Irregular patterns of flowering and fruiting and androdioecy in *Phillyrea latifolia* L. in Israel

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Study Questions

- What stands behind the irregular patterns of the reproductive traits of *Phillyrea latifolia*?
- Whether and how androdioecy is related to the irregular patterns of flowering and fruit production in *Phillyrea latifolia*?

Phillyrea latifolia L. - Natural History in brief

Evergreen sclerophyllous shrub (fig. 1) Widely distributed through the Mediterranean biogeographic region (Feinbrun-Dothan, 1978; Browitz, 1984; Zohary, 1973). Dominant in some Mediterranean shrub communities in Israel.

Flowering and new vegetative growth occur in spring. The small yellowish flowers contain 2 sepals, 4 petals 2 stamens and a gynoecium consisting of an ovary with 2 ovules, style and 2 lobed stigmas. Wind pollinated.

Androdioecious species by which the hermaphroditic individuals have flowers with big stigmas (figs 2,3), whereas the "males" bear flowers with normal ovaries and styles, but have small and degenerated stigmas (figs 4,5) or lack female parts at all (Herrera, 1994; Aronne and Wilcock, 1994, Pollak and Schwartz-Tsachor, 2003).

Ripe fleshy bluish-black fruits are found in September-January (fig. 6).

Figure 1. Shrubs of *P. latifolia* at Ramat Hanadiv Park

Figure2. Hermaphroditic flower with big stigma (X30)

Figure 3. Hermaphroditic stigma (SEM)

Figure 6. Ripe fruits of *P. latifolia*

Figure 4. "Male" flower with small stigma (X16)

Figure 5. "Male" stigma (SEM)

Study sites

1 - Harashim, mean annual precipitation: 940 mm.
2 - Ramat Hanadiv, mean annual precipitation: 650 mm
3 - Nehusha, mean annual precipitation: 450 mm

Main study site:

Ramat Hanadiv Nature Park, at the southern edge the Carmel ridge, Israel. (fig 1)

Observation plots

1. Natural vegetation stand - undisturbed at least for 50 years.
   -Four management treatments exhibiting various degrees of disturbance
2. Control: no disturbance since last fire in 1980
3. Shrub removal: partly removal of shrubs and sub-shrubs, including *P. latifolia*, prior to the study, at 1992.
4. Grazing: 150 cattle were introduced every year during the study period for 7-10 days at the beginning of April.
5. Shrub removal + grazing: combination of 3+4.

Results

Table 1. Sex types in populations of *P. latifolia* along climatic gradient

Population	Mean annual precipitation (mm)	No.	"Male" (%)	Hermaphrodite (%)	Unknown[1] (%)
Harashim	940	53	43.4	30.1	26.5
Ramat Hanadiv	650	200	37.5	42.0	20.5
Nehusha	450	43	44.2	39.5	9.3

The proportion of "males" individuals is rather similar along an aridity gradient. A higher proprtion of flowering-avoiding individuals was found in the humid habitat.

Table 2. Flowering characteristics of "males" and hermaphrodites

Trait	"male"	hermaphrodite	Significance (t test)
% of twigs with flowers (n = 135)	75 ± 24	63 ± 24	**
No. of inflorescences per twig (n = 195)	6.09 ± 3.1	3.9 ± 2.2	***
No. of flowers per inflorescence	6.4 ± 1.7	5.9 ± 1.6	*
No. of flowers per twig	986	522	***
No. of pollen grains per flower	91874 ± 43844 (n = 7)	83524 ± 35241 (n = 10)	ns

"Males" produce more pollen than hermaphrodites, mainly due to more flowering twigs and more inflorescences per twig, probalbly reflecting different resource allocation to reproductive functions between the two sex types.

Table 3. Annual fluctuations in flowering and fruiting rates

Year	Rainfall (mm)	Flowering (%)	Fruiting (%)
1994	465.8	43.0 b	19.8 ab
1995	900.6	59.5 b	9,5 b
1996	476.1	81.5 a	31.5 ab
1997	625	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.

Flowering and fruiting rates are highly variable. Many individuals do not flower every year and 20% avoided flowering at all. Fruiting rates are even lower and the majority of the hermaphroditic shrubs avoid ripe fruits at all. On the basis of the 5 year observation period, each hermaphroditic shrub showed a probability of 37% to bear ripe fruits, No correlation was found between flowering and fruiting rates and annual amount of rain.

Table 4. Frequency and intensity of flowering and fruiting in "males" and hermaphrodites.

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

Figures are averages of 5 years observations and refer to those individuals which flowered at least once during the study period and whose sex type was certainly determined.
Different letters in each column indicate significant differen.

"Males" tend to flower more frequently and with higher intensity than hermaphrodites. The frequency and the intensity of fruiting in hermaphrodites is much lower than flowering, which means failure of many flowering hermaphrodites to set fruit.

Table 5. The effect of disturbances on flowering and fruit yield

Management treatment	Flowering			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	1.13ab	24.1 ab	0.36 a

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

Flowering

The flowering 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.

Fruiting

The values for fruiting rate in the population, and fruiting frequency and fruit yield intensity of the individuals, were very low at all treatments, compared with blooming values. The highest amount of ripe fruits was found in the shrub removal plot. Fruiting frequency and intensity were significantly higher in shrub removal and shrub removal + grazing treatments.

Ovary galls of *Probruggmanniella phillyreae* (Diptera, Cecidomyidae)

A part of the flowers, develop ovary galls that look like distorted fruits which remain green (fig. 7), instead of normal fruits. These galls appear on "males" and on hermaphrodites as well. Probruggmanniella phillyreae (Diptera, Cecidomyidae) females lay eggs into the ovaries (fig.8), which develop to a gall, without seeds.

Figure 7. Ovary Galls, a. pupa emerging from gall

Figure 8. *Probruggmanniella phillyreae* laying eggs in ovary

Conclusions

- "Male" individuals of *Phillyrea latifolia* contribute more pollen and flower more frequently and intensively than hermaphrodites, reflecting probable resource constraint in fruiting hermaphrodites .
- The "male" proportion in populations is rather constant and is not correlated to water stress.
- High inter-annual variability and reproductive avoidance are not related to water availability but to disturbance: Shrub removal increased flowering and fruit production, providing better chances for colonization.
- Irregular pattern, high variability and avoidance of flowering and fruit production, can be explained as an adaptation to avoid pest damages, as is exampled by the ovary galls caused by *Probruggmanniella phillyreae*.
- Androdioecy may contribute to lowering chances of mosquito attacks on hermaphrodite ovaries, due to infection of "male" ovaries.

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