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Dynamics of cohorts of cladodes and related effects on reproduction in the shrub *Retama sphaerocarpa* in semi-arid south-eastern Spain

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Abstract

Changes in the size and age structure of the canopy of the leguminous shrub *Retama sphaerocarpa* in semi-arid south-eastern Spain were investigated by monitoring growth and survivorship of cladodes (photosynthetic stems) on marked shoots over a period of 26 months. Three basic morphological types of cladodes – long shoots, short shoots, and secondary short shoots – were distinguished.

The canopy of the shrubs contained three annual cohorts of cladodes in spring and summer. The number and size of shoots produced each year was highly variable and was apparently related to the amount of rainfall during the preceding cool season. The spring cohort of 1994 produced only 37% of cladodes compared with 1993. Two cohorts of shoots were actually initiated in spring and late summer of each year, but the second cohort produced only 2–12% of the number of cladodes compared with the spring cohort. The proportions of the different cohorts in the canopy changed rapidly from April to August, but only slowly during the remainder of the year when only two annual cohorts remained after extensive litterfall in late summer. This late summer litterfall caused a substantial reduction in green canopy area (40–50%) which was achieved mainly be shedding of one year old cladodes. The life expectancy of cladodes decreased with increasing order of their morphological type from 850 ± 25 days in long shoots to 563 ± 4 days and 546 ± 9 days in short shoots and second order short shoots, respectively.

Flowering and fruiting took place from May to July, almost exclusively on one year old cladodes, and coincided with the maximum development of the canopy. Flowering intensity was high in 1994, when individual shoots supported a mean number of approximately 150 flowers. Shoots produced an average of 12.6 ± 0.6 and 5.3 ± 1.0 fruits per shoot in 1993 and 1994, respectively. Most of the annual fruit crop (80–90%) was shed during litterfall in late summer. A proportion of 10–20% was retained in the canopy for up to 12 months, however, with some fruits persisting for more than 22 months.

Introduction

Dry Mediterranean climates are strongly periodic with variable amounts of rainfall, mainly from autumn to spring, and an extended dry season with high temperatures and low absolute humidities in the summer. Biological activity in many plants is thus limited to comparatively short periods of the year (Mooney et al. 1974). Although growing and resting seasons are usually predictable, year-to-year differences in climate can lead to large variation in the timing and amount of new growth and leaf abscission, and hence, both in the size and age structure of plant canopies which strongly affects their current assimilation, biomass production and water use. In dryland ecosystems, this variation in plant productivity is determined mainly by the total amount and seasonal distribution of rainfall (e.g., Le Houérou 1984). A rise in mean temperature of 3.0 ± 1.5 °C predicted for the Mediterranean Region as a result of rising carbon dioxide levels (e.g., Le

Houérou 1990) will be associated with higher potential evapotranspiration and more erratic rainfall. These climatic changes are likely to produce environmental conditions which are more arid and more variable in time than those prevailing at present and will thus cause considerable reductions in plant productivity and vegetative cover and, ultimately, in landscape stability.

A common feature of many shrubs of arid and dry Mediterranean climate ecosystems is the utilisation of current season, and often also older stems, as primary organs for photosynthetic assimilation (e.g., Adams & Strain 1968, 1969; Comstock & Ehleringer 1988; Comstock et al. 1988; Bossard & Rejmanek 1992). While most of these shrubs also produce leaves, some species rely almost exclusively on stem photosynthesis for carbon gain (Comstock et al. 1988). The annual turnover of the photosynthetically active organs – leaves and/or stems – is often strictly seasonal with predictable effects on canopy area and architecture, while between-year variation in the amount of reproductive versus vegetative structures may impose further, longer term variation (Comstock et al. 1988). When the life span of leaves or stems exceeds one year, the shrubs' canopies contain more than one annual cohort of photosynthetic organs, hence annual turnover of canopy area becomes less predictable. Furthermore, desert shrubs often produce more than one cohort of stems and/or leaves per year (e.g., Nilsen et al. 1987) and each of these cohorts may have different life expectancies and different physiological properties (Orshan 1954). Seasonal and between-year variations in canopy area impose equally large variations on gas exchange and water use of individual shrubs as well as whole shrublands (e.g., Haase et al. 1999a).

We report here the seasonal and year-to-year differences in the size and age structure of populations of photosynthetic stems (cladodes) in the canopy of the shrub *Retama sphaerocarpa* (L.) Boiss.. The aim of this research was to collect field data on phenology and productivity, relate these to climatic variables, and to estimate the proportions of different cohorts of cladodes and their seasonal changes in the canopy. Monitoring of reproduction was included since flowering and fruit development affect the shrubs' morphology and can potentially divert resources from vegetative growth. Information on the responses in phenology and productivity of the shrubs to variations in present climate can be used to assess potential effects of changing regional climatic conditions on the shrublands.

Table 1. Rainfall (mm) at the Rambla Honda field site for the 12-month period (October–September), and winter (October–March), spring (April–June), and summer (July–September) from 1991/92 to March 1995.

Year	Annual	Seasonal		
	Oct.–Sept.	Oct.–March	April–June	July–Sept.
1991/92	288	205	83	0
1992/93	294	247	46	1
1993/94	137	99	23	15
1994/95		176		

Methods

Field site

The research was carried out from April 1993 to May 1995 at a field site in the Rambla Honda, a dry valley on the southern slope of the Sierra de los Filabres, ca. 40 km north of Almería, Andalucía, Spain (37°08′ N, 2°22′ W, 630 m a.s.l.). Climatic data at the field site have been recorded with an automatic weather station since 1990 (Puigdefábregas et al. 1996). The regional climate is semi-arid; the 5-year record 1990–94 gives a mean annual temperature of 15.7 °C (January 7.5 °C, August 25.4 °C) and mean annual rainfall of 259 mm (R. Lázaro, unpublished data). There is a pronounced dry season from May to September, often with almost no rainfall from June to August. In 1993, the spring rains ceased in early May and the almost rainless dry season lasted until mid-October. Less than 50% of the average rainfall were received during the following cool season and practically no rain fell from mid-April to late September 1994 (Table 1). Longer-term (1965–91) climatic records for Tabernas (490 m; 17.9 °C, 218 mm), 10 km to the south of the field site, indicate high between-year variation both in the pattern and total amounts of rainfall (Lázaro & Rey 1991) and show that prolonged periods with low rainfall are not unusual in this semi-arid region.

The local bedrock is mica-schist with some quartzite beds and supports a thin regolith soil (Puigdefábregas et al. 1996). There are extensive alluvial fan systems and colluvial deposits at the base of the mountain slopes. The valley bottom is filled with thick, poorly sorted fluvial sediments consisting of sands and gravels.

Except for high elevation pine forests, the regional climate only supports semi-arid vegetation types, consisting of scattered shrublands, but at the drier end of the rainfall gradient perennial tussock grasses become the dominant species and may form extensive grasslands (Freitag 1971; Puigdefábregas et al. 1996). In Rambla Honda, three distinct semi-natural vegetation types can be distinguished along a hill slope – valley bottom catena. *Stipa tenacissima* L. tussock grassland covers the rocky slopes up to the ridgetops at 800–1000 m; summer-deciduous *Anthyllis cytisoides* L. shrubland occupies the alluvial fans at the foot of the mountain slopes, and evergreen shrubland of *Retama sphaerocarpa* covers the valley bottom.

Natural history of Retama sphaerocarpa

Retama sphaerocarpa is a leafless shrub with photosynthetic stems that occurs in the Mediterranean part of northern Africa and the southern Iberian Peninsula. It is particularly common along drainage lines over alluvial sediments, where it can form open shrublands. In spring, the shrubs produce simple sessile lanceolate leaves, only 5 × 1 mm in size, at each node of the extending new long shoots (Haase et al. 1999a). The leaves only persist for 3–4 weeks until their axillary cladode has completed extension growth and the shrubs are therefore essentially leafless. *Retama sphaerocarpa* possesses a deep root system which may penetrate to depths of 25 m and more, giving it access to phreatic water or moist soil layers (Haase et al. 1996a) and it is able to maintain comparatively high xylem water potentials throughout the year (Lansac et al. 1994; Haase et al. 1999a). The shrubs are focal points or 'islands' of biomass production and plant (biological) diversity in this otherwise sparsely vegetated ecosystem by facilitating establishment and growth of other perennial and in particular, annual plants (Haase et al. 1996b; Pugnaire et al. 1996a,b; Moro et al. 1997a, b). The cladodes contain alkaloids (Martín-Cordero et al. 1993) which make them unpalatable to livestock, but rabbits (*Oryctolagus cuniculus* L.), which use the shrubs for shelter, may browse heavily on young shoots affecting the shrubs morphology (Gómez Sal et al. 1999) and also feed on the fruits thereby dispersing the seeds (Cerván & Pardo 1997). Possessing typical fabaceous flowers, *R. sphaerocarpa* is pollinated by winged insects, but Gómez et al. (1996) also described ants as important pollinators.

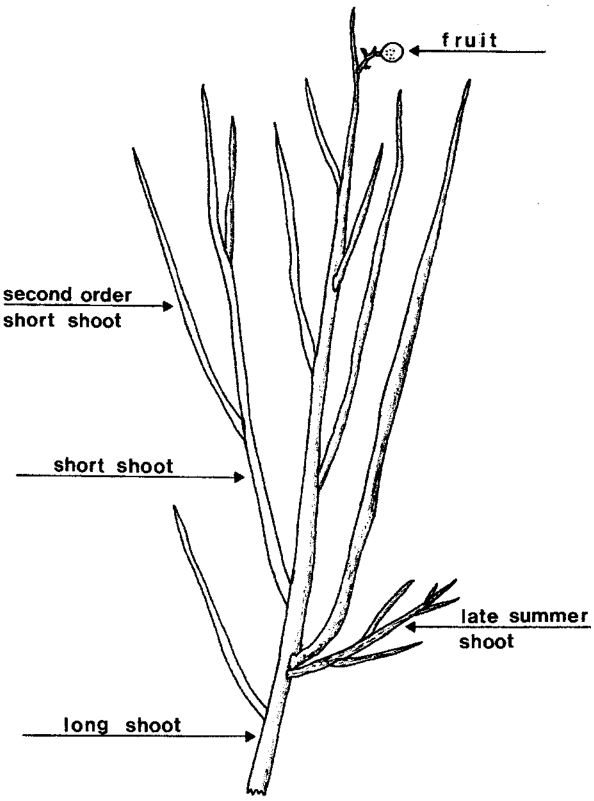

Figure 1. Sketch of a shoot of *Retama sphaerocarpa* with the three types of modules recognised. Depicted is a shoot of the spring cohort of the previous season in late summer to early autumn of its second (reproductive) season. It also supports a developing shoot of the late summer cohort.

Monitoring of phenology

Following the modular concept of shrub architecture (Ginocchio & Montenegro 1992), the evergreen stems (cladodes) of *R. sphaerocarpa* were divided into three types of basic morphological units or 'modules' (Figure 1). *Long shoots* arise from overwintering buds on one and two year old and occasionally older shoots and have the potential to develop into woody branches. *Short shoots* arise from axillary buds of the current season's long shoots. These short shoots, which are normally temporary, make up the largest part of the green canopy area. The short shoots may support *second-order short shoots.* The term 'shoot', if used without further qualification in the following, refers to a long shoot complete with all short shoots, while 'cladodes' or 'modules' are single stems of any branching order.

In April 1993, 10 shrubs were selected for continuous monitoring along a 70 m long E–W transect, traversing the dry floodplain of Rambla Honda. On each shrub, 10 long shoots dating from the previous season (i.e., 1992) were randomly selected around the outer canopy and marked with a short section of coloured drinking straw. The length of these long shoots, and of all the short shoots they were supporting, was measured and the condition of each cladode was described as green, yellow, or dry. The shoots were inspected every 1–2 weeks during spring and summer and at approximately monthly intervals in autumn and winter and all photosynthetically non-functional cladodes were recorded as yellow, dry, or shed. The current length of new long shoots which were produced during 1993 and 1994 on the marked shoots was measured weekly to bi-weekly and a complete inventory of new cladodes was made after extension growth had ceased in early summer. Only two field visits were made in the spring of 1995. Emergence of new shoots from the buds was noted as the 'birth' date of the long shoot. Observation of subsequent production of short shoots had indicated a time span of approximately two days between the emergence of successive short shoots on the long shoot. This interval was used to estimate birth dates for individual short shoots as a function of their nodal position. A mean date of birth was estimated for all long shoots of the 1992 cohort. After a particular module had become non-functional, its date of death was taken to be the mid-point between the two last observations and its life span was estimated. The number of shed modules recorded at each observation was used to calculate the seasonal distribution of litterfall.

The proportions of the different cohorts of cladodes in the canopy were calculated for each observation from April 1993 to May 1995. Although only a small subsample of the total canopy of the 10 shrubs was monitored, the observed seasonal changes in the proportions of the different cohorts of cladodes were assumed to be representative for the total canopy (cf., Comstock et al. 1988; Haase et al. 1999a).

Because of their large numbers, floral buds and flowers were counted on randomly selected subsamples of the marked shoots or modules. The fruits on all marked shoots were counted at the observation dates between July 1993 and May 1995 and total numbers of fruits remaining in the canopy of the monitored shrubs were counted in mid-May 1994.

Results

Shoot production and extension growth

After bud-break in spring, three cohorts of cladodes, dating from the current year and the two previous years, were present in the canopy of *R. sphaerocarpa* from spring to mid-summer, while only two cohorts remained after extensive litterfall in late summer. Approximately one third (37% and 34% in 1994 and 1995, respectively) of the new shoots of the spring cohort were produced on one year old shoots, while the majority of the new growth originated from buds of two year old shoots (63% and 59% in 1994 and 1995, respectively) and a smaller proportion developed on three year old shoots (no data for 1994, 7% in 1995). Shoot growth from dormant buds of still older shoots also occurred, but was not quantitatively estimated because the method of observation was based on the selected shoots of the 1992 cohort and did not consider complete branches including older woody parts.

Shoot extension growth began in early April in 1993 and in mid-March in 1994 and lasted for ca. three months (Figures 2 and 3). Maximum rates of shoot extension growth of 4–6 mm d^{-1} were determined in May to early June 1993 but then declined rapidly. In a few shoots, extension growth continued at a low rate until July. Occasional new short shoots or secondary short shoots, and sometimes also new long shoots were initiated late in the dry season. This second annual cohort attained maximum rates of extension of 2–3.5 mm d^{-1} in mid-September 1993 and continued to grow until mid-October. The same maximum rates of shoot extension (2–3.5 mm d^{-1}) were determined for the new spring cohort in mid-April to mid-May 1994, which was significantly lower ($P < 0.001$; *t*-test) compared to the spring growth of 1993.

The cohort of 1992 (as at April 1993) and the spring cohorts of 1993 and 1995 all produced similar numbers of cladodes on the 100 monitored shoots (Table 2). In 1994, however, new spring growth was much lower and only 37% of cladodes, compared with the previous season, were produced. In 1994, the mean length of all three types of modules was also significantly less than in any of the three other years ($P < 0.05$; except second-order short shoots in 1993; Table 2). Although shoot extension of the 1995 cohort of cladodes was still not completed when measured in mid-May, the mean length of cladodes was significantly larger than in any of the previous seasons ($P < 0.05$; except long shoots in 1992; Table 2). The

Table 2. Number (*n*) and mean length (± SE) of modules produced by 100 long shoots of *Retama sphaerocarpa* (L.) Boiss. from 1992 to 1995. Different superscript numerals indicate significant differences between years ($P < 0.05$; pairwise *t*-test).

Type of module	*n*	Length / mm
Spring growth		
Long shoot		
1992	100	319.6 ± 9.7^1
1993	219	211.5 ± 8.2^2
1994	127	145.6 ± 8.2^3
1995	180	247.4 ± 10.4^4
Short shoot		
1992	1078	148.2 ± 2.1^1
1993	1094	143.3 ± 2.0^1
1994	362	117.5 ± 3.7^2
1995	1097	164.3 ± 2.3^3
2nd-order short shoot		
1992	224	91.2 ± 3.5^1
1993	152	$87.7 \pm 3.4^{1,2}$
1994	47	73.7 ± 7.7^2
1995	156	104.7 ± 3.6^3
All modules		
1992	1402	151.3 ± 2.3^1
1993	1465	147.7 ± 2.1^1
1994	536	120.3 ± 3.3^2
1995	1433	168.3 ± 2.4^3
Late summer growth		
All modules		
1993	31	78.5 ± 7.6^1
1994	64	118.8 ± 9.7^2

late summer cohorts of 1993 and 1994 produced approximately 2% and 12%, respectively, of the number of cladodes compared with their corresponding spring cohorts (Table 2).

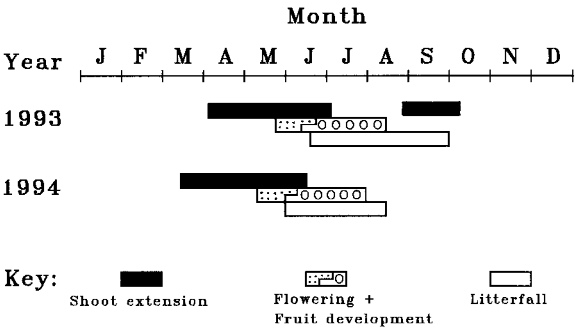

Figure 2. Phenogram for *Retama sphaerocarpa* shrubs at the Rambla Honda field site in 1993 and 1994 (data for late summer growth in 1994 are not available).

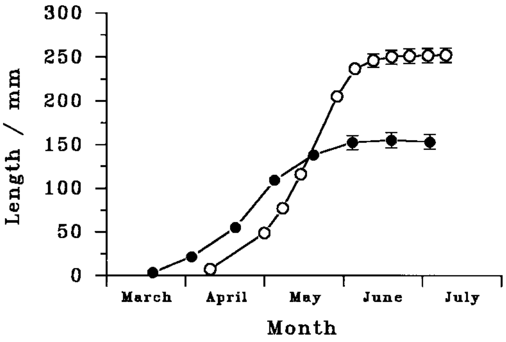

Figure 3. Extension growth of long shoots in *Retama sphaerocarpa* shrubs in 1993 and 1994 (mean ± SE; ○, 1993 cohort, $n = 208$; ●, 1994 cohort, $n = 126$).

Flowering

In the spring of their second growing season, all types of modules produced racemes of small, yellow flowers. Flowering started in late May 1993 and early to mid-May 1994 and lasted for four weeks (Figure 2). In June 1993, a random sample of one year old shoots ($n = 56$) from two shrubs, selected visually for 'medium' and 'high' flowering intensity, yielded 51 ± 9 and 149 ± 23 individual flowers per shoot, respectively. In mid-May 1994, all 10 monitored shrubs were considered in a stratified sampling method. One year old shoots had produced inflorescences on 19.7 ± 1.7 nodes per shoot ($n = 179$), each node ($n = 135$) supporting 7.6 ± 0.6 single flowers, which yielded an average of 149 flowers per shoot, a number corresponding to the 'high' flowering intensity of 1993. Most racemes were produced on the distal parts of long shoots where the nodes had not produced vegetative short shoots. These racemes were larger and more likely to produce fruits than racemes produced on short shoots.

Fruit production and shedding

The fruits, which are mostly one-seeded pods, developed during June and July (Figure 2). Although one node can produce up to three racemes with 10–30 flowers each, fruiting was mostly limited to one fruit per raceme. The other flowers were infertile or the fruits aborted or were damaged by predators during development. One of the 10 shrubs monitored did not produce any fruits in 1993. In the remain-

Table 3. Number of fruits (produced in 1993) remaining on 10 *Retama sphaerocarpa* shrubs in mid-May 1994, mean proportion of fruits remaining on 10 selected shoots of each shrub, and extrapolated initial number of fruits per shrub.

Shrub	Fruits *n*	Proportion %	Extrapolated *n*
1	0		0
2	10	11.8	85
3	189	10.0	1598
4	80	8.3	676
5	2061	4.4	17422
6	2725	13.1	23035
7	533	44.6	4505
8	327	6.0	2764
9	243	2.5	2054
10	1789	5.8	15123
Mean ± SE	796	11.8	6726
	317	4.3	2678

ing shrubs, the total number of fruits in the canopy was too large to be counted, but in mid-May 1994 between 10 and 2725 fruits remained on individual shrubs (Table 3). Extrapolations, based on the mean proportions of fruits retained on the 100 monitored shoots at this time, yielded estimates ranging from 0 to approximately 23 000 fruits per shrub (Table 3).

In mid-July 1993, an average of 12.6 ± 1.7 sound green fruits per shoot were counted on the monitored shoots. Almost 46% of these fruits were shed during extensive litterfall in August, and this was followed by a further rapid decline in fruit numbers until mid-October (Figure 4). A continuous slow decline in fruit numbers was observed during the remainder of the period of observation and only 0.8% of the fruits persisted on the shrubs in mid-May 1995. Shedding of fruits was correlated with the number of cladodes shed during the same period ($r = 0.90$, $P < 0.01$, $n = 23$ observations). While most of the dry fruits were shed individually, a proportion of the fruits (10–20%) dropped while still attached to their supporting cladodes. Not all fruiting cladodes became dry and not all cladodes were shed immediately after drying, however, and attached fruits were thus stored in the canopy for some time.

Although visual observations suggested that flowering intensity was higher in 1994 than in 1993, shoots of the 1993 cohort only supported an average of 5.3 ± 1.0 sound fruits per shoot in late June 1994 which is considerably less than in 1993. Fruits were shed rapidly during July–August 1994 (Figure 4).

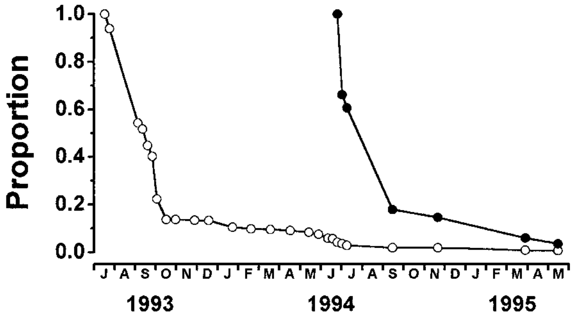

Figure 4. Proportion of fruits retained in the canopy of 10 *Retama sphaerocarpa* shrubs in 1993 and 1994 (○, 1993 fruits; ●, 1994 fruits).

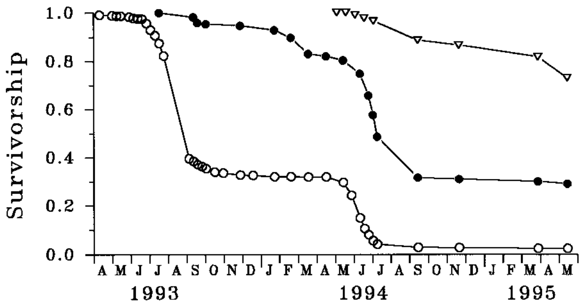

Figure 5. Survivorship of three cohorts of cladodes in *Retama sphaerocarpa* shrubs (○, 1992 cohort, ●, 1993 cohort, ▽ 1994 cohort; $n = 10$ shrubs).

Litterfall

Only 2% of the (one year old) cladodes of the 1992 cohort were shed between April and late June 1993 (Figure 5). Litterfall accelerated in early July and particularly in August and 49% of cladodes of the cohort had been shed by early September 1993 (Figure 5). Few cladodes were shed from mid-October 1993 to late May 1994, but after the subsequent period of summer litterfall in June–August 1994 only 5% of the cladodes of the 1992 cohort remained on the shrubs. About half of these remaining cladodes were already dry; the surviving cladodes were mostly long shoots which had developed into woody branches.

Litterfall of the newly produced 1993 cohort occurred at a low rate, but more or less continuously and without a defined late summer maximum (1.9%), from July 1993 to mid-May 1994 when 19% of the cohort had been shed (Figure 5). Litterfall accelerated in June and July 1994, i.e., earlier and with a more pronounced

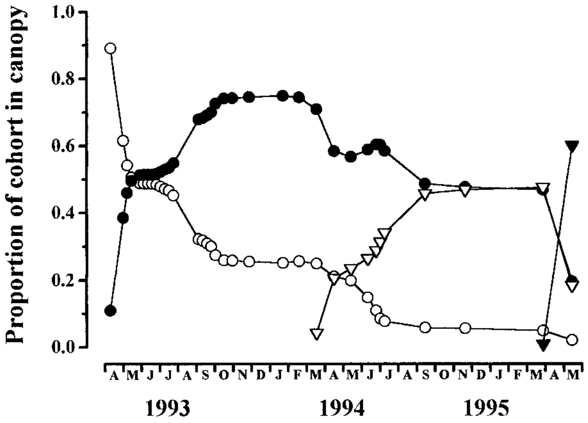

Figure 6. Change in the proportions of four cohorts of cladodes in the canopy of *Retama sphaerocarpa* shrubs from 1993 to 1995 (○, 1992 cohort; ●, 1993 cohort; ▽, 1994 cohort; ▼, 1995 cohort).

peak than in 1993, and 68% of the cohort had been shed by mid-September 1994.

The spring cohort of 1994 shed a higher proportion (12.8%) of its cladodes during the first (1994) summer litterfall (Figure 5). While litterfall in *R. sphaerocarpa* thus occurred throughout the year, its seasonal distribution showed a pronounced maximum in late summer. This summer litterfall mainly affected cladodes of the cohort which was produced during the spring of the preceding year.

Dry cladodes often persisted in the canopy for some time before being shed. The difference between the death (drying) of a cladode and its shedding varied depending on the type of module and decreased from 144 ± 21 days in long shoots ($n = 66$) to 22 ± 2 days in short shoots ($n = 1077$) and to 18 ± 5 days in second-order short shoots ($n = 224$) of the 1992 cohort. The difference between the two latter types of modules was not significant, however.

Cohort dynamics and life expectancy of cladodes

The proportions of cladodes of the different cohorts in the canopy changed rapidly during spring growth and also during litterfall in late summer, but there was little change during the cool season (Figure 6). In 1993 and 1995, the cladodes of the new spring cohort superseded the previous year's cohort in numbers before or during the period of summer litterfall (Figure 6). Because of the small spring cohort of 1994, however, cladodes of the 1993 cohort comprised the largest proportion in the canopy until the spring of 1995.

Table 4. Mean life expectancy in days (± SE) of modules produced by 100 long shoots of *Retama sphaerocarpa* (L.) Boiss. in 1992 and 1993. Data are underestimates because shedding was incomplete (97.5%, 70.3%, 90.4% for the 1992, 1993 spring, and 1993 late summer cohort, respectively).

Type of module	*n*	Longevity / d
Cohort of 1992		
All modules	1402	580 ± 5
Long shoots	100	850 ± 25
Short shoots	1078	563 ± 4
2nd-order	224	546 ± 9
Spring cohort of 1993		
All modules	1465	500 ± 5
Long shoots	219	514 ± 14
Short shoots	1094	501 ± 5
2nd-order	152	477 ± 13
Late summer cohort of 1993		
All modules	31	308 ± 25
Long shoots	3	
Short shoots	26	313 ± 23
2nd-order	2	

Only 35 of the 1402 modules of the 1992 cohort counted in April 1993 persisted on the shrubs alive in May 1995. Of these, 34 were long shoots, 27 of which had developed into woody branches and were unlikely to be shed, and one was a short shoot. The mean life span varied between the three types of modules (Table 4). While the small and statistically insignificant difference between the life spans of short shoots (563 ± 4 days) and secondary short shoots (546 ± 9 days) is accounted for by the slightly earlier birth of short shoots, the much longer life span of long shoots (850 ± 25 days) reflects the importance of these types of modules in canopy architecture.

Only 70.4% of the cladodes of the 1993 spring cohort, but 90.3% of the 1993 late summer cohort had been shed by May 1995 (Table 4). A comparison between the two 1993 cohorts shows, however, that the mean life span of their modules varied by 192 days. This significant difference ($P < 0.001$; *t*-test) is mostly accounted for by the later initiation of the late summer cohort by ca. 4 months. The cladodes of both 1993 cohorts were shed at the same time, mostly during the late summer litterfall of the following season, and the life expectancy of the late summer cohort is therefore considerably shorter.

Discussion

Phenological adaptation to variation in environmental conditions

As in many Mediterranean and arid-zone woody plants (e.g., Comstock et al. 1988; de Lillis & Fontanella 1992), the major flush of new shoot growth in *R. sphaerocarpa* shrubs was concentrated in a comparatively short period in spring. A secondary period of shoot production, although only observed on a much smaller scale and only in some shrubs, lasted from the end of the summer drought to early autumn. A similar pattern of shoot growth, with a major spring flush and an additional minor flush in late summer, has been described for North American arid-zone shrubs and trees (Nilsen et al. 1983; Comstock et al. 1988). The climatic conditions during or at the end of the summer drought appear to be important for the initiation of the usually minor, late summer flush of new shoot growth in *R. sphaerocarpa*. After substantial rainfall in June 1992 (77 mm), regrowth was noted on shrubs at the field site during July (L. Gutiérrez, pers. comm.). After 139 mm of rain fell from late September to early November 1994, when autumn temperatures were 1–2 °C above average, numerous new shoots were observed on many *R. sphaerocarpa* shrubs at the field site (P. Haase, pers. observation), but not on the 10 shrubs monitored for the research which had produced a small late summer cohort by mid-September.

The environmental conditions during the cool season are generally suitable for vegetative growth, as suggested by the sometimes substantial rates of leaf and shoot growth in other perennial plants at the field site, e.g., the tussock grass *Stipa tenacissima* and the drought-deciduous dwarf-shrub *Anthyllis cytisoides* (Puigdefábregas et al. 1996; Haase et al. 1999b). In *R. sphaerocarpa*, however, shoot growth of the spring cohort practically ceased in June, and fruit development was completed by late July to early August. While some of the carbon assimilated from August to February may be utilised for cambial growth, as in other, often deep-rooted evergreen shrubs in Mediterranean-climate regions (Mooney et al. 1977), we assume that *R. sphaerocarpa* shrubs also accumulate and store substantial amounts of carbohydrate in their large root systems (cf., Haase et al. 1999a) which can account for ca. 90% of their biomass (Puigdefábregas et al. 1996).

Many evergreen species of arid or Mediterranean-climate regions, which build up pools of carbohydrate during the winter (Mooney et al. 1974, 1977), remobilise these reserves during the period of spring flushing. Flowering occurs before, at the same time, or after the main period of growth of the new shoots in different evergreen species (Mooney et al. 1977). *Retama sphaerocarpa* is in the last category. Although the two phenological events – shoot growth and flowering – overlap in time (Figure 2), their peaks are staggered, i.e., allocation of carbohydrate to different sinks occurs at different times of the growing season. A further postponement of the usually abundant flowering into mid to late summer is possibly precluded by the seasonal availability of pollinators (e.g., Mooney & Kummerow 1981). Anecdotal evidence suggests that winged insects were most abundant at the field site from April to June, but were rare or absent during the dry season. On the other hand, Gómez et al. (1996), who reported 18 insect species from 12 different families as flower visitors on *R. sphaerocarpa*, found that 74% of all visitors were ants of the species *Camponotus foreli* Emery, which clearly acted as pollinators. A further, and probably more important advantage of this particular phenological timing is that the reproductive phenological phase of *R. sphaerocarpa* coincided with the period of maximum canopy development and long daylight hours which enabled potential maximum ‘light harvest’ by the shrubs. At least in wetter years, when soil moisture does not impose restrictions on transpiration and photosynthesis, carbon allocation from current assimilation to reproductive structures can thus be maximised.

In many evergreen woody plants of temperate regions, maxima of litterfall coincide with development of new foliage in late spring to early summer. Nutrients withdrawn from old leaves before shedding can thus be allocated to developing shoots. In *R. sphaerocarpa*, and also in other arid-zone shrubs and trees (Mooney et al. 1977), there is a delay between the maxima of shoot growth and shedding of old twigs or leaves. The reserves for the growth of the new spring cohort of cladodes may be made available or supplemented by the large carbohydrate pool in the root system of *R. sphaerocarpa* and to a lesser extent by translocation from older cladodes. However, resources appear to be translocated from older cladodes to developing fruits before the former are shed in the dry season. By thus extending the life span of the older photosynthetic organs, maximum canopy size can be maintained for approximately three months under maximum levels of irradiance and often adequate water supply in spring to early summer.

Our data suggest that cladodes of the small late summer cohort have a shorter life expectancy compared to the spring cohort of the same year. The summer litterfall of the following year did not discriminate between these two cohorts, then 12 and 15 months old, while the youngest cohort (then 3 months old), which was initiated in the current year, only shed very few cladodes at the same time. Investment of structural carbohydrate into the spring cohort of cladodes therefore yields a larger return than into an equally large late summer cohort.

Bud break, shoot extension, and flowering and fruiting occurred approximately three weeks earlier in 1994 than in 1993, because of higher late winter and spring temperatures. Besides the different phenological timing, there was also high between-year variation in the amount of both vegetative and reproductive growth of *R. sphaerocarpa*. Although the lower vegetative growth in 1994 (37% of 1993) was probably related to the equally low winter rainfall (40% of 1992/93), it could also, or additionally, be due to morphological constraints ensuing from the higher flower density of the 1993 spring cohort in 1994. A single node can either produce a shoot or a flower raceme in any one year and in 1994 flowers were more numerous than in 1993. In woody plants, resting buds containing vegetative or reproductive primordia are usually initiated during the growing season preceding the extension growth of the bud and current climatic conditions often act as cues to switch between vegetative and reproductive development (e.g., Jackson & Sweet 1972). Reproductive modules have a determinate life span, however, and thus also impose restrictions on subsequent growth of structures. With the comparatively small number of shoots produced in 1994, it had been assumed that both vegetative and reproductive growth would be negatively affected in 1995. This applied only to reproductive growth, however, because the vegetative shoots were produced mainly on twigs older than one year.

Drought stress and reduction of canopy area

Although *Retama* shrubland is most commonly associated with drainage lines and fluvial deposits, *R. sphaerocarpa* is not a typical phreatophyte because it also grows in a range of other habitats including on non-calcareous bedrock with thin soil profiles (Freitag 1971). In the Rambla Honda, even the particularly deep root system does not assure access to a free water table (Haase et al. 1996a, 1999a). Shrubs tap the water resources of deep-seated moist soil layers which only yield a limited rate of supply, insufficient to maintain high stomatal conductances at high temperatures, vapour pressure deficits and irradiances, so that some degree of drought stress developes in the course of the day (Haase et al. 1999a). After a winter with low rainfall in 1993/94, cladode water potentials and rates of assimilation of the shrubs at the field site were greatly reduced in the summer of 1994 (Haase et al. 1999a).

The architecture and morphology of the canopy of *R. sphaerocarpa* shows adaptations for water conservation, e.g. extreme reduction of leaf area through production of very small leaves, which are only present for a brief period in spring, and photosynthetic stems which are oriented vertically thereby minimising light interception and conductive overheating. Nevertheless, a substantial reduction in transpiring canopy area (40–50%) occurred in the shrubs at the field site during the hottest part of the summer which was achieved mainly by shedding of one year old cladodes some of which supported ripe and dry pods at this time. Therefore, the shedding of dead fruiting cladodes also serves to disperse the fruits which are deposited on the ground before the autumn rain season. These rains often cause local flooding in *R. sphaerocarpa* shrublands on alluvial sites which can lead to long distance dispersal of fruits and seeds by running water. Although shedding of ripe fruits was correlated with litterfall during the peak of the dry season, a substantial proportion of fruits (ca. 20%) remained in the canopy in early autumn (October) and 2% of the 1993 crop even persisted after the second summer litterfall. This long-term retention and slow release of fruits from the canopy may be part of the disturbance-initiated mode of regeneration of *R. sphaerocarpa*. Fruits dispersed by flood waters are likely to become buried in moist soil while those remaining on the soil surface for a long time are likely to be destroyed by predators before the next disturbance event. Rabbits (*Oryctolagus cuniculus* L.) eating the fruits of *R. sphaerocarpa*, however, pass germinable seeds in their pellets. Although this mode of dispersal is usually limited within a range of 500 m (Cerván & Pardo 1997), it can, unlike running water, disperse seed in the uphill direction.

The phenological timing of litterfall with a pronounced maximum in the dry season and before the beginning of the autumn rains also has a distinct facilitative effect on its understorey. The litter layer under the shrubs' canopies provide shelter for a variety of seeds from predators and excessive solar radiation and drying. These seeds, mainly of annual plants, germinate soon after the onset of the autumn rains. Although an experimental litter layer of typical thickness was found to reduce total germination and establishment, plant diversity increased significantly (Moro et al. 1997a).

Conclusions

The phenological timing in *R. sphaerocarpa* is typical of the often deep-rooted evergreen shrubs in the Mediterranean and arid regions of North America (e.g., Mooney 1977, 1981). The annual maximum of canopy development, coinciding with the reproductive phase, occurs in spring to summer during long days and with maximum levels of irradiance. Physiological constraints may arise through limitations in the water supply, however. Although we only analysed three years' data, we assume that the observed between-year variation in the shrubs' phenology and productivity was predominantly a result of the different rainfall regimes during this period. Taking into account information on rooting depth in *R. sphaerocarpa* (Haase et al. 1996a), we postulate that after a cool season with average to high rainfall, vegetative growth will be enhanced in the following spring leading to an increase in canopy size. This precipitation recharges the moisture of deep sediment layers accessed by the shrubs' root systems, which ensures adequate supplies of water throughout late spring and summer enabling high rates of growth and assimilation. A cool season with low rainfall, on the other hand, appears to cause a smaller than average increment in canopy size. The evapotranspiration by these smaller canopies uses less water which can be more easily supplied by the now limited soil water resource in the following spring and summer. A further adjustment to limited water supply can be achieved by variation in the timing and extent of late summer litterfall. It is possible that the effect of this between-year variation in rainfall on vegetative and reproductive development can be buffered by storage of carbon in the large root system of the shrubs. This large reservoir of carbon may enable a fast recovery of the canopy after years with low canopy area or ensure survival through a sequence of dry years with little growth.

Large variation in rainfall within and between years is typical of semi-arid south-eastern Spain (Puigdefábregas et al. 1996) and this may produce a much larger variation in the phenology and productivity of the shrubs than observed during the period of field work. In particular, the second annual flush in late summer or autumn will probably show a much larger contribution to the canopy area in years with substantial rainfall in summer.

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