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Exceptional photosynthetic performance of *Capparis spinosa* L. under adverse conditions of Mediterranean summer

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Abstract

Diurnal and seasonal fluctuations in water potential (Ψ), stomatal conductance (g_s), transpiration rate (E), and net photosynthetic rate (P_N) were monitored in *Capparis spinosa* L., a Mediterranean plant growing during summer, *i.e.* at the period considered the most stressful for local plant life. In spite of the complete absence of rain, Ψ exhibited a modest drop at midday (–2.7 MPa), but was fully recovered overnight, indicating sufficient access to water sources. The stomata remained open throughout the day and season and the high E resulted in leaf temperatures up to 3.9 °C below air temperature. Additionally, P_N of the fully exposed leaves was higher than 25 μmol m^{-2} s^{-1} for more than 10 h per day throughout the summer growth period. No symptoms of photooxidative stress were shown, as judged by maximum photosystem 2 photochemical efficiency (F_v/F_m) and the function of xanthophyll cycle. Indeed, diurnal inter-conversions of the xanthophyll cycle components were modest during the summer and a more intensive function of the cycle was only evident during leaf senescence in autumn. In comparison with a semi-deciduous and an evergreen sclerophyll co-existing in the same ecosystem, *C. spinosa* assimilated up to 3.4 times more CO_2 per m^2 during its growth period (May to October) and up to 1.8 times more on an annual basis.

Additional key words: chlorophyll fluorescence; daily and seasonal photosynthesis; net photosynthetic rate; stomatal conductance; summer perennial; transpiration rate; water potential.

Introduction

In Mediterranean and arid ecosystems the most unfavourable period of the year for plant growth is the dry summer period (Mooney 1983). The conditions prevailing during the summer months are characterized by high irradiance, high temperature, and, in extreme cases, by complete lack of precipitation (Di Castri 1973). Concerning plant responses to these adverse conditions, two major groups can be distinguished, depending on the growth strategy that they follow. Perennial evergreen plants adopt a "preservation" strategy during the summer, whereas the optimal seasons for growth are spring and autumn. Through their morphological and physiological characteristics, these plants respond to the multiple stress (water, temperature, high irradiance) by minimizing the effects and/or repairing the produced damage (Orshan 1963, Lange 1988, Kyparissis *et al.* 1995, Werner 2000, Chaves *et al.* 2002, Munné-Bosch *et al.* 2003). An exceptionally prolonged drought may surpass their adaptive abilities and become lethal. Alternatively, the southern and northern distribution limits for these plants are defined by the mean values of the environmental parameters, *e.g.* precipitation and temperature (Mitrakos 1980, Larcher 2000). Evergreen sclerophylls and semi-deciduous shrubs may be ranked in this group. On the other hand, a more "aggressive" strategy is adopted by annual or perennial shrubs, whose growth cycle commences in spring and is completed in summer or early autumn (summer greens). The plants of this group do not preserve any aboveground parts during the rest of the year (Orshan 1989). Such plants may not suffer a summer stress either due to morphological and/or physiological characteristics, which support a more efficient exploitation of the available resources, or due to adequate protective mechanisms.

Even though many studies have been conducted

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Abbreviations: Chl, chlorophyll; E, transpiration rate; F_v/F_m, maximum (dark adapted) photosystem 2 photochemical efficiency; g_s, stomatal conductance; P_N, net photosynthetic rate; PAR, photosynthetically active radiation; PS, photosystem; Ψ, water potential.

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concerning sclerophylls (Valladares *et al.* 1997, Peñuelas *et al.* 1998, Larcher 2000, Chaves *et al.* 2002, Medrano *et al.* 2002) and semi-deciduals (Kyparissis *et al.* 1997, Gratani and Bombelli 1999, Karavatas and Manetas 1999, Kyparissis *et al.* 2000, Munné-Bosch *et al.* 2003), little is known about Mediterranean summer growing species. In order to fill this gap, this study explores the eco-physiological characteristics of the summer growing species *Capparis spinosa* L.

C. spinosa is a summer perennial shrub growing in the Mediterranean and semiarid ecosystems (Sozzi 2001). Its annual above-ground growth commences during the end of spring (May) and concludes during early autumn (October). It usually thrives in rocky and anhydrous habitats, fully exposed to the sunrays, and is able to withstand temperatures above 40 °C.

Materials and methods

Field site and sampling: All samplings and measurements were carried out on four tagged individuals of *C. spinosa* L. growing wild within the campus of Patras University (38°15'N, 21°44'E, 50 m a.s.l.). Measurements were conducted with fully expanded leaves during the summer of 1998 on the following dates: June 23, July 8, August 6, August 20, and October 1. The October 1 measurements were started later in the morning and finished earlier in the evening, compared to the measurements of the other dates, due to the shorter day-length of that season. 40 leaves belonging to eight branches (5 leaves per branch, 2 branches per plant) were tagged and used for all non-destructive measurements [net photosynthetic rate, P_N; stomatal conductance, g_s; transpiration rate, E; temperature; chlorophyll (Chl) fluorescence]. Destructive measurements (water potential, Ψ; content of xanthophylls) were carried out on leaves from different stems of the same plants. Care was taken so that the orientation of the stems and leaves used in both destructive and non-destructive measurements was similar.

For Ψ determination, four shoots (1 shoot per plant) were wrapped in plastic bags, cut, and transferred to the lab immediately for measurement. For pigment analysis, 16 leaves (4 leaves per plant) were cut and immediately immersed in liquid nitrogen, where they remained until measurement. For each sample, four leaves (1 leaf per plant) were pooled.

Measurements: P_N and photosynthetically active radiation (PAR) were measured with a *LI-6200* portable photosynthesis system (*Li-Cor*, Lincoln, NE, USA). E, g_s, and leaf (T_l) and air (T_a) temperatures were measured with a *LI-1600* porometer (*Li-Cor*, Lincoln, NE, USA). Ψ was measured with a Scholander-type pressure bomb (*SKPM 1400*, Skye, UK), which had a measuring lower limit at –4.4 MPa.

Chl fluorescence parameters were measured in the field using a *Hansatech* (Norfolk, UK) Plant Efficiency Analyser. The exciting irradiance was 1 500 µmol m^{-2} s^{-1} and the leaves were pre-adapted in the dark for 30 min. Pigment extraction was performed in dim radiation by grinding the frozen samples in a mortar with 100 % purified acetone in the presence of a small amount of $CaCO_3$. The extract was centrifuged at 5 210×*g* for 10 min at 2 °C, and the supernatant was further cleared by passing through a 0.45 µm filter. Chl content was measured spectrophotometrically, using a *Shimadzu UV-160A* double beam spectrophotometer and the equations of Lichtenthaler and Wellburn (1983). Carotenoid separation was performed with a *Shimadzu LC-10 AD* HPL chromatograph equipped with a non-endcapped *Zorbax ODS* (4.6×250 mm) column (*Rockland Technologies*, Chadds Ford, PA, USA) and calibrated against purified β-carotene (*Sigma Chemical*, St. Louis, MO, USA) and carotenoids freshly prepared by TLC, as previously described (Kyparissis *et al.* 1995). Development was performed isocratically at 1 cm^3 min^{-1}, according to Thayer and Björkman (1990): 20 min with acetonitrile : methanol, 85 : 15, v/v, and 20 min with methanol : ethyl acetate, 68 : 32, v/v. Pigments were detected by measuring absorbance at 445 nm, using a *Shimadzu SPD-10A* UV-VIS detector. Peak areas were integrated by a *Shimadzu C-R6A Chromatopac*.

Meteorological data were recorded by a solar powered *Mini-Met* (*Skye*, UK) meteorological station on a 30-min basis.

Statistics: Significance of differences between air and leaf temperature was assessed by a paired *t*-test (*SPSS 9.0* statistical package), since both parameters were recorded simultaneously at each leaf.

Results

The conditions prevailing during the growth period of *C. spinosa* in the study area were typical Mediterranean (Fig. 1). Growth commenced in May, when temperatures were mild and precipitation events were still frequent (total precipitation of May was 44 mm). The summer period was characterized by the complete absence of precipitation and high temperature with seasonal maximum of 43.2 °C. Despite these adverse conditions, plants of *C. spinosa* did not seem to suffer any water stress. Early in the summer period (June 23), Ψ showed a midday depression down to –2.0 MPa and was fully recovered at the end of the afternoon (Fig. 2*A*). During the hottest summer day (August 6) and after two months of complete lack of precipitation, midday Ψ did not drop bellow –2.7 MPa and was still fully recovered overnight. This water utilization pattern continued until the end of the growth period (Fig. 2*A*).

This extraordinary capacity of *C. spinosa* to exploit the limited water resources of the ground allowed the plants to maintain open stomata throughout the day (Fig. 2*B*). This pattern has a dual benefit for the plants. At first, the accompanying high *E* (Fig. 2*C*) lead to a statistically significant decrease in T_l (p<0.001) on a diurnal basis for all summer sampling dates. This was distinctly profound on August 6, when midday T_l was 3.5 °C below T_a (Fig. 2*D*). Secondly, open stomata allowed CO_2 to reach easily the carboxylation sites, resulting in high P_N throughout the growth season (Fig. 3*A*). Furthermore, P_N was maintained higher than 25 μmol m^{-2} s^{-1} for more than 10 h per day. During these hours, the irradiance at the leaf level was higher than 1 300 μmol m^{-2} s^{-1}, with maximum values of 1 800 μmol m^{-2} s^{-1} recorded around midday (data not shown). However, *C. spinosa* showed no symptoms of either chronic or dynamic photoinhibition. Maximum (dark adapted) photosystem (PS) 2 photochemical efficiency (F_v/F_m) exhibited a modest depression only for about two hours during August middays and was fully recovered in the afternoon (Fig. 3*B*). Additionally, even though the xanthophyll pool size (violaxanthin+antheraxanthin+zeaxanthin) was kept high throughout the growth season [77.91±6.52 mmol mol^{-1}(Chl); values not shown], the xanthophyll cycle, as judged by its conversion state, did not seem to be intensively used for photoprotection by the plant, until the end of the growth season, when leaves started to senesce (Fig. 3*C*).

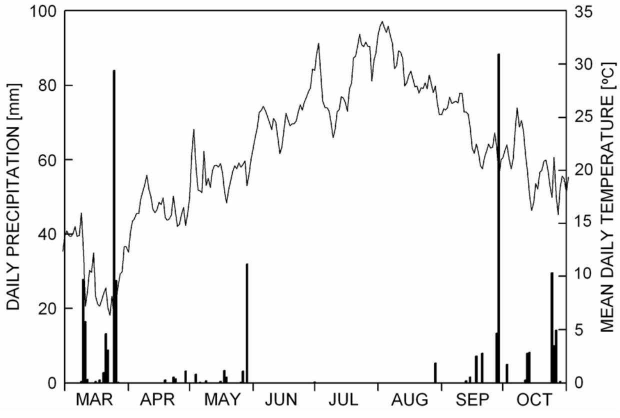

Fig. 1. Daily precipitation (*bars*) and mean daily temperature (*line*) for the sampling site throughout the experimental period.

Discussion

C. spinosa is well adapted to the adverse environment of the Mediterranean summer. Most of its above-ground development (including flowering and fruiting) takes place almost in the absence of any precipitation. Additionally, it needs well-drained substrates in order to have a successful growth (Sozzi 2001). Despite the above, it probably does not suffer any water stress throughout the growth period. The lowest midday Ψ recorded in this study was –2.7 MPa during the hottest day of the summer (August 6), while similar values have been reported by Rhizopoulou *et al.* (1997). Compared to other plants coexisting in the same or similar ecosystems, this value may be considered relatively high. For example, respective values for semi-deciduous species like *Phlomis fruticosa* and *Cistus* sp. may drop to –7.5 MPa and similar values have been recorded for evergreen sclerophylls such as *Phillyrea latifolia*, *Phillyrea angustifolia*, *Erica arborea*, and *Olea europaea* (Kyparissis *et al.* 2000, Werner *et al.* 2002). Additionally, these midday depressions of Ψ are poorly recovered overnight for the above mentioned semi-deciduous and sclerophyllous species, whereas for *C. spinosa* full recovery was recorded either late in the afternoon (early summer) or during the night (midsummer). This seasonal difference may be attributed to higher soil water availability early in the season and/or higher evaporative demand (higher temperatures) during midsummer. The extraordinary capacity of *C. spinosa* to maintain a satisfactory water balance under limited water resources may be explained by two factors. Firstly, its root system is significantly deep (up to 10 m long, Sozzi 2001) and dense (Rhizopoulou 1990), comprising the 65 % of the total biomass during the summer (Sozzi 2001). It also excretes acidic compounds, which helps to penetrate through cracks in rocks and reach deep and well-protected water resources (Oppenheimer 1960). Secondly, root and stem wood show anatomical characteristics, which favour high hydraulic conductivity, *i.e.* wide and short vessel elements with simple perforation plates and vessel grouping for cavitation avoidance (Psaras and Sofroniou 1999).

This efficient system for water supply disengages *C. spinosa* from stomatal opening control of water balance regulation. Consequently, the stomata are kept open throughout the day and the growth season, leading to enhanced evapotranspiration, with a strong cooling effect on leaf temperature. This stomatal opening pattern is in contrast to the corresponding pattern that sclerophylls and semi-deciduals follow during the same period. Sclerophyllous shrubs and trees—with relatively deep root system—exhibit midday stomatal closure during the summer (Kummerow 1981, Lange 1988, Nardini *et al.* 2000) and semi-deciduals—possessing more shallow root systems—maintain their stomata open only for two or three hours early in the morning, when evaporative demand is still low (Harley *et al.* 1987, Tenhunen *et al.* 1990, Nunes *et al.* 1992, Grammatikopoulos *et al.* 1995, Kyparissis *et al.* 1995, Munné-Bosch *et al.* 2003).

These differences in stomatal opening between the three growth patterns result in respective differences in photosynthesis. During the summer months, sclerophyllous and semi-deciduous species maintain low P_N, which may lead to photoinhibitory conditions (Harley *et al.* 1987, Chaves *et al.* 2002). Low F_v/F_m, high contents of the xanthophyll cycle components (antheraxanthin, violaxanthin, zeaxanthin), and intense function of the xanthophyll cycle are common responses of these plants during summer (Faria *et al.* 1998, Karavatas and Manetas 1999, Kyparissis *et al.* 2000, Larcher 2000, Werner *et al.* 2002, Munné-Bosch *et al.* 2003). In contrast to the above, *C. spinosa* utilizes efficiently the high irradiance throughout the growth season, without showing any symptoms of sustained photoinhibition. Nevertheless, the xanthophyll pool size is kept relatively high, probably serving as an auxiliary photoprotective mechanism to be used at more intense drought. The highly functional xanthophyll cycle recorded during October may be related to leaf senescing processes. Garcia-Plazaola and Becerril (2001) have reported that during senescence of *Fagus sylvatica* leaves, degradation of Chls was accompanied by conversions of violaxanthin to zeaxanthin.

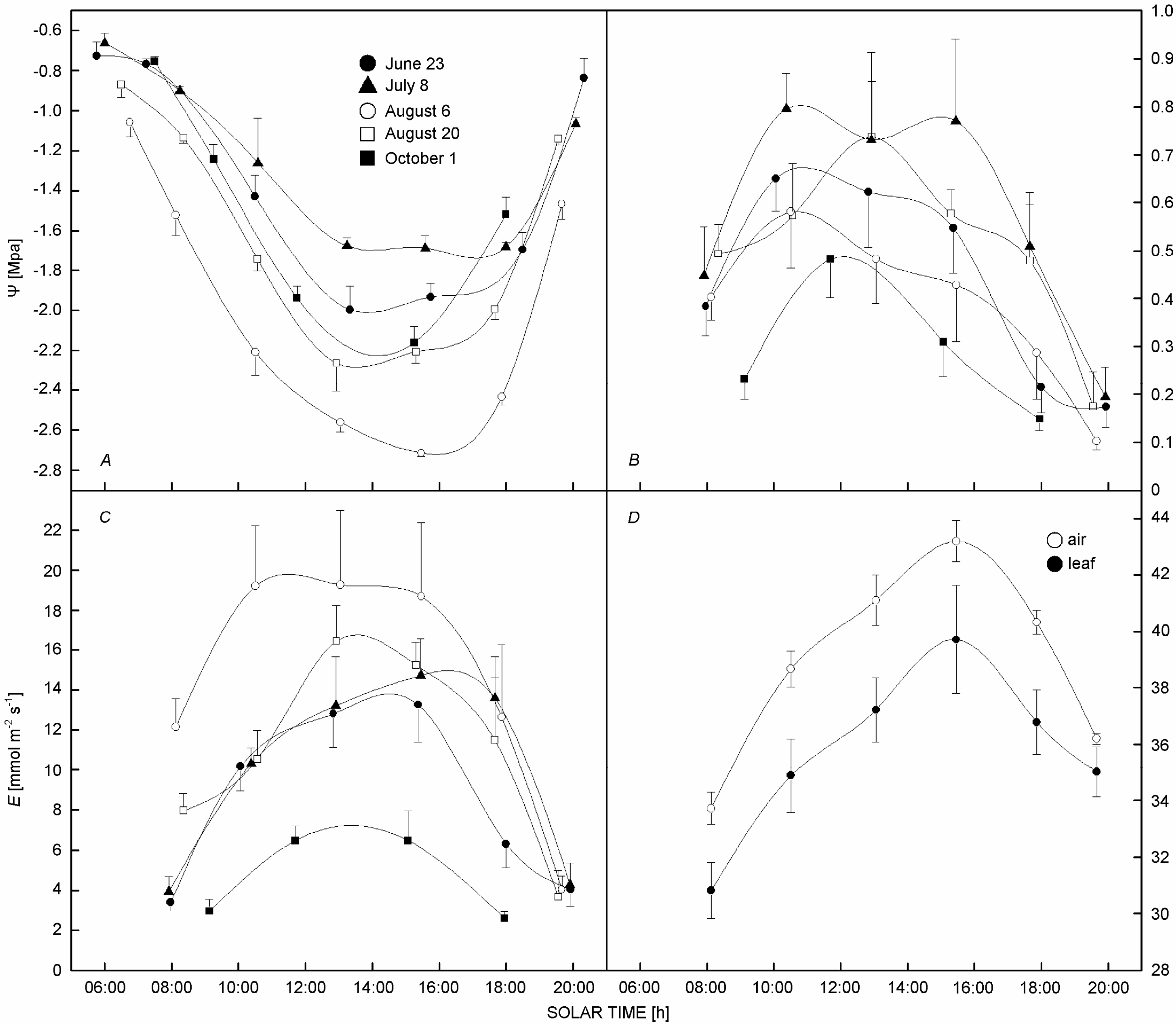

Fig. 2. Daily variations of (*A*) water potential, Ψ, (*B*) stomatal conductance, g_s, and (*C*) transpiration rate, *E* for the 5 sampling dates, and (*D*) air and leaf temperature for one representative date (August 6). Values of Ψ are means±SD from 4 independent measurements; values of all the other parameters are means±SD from 4 individuals (10 measurements per plant). Differences between air and leaf temperature were statistically significant at $p<0.001$.

As shown above, *C. spinosa* exhibits a short growth period (*ca.* 5 months), with high P_N. On the other hand, the co-existing adjacent sclerophylls and semi-deciduals retain low P_N during the same period, while their photosynthetic activity expands throughout the year. On an ecosystem level, useful information might be derived from an estimation of the total CO_2 fixed on an annual basis for the three growth forms discussed so far. In Fig. 4, a comparison concerning the daily P_N throughout the year is presented among *C. spinosa* (summer perrenial), *Phlomis fruticosa* (semi-decidual, data from Kyparissis *et al.* 1997), and *Phillyrea latifolia* (evergreen sclerophyll, data from Tretiach 1993). The three species grow in close vicinity to each other in our sampling site. It has to be noted that calculations for P. fruticosa and *P. latifolia* are overestimated, since these plants have a dense canopy with sun and shade leaves, whereas the leaves used for photosynthesis measurements are fully exposed (on the top and/or the edge of the canopy). On the other hand, all leaves of *C. spinosa* receive similar PAR irradiances due to the flat and open shape of its canopy. Even without taking these overestimations into account, it seems that from May 15 to October 15 *C. spinosa* assimilates 3.1 times more CO_2 per m^2 compared to *P. fruticosa* and 3.4 times more than *P. latifolia* (Table 1). Furthermore, even on an annual basis, carbon fixation is higher in *C. spinosa* than in *P. fruticosa* or *P. latifolia* (1.1 and 1.8 times higher, respectively).

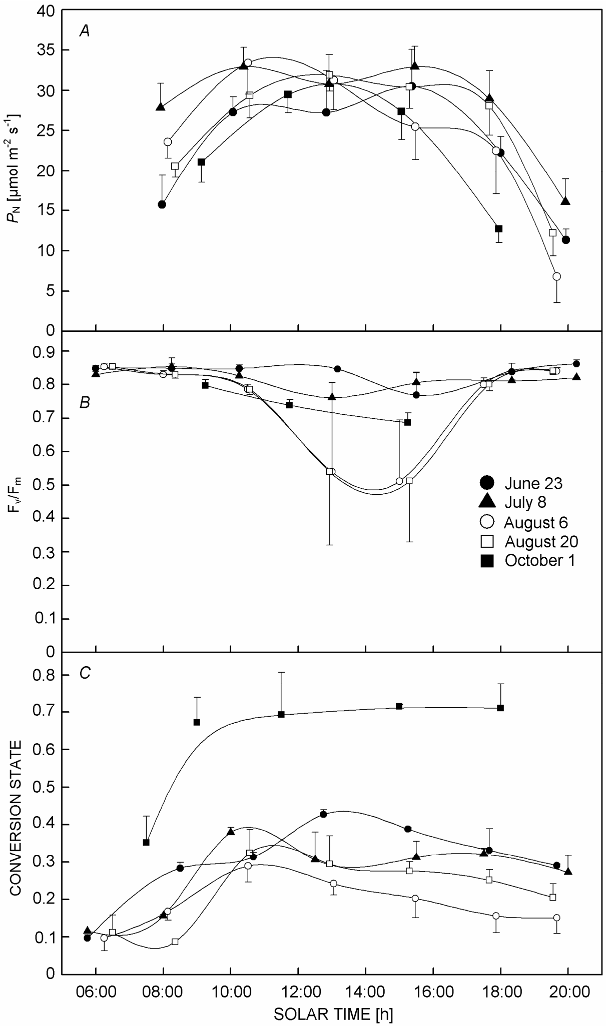

Fig. 3. Daily variation of (*A*) net photosynthetic rate, P_N, (*B*) maximum photosystem 2 photochemical efficiency, F_v/F_m, and (*C*) the conversion state of the xanthophyll cycle (antheraxanthin+zeaxanthin/violaxanthin+antheraxanthin+zeaxanthin) for the 5 sampling dates. Values of P_N and F_v/F_m are means±SD from 4 individuals (10 measurements per plant). Values concerning xanthophyll cycle components are means±SD from 4 independent measurements.

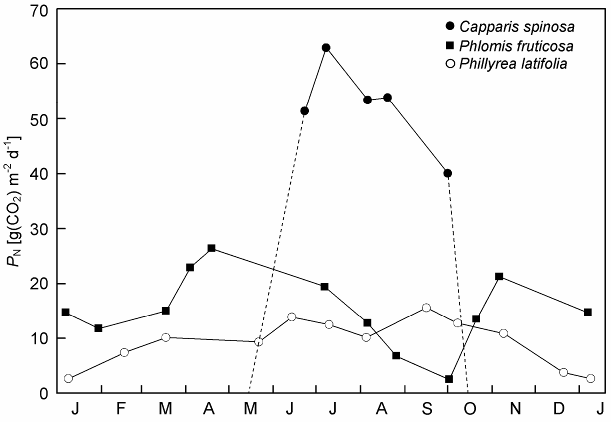

Fig. 4. Annual course of the daily net photosynthetic rate, P_N for *Capparis spinosa*, *Phlomis fruticosa* (semi-decidual), and *Phillyrea latifolia* (evergreen sclerophyll). The diurnal P_N was calculated by integrating the daily curves from sunrise to sunset. Zero values at May 15 and October 15 for *C. spinosa* denote the onset and conclusion of the growing period, respectively. Values for *P. fruticosa* were extracted from Kyparissis *et al.* (1997) and for *P. latifolia* from Tretiach (1993).

Table 1. Integrated values of daily net photosynthesis [g(CO_2) m^{-2} d^{-1}] for *Capparis spinosa*, *Phlomis fruticosa* (semideciduous), and *Phillyrea latifolia* (evergreen sclerophyll). Values were calculated from Fig. 4 on annual basis and for the period May 15–October 15, which corresponds to the growth period of *Capparis spinosa*.

	Net carbon assimilation Annual	 May 15–October 15
Capparis spinosa	6549	6549
Phlomis fruticosa	5837	2090
Phillyrea latifolia	3587	1899

In conclusion, *C. spinosa* has evolved a highly effective system concerning the exploitation of the limited water resources (deep roots and highly conductive wood). Stomata remain open throughout the day and season resulting in high *E*, with strong cooling effect on T_l, as well as exceptionally high P_N on a seasonal basis, compared to other co-occurring species. This superb photosynthetic performance during the most stressful period of the year, when semi-deciduals and sclerophylls show their minimum growth rates, provides *C. spinosa* with a competitive advantage against these species. Additionally, summer-greens like *C. spinosa* may play an important role in the stability and dynamics of Mediterranean ecosystems through their aggressive pattern of carbon and nutrients allocation.

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