and fruit set, are examined by the timing, rate, frequency and intensity. Thus, it reflects varied internal resource allocation at different stages of life history, adjusted to the availability of external resources and to the impacts of environmental stress. (Le Roux et al., 1984; Orshan, 1989). Usually, phenological patterns are highly correlated with climate (Larcher, 1995). Evergreen sclerophyllous shrubs and trees are very typical to Mediterranean ecosystems and their phenological pattern is characterized generally by short intensive vegetative growth and blooming in the spring. This is correlated with deep root system and is synchronized with the availability of water and temperature rise (Mooney and Kummerow, 1981). Fruits, mostly animal dispersed, ripen in autumn.

The evergreen sclerophyllous shrub *Phillyrea latifolia* L, was chosen as a model plant for the study of the effects of management interventions on the phenological pattern. *P. latifolia* is widely distributed through the Mediterranean biogeographic region (Feinbrun-Dothan, 1978; Browitz, 1984; Zohary, 1973). In some Mediterranean evergreen maquis communities in Israel it is a dominant species (Rabinovitch-Vin, 1986; Pollak and Schwartz-Tsachor, 2003). The phenological pattern of *P. latifolia* is typical for Mediterranean evergreen sclerophyllous shrubs and trees. Blooming and new vegetative growth occur in spring and ripe fleshy bluish-black fruits are found in September-February (Feinbrun-Dothan, 1978; Perevolotsky and Haimov, 1992; de-Lillis and Fontanella, 1992). Special spring vegetative growth in the form of elongated shoots was also observed. The growth of these elongated shoots was induced by cutting and grazing and exhibited lateral orientation, probably as a compensation reaction to the removal of plant parts (Perevolotsky and Haimov, 1992). A second period of spontaneous growth of elongated shoots was documented in Israel also in late summer and autumn (Rabinovitch-Vin, 1986). Information on blooming, refers mainly to the sex types in natural populations in Spain and Italy. *P. latifolia* is an androdioecious species by which the hermaphroditic individuals have flowers with big stigmas, whereas the "males" bear flowers with ovaries, style and degenerated stigmas or lack female parts at all (Herrera, 1994; Aronne and Wilcock, 1994). Only the hermaphroditic plants produce fruits. Fruit yield in populations in Spain was very irregular and variable. In observations over a period of 15 years (1978-1992), high fruit production was found only in 2 of the years, whereas in the other years the total fruit yield was very low (Herrera et al, 1994).

In this study, we assess the basic phenological pattern of east-Mediterranean populations of *P. latifolia* and its natural fluctuations. Distinction is made between long-term adaptation to the current environment, due to phylogenetic heritage, and the short-term reactions, expressed by phenotypic plasticity. Management treatments like shrub-removal and grazing, serve as factors that induce short term reactions, which may modify the basic phenological pattern. These modifications are interpreted by the parameters of timing, frequency, rate and intensity of the phenological events and are examined in terms of resource allocation and trade-off mechanisms.

2 STUDY AREA AND RESEARCH PLOTS

The study area is located at Ramat Hanadiv Park, at the southern edge the Carmel ridge, Israel. The annual average precipitation in Zikhron Yaacov, adjacent to the study area, is 650 mm. Table 1 presents the rainfall amounts during four study seasons (1993/4 – 1996/7) and the relative proportion of early winter rain (October-December). The geological substrate consists of cenomanic hard limestone and dolomite rocks, covered partly with brown-reddish terra-rossa soil. The research plots were set at 2 sites: Site 1 is located at 14582183 Israel grid, altitude 120 m., on a slight slope facing south-east. The natural vegetation, recovered from a fire in 1980, exhibits a transition state between shrubland and a degraded maquis, defined as "sparse" *Phillyrea latifolia* vegetation unit (Cohen, 1987). This plant community is dominated by *P. latifolia*, accompanied by *Pistacia lentiscus*, *Calycotome villosa*, *Rhamnus lyciodes*, *Sarcopoterium spinosum*, *Rubia tenuifolia*, *Asparagus aphyllus* and *Smilax aspera*.

Table 1. Annual precipitation at Zikhron Yaacov for 1993/4 – 1996/7

Season	total annual amount (mm)	Accumulated rainfall September – December	
		Mm	%
1993/4	465.8	89.5	19
1994/5	900.6	617.7	69
1995/6	476.1	122.9	26
1996/7	625.0	217	35

This area serves as a "fire break" aimed to diminish spread the spread of fire into the park from adjacent settlements (Perevolotsky et al., 2003). Four management regimes were applied in different plots at this fire break: 1. "Control" (no intervention). 2. "Shrub-removal" - removal of the shrubs and sub-shrubs, mainly *Sarcopoterium spinosum* and *Calycotome villosa*, prior to the study, at 1992. 3. "Grazing" – herd of beef cattle (150-200 heads) was introduced to the fire break producing very high grazing pressure for a short duration (7-10 days), at the beginning of April. 4. Shrub-removal + grazing – combination of 3 and 4.

Site 2 is located at 14462174 Israel grid, at 100 m. altitude, on a moderate slope facing the north. No documentation exists about fires in the last 50 years. The vegetation is a transition formation between open and dense maquis, defined as "typical" *P. latifolia* unit (Cohen, 1987). Plant species composition is similar to site 1, except for the more prominent domination of *P. Latifolia*. At this site only one plot was established and was named "natural".

These five plots represented increasing degree of intervention and disturbance in the following order: Natural → control → shrub-removal/grazing → shrub-removal + grazing.

3 METHODS

3.1 *Phenological records*

The monitoring of vegetative growth, blooming and fruiting took place between 1.1.1994 – 31.12.98. Two hundreds shrubs, 40 in each of the 5 plots, were randomly chosen, numbered and tagged. at the beginning of the investigation. Each plant was visited regularly twice a month. Between mid February and the end of April, the plants were visited and recorded weekly and in June-September, only once a month. Vegetative growth was defined as the appearance of new short twigs bearing usually 4-10 leaves, developed from vegetative buds. Special vegetative growth of longer twigs (15-40 cm long), was characterized as "elongated shoots". Blooming was identified when branched inflorescences developed from reproductive buds on woody twigs from previous years. Presence of fruits was recorded at every observation, and the values for ripe fruits refer to October

3.1.1 *Timing*

Dates of start, peak and end of vegetative growth, blooming and ripe fruits were recorded both in population (total for all investigated plants or per treatment) and for each individual. Timing data refer to 1994-1997.

3.1.2 *Rate*

The rates of vegetative growth (including elongated shoots), blooming and ripe fruits were calculated at the population level, as percentage of individuals by which at least one growing twig, inflorescence or ripe fruit was present.

3.1.3 *Frequency*

Frequency of vegetative growth, blooming and the presence of ripe fruits was calculated for each shrub as the proportion of number of years in which each individual performed each activity, out of a total 5 years of observations (1994-1998).

3.1.4 *Intensity*

Total numbers of vegetative twigs, inflorescences and ripe fruits per individual shrub, were estimated qualitatively by visual observation and defined as intensity category. The intensity was ranked on 0-3 scale, when 0 = no, 1 = few, 2 = intermediate, 3 = many. As vegetative growth was always highly intensive, only intensity values of blooming and ripe fruits are presented in the results. Intensity values for blooming and fruits refer to 1995-1998.

3.2 Leaf measurements

Leaves were randomly sampled in the natural and the shrub removal + grazing plots (40 in each plot) in May 1994. Leaf area was measured by planimeter. Dry weight was determined by an analytic balance after oven-desiccation at 90°C. The ratio of dry weight/leaf area (one side) was used as an indication for leaf sclerophylly.

3.3 Sex type

The small yellowish flowers on all blooming shrubs contained 2 sepals, 4 petals 2 stamens and a gynoecium consisting of an ovary with 2 ovules, style and 2 lobed stigmas. However, *P. latifolia* is considered as an androdioecious species (Herrera, 1994). The two gender types were distinguished among the investigated shrubs, according to the stigma shape and size: 1. Hermaphrodites, whose flowers contain bigger and developed stigmatic surfaces and have the potential capacity to produce fruits. 2. "Males", which possess smaller and undeveloped stigmata, sometimes reddish in the tip and did not produce fruits. The assessment of the sex type was made during the visits at blooming time by observations with magnification glass. This was supplemented by stereoscope observations on alcohol-preserved flowers in the laboratory.

3.4 Statistical analysis

The significance of differences between means of various parameters was determined by Duncan's Multiple Range test (GLM procedure) of the SAS software. Percentage data were transformed to arcsine.

4 RESULTS

4.1 General phenological pattern

Fig. 1 presents the general pattern of the phenological events of *P. latifolia* at the population level. Spring is the main activity season. Blooming peaking in March precedes vegetative growth which reaches its' peak in April. The overlap of blooming and vegetative growth periods is partial. Ripe fruits are found between the end of September and January.

4.1.1 Vegetative growth

Twigs of 2-8 cm long are developed in spring from apical and axillar vegetative buds, located on previous years branches. Each twig bears 3-7 pairs of opposite leaves. During all study seasons, in all the management plots, vegetative growth occurred regularly every year in all individual shrubs, with plenty of twigs per individual. At the population level, the vegetative growth could last for 2 months, but the main flush occurs during a short peak period of 2-4 weeks. At the individual level, the duration of the vegetative growth generally does not exceed 10 days. The timing of the peak period at the population level varied very slightly during the study years. In 1995 the vegetative growth occurred 3-4 weeks earlier than in other seasons, while in 1997 it occurred a bit later, so the fluctuations are in a 3-4 weeks range (fig.1). In addition to the main spring vegetative growth, a second vegetative growth season was observed, in November and December (fig. 1). This early winter vegetative growth was sporadic and much less intensive. In 1994 early winter vegetative growth occurred in 25% of the shrubs and in 1996 only in 9%.

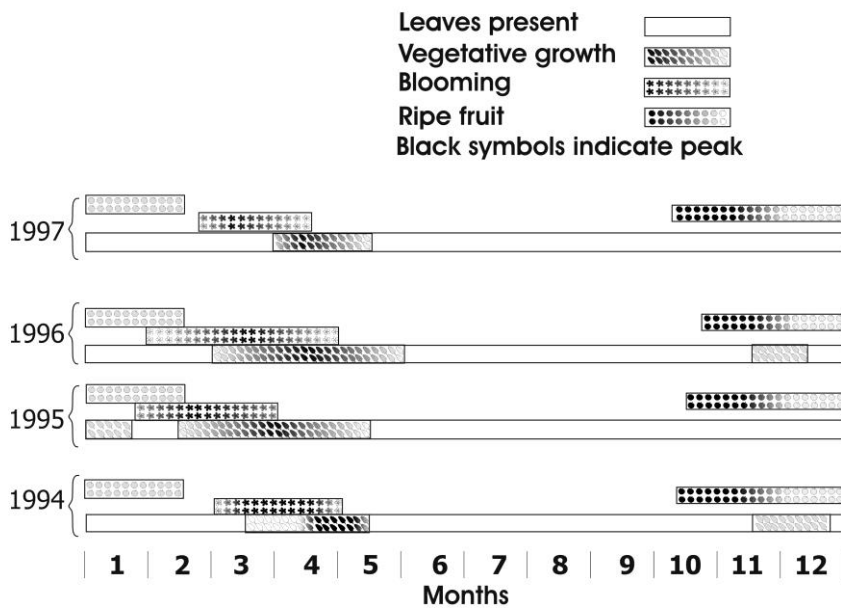


Figure 1. The timing of vegetative growth, blooming and ripe fruits in *Phillyrea latifolia*.

4.1.2 Blooming

Flowers are arranged on branched racemes and develop from reproductive buds, located on the previous year's branches. At the population level, the average rate of blooming for all management plots throughout all the study years was 58% (Table 1). Many individuals avoided blooming in certain years and about 20% of the shrubs had never bloomed during the study period. Significant high blooming rate was recorded in 1996. Blooming frequency; rate and intensity were significantly higher in the "male" shrubs (Table 2). At the population level, total blooming period lasted 2 months, but main blooming occurred throughout 3-4 weeks in March. At the individual level, the duration of blooming is generally 2-3 weeks long. The inter-annual fluctuation range of blooming timing is similar to that of the vegetative growth (Fig. 1). In 1995, blooming occurred in February, 3 weeks earlier than in other years.

Table1. Rates of blooming and fruiting at the population level during the study period (1994-1997)

Year	Blooming (%)	Fruiting (%)
1994	43.0 b	19.8 ab
1995	59.5 b	9.5 b
1996	81.5 a	31.5 ab
1997	47.2 b	20.0 a
Average	57.8	20.2

Percentages refer to the total studied population, in all management treatments (N=200). Identical letters indicate non-significant differences.

4.1.3 Fruiting

Fruits set gradually after blooming during the late spring and summer, in the hermaphroditic individuals. Fleshy dark-blue fruits are found on the shrubs between October and January (Fig. 1). During that period the fruits are gradually removed by birds or fall spontaneously. At the popu-

lation level, the average percentage of shrubs bearing ripe fruits was very low - 20.2% on average (Table 1). This means, that on the base of a 5-year period, the majority of the hermaphroditic shrubs avoid ripe fruits at all. Fruiting frequency and average fruiting intensity in the individual shrubs throughout the observation years, was also very low (Table 2).

Table 2. Frequency and intensity of blooming and fruiting in hermaphroditic and "male" plants (average of categories)

Sex type	Blooming frequency	Blooming intensity	Fruiting frequency	Fruiting intensity
Hermaphroditic	3.15 b	1.29 b	1.84	0.60
"Male"	3.77 a	1.83 a	0	0

Hermaphroditic – Individual with large stigma in the flower. "Male"– Individual with small stigma in the flower.

Figures are averages of 5 years of observations and refer to those individuals which bloomed at least once during the study period and whose sex type was certainly determined.

Different letters in each column indicate significant difference.

4.1.4 *Growth of elongated shoots*

Management treatments stimulated the growth of elongated shoots which sequenced the growth of regular twigs during the spring vegetative growth flush. These twigs continued to grow and developed additional leaves. This process occurs during 3-4 weeks beyond the usual spring growth and came to an end not later than the middle of May. These elongated shoots were usually 15-40 cm long. The elongated shoots appear in all parts of the shrub canopy and emerge also from woody parts in the base. Elongated shoots developed on plants in all observation plots, but were especially frequent in the grazing + shrub removal treatment. Strong response was found also in grazing and shrub-removal treatments. The percentage of shrubs with elongated shoots in the natural and control plots was very low (Table 3).

Table 3. The Effect of management treatments on the growth of elongated shoots

Natural	Control	Shrub removal	Grazing	Shrub removal +Grazing	All
7.5 cd	5.6 d	31.3 b	25.6 bc	73.8 a	28.9

Figures indicate the average percentage of plants which developed elongated shoots at 1994 – 1997.

Different letters indicate significant difference.

4.1.5 *Leaf weight, leaf area and their ratio*

The average leaf weight, leaf area and ratio weight/area were significantly lower in the shrub removal + grazing treatment (Table 4). This indicates less scleromorphic leaf structure. Tendency toward less scleromorphic leaf was also observed in grazing treatment, but was not significant.

4.2 The effect of management treatments on blooming and fruit yield

The timing and the duration of blooming were not affected by management treatments. However, the blooming frequency of the individual shrubs, the rate of flowering plants in the population and the blooming intensity of the individuals, were significantly higher in the shrub-removal and shrub-removal + grazing treatments (Table 5). The figures for the grazing treatment were especially low and lower even than those of the natural and the control plots. The values for fruiting rate in the population, fruiting frequency and fruit yield intensity of the individuals, were very low at all treatments, compared with blooming values. The highest amounts of ripe fruits were found in the shrub-removal plot. Fruiting frequency and intensity were significantly higher in shrub-removal and shrub-removal + grazing treatments. Values in the grazing treatments were very low (Table 5)

Table 4. The effect of management treatments on leaf dry weight, leaf area and the ratio dry weight/leaf area

Treatment	Dry weight (gr.)		Area (cm ²)		Dry weight/area	
Natural (n=39)	0.036±0.021	a	1.680±0.086	a	0.0212±0.008	a
Control (n=40)	0.030±0.012	a	1.522±0.535	ab	0.0194±0.003	a
Shrub-removal (n=39)	0.031±0.017	a	1.477±0.610	ab	0.0203±0.004	a
Grazing (n=39)	0.029±0.008	ab	1.524±0.392	ab	0.0189±0.003	ab
Shrub-removal + Grazing (n=40)	0.023±0.011	b	1.261±0.410	b	0.0173±0.004	b

Leaf area refers only to one side.

Different letters in each column indicate significant difference.

Table 5. The effect of management treatments on frequency, rate and intensity of blooming and fruiting, during the study period (1994-1998)

Management treatment	Blooming			Fruiting		
	Frequency	Rate	Intensity	Frequency	Rate	Intensity
Natural	2.68 b	51.3 bc	1.33 b	0.80 bc	16.3 b	0.26 ab
Control	2.43 bc	51.9 bc	0.91 c	0.70 c	18.1 ab	0.26 ab
Shrub removal	3.53 a	75.0 a	1.61 a	1.28 a	33.8 a	0.40 a
Grazing	2.00 c	39.6 c	0.88 c	0.40 c	8.9 b	0.13 b
Shrub removal + grazing	3.50 a	71.3 ab	1.56 ab	1.13 ab	24.1 ab	0.36 a

Frequency: No. of blooming/fruiting events per individual during 1994-1998. Scale: 0-5.

Rate: % of blooming/fruiting plants for each population averages for 1994-1997.

Intensity: Estimated flowers/fruits amount per individual on scale 1-3. Averages for 1995-1998.

Different letters in each column indicate significant difference.

5 DISCUSSION

The timing of the phenological events in *P. Latifolia* exhibits a consistent pattern, with slight inter-annual fluctuations. This process is in accordance with previous reports on the phenology of evergreen sclerophyllous Mediterranean trees and shrubs (Miller, 1983; Mooney and Kummerow, 1981; Orshan, 1989; Perevolotsky and Haimov, 1992). This pattern reflects a long term adaptation to the Mediterranean climate regime. The short and intense phenological activity in spring is generally related to deep root systems (Castro-Diez and Montserrat-Marti, 1998). The inter-annual fluctuations can be explained by the changing availability of water: when rains occur in early winter, spring vegetative growth and blooming occur earlier and reflect short-term phenotypic plasticity. High cumulative rainfall until December induces the sporadic winter vegetative growth. No vegetative growth, neither spontaneous as reported by Rabinovitch-Vin (1986), nor in reaction to artificial disturbances (Giovannini. et al., 1992) was found in summer and autumn.

The frequency, rate and intensity of the vegetative events in *P. latifolia* differed significantly from those of the reproductive events. Spring vegetative growth occurred every year in all plants and was very intensive. Contrary to that, blooming and fruiting exhibited low rates and high inter-annual variability both at the population and the individual levels. Many individuals avoided blooming and fruiting on an irregular pattern. This pattern is not unique to Ramat Hanadiv, and was observed in other populations in Israel (Pollak and Schwartz-Tsachor, 2003). Irregular pattern characterizes the fruit production of *P. latifolia* also in Spain (Herrera et al., 1998). Such low frequency, low rates, avoidance and high variability in blooming occurrence and in fruit yields, are very exceptional in other evergreen sclerophyllous shrubs. The difference in blooming rates, frequency and intensity between hermaphroditic and "males", suggests resource trade-off (Crawley, 1997). Higher blooming frequency, rate and intensity in males, compared with hermaphroditic potential fruit producers, can be explained by lower demand for internal resources investment in males. This idea is supported by the findings in *P. angustifolia* (Pannell and Ojeda, 2000). The very low frequency, rate and intensity of fruiting at the individual and population level, is caused not only by the low and variable performance of the blooming hermaphrodites, but probably also by pollination and fertilization constraints, fruit abortion and insect attacks (Herrera et al., 1994; Prophetou-Athanasiadou, 1996). The ovaries of *P. latifolia* are attacked by *Probruggmanniella phillyreae* (Cecidomyiidae), and galls are formed instead of normal fruits (Pollak and Schwartz-Tsachor, 2003). Formation of ovary galls was reported also in *P angustifolia* (Traveset, 1994). We assume, that low and irregular reproductive performance can be explained, at least partially, as a selection against insect damage.

Intensive management interventions modify part of the vegetative growth of *P. latifolia* toward aggressive production of elongated shoots. Spontaneous growth of elongated shoots without artificial disturbance was negligible. This reaction expresses short-term phenotypic plasticity, which can be interpreted as a compensation growth under grazing and thinning (Perevolotsky and Haimov, 1991, 1992). Elongated shoot growth under strong disturbance was accompanied by the appearance of smaller and less sclerophyllous leaves, at least at the early stage of leaf development. This trend was reported also in *Quercus coccifera* in Greece (Papatheodorou et al., 1998) and can be interpreted as trade-off of resource allocation between massive shoot elongation and deposition of wall material in leaf cells which contributes to high sclerophilly index.

Management treatments, like shrub-removal and the combination of shrub-removal and grazing, induce an increase of the frequency, rate and intensity of blooming and fruiting and decreased reproductive avoidance. Shrub-removal may cause better light penetration, thus enabling more blooming. From long-term adaptation point of view, enhanced reproductive performance under disturbance can be explained as selection for potential ability to colonize new gaps by more dispersed fruits. We have difficulty suggesting an explanation as to why grazing alone differs from the other management treatments and actually does not enhance blooming and fruit production. The strategy

of increased reproductive investment in *P. latifolia* under certain disturbance types differs from the decrease in blooming rates and the increase of blooming avoidance under disturbance and stress, reported in *P. angustifolia* (Pannell and Ojeda, 2000). It seems that the relationship between disturbances and reproductive performance is rather complex and may involve other factors. Further investigation is needed.

6 CONCLUSION

The basic phenological timing pattern of *P. latifolia* represents a long-term adaptation to Mediterranean climate, mainly to the rainfall regime. The slight inter-annual fluctuations in timing reflect phenotypic response to the current availability of water. The irregularity, low performance and partial avoidance of blooming and fruit production, suggest long-term adaptation to other selective forces, probably constraints of floral biology, dispersal biology and insect attacks. Deliberate management treatments modify certain pheno-morphological components in a manner that may contribute to the success in the dynamic processes in the community. This short-term effects at the population and individual levels of one species should be considered when management treatments are applied.

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