Lagascalia 19(1-2): 445-454 (1997)

REPRODUCTIVE PHENOLOGY IN MEDITERRANEAN MACCHIA VEGETATION

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Abstract

Reproductive phenology of the woody perennials of a Mediterranean shrubland in Southern Italy is investigated in relation to the Mediterranean climate and evolutionary origin of its flora. No single reproductive phenology was adopted by these perennials; in fact, less than one fifth of the species avoided the summer aridity by reproducing in spring; the remainder being equally divided between those species which, despite the drougth stress, either undertook most or the whole cycle in the summer or spent the summer developing their fruits, in spite of flowering and fruiting in spring and autumn. Most species flowered in spring rather than in autumn, while the number of species bearing ripe fruits is uniformly distributed throughout the seasons. New Mediterranean species reproduced in spring and/or summer with a cycle no longer than 24 weeks. Tropical remnants reproduced throughout the year and had cycles of different lengths. The overall view of phenology, reproductive characteristics and origin of the Mediterranean shrubs is discussed and three groups of species linked by one evolutionary trend are identified.

Introduction

Mediterranean ecosystems are characterized by seasonal changes in temperature and light, and by annual fluctuations of soil water content and mineral nutrients which are considered limiting factors in these enviromnents (ASCHMANN, 1973; MILLER, 1981).

In all mediterranean environments the two adaptive strategies reported to allow species to survive the summer drought are avoidance or tolerance (MONTENEGRO & al., 1979; ARIANOUTSOU-FARAGGITAKI & DIAMANTOPOULOUS, 1985; MONTENEGRO, 1987; ORSHAN & al., 1988; DE LILLIS & FONTANELLA, 1992). The occurrence in Mediterranean shrublands of species apparently not affected by aridity has been interpreted as a specific kind of drought tolerance (DE LILLIS & FONTANELLA, 1992). spring flowering and autumn fruiting have also been reported as adaptations of plants to interactions with animals, specifically for pollination and seed dispersal respectively in the two seasons (HERRERA, 1986; IZHAKY & SAFRIEL, 1985).

The present work aims to investigate the reproductive phenology of the woody perennials of a Mediterranean shrubland in Southern Italy, in relation to the Mediterranean climate and evolutionary origin of its flora.

Study area

Geology.- Most of the field observations were conducted at the Nature Reserve of Castelvolturno on the Tyrrhenic coast, north of the Bay of Naples, Southern Italy, during the period 1990-1995. This study area is on a coastal plain of alluvial origin lying in a tectonic depression generated during Plio-Quaternary times and related to the opening of the Tyrrhenian Sea.

Since historical time the widespread mosaic of environments typical of the region around Naples has been superimposed by extreme anthropogenic disturbance. The main human activities have been, and still are, intensive urban development and fire.

Vegetation.- The pioneer successions on the primary dunes have almost completely disappeared because of tourism. The inner lands were completely reclaimed in the 50's and are now drained and mostly cultivated. The central strip, which is on a stabilized dune system, is characterized by a mosaic of sclerophyllous vegetation, with restricted relict areas of *Quercus ilex* L. forest. Within the macchia there are patches of vegetation, 0.5-1.5 m in height, dominated either by *Cistus salvifolius* L. or by *Pistacia lentiscus* L. and *Myrtus communis* L., *Rosmarinus officinalis* L., *Juniperus oxycedrus* L. var. *macrocarpa* and *Daphne sericea* Vahl. These are thoroughly mixed with patches of vegetation 1.5-3.0 m in height and dominated by *Quercus ilex* L., *Phillyrea latifolia* L., *Rhamnus alaternus* L., *Arbutus unedo* L. (BUONANNO & al., 1993).

Climate.- The climate of the coastal part of Campania is typically Mediterranean (DAGET, 1977; NAHAL, 1981) with precipitation concentrated in autumn and winter and a dry summer. The dominant winds blow from the south-west, which is also the souce of other meteorological events. Referring to the climatic data of the period 1974-1983, mean rainfall is 761 mm per year with maximum precipitation in October (117 mm) and December (118 mm) and minimum in July (3 mm). Mean monthly temperature is highest in July-August (21oC) and lowest in January (7oC). Following the method of BAGNOULS & GAUSSEN (1957), the summer aridity period lasts from the middle of May to the end of August. According to the climate of the area, we defined the seasons as follows: spring (10 weeks) from the begining of March to mid-May; summer (14 weeks) from mid-May to end of August, in accord with the aridity period; autumn (14 weeks) from the begining of September to mid-December; winter (14 weeks) from mid-December to end of February. Further references to season refer specifically to these time periods.

Materials and methods

During the period 1990-1995, the reproductive phenology of 21 woody perennial species co-occurring at Castelvolturno was bi-weekly recorded, checking for the following stages: a) flowering, b) fruit development, c) ripe fruit. Each stage was considered to have started when it was present on more than 50% of the plants and to have ended when present on less than 50% of the plants.

Species were categorized "old" or "new" taxa on the basis of whether, or not, following RAVEN (1971), RAVEN & AXELROD (1974), PONS (1981) and SUC (1984), they could be regarded as surviving descendents of once widespread vegetation developed at the edges of the tropics during the Tertiary and from which similar species differentiated into the semi-arid areas of California and the Mediterranean.

Statistical analysis was done on some characters of the woody perennials of Castelvolturno, but, because of its complex phenology, *Ruscus aculeatus* L. was not included in the analysis.

Nomenclature follows PIGNATTI (1982).

Results

No single reproductive phenology was exhibited by the woody perennials of Castelvolturno. They also showed a large variety in length of the reproductive cycle (Fig. 1). More than one third of the species needed 9-16 weeks from the begining of flowering to the begining of fruiting and none of the species had a reproductive cycle shorter than this. About one fourth of the species needed 17-24 weeks for reproduction and the same proportion of species needed more than one year to produce fruit. Cycles of intermediate length were less frequent. When the origin of the species is considered, new Mediterranean ones had reproductive cycles no longer than 24 weeks, while tropical remnants were represented in all of the groups.

In Fig. 2, we compare the reproductive phenology of the 21 woody perennials of Castelvolturno. Each reproductive stage was well represented throughout the year.

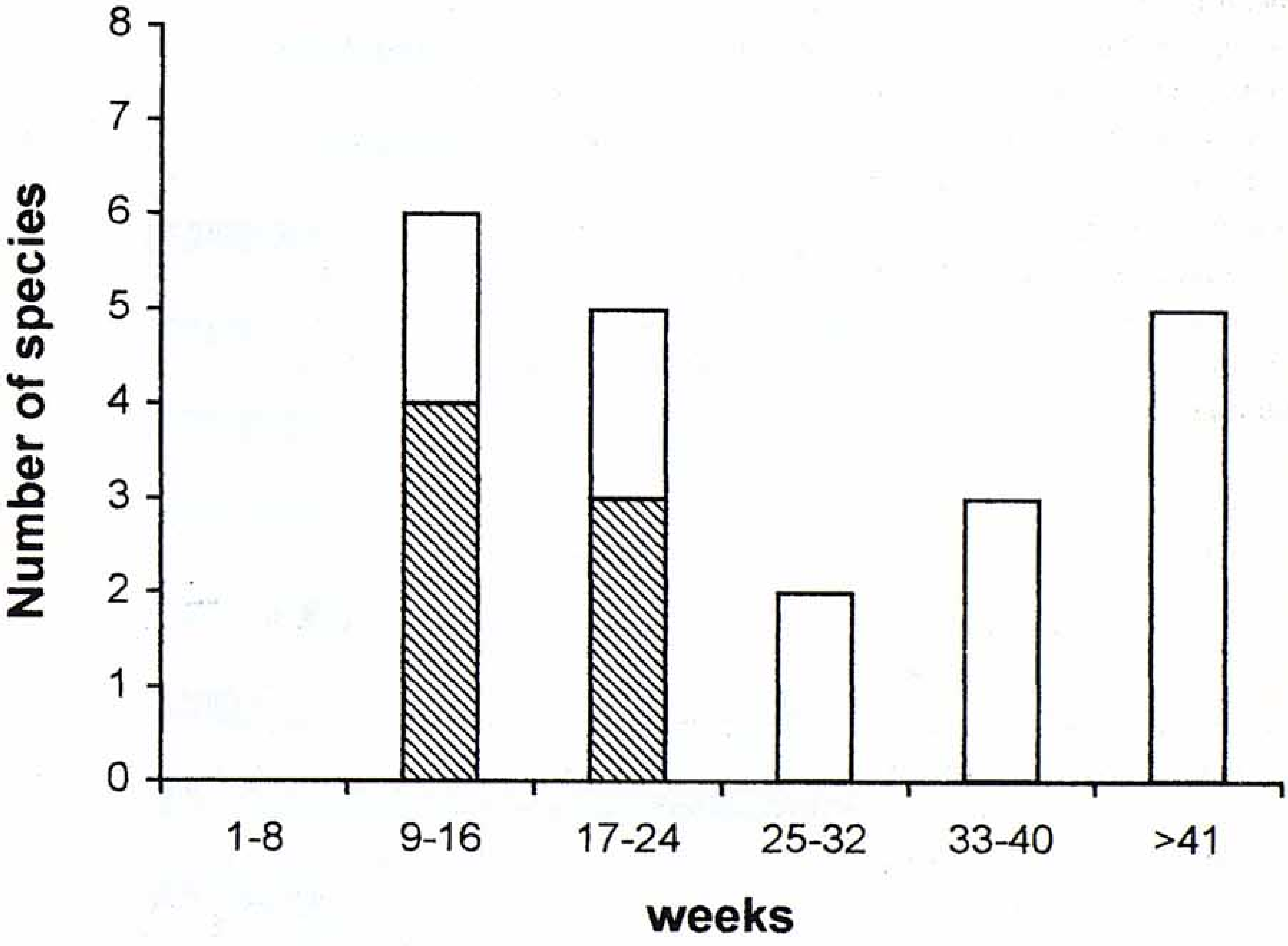
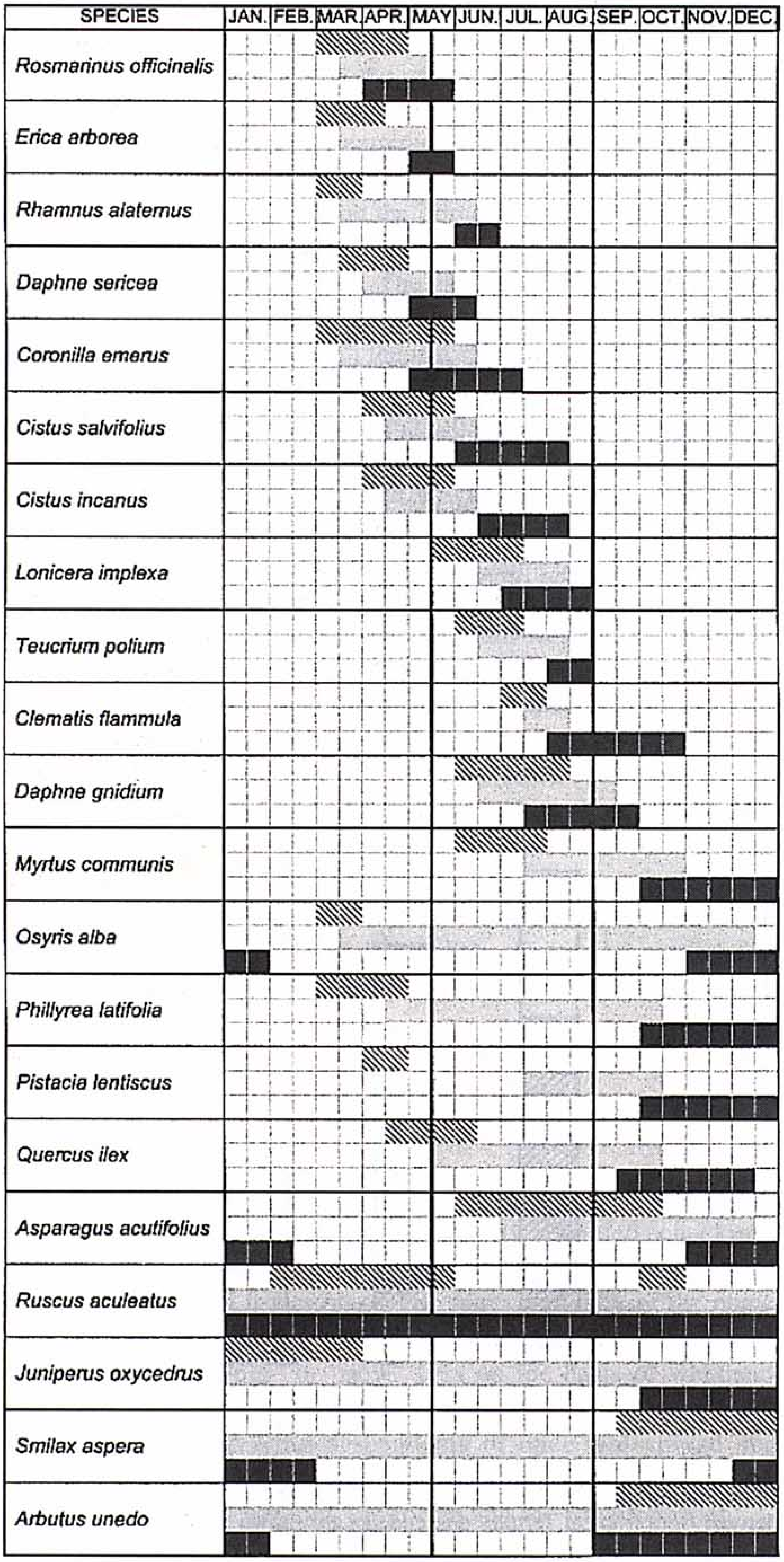


Fig. 1. Maturation time for 21 woody perennials of the macchia at Castelvolturno. The proportion of species derived from tropical Tertiary descendents are shown in white and those newly evolved in the Mediterranean are shown hatched respectively.


SPECIES
JAN.
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.
Rosmarinus officinalis
Erica arborea
Rhamnus alaternus
Daphne sericea
Coronilla emerus
Cistus salvifolius
Cistus incanus
Lonicera implexa
Teucrium polium
Clematis flammula
Daphne gnidium
Myrtus communis
Osyris alba
Phillyrea latifolia
Pistacia lentiscus
Quercus ilex
Asparagus acutifolius
Ruscus aculeatus
Juniperus oxycedrus
Smilax aspera
Arbutus unedo

However, no species started to flower or to fruit during the winter. *Rosmarinus officinalis, Erica arborea* L., *Daphne sericea* and *Coronilla emerus* L. reproduced in spring, starting seed dispersal before the onset of the summer drought. No species developed the whole of their reproductive cycle during the autumn and none during the winter, while *Lonicera implexa* Aiton, *Teucrium polium* L., *Clematis flammula* L. and *Daphne gnidium* L. reproduced during the summer aridity period. *Rhamnus alaternus, Cistus salvifolius* and *Cistus incanus* L. flowered in spring and fruited in summer. Reproduction started in summer and finished in autumn for both *Myrtus communis* and *Asparagus acutifoliu. Osyris alba* L., *Phillyrea latifolia*, *Pistacia lentiscus* and *Quercus ilex* flowered in spring, spent the all summer developing fruits which reach maturity in autumn. Although a similar phenology occurs in *Pistacia lentiscus*, at the end of the anthesis female flowers spend 2-3 months in a latent-ovary stage, fruit development not starting until the end of the summer. *Ruscus aculeatus* flowered twice in the same year while both developing and ripe fruits were always present in the population. In *Juniperus oxycedrus, Smilax aspera* L. and *Arbutus unedo,* more than 12 months were necessary for the production of ripe fruits from flowering. In summary, fewer than one fifth of the species avoided the summer aridity by reproducing in spring; two fifths of the species, despite the drought stress, undertook most or the whole of their cycle in the summer and two fifths, although flowering and fruiting in spring or autumn, spent the aridity period developing their fruits.

Statistical analyses were done on some characters of the woody perennial of the macchia at Castelvolturno. In Table 1 a significant association between season and the number of flowering species is shown. A larger proportion of species flowered in spring than in autumn while there is no deviation from expectation in summer. A similar analysis (Table 2), showed that fruiting was independent of season. This leads to the conclusion that, in the woody perennials of Castelvolturno, while species flower predominantly in spring, the number of species with ripe fruits is uniformly distributed throughout the seasons. However, when the kind of fruit (dry or fleshy) was considered, a significant association was found (Table 3). A larger proportion of dry fruited species ripen fruits in spring and summer rather than in autumn, while the opposite occurred for fleshy fruited species which tended to ripen their fruits more in autumn than in spring and summer.

Discussion

The coincidence of highest temperature and minimum rainfall during summer has been considered a limiting factor for the survival of mediterranean species and several mechanisms of avoidance or tolerance of this stress have been identified (MONTENEGRO & al., 1979; MONTENEGRO, 1987; ORSHAN & al., 1988; DE LILLIS & FONTANELLA,

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Fig. 2. Reproductive phenology of 21 woody perennial species co-occurring in the shrubland of Castelvolturno (Southern Italy). Flowering period (dashed bars), period of fruit developement (grey bars) and period of ripe fruit (black bars).

	Spring		Summer		Autumn	
	obs.	exp.	obs.	exp.	obs	exp
Number of flowering species	12	5.2	6	7.4	2	7.4

n = 20; chi squared = 13.05; $p < 0.01$.

Table 1. Relationship between season and number of flowering species. Number of species in each category are reported (obs.), with expected numbers adjusted for lenght of season based on a null hypothesis of no association (exp.).

	Spring		Summer		Autumn	
	obs.	exp.	obs.	exp.	obs	exp
Number of fruiting species	4	5.2	7	7.4	9	7.4

n = 20; chi squared = 0.65; not significant.

Table 2. Relationship between season and number of fruiting species. Number of species in each category are reported (obs.), with expected numbers adjusted for lenght of season based on a null hypothesis of no association (exp.)

	Spring		Summer		Autumn	
	obs.	exp.	obs.	exp.	obs	exp
Dry	3	1.6	4	2.8	1	3.6
Fleshy	1	2.4	3	4.2	8	5.4

3x2 contingency table; n = 20; chi squared = 6.03; $p < 0.05$.

Table 3. Relationship between season and kind of fruit. Number of species in each category are reported (obs.), with expected numbers based on a null hypothesis of no association (exp.)

1992; NEEMAN, 1993). However, the presence of many species which did not stop to grow and/or to reproduce during summer has been reported from several shrublands of the Mediterranean region (ARIANOUTSOU-FARAGGITAKI & DIAMANTOPOULOUS, 1985; HERRERA, 1986; DE LILLIS & FONTANELLA, 1992). In the macchia vegetation of Southern Italy, the great majority of the species spent the summer reproducing.

Moreover, many of them developed new shoots at the same time as fruit development (ARONNE, 1994). This suggests that functional adaptations to the uptake and allocation of nutrients to different plant organs might occur in these species, in contrast to the well known strategy adopted by "typical" mediterranean species which confine growth and reproductive events to the spring season, before water deficit could limit photosyntesis and respiration (OECHEL & al., 1981).

The spring flowering of most of the species at Castelvolturno is in agreement with that found in other sites characterized by a mediterranean climate (HERRERA, 1986; DE LILLIS & FONTANELLA, 1992) and has often considered as an evolutionary response to the high activity of the insects which effect pollination. Nevertheless this happens also in wind pollinated species, such as *Phillyrea latifolia, Pistacia lentiscus, Quercus ilex* and *Juniperus oxycedrus*, which exhibit a growing and reproductive stasis in winter but are apparently little or not affected by the "unfavourable" conditions of the summer. This, together with the many summer-flowering species compared with the few autumn-flowering ones, suggest that selection for winter avoidance might have occurred in many shrubs of the Mediterranan region. The presence of two unfavourable periods for Mediterranean plants has been reported by MITRAKOS (1980), who suggested that a drought stress during the summer and a cold stress during the winter are responsible for the spread of the evergreen sclerophyllous shrubs into the Mediterranean environments.

The strong association found in Southern Italy between dry fruit and fruit maturation in spring or summer, in contrast with that of fleshy fruits and autumn maturation, is consistent with that reported in other Mediterranean shrublands and has been interpreted as an adaptation to different mechanisms of seed dispersal (HERRERA, 1986; IZHAKI, & SAFRIEL, 1985; DE LILLIS & FONTANELLA, 1992). However, although most of the species flowered in spring, the distribution of ripe fruits was uniform throughout the year, because of the variety in length of fruit maturation.

We showed that species fruiting in spring or summer are generally characterized by a short reproductive cycle. Moreover, they have hermaphrodite, insect pollinated flowers and dry, many-seeded fruits dispersed by insects or abiotic vectors. In contrast, species fruiting in autumn-winter have a long reproductive cycle, are generally dioecious, insect or wind pollinated and have fleshy, few-seeded fruits that are bird dispersed. (ARONNE & WILCOCK, 1994 a). It is relevant that the second group is represented only by species which are remnant from the tropical period while the first group is represented both by tropical remnants and by more recently, mediterranean species (RAVEN, 1971; RAVEN & AXELROD, 1974; PONS, 1981; SUC, 1984). A long reproductive cycle, with lack of synchrony between flowering and fruiting periods is characteristic of tropical species (SWAINE & HALL, 1988), while a short seasonal reproduction is characteristic of "r" strategy species which are charcteristic of pioneer habitat and have short life span (RICHARDS, 1986). The overal view of phenology and reproductive characteristics of the Mediterranean shrubs leads to the identification of three groups of species. A group of tropical remnants with a drought and cold tolerance strategy continuously reproducing because of the overlapping of very long reproductive cycles; a second group of tropical remnants with drought tolerance and cold avoidance strategy which have reduced the reproductive cycle to slightly less than one year and a third group of more recent mediterranean species with short reproductive cycles which allows a drought and cold avoidance strategy. Going from the first to the third group an adaptive trend seems evident and a further extension of this trend might be represented by the annuals which have a restricted life cycle of a few months, avoiding the less favourable seasons of the year. In this frame the case of *Rhamnus alaternus* (ARONNE & WILCOCK, 1994 b, 1995) is relevant because, although it is a descendant of the tropical vegetation of the region, and is dioecious and fleshy fruited, it has a short fruit maturation period and a specific adaptation to ant dispersal which suggest the species is under selective pressure to switch from a "tropical" to a more "mediterranean" reproductive strategy.

Acknowledgements

This work began with the financial support of an Italian 40% MURST grant and concluded with that by the European Commission (DG XII/D2), MODMED Project, Contract n. EV5V-CT94-0489.

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