

Spreading of the invasive *Carpobrotus* aff. *acinaciformis* in Mediterranean ecosystems: The advantage of performing in different light environments

Traveset, A.^{1*}; Moragues, E.^{1,2} & Valladares, F.^{3,4}

¹Institut Mediterrani d'Estudis Avançats (CSIC-UIB). C/ Miquel Marqués 21, 07190 Esporles, Mallorca, Balearic Islands, Spain; ²University of the Balearic Islands, Ctra. Valldemossa km 7'5, 07071-Palma de Mallorca, Spain; ³Instituto de Recursos Naturales, Centro de Ciencias Medioambientales (CSIC). C/ Serrano 115, E-28006, Madrid, Spain; ⁴Departamento de Biología y Geología. Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/ Tulipán s/n, 28933 Móstoles, Spain;

*Corresponding author; Fax +34 971173184; E-mail atraveset@uib.es

Abstract

Question: Do specific environmental conditions affect the performance and growth dynamics of one of the most invasive taxa (*Carpobrotus* aff. *acinaciformis*) on Mediterranean islands?

Location: Four populations located on Mallorca, Spain.

Methods: We monitored growth rates of main and lateral shoots of this stoloniferous plant for over two years (2002-2003), comparing two habitats (rocky coast vs. coastal dune) and two different light conditions (sun vs. shade). In one population of each habitat type, we estimated electron transport rate and the level of plant stress (maximal photochemical efficiency F_v/F_m) by means of chlorophyll fluorescence.

Results: Main shoots of *Carpobrotus* grew at similar rates at all sites, regardless habitat type. However, growth rate of lateral shoots was greater in shaded plants than in those exposed to sunlight. Its high phenotypic plasticity, expressed in different allocation patterns in sun and shade individuals, and its clonal growth which promotes the continuous search of available resources, contributed to a good growth and photochemical efficiency of *Carpobrotus* in the relatively moderate shade of the understories of Mediterranean shrublands and woodlands. Each main shoot of a *Carpobrotus* clone (which can have several dozens main shoots) grows ca. 40 cm per year, which explains its vigorous habitat colonization capacity.

Conclusion: The highly plastic morphological response to different light regimes of this taxon contributes to a rapid colonization of heterogeneous coastal Mediterranean environments spreading well beyond the open sand dune systems where it has been often reported.

Keywords: *Aizoaceae*; Balearic Islands; Clonal growth; Colonization rate; Invasion pattern; Photochemical efficiency.

Nomenclature: Tutin et al. (1964-1980).

Abbreviations: DSF = Direct site factors; ETR = Electron transfer rate; F_v/F_m = Maximal photochemical efficiency; ISF = Indirect site factors; PAR = Photosynthetically active radiation; RDPI = Relative distance phenotypic index; RFR = Red/far-red ratio; UV = Ultraviolet.

Introduction

The relationship between the characteristics of an invading species (such as effective vegetative reproduction) and the features of the invaded ecosystem is crucial to the success of the invasion (Heger & Trepl 2003; Vilà & Weiner 2004). This relationship can influence the evolution, adaptation and population dynamics of introduced species and can contribute to their establishment in new areas, while outcompeting native species (Myers & Bazely 2003). Clonal growth, together with other life history traits, has been shown to increase invasion success (Mack 2003). Clonal plants are one of the most successful growing strategies in the plant world, they are found in almost all terrestrial and aquatic habitats (de Kroon & van Groenendael 1997) and predominate in a variety of habitat types, including severely stressed (Callaghan et al. 1992) and disturbed habitats (Sebens & Thorne 1985). There are several advantages associated with the reliance on clonal growth for population expansion (Lambrecht-McDowell & Radosevich 2005 and references therein): (1) increases the potential to access unevenly distributed resources, such as light and water (Stuefer et al. 1996), (2) increases the capacity to recover from stresses such as defoliation, (3) rapidly captures and dominates an area, competitively excluding other species (Sammul et al. 2004) and (4) changes the spatial and/or temporal distribution of ramets (Elberse et al. 2003).

An intrinsic characteristic of clonal growth that confers competitiveness is the efficient distribution of tasks among ramet modules which, coupled with phenotypic plasticity, can lead to enhanced resource exploitation (Stuefer et al. 1996). Clonal plants build a variety of architectural forms by modifying the lengths of spacers (rhizomes or stolons), branching frequencies and branching angles (Bell 1980; Lovett Doust 1981; Hartnett & Bazzaz 1983; Salzman & Parker 1985; Slade & Hutchings 1987). These architectures differ among

plant species or within a species in different environments (Bell 1980; Lovett Doust 1981; de Kroon & Knops 1990; Hutchings & de Kroon 1994). Plasticity in clonal architecture has actually been considered an adaptive plant trait (Hartnett & Bazzaz 1983). Plasticity in horizontal growth provides a clonal species with special capacity for resource capture (de Kroon & Hutchings 1995) and for producing ramets growing in numerous directions and at long distances (Oborny & Bartha 1995). Hence, clonal growth is particularly well-suited for the colonization of spatially heterogeneous environments, such as forest understories (Stuefer et al. 1996).

Most clonal plants produce both seeds and vegetative propagules, which are alternative means for dispersal. As a general trend, vegetative reproduction is specialized for efficient local dispersal and persistence (Silander 1985). The cost of vegetative reproduction is generally lower than the cost of producing seeds and the establishment of the progeny is more successful in a wider range of habitat types (Oborny & Bartha 1995). In a community, the occurrence of monodominant patches of clonal species strongly determines the spatial structure and, if the patches cover a large area, may increase the resistance of the whole community to invasion by a new species (Bartha 1992).

The genus *Carpobrotus* includes species that are very aggressive and invasive in Mediterranean ecosystems, especially in open areas such as dunes and rocky coasts in western Mediterranean islands (Delanöe et al. 1996; Suehs et al. 2004; Moragues 2006; Vilà et al. 2006). Its clonal growth and its ability to survive in extreme environmental conditions make it a very competitive plant, with high rates of space colonization (Sintes et al. 2007), and with a subsequent negative impact on the native flora (D'Antonio & Mahall 1991; D'Antonio et al. 1993; Weber et al. 1998; Moragues & Traveset 2005; Vilà et al. 2006).

Besides determining the seasonal growth patterns of *Carpobrotus* spp. in different localities and assessing whether there is a differential growth rate between long and short shoots, one main goal of this study was to compare the ecophysiological performance (growth and photochemical efficiency) between microhabitats differing in light availability (open vs understory sites). Specifically, we test the following hypotheses:

1. Phenotypic plasticity of *Carpobrotus* is relatively high, as typically expected for invasive plants (e.g. Ninemets et al. 2003);
2. Growth and ecophysiological performance of the taxon is poor in the shade since it has been reported as a heliophilous plant, colonizing or invading open, coastal sites (Weber et al. 1998; Wisura & Glen 1993).

Material and Methods

Study species

Our focal species is *Carpobrotus* aff. *acinaciformis* (*Aizoaceae*) (hereafter *Carpobrotus*), which belongs to a complex of species that easily hybridize (Suehs et al. 2004) and that are difficult to distinguish unless they bear flowers. *C. edulis* is the only member of the genus to have distinctly yellow flowers (Wisura & Glen 1993) while *C. aff. acinaciformis* typically has magenta flowers. The genus is native to South Africa and was introduced in Europe around the 19th century as an ornamental plant because of its fast clonal growth, its low water requirements and its conspicuous large (5–12 cm) flowers (Wisura & Glen 1993; Suehs et al. 2004). *Carpobrotus* can form large mats on coastal rocks, cliffs and sand dunes, and is considered a serious threat to several plant species and coastal habitats (D'Antonio & Mahall, 1991; Delanöe et al. 1996; Moragues 2006). The plant produces indehiscent fleshy fruits (each bearing a large number, often over a thousand, of small seeds) that are eaten and dispersed by rabbits (D'Antonio 1990) and rats (Bourgeois et al. 2005; Traveset & Richardson 2006).

Each *Carpobrotus* clone expands horizontally and radially in all directions, occupying ca. 130 m². It forms dense mats that, in natural conditions, tend to trail among other elements of the vegetation (Wisura & Glen 1993). The shoots grow along the substrate surface according to a regular structure of internodes between consecutive nodes, where internodes are the distances between two nodes and a node is the point on the shoot at which one or more leaves are inserted. There are two different kinds of shoots: long (main) shoots and short (lateral or secondary) shoots; both are macroblasts, although they appear to have different functions (Moragues 2006; Sintes et al. 2007). The main shoots (stolons, in botanical terms) have the capacity to form functional individuals (ramets) by rooting some shoot nodes spreading alone. Each ramet is potentially autonomous, being able to develop all the organs possessed by a whole plant.

Study sites

The study took place in four coastal localities of Mallorca (the largest island of the Balearic Archipelago in the western Mediterranean basin). Two were located on cliffs in the southwest part of the island (Cala Figuera and Cap Enderrocat), one at the southeast of Mallorca on a rocky coast near the sea (Ses Salines) and the fourth was at the north of the island, in a dune habitat (Son Serra). The vegetation of the first two localities consisted of the typical coastal, open, xerophytic shrubland, with predominance of *Olea europaea* var. *sylvestris*, *Pistacia*

lentiscus, *Cistus monspeliensis* and *Anthyllis cytisoides*. The site of Ses Salines is located at sea level and was dominated by a few shrub species (mainly *Pistacia lentiscus* and *Juniperus phoenicea* ssp. *turbinata*). Finally, Son Serra was characterised by the typical west Mediterranean dune flora where species such as *Ammophila arenaria*, *Cistus salviifolius*, *Pistacia lentiscus* and *Lotus cytisoides* predominate. Both in Cala Figuera and Son Serra, *Carpobrotus* also occurred in the understory of *Pinus halepensis* (Aleppo pine) forests that were in a second line of vegetation (ca. 500 m from the coast) (Fig. 1).

In each of the four populations we selected three mature, healthy and isolated individuals (clones) of *Carpobrotus* of similar size. We are confident that all were *C. aff. acinaciformis* as they produced magenta flowers; in fact, the yellowish flowers of *C. edulis* were exclusively observed in the locality of Son Serra. In the two localities where *Carpobrotus* grew in both sun and shade sites (Cala Figuera and Son Serra), we measured growth from three randomly selected clones in each microhabitat. The ecophysiological measurements were performed in these two localities, for which we used a total of eight clones (known to produce magenta flowers) per microhabitat and locality.

Field measurements

The traits measured to estimate performance of *Carpobrotus* were related to growth, dry mass allocation and photochemical efficiency. All of them have been shown to be correlated with the ecological success of plants and they have been frequently used as surrogates of fitness, particularly in long-lived plants (e.g. Verdú et al. 2004). The rationale for considering these three kinds of traits was to include short and long-term estimators of performance since ecophysiological variables such as photochemical efficiency can change rapidly over a few days, while dry mass allocation and growth rate respond in the scale of months and years. From each individual clone, we randomly chose and marked one main shoot and one lateral shoot. Bimonthly over two years (2002-2003), we measured the increase in length in each type of shoot in all individuals. At each visit, we recorded both the number of new nodes and the distance between them.

The immediate light environment under which individual clones grew was monitored during late spring (May 25 and 26, 2004 at both localities) by two means:



Fig. 1. Shade (A, B) and sun (C, D) microhabitats where *Carpobrotus* was found in two coastal Mallorca sites (rocky outcrops in Cala Figuera (A and B) and sand dunes in Son Serra (C and D)). Individual *Carpobrotus* plants can be seen in the foreground of B and C. The canopy was dominated by *Pinus halepensis* and *Pistacia lentiscus* at both sites, while plants co-occurring with *Carpobrotus* in the open were *Olea europaea* var. *sylvestris*, *Cistus monspeliensis* and *Anthyllis cytisoides* in Cala Figuera, and *Ammophila arenaria*, *Cistus salviifolius*, *Lotus cytisoides* and *Helichrysum stoechas* in Son Serra.

(1) hemispherical photography (Percy 1989), which provided an integrated measure of annual mean availability of light and (2) three different sensors, which provided quantitative (although instantaneous) measures of irradiance quantity and quality. Photographs were taken at a height of 0.25 m above the ground using a horizontally-levelled digital camera (CoolPix 995 digital camera, Nikon, Tokyo, Japan) and aimed at the zenith, using a fish-eye lens of 180° field of view (FCE8, Nikon). All photographs were taken in overcast conditions to ensure homogeneous illumination of the overstorey canopy and a correct contrast between the canopy and the sky. Photographs were analysed using Hemiview canopy analysis software version 2.1 (1999, Delta-T Devices Ltd, Cambridge, UK) and the following variables were estimated: (1) direct and indirect site factors (DSF and ISF, respectively), which we defined as the proportion of direct and diffuse radiation received below the canopy as a fraction of that received above the canopy (Rich 1990) and (2) ground cover, defined as the vertically projected canopy area per unit ground area. The red/far-red ratio (RFR: 660/730 nm) was measured with a SKR 110 sensor attached to a SKR 100 meter (Skye Instruments Ltd., Powys, UK). Photon flux density ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$) of photosynthetically active radiation (PAR: 400–700 nm) and ultraviolet a, b and c (UV: 250–400 nm) were measured with a PAR quantum meter and a UV meter (BQM-SUN and UVM, respectively, both from Apogee-Instruments Inc., Logan, UT, USA).

On the same dates that irradiance measurements were obtained, and by means of a pulse-modulated fluorometer (FMS2, Hansatech Instruments, Norfolk, UK), we also determined the photochemical efficiency of photosystem II (F_v/F_m) of fully expanded, representative leaves of both short and long shoots of sun and shade individuals of *Carpobrotus* at each locality. One green leaf of each shoot type was first darkened for 30 minutes with leaf clips containing a shutter that could be opened when the fluorometer probe was attached and maximal photochemical efficiency (F_v/F_m) measurements were made.

Most individuals exhibited a varying number or reddish, apparently senescing leaves and the relative abundance of these leaves was visually estimated from ca. 30 randomly chosen individuals (including those used for the measurements) at each locality using a categorical variable from 0 to 3 (0 = < 5%; 1 = 5–25%; 2 = 25–60%; 3 = > 60%). In order to assess the senescent nature of such reddish leaves, we also compared the relative quantum yield of PSII photochemistry ($\Phi_{\text{PSII}} = (F_m' - F_t)/F_m'$) under moderate light ($350 + 20 \mu\text{mol m}^{-2}\text{s}^{-1}$, leaf temperature 24 ± 1 °C) to estimate apparent rate of electron transport ($\text{ETR} = \Phi_{\text{PSII}} * \text{PAR} * 0.5$) of green and reddish leaves in sun and shade individuals. For this,

we measured one leaf of each type from a total of seven clones in each microhabitat and locality.

On the same date of these measurements, one long and one short shoot were collected from each of the eight selected *Carpobrotus* clones in each locality to determine dry mass allocation to leaves and stems (internodes) and their water content. Shoots were placed in plastic bags and transported immediately to the laboratory for fresh mass determinations after measurement of shoot length. All plant material was then placed in an oven at 70 °C to determine the dry mass of all leaves (the number of which was also recorded) and stems separately for each shoot unit. Dry mass per unit of shoot length was thus obtained, which allowed us to transform the shoot length measured in the field into units of biomass increase over time.

Plastic phenotypic changes in response to light were estimated by calculating the relative distance plasticity index (RDPI) as described in Valladares et al. (2006). RDPI was estimated from all phenotypic distances between sun and shade individuals for each morphological, physiological and growth variable by pooling data from both sites. In this hybrid taxon, phenotypic changes may be due not only to the environment but also to genetic factors. Thus, the phenotypic plasticity estimated in this study is for the population, not for a given genotype as is the case for plasticity *sensu stricto* (see also Niinemets et al. 2003 for a similar approach).

Statistical analyses

To analyse the variance in annual growth rate (cm/year) among the four populations and between main and lateral shoots we performed two general linear models (Proc GENMOD in SAS v. 9.0). In the first we included population as a fixed factor, type of shoot as a within-subject factor (i.e. repeated measures) and individuals as a random factor (subject). Only clones in the sun were considered in this analysis to make the four populations comparable. In the second one, we added microhabitat (sun vs. shade) as a fixed factor and considered only the two populations in which this effect was tested (Cala Figuera and Son Serra). After checking (by means of a paired sample *t*-test) that the two years of the study did not differ in annual growth rate, the mean value of this parameter was calculated and transformed by means of the square root to be normalized. Seasonal differences in growth rate were examined by means of an ANOVA, after pooling data from all populations as the interaction season × population was not significant. Finally, the relationship between annual growth rate, number of nodes and length between them was examined by means of a Pearson's correlation.

The procedure GENMOD was also used to test for

differences in variables that quantified the incident light (ISF, DSF, %PAR and UV). For all those models, we used the gamma distributions and the power (-1) link function. On the other hand, differences in (1) Fv/Fm, (2) dry stem biomass/cm, (3) dry leaf biomass/cm, (4) number of leaves/cm and (5) shoot water content were tested using the normal error distribution and the identity as link function. For each locality, a Mann-Whitney U test was performed to test for differences between sun and shade clones in the physiological parameters that could not be normalized (abundance of red leaves and apparent electron transport rate in red leaves).

Results

There were no significant differences in annual growth rate among populations ($\chi^2_3 = 3.88$; $P = 0.28$). Main shoots were observed to grow at a higher rate than lateral ones ($\chi^2 = 5.16$; $P = 0.02$); this was consistent among populations (i.e. there was no interaction between population and type of shoot ($\chi^2_3 = 5.16$; $P = 0.16$)). When testing for differences in growth rate among seasons (every four months), we observed that there were significant differences among them ($F_{2,198} = 29.36$; $P < 0.0001$). The period encompassing the spring season (from March to June) showed the highest growth rate, whereas growth was minimal from late summer to early autumn (from July to October). From November to February, growth was intermediate between those two periods (Fig. 2).

The *P. halepensis* forests found near the coast at Son Serra and Cala Figuera and where *Carpobrotus* establishes had open canopies (cover ca. 67%), which led to relatively bright understories (20-30% of full sunlight, with both sensors and hemispherical photographs giving similar values, Table 1). Clones in the shade had significantly lower RFR ($\chi^2 = 14.83$; $P < 0.01$), PAR ($\chi^2 = 14.25$; $P < 0.01$), ISF ($\chi^2 = 15.09$; $P < 0.01$), DSF ($\chi^2 = 12.97$; $P < 0.01$) and UV ($\chi^2 = 13.85$; $P < 0.01$) than clones in the sun, although the differences were smaller in Son Serra for the factors: RFR ($\chi^2 = 8.81$; $P < 0.01$), PAR ($\chi^2 = 9.79$; $P < 0.01$) and UV ($\chi^2 = 8.25$; $P < 0.01$).

Clones in the sun grew more slowly than clones in the shade ($\chi^2 = 4.09$; $P = 0.04$; Fig. 3). We again found no differences between the two populations compared ($\chi^2 = 0.07$; $P = 0.79$) and the effect of microhabitat was consistent in the two populations (interaction not significant: $\chi^2 = 0.37$; $P = 0.55$). The type of shoot had a marginally significant effect on growth, main shoots growing more rapidly than lateral ones ($\chi^2 = 3.29$; $P = 0.07$); however, lateral shoots grew significantly faster in the shade than in the sun ($\chi^2 = 5.41$; $P = 0.02$; Fig. 4). There was also a significant interaction between popula-

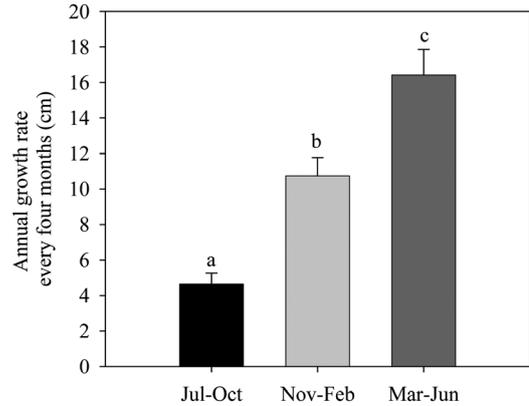


Fig. 2. Seasonal growth rate (cm/four months) (mean \pm SE). All four populations pooled after finding no significant interaction season \times population. The different letters above the bars indicate significant differences among periods ($P < 0.001$) (Tukey's test).

tion and type of shoot ($\chi^2 = 4.86$; $P = 0.03$), as the two types of shoots differed more in growth in Cala Figuera than in Son Serra. Finally, the interaction of the three factors was not significant ($\chi^2 = 0.07$; $P = 0.80$). Results were identical when biomass growth rate rather than length growth rate was used as the dependent variable (data not presented).

The number of new nodes produced per year by a

Table 1. Sun and shade environments in Cala Figuera and Son Serra. Values are the mean and the SD of red-far red ratio (RFR); photon flux density of photosynthetically active radiation (PAR) and ultraviolet radiation (UV); indirect and direct site factors (ISF and DSF, respectively, both obtained with hemispherical photography); ground cover by vegetation; and chlorophyll fluorescence variables (maximum photochemical efficiency of dark-adapted leaves, Fv/Fm, and apparent electron transport rate ETR under moderate light, $\mu\text{mol photon m}^{-2}\cdot\text{s}^{-1}$, which was measured both in green (ETR gl) and reddish (ETR rl) leaves. All values except RFR, Fv/Fm and ETR are expressed as percentage of a completely open site. Variables with asterisks were significantly different between sun and shade microhabitats at both sites (see text for details). $N = 16$ (2 shoots/clone, 8 clones) in all cases, except for ETR (7 clones).

	Cala Figuera		Son Serra	
	Sun	Shade	Sun	Shade
RFR (*)	1.1 \pm 0.03	0.8 \pm 0.05	1.1 \pm 0.02	1.0 \pm 0.08
PAR (*)	91.9 \pm 7.7	21.2 \pm 6.8	65.9 \pm 0.0	25.2 \pm 8.0
UV (*)	90.3 \pm 7.0	20.3 \pm 10.2	66.1 \pm 9.3	21.7 \pm 6.6
ISF (*)	92.8 \pm 5.5	25.7 \pm 3.8	74.4 \pm 1.0	26.4 \pm 2.8
DSF (*)	91.6 \pm 1.0	27.4 \pm 7.2	64.2 \pm 4.6	29.7 \pm 12.2
Cover	0.01 \pm .00	66.1 \pm 9.7	5.6 \pm 9.5	67.0 \pm 3.9
Fv/Fm	0.82 \pm .02	0.84 \pm 0.02	0.87 \pm 0.01	0.86 \pm 0.01
ETR gl	126.4 \pm .2	133.4 \pm 2.7	136.3 \pm 8.2	137.7 \pm 6.5
ETR rl	96.2 \pm 9.5	116.0 \pm 14.4	80.5 \pm 32.7	115.5 \pm 19.4

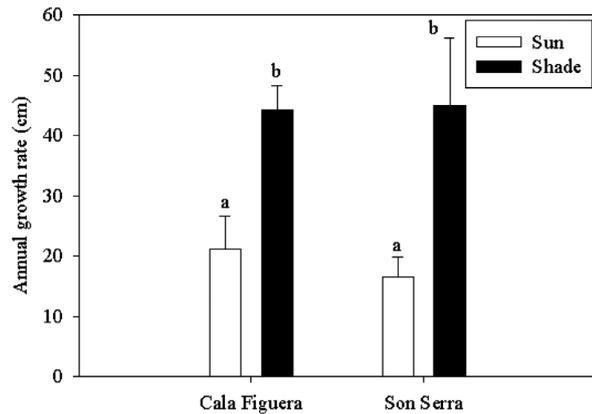


Fig. 3. Annual growth rate in the two microhabitats examined (mean \pm SE). Bars with the same letter are not significantly different.

given shoot was highly correlated with its annual growth rate ($r^2 = 0.64$, $p < 0.001$). Main shoots formed a mean of 8.28 ± 0.49 nodes by year (Mean \pm SE; $n = 36$), whereas the laterals produced only 5.42 ± 0.68 ($n=31$) nodes. Likewise, the internodal distance was also highly correlated with growth rate ($r^2 = 0.8479$, $p < 0.001$). The mean internodal annual growth rate (cm) was 4.53 ± 0.17 cm ($n = 36$) for main shoots and 3.45 ± 0.28 cm ($n = 31$) for the lateral ones. Mean horizontal growth of the main shoots of *Carpobrotus* was ca. 40 cm/yr.

At both localities, *Carpobrotus* showed values of photochemical efficiency (Fv/Fm) generally above 0.8. There were no differences between localities, but there was a significant interaction between population and microhabitat; in Cala Figuera, Fv/Fm was slightly lower

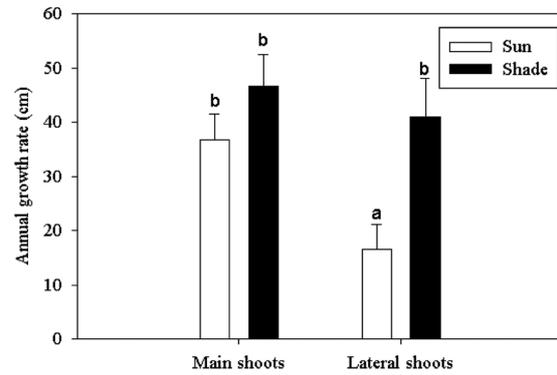


Fig. 4. Annual growth rate for each type of shoot in the two different environmental conditions (mean \pm SE). Bars with the same letter are not significantly different.

in the sun than in the shade ($\chi^2 = 7.06$; $P < 0.01$; Table 1). This ratio was found to differ, although only marginally, between main and lateral shoots ($\chi^2 = 3.61$; $P = 0.06$); consistently in both localities and both microhabitats (interaction not significant), main shoots had slightly lower Fv/Fm than lateral shoots (0.848 ± 0.026 vs. 0.849 ± 0.026 , respectively).

Reddish leaves had lower electron transport rates than their green counterparts (Table 1), which confirmed the senescing nature of the former. In both localities, individuals in the sun had a greater number of red leaves than individuals in the shade ($Z > 3.14$; $P < 0.002$), and such red leaves showed values of electron transport rate somewhat lower in the sun than in the shade ($Z = -1.75$; $P = 0.08$).

Consistent with a greater growth length in the shade,

Table 2. Allometric values and water content (percentage of shoot weight) determined in sun and shade *Carpobrotus* from two localities and for both types of shoots. Values are the mean and SE for measurements on eight independent individuals at each microhabitat and locality. LS = long shoots, SS = short shoots.

Variable	Cala Figuera				Son Serra				Significance of factors
	Sun		Shade		Sun		Shade		
	LS	SS	LS	SS	LS	SS	LS	SS	
Dry stem biomass (g/cm)	0.17 \pm 0.01	0.13 \pm 0.02	0.09 \pm 0.01	0.10 \pm 0.01	0.18 \pm 0.01	0.13 \pm 0.01	0.16 \pm 0.02	0.10 \pm 0.02	Locality: $\chi^2 = 1.58$; $P = 0.21$ Microhabitat: $\chi^2 = 6.36$; $P = 0.01$ Shoot type: $\chi^2 = 8.80$; $P < 0.01$
Dry leaf biomass (g/cm)	0.68 \pm 0.09	0.50 \pm 0.07	0.28 \pm 0.04	0.39 \pm 0.07	0.70 \pm 0.08	0.46 \pm 0.05	0.43 \pm 0.09	0.34 \pm 0.07	Locality: $\chi^2 = 0.18$; $P = 0.67$ Microhabitat: $\chi^2 = 7.49$; $P < 0.01$ Shoot type: $\chi^2 = 4.96$; $P = 0.03$
Number of leaves/shoot length (cm)	2.43 \pm 0.20	1.73 \pm 0.20	1.57 \pm 0.10	1.48 \pm 0.31	2.85 \pm 0.17	2.05 \pm 0.17	1.78 \pm 0.17	1.36 \pm 0.16	Locality: $\chi^2 = 4.51$; $P = 0.03$ Microhabitat: $\chi^2 = 8.78$; $P < 0.01$ Shoot type: $\chi^2 = 7.40$; $P < 0.01$
Water content	84.88 \pm 0.67	85.49 \pm 0.94	89.22 \pm 0.79	90.12 \pm 0.79	87.45 \pm 0.75	87.20 \pm 0.84	90.21 \pm 0.96	90.24 \pm 0.95	Locality: $\chi^2 = 4.02$; $P = 0.04$ Microhabitat: $\chi^2 = 9.99$; $P < 0.01$ Shoot type: $\chi^2 = 0.71$; $P = 0.40$

significant differences in plant water content were also found between sun and shade (Table 2). Individuals in the shade had a greater water content than those in the sun, and this was consistent in the two populations (interaction: $\chi^2 = 1.13$; $P = 0.29$). This water content was also greater at Son Serra than at Cala Figuera. Likewise, the number of leaves/cm was also higher in Son Serra than in Cala Figuera (Table 2). By contrast, neither dry biomass of leaves or stems/cm differed between populations. These three variables were consistently greater in sunny than in shady conditions. Lastly, main shoots had consistently greater dry leaf and stem biomass and a higher number of leaves per unit length than lateral shoots (Table 2).

Plastic phenotypic responses to the light environment differed in extent and pattern among the different variables studied (Table 3). Plasticity for photochemical efficiency and electron transport rate was very low, while annual growth of lateral shoots was highly plastic; annual growth of main shoots, stem and leaf biomass and water content exhibited intermediate values.

Discussion

Carpobrotus showed a remarkably constant performance in the four study sites (despite the fact that one was a sand dune and the others were located on rocky coasts). This was evidenced by similar growth rates of main shoots and similar photochemical efficiency and electron transport rates in sun and shade habitats. Furthermore, even though the plant usually inhabits open areas near the sea, it grows well in the forest understorey, which certainly contributes to the invasion success of the genus. A wide ecological amplitude had already been described for *C. edulis* in California (D'Antonio 1993),

Table 3. Plastic phenotypic responses to light availability in the field. Plasticity is given as a relative distance phenotypic index (RDPI) ranging from 0 (no response) to 1 (maximal response) together with the standard deviation. Variables are arranged in increasing order of plasticity. RDPI is calculated as in Valladares et al. (2006) = 22 individuals; data from both localities were pooled.

Variable	RDPI	SD
ETR _{gl}	0.022	0.002
Fv/Fm	0.023	0.002
Annual growth of main shoots	0.208	0.017
ETR _{rl}	0.243	0.019
Dry stem biomass	0.267	0.021
Number of leaves per stem length	0.314	0.025
Water content	0.323	0.026
Dry leaf biomass	0.379	0.030
Overall mean annual growth	0.578	0.046
Annual growth of lateral shoots	0.628	0.050

which occurs in coastal habitats and also in a number of non-saline environments such as road edges, grass slopes and forest edges.

The relatively homeostatic response in key variables such as growth of main shoot was achieved by plastic adjustments of dry mass distribution, so stems and leaves were heavier in the sun than in the shade but lateral shoots grew faster in the shade than in the sun. In fact, plasticity for variables such as growth of lateral shoots was as high as 0.63, which is a high value of plasticity – compare with values in Gratani et al. (2003) or Valladares et al. (2000, 2006) for Mediterranean and tropical plants, respectively). Long shoots contribute to ‘explore’ the environment extending the framework of the plant into new territory, similar to observations in other clonal plants (Marbà & Duarte 1998). In contrast, short shoots are located along the long shoots and serve to ‘exploit’ the occupied site; they contribute to increase the volume of the plant and its relative leaf surface area, without or with little influence on horizontal plant growth (Sintes et al. 2007). A predictably short shoot bud may occasionally develop as a long shoot if its bearing axis is damaged and often has a precise and consistent number of foliar components for each increment of growth (Bell 1993). Such shoots were found to be shorter in the sun than in the shade, but this did not occur with the main shoots. This is unlikely to be due to the only marginal significant differences in photochemical efficiency between main and lateral shoots.

Carpobrotus showed no sign of high light stress in any of the two localities where this was examined, as values of photochemical efficiency were in general above 0.8, except for the case of reddish shoots. Although *Carpobrotus* exhibited a remarkable capacity to cope with both high and low light, those plants in full sunlight exhibited slightly, but significantly lower photochemical efficiency, an indication of minor but chronic photoinhibition, as found in other species (Werner et al. 2002), and a larger proportion of reddish, senescing leaves. Individuals grew at a higher speed in the shade than in the sun, and we attribute such difference to the search for light by shaded shoots. Studying plant morphological plasticity to various light regimes in seedlings, Kuo et al. (1999) showed that as light intensity decreased, plant height of *Lea guineensis* and *Maba buxifolia* increased significantly. An increase of leaf area in shaded conditions has also been reported for *Echinochloa oryzoides* (Gibson & Fischer 2001). In all these cases, the increased growth was in fact part of the shade avoidance response, while *Carpobrotus* exhibited a more subtle and complex response, keeping growth of main shoots rather stable but significantly enhancing growth of lateral shoots, which have slightly different functions, as discussed above.

Lower foliage density, lower dry leaf and stem bio-

mass and longer stem elongation in the shade are usual plant responses to low light conditions, particularly when not only the intensity but also the spectrum (red-far red ratio) is modified. In fact, shade-tolerant grasses often increase yield under moderate light levels (Samarakoon et al. 1990). Lower evaporative demand and different tissue properties led to higher water content in the shade than in sun leaves, a pattern that has been often observed (Niinemets & Valladares 2004). The good performance of *Carpobrotus* in the shade in terms of growth was due not only to its phenotypic plasticity, expressed in different allocation patterns in sun and shade individuals, and to its clonal growth, which allowed for the continuous search of the best neighbour patches, but also to the relatively moderate shade of the particular understories studied. Shade was not very intense, although enough for a remarkable elimination of the high light stress as revealed by the optimal photochemical efficiency values and the reduced UV radiation reaching shade *Carpobrotus* individuals (UV was significantly more reduced in the shade than PAR, Table 1). The phenotypic plasticity in response to light shown by *Carpobrotus*, which affected primarily the lateral shoots, seems to allow for an efficient space occupation, which is one of the common traits conferring invasiveness (Mooney & Hobbs 2000; Niinemets et al. 2003).

Two functional strategies can be distinguished in clonal plants: (1) *phalanx* strategy, which involves the production of frequently-branched shoots with short spacers and occupy local resource patches with dense populations, and (2) *guerrilla* strategy, with fewer branched shoots, and longer spacers growing out of a patch to explore adjacent patches (Lovett Doust 1981). The extensive intergrowth of individual plants (genets) and the larger growth of long vs. short shoots indicate that *Carpobrotus* exhibits a guerrilla-type clonal morphology, such as that reported for an invasive fern (Parks & Werth 1993). However, *Carpobrotus* is capable of switching to a phalanx strategy under optimal environmental conditions (in our case, enough light). The greatest shoot growth of *Carpobrotus* takes place in spring (from March to June), when temperatures are moderate (13 °C to 23 °C) and the first rains fall. The lowest growth rate occurs in summer and early autumn (from July to October), during the most extreme drought periods. This different growth performance over the seasons could be due to water stress and extreme temperatures during summer and winter periods as has been shown for many perennial Mediterranean plants that co-occur with *Carpobrotus*. Its high annual growth of main shoots, ca. 40 cm, explains its capacity for a vigorous habitat colonization.

In short, *Carpobrotus* performs very well in open areas near the sea, regardless if it is on a dune or on the rocky coast, as it is able to successfully cope with exces-

sive light. However, the moderate shade of Mediterranean forests dominated by *P. halepensis* facilitates the inland spreading of *Carpobrotus* by reducing high light stress without exerting strong limitations for growth. The clonal growth and the plastic morphological response to light of this highly invasive plant are efficient mechanisms for its rapid colonization of space and successful establishment in the vicinities of the coastal zones in Mediterranean environments.

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