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Lantana camara L.: a weed with great light-acclimation capacity

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Abstract

Plant invasions may be limited by low radiation levels in ecosystems such as forests. *Lantana camara* has been classified among the world's 10 worst weeds since it is invading many different habitats all around the planet. Morphological and physiological responses to different light fluxes were analyzed. *L. camara* was able to acclimate to moderately shaded environments, showing a high phenotypic plasticity. Morphological acclimation to low light fluxes was typified by increasing leaf size, leaf biomass, leaf area index and plant height and by reduced stomatal density and leaf thickness. Plants in full sunlight produced many more inflorescences than in shaded conditions. Physiological acclimation to low radiation levels was shown to be higher stomatal conductance, higher net photosynthetic rates and higher efficiency of photosystem II (PSII). *L. camara* behaves as a facultative shade-tolerant plant, being able to grow in moderately sheltered environments, however its invasion could be limited in very shady habitats. Control efforts in patchy environments should be mainly directed against individuals in open areas since that is where the production of seeds would be higher and the progress of the invasion would be faster.

Additional key words: chlorophyll fluorescence; gas exchange; leaf growth rate; light acclimation; photosynthetic pigments; trade–off.

Introduction

Several features of plant form, physiology, and resource allocation vary with the level of irradiance to which plants are acclimated and/or ecologically restricted (Givnish 1988); thus, plants exposed to high irradiance levels generally have higher photosynthetic rates, chlorophyll (Chl) *a*/*b* ratio, leaf thickness, stomatal density and reproductive efforts, and smaller stomatal size than plants at low light conditions (Boardman 1977, Björkman 1981, Bazzaz *et al*. 1987, Givnish 1987).

Leaf morphology and anatomy, gas exchange, water relations, water-use efficiency, stomatal conductance (g_s), biomass and photosynthesis of sun-adapted plants can be altered when growing in a light-limiting environment (Björkman 1981, Muthuchelian *et al*. 1989). In addition, shade diminishes reproductive potential directly by decreasing flowering, fruit set and fruit size (Hampson *et al.*1996). To avoid negative effects of low radiation levels, some plants show a high degree of phenotypic plasticity in response to low light conditions, manifested in increased leaf area and stem biomass, reduced leaf thickness, increased specific leaf area and increased photosynthetic pigment concentration for maximization of light absorption (Björkman 1981, Turnbull 1991, Poorter and Perez-Soba 2001, Sage and McKown 2006).

Invasive plant species may show a high tolerance to different abiotic environmental factors (Mack 1996) but their colonization may be limited by extreme conditions such as low radiation levels (Dawson *et al.* 2009). In this context, the tolerance of invasive species to harsh environments may be related to rapid evolutionary changes (Lambrinos 2004) and high phenotypic plasticity (Daehler 2003).

L. camara L. (Verbenaceae) has been classified among the world's 10 worst weeds, invading a wide variety of habitats in tropical, subtropical and temperate regions (Holm *et al.* 1977, Sharma *et al*. 1988, Day *et al*. 2003).

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Abbreviations: C_i – intercellular CO_2 concentration; Car – carotenoids; Chl – chlorophyll; F_m – maximal fluorescence level in the dark-adapted state; F_0 – minimal fluorescence level in the dark-adapted state; F_v/F_m – maximum quantum efficiency of PSII photochemistry; g_s – stomatal conductance; LAI – leaf area index; LCP – light compensation point; LGR – leaf growth rate; LSP – light saturation point; NPQ – nonphotochemical quenching; P_{max} – maximum photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PSII – photosystem II; q_P – photochemical quenching; R_D – dark respiration rate; SLA – specific leaf area; WUE_i – intrinsic water-use efficiency; Φ_{PSII} – quantum efficiency of PSII.
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Researchers have described *L. camara* as mostly occupying open sunny places such as degraded lands, grasslands, crops and forest edges, abandoned crops, coastal areas or disturbed forests (Parsons and Cuthbertson 2001, Sharma *et al*. 2005), and as not developing properly in very shady habitats such as well-conserved forests (Thakur *et al.* 1992, Fensham *et al*. 1994, Gentle and Duggin 1997). However, our field observations of invasive populations of *L. camara* in the Galapagos Islands and in the Southwest Iberian Peninsula showed that they were able to grow in unaltered forests. There has been no prior research specifically studying the responses of *L. camara* to different radiation environments.

Our observations in the field led us to hypothesize that *L. camara* would be able to grow in shady environments, showing high phenotypic plasticity in response to different light environments. To test this hypothesis, this work analyzes a series of morphological and physiological responses of *L. camara* to four contrasted light fluxes.

Materials and methods

Plant material and light treatments: Plant material was collected in May 2009, consisting in stem cuttings of ten adult individuals of *L. camara* (4 cuttings per individual) collected from an invading population growing at an open, unshaded site on the Asperillo Sea Cliff, Southwest Iberian Peninsula (37º06'N – 6º46'W). Cuttings with similar sizes (*ca*. 20 cm long and *ca*. 1 cm diameter) were cultivated in perlite substrate until they developed abundant roots and then were transplanted to plastic pots (diameter: 16.5 cm; depth: 15.0 cm) in peat soil and immediately exposed to the light treatments. Every pot contained just one cutting that was chosen randomly from those collected in the field.

Our experiment was conducted in the open-air area of the greenhouse facilities of the University of Seville (37º21'42''N – 5º59'15''W) from July to December 2009. Pots were randomly assigned to one of four light treatments: (T1): 100% of full sunlight, (T2): 55% of full sunlight, (T3): 37% of full sunlight and (T4): 23% of full sunlight (n = 4 plants per treatment). Irradiance was controlled with neutral shade cloth (Hummert International, Earth City, MO USA). Although deep shade (<5%) is traditionally used in shade-tolerance studies, we used 23% of full sunlight because it represents the deepest shade generally found in the natural forests of Galapagos Island and coastal areas of Southwest Iberian Peninsula where *L. camara* is invading (Carrión-Tacuri, unpublished data). Maximum daily photosynthetic photon flux density (PPFD) during the experiment ranged from 1,900 µmol(photon) m^{-2} s^{-1} in July to 1,100 µmol(photon) m^{-2} s^{-1} in December. Pots were permanently submerged 1 cm deep in water and watered gently once a day to avoid water stress.

Gas-exchange measurements were taken for the youngest fully developed leaf of randomly chosen stems using an infrared gas analyzer in an open system (*LI-6400, Li-COR Inc.*, Lincoln, NE, USA). Net photosynthetic rate (P_N), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i) were recorded in October 2009 within light saturation curves (n = 2 curves per treatment, Martínez-Ferri *et al*. 2004). Measurements were taken at 23ºC, 380 µmol mol^{-1} of CO_2 concentration. Vapour pressure deficit (VPD) was held at a constant range from 1–1.3 kPa. P_N, g_s, and C_i were calculated according to von Caemmerer and Farquhar (1981). Intrinsic water-use efficiency (WUE_i) was calculated as the ratio between P_N and g_s (Moutinho-Pereira *et al.* 2004). The photosynthetic response of the leaves to photosynthetic photon flux density (PPFD) was modelled by a rectangular hyperbola quadratic equation presented by Chartier and Prioul (1976), where the light compensation point (LCP) and the dark respiration rate (R_D) were estimated from axis intercepts. The light saturation point (LSP) was defined as the lowest value of PPFD at which maximum photosynthetic rate (P_{max}) was reached.

Chl *a* fluorescence parameters were also recorded in October 2009 at predawn and at midday at the light flux of each treatment. Measurements were taken at 23ºC air temperature with 62% air relative humidity at predawn and at 24ºC with 58% humidity at midday.

Fluorescence was measured in the adaxial leaf surface of the youngest fully developed leaf of randomly chosen stems (n = 4 plants per treatment; 4 leaves per plant) using a portable modulated fluorimeter (*FMS-2, Hansatech Instruments Ltd*., King´s Lynn, UK). Leaves were adapted to dark conditions for 30 min using leaf clips. The minimal fluorescence level in the dark-adapted state (F_0) was measured using a modulate pulse [PPFD < 0.05 µmol(photon) m^{-2} s^{-1} for 1.8 µs] too small to induce significant physiological changes in the plant (Schreiber *et al*. 1986). The data recorded were averages taken over a 1.6-s period. Maximal fluorescence in this state (F_m) was measured after applying a saturating actinic light pulse of 15,000 µmol(photon) m^{-2} s^{-1} for 0.7 s (Bolhàr-Nordenkampf and Öquist 1993). The value of F_m was recorded as the highest average of two consecutive points. Values of the variable fluorescence ($F_v = F_m - F_0$) and the maximum quantum efficiency of PSII photochemistry (F_v/F_m) were calculated.

The same leaf section of each plant was used to measure light-adapted parameters. Steady state fluorescence yield (F_s) was recorded after adapting plants to ambient light conditions [with full sunlight of 1,150 µmol(photon) m^{-2} s^{-1}]. A saturating actinic light pulse of

15,000 µmol(photon) m^{-2} s^{-1} for 0.7 s was then used to produce the maximum fluorescence yield (F_m') by temporarily inhibiting PSII photochemistry. With both light- and dark-adapted states fluorescence parameters, the following were calculated: quantum efficiency of PSII [$\Phi_{PSII} = (F_m' - F_s)/F_m'$], photochemical quenching [$q_P = (F_m' - F_s)/(F_m' - F_0)$], and nonphotochemical quenching [$NPQ = (F_m - F_m')/F_m'$] (Bilger and Björkman 1990).

Photosynthetic pigments of the same leaves used for Chl fluorescence measurements (n = 4; 1 leaf per plant) were extracted in October 2009 using 0.1 g of fresh material in 5 ml of 80% aqueous acetone. After filtering, 0.5 ml of the suspension was diluted with a further 2 ml of acetone and Chl *a*, Chl *b,* and carotenoids (Car) concentrations were determined with a *Hitachi U–2001* spectrophotometer (*Hitachi Ltd., Japan*) using three wavelengths (663.2, 646.8, and 470.0 nm). Concentrations of pigments [mg g^{-1}(FM)] were obtained through calculation (Lichtenthaler 1987).

Stomatal density (SD) [number of stomata mm^{-2}(leaf blade)] was determined for youngest fully developed leaves in December 2009 (n = 4; 1 leaf of each plant per treatment). From the abaxial surface of each leaf, a sample was taken using the imprint technique (Meister and Bolhàr-Nordenkampf 2003), three random fields (0.14 mm^2) were observed and the number of stomata was counted on each sample using an *OLYMPUS BX61 Motorized System Microscope* (Horanic and Gardner 1967).

Leaf growth and leaf morphology: Relative leaf growth rate (LGR) was measured for the youngest leaf (n = 4 plants per treatment; 3 leaves per plant) using an *Electronic Digital Caliper* in October 2009. Leaves were marked with inert sealant and their length was recorded just after marking them and again 1 week later. LGR was calculated as the net growth in length after 1 week, divided by the initial leaf length (Ewing *et al*. 1995). Leaf area was calculated applying the ellipse formula after recording maximum length and maximum width of adult leaves (n = 4 per treatment; 5 leaves per plant).

Leaf area index and specific leaf area: To calculate the leaf area index (LAI) at the end of the experiment we recorded the area covered by each plant and the dry mass of four leaf drilled circular pieces (1.3 cm diameter) per plant (n = 4 plants). Then to calculate total leaf area and LAI per plant, we used the mass of the circular pieces with a known area and the recorded total leaf dry mass per plant as reported previously. The specific leaf area (SLA) was calculated as the ratio of leaf area to leaf dry mass [cm^2 g^{-1}] pursuant to Garnier *et al*. (2001).

Plant morphology, number of inflorescences and biomass allocation: At the end of the experiment, maximum plant height, occupied area (by measuring maximum length and width) and the number of inflorescences were recorded for each plant. Finally plants were removed from the pots, carefully washed and divided into leaves, stems and roots. The components of each plant were dried separately in a forced-air oven (80ºC for 48 h) and dry mass was recorded.

Statistical analysis: All statistical tests were conducted using *SPSS v.17* (*Statistic Inc*.). The *Kolmogorov-Smirnov* test was used to test for data normality and the *Levene test* for homogeneity of variance. When necessary, dependent variables were transformed using the functions 1/x, ln(x) or √x to achieve requirements of normality. Analysis of variance (*ANOVA*) was used to detect differences between light treatments and *Tukey's Honest Significant Difference* (HSD) test was used to detect differences between two treatments only if *F*-test was significant at the 0.05 level of probability. *Kruskal-Wallis* nonparametric *ANOVA* was used to compare treatments when normality or homogeneity of variance were not reached after transformations, followed by the *Mann-Whitney U*-test to compare two treatments. Deviations were calculated as standard deviation (SD).

Results

Gas exchange: P_N for T3 was higher than for the other treatments (Fig. 1), showing the P_{max} [*ca*. 10 µmol(CO_2) m^{-2} s^{-1}] at high light fluxes [1,750 µmol (photon) m^{-2} s^{-1}] whereas T2 showed the lowest P_{max} [*ca*. 6 µmol(CO_2) m^{-2} s^{-1}]. LSP was much higher for the plants at shade conditions [*ca*. 2,000 µmol(photon) m^{-2} s^{-1}] than for those at full sunlight [*ca*. 1,125 µmol(photon) m^{-2} s^{-1}]. LCP was the highest for T1 [*ca*. 12 µmol(photon) m^{-2} s^{-1}] and the lowest for T2 [*ca*. 4 µmol(photon) m^{-2} s^{-1}] while the other treatments showed intermediate values [*ca*. 5 to 8 µmol(photon) m^{-2} s^{-1}]. T1 showed the maximum R_D [–0.80 µmol(CO_2) m^{-2} s^{-1}] and T2 the minimum [–0.35 µmol(CO_2) m^{-2} s^{-1}] with T3 and T4 showing values *ca*. –0.5 to –0.7 µmol(CO_2) m^{-2} s^{-1} (Table 1).

Plants exposed to full sunlight (T1) showed the smallest and almost constant g_s [*ca*. 90 mmol(H_2O) m^{-2} s^{-1}]. The g_s values for T2 were similar to those for T1 at the lowest light fluxes, increasing to *ca*. 300 mmol(H_2O) m^{-2} s^{-1} at higher PPFD. g_s for T3 and T4 was higher than for T1 and T2, being *ca*. 300 mmol(H_2O) m^{-2} s^{-1} at lower radiations and increasing to *ca*. 550 mmol(H_2O) m^{-2} s^{-1} with PPFD (Fig. 1).

C_i for T1 ranged from *ca*. 210–380 µmol mol^{-1}, being lower than the C_i for all treatments from 100 µmol (photon) m^{-2} s^{-1} onwards. C_i for T2, T3 and T4 was *ca*. 340 µmol mol^{-1}. WUE_i for T1 was higher (maximum *ca*. 74 mmol mol^{-1}) than for the other treatments (*ca*. 18 mmol mol^{-1}) (Fig. 1).

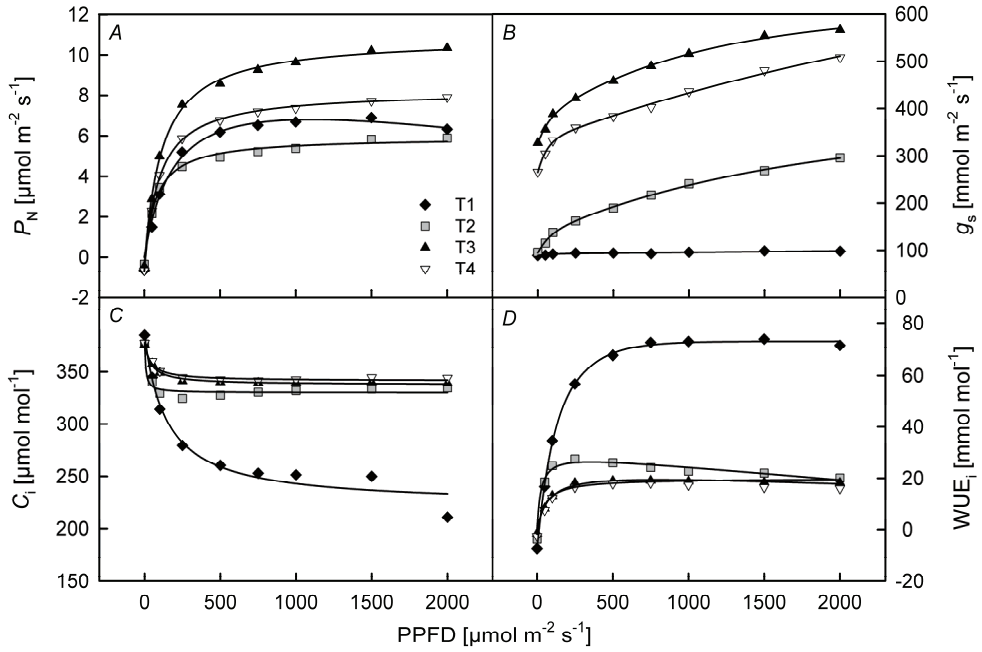

Fig. 1. *A*: Net photosynthetic rate (P_N), *B*: stomatal conductance (g_s), *C*: intercellular CO_2 concentration (C_i) and *D*: intrinsic water-use efficiency (WUE_i) against photosynthetic photon flux density (PPFD) for *Lantana camara* in four light treatments (T1: 100% sunlight; T2: 55% sunlight; T3: 37% sunlight; T4: 23% sunlight). Data are means (n = 2).

Table 1. Maximum photosynthetic rate (P_{max}), light compensation point (LCP), dark respiration rate (R_D); and light saturation point (LSP) for *Lantana camara* in four light treatments (T1 – 100% sunlight; T2 – 55% sunlight; T3 – 37% sunlight; T4 – 23% sunlight). (mean ± SD, n = 2 light curves per treatment).

Variables/Treatments	T1	T2	T3	T4
P_{max} [µmol(CO_2) m^{-2} s^{-1}]	6.9 ± 1.4	5.9 ± 1.9	10.4 ± 0.1	7.9 ± 1.4
LCP [µmol m^{-2} s^{-1}]	11.9 ± 1.3	3.8 ± 0.0	5.3 ± 2.1	8.3 ± 2.1
R_D [µmol m^{-2} s^{-1}]	–0.8 ± 0.1	–0.3 ± 0.0	–0.5 ± 0.1	–0.7 ± 0.1
LSP [µmol m^{-2} s^{-1}]	1,125 ± 530	1,750 ± 354	1,750 ± 354	2,000 ± 0

Chlorophyll fluorescence: At predawn, Φ_{PSII} (*ca*. 0.800), q_P (*ca*. 0.98), F_0 (*ca*. 209 r.u.) and F_v/F_m (*ca*. 0.850) were similar for every treatment. F_m, F_v and NPQ for T1 were lower than for the other treatments (*Tukey*'s test, p<0.01).

Φ_{PSII} at midday for T1 (0.375 ± 0.12) was lower than for the other treatments (*ca*. 0.700) (*Kruskal-Wallis ANOVA*, χ^2 = 10.147, p<0.05; *Mann-Whitney U*-test, p<0.05). q_P was also lower for T1 (0.78 ± 0.06) than for T4 (0.89 ± 0.02), showing T2 and T3 intermediate values (*ANOVA*, F = 4.738, p<0.05; *Tukey*'s test, p<0.05). NPQ was much higher for T1 (1.61 ± 0.52) than for the other three treatments (*ca*. 0.29) (*Kruskal-Wallis ANOVA*, χ^2 = 9.551, p<0.05; *Mann-Whitney U*-test, p<0.05). T2, T3 and T4 showed a higher F_v/F_m (*ca*. 0.825) than T1 (*ca*. 0.788) (*Kruskal-Wallis ANOVA*, χ^2 = 9.288, p<0.05; *Mann-Whitney U*-test, p<0.05). Lower values of F_v/F_m for T1 were due to lower F_m (*Tukey's* test, p<0.05) with similar F_0 (*ca*. 200 r.u.; Fig. 2).

Photosynthetic pigments: T1 showed the lowest concentrations of every photosynthetic pigment. T3 had the highest content of Chl *a* [1.67 ± 0.10 mg g^{-1}(FM)] (*ANOVA*, F = 7.115, p<0.01; *Tukey's test*, p<0.01) and T2 showed the highest Chl *b* content [0.69 ± 0.12 mg g^{-1} (FM)] (*Kruskal-Wallis*, χ^2 = 5.333, p<0.05; *Mann-Whitney U*-test, p<0.05). Car showed similar values for every shade treatment [*ca*. 0.75 mg g^{-1}(FM)] which were all higher than for the full sunlight treatment [*ca*. 0.48 mg g^{-1}(FM)] (*ANOVA*, F = 4.014, p<0.05; *Tukey*'s test, p<0.05). Chl *a*:Chl *b* ratio varied between 2.42 and 2.98; T2 and T3 showed higher values than T1 (*Mann-Whitney U*-test, p<0.05). Chl (*a*+*b*):Car ratio was higher for T2 [3.19 ± 0.25 mg g^{-1}(FM)] than for T4 [2.38 ± 0.49 mg g^{-1} (FM)], showing T1 and T3 intermediate values (Table 2).

Stomatal density, leaf growth rate and leaf morphology: SD was higher for T1 [283 ± 23 stomata mm^{-2}(leaf blade)] than for darker treatments [*ca*. 170 stomata mm^{-2} (leaf blade)]; *Kruskal-Wallis ANOVA*, χ^2 = 9.345, p<0.05; *Mann-Whitney U*-test, p<0.05; Table 2).

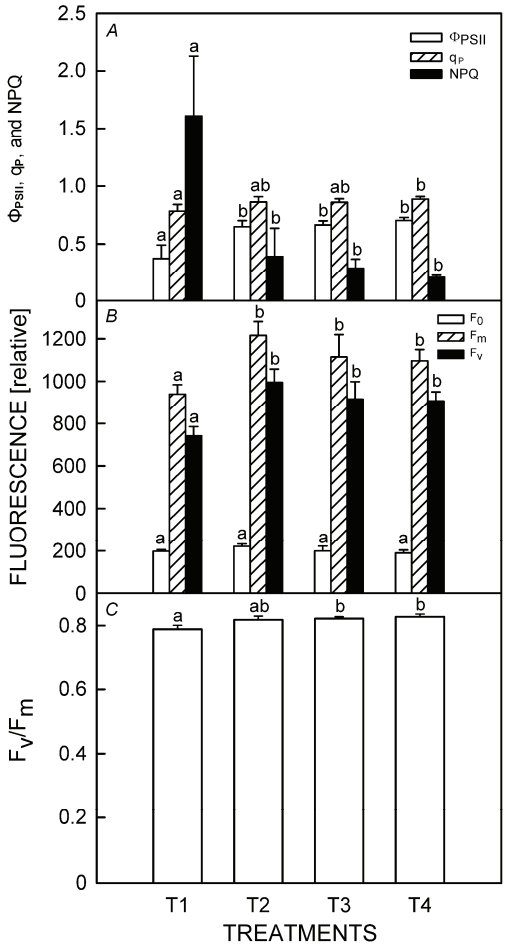

Fig. 2. *A*: Quantum efficiency of PSII (Φ_{PSII}), photochemical quenching (q_P), nonphotochemical quenching (NPQ), *B*: basal fluorescence (F_0), maximum fluorescence (F_m), variable fluorescence (F_v) and *C*: potential photochemical efficiency (F_v/F_m) for *Lantana camara* in four light treatments during midday (T1: 100% sunlight; T2: 55% sunlight; T3: 37% sunlight; T4: 23% sunlight), (mean ± SD, n = 4).

LGR tended to increase at darker treatments, varying between *ca*. 0.85 and 2.40 mm week^{-1} mm^{-1}. Leaf mean width varied between 4.5 ± 0.1 cm and 7.9 ± 0.2 cm and leaf mean length between 6.9 ± 0.3 cm and 11.8 ± 0.9 cm. Leaves were larger at darker treatments, changing between 24.3 ± 3.0 cm^2 for T1 and 74.0 ± 10.3 cm^2 for T4 (*ANOVA*, F = 15.423, p<0.01; *Tukey*'s test, p<0.05; Table 2).

Leaf area index and specific leaf area: T3 showed a much higher LAI (*ca*. 21) than T1 and T2 (*ca*. 8) (*ANOVA*, F = 10.240, p<0.01; *Tukey*'s test, p<0.05). SLA was lower for T1 (19.67 ± 3.32 cm^2 g^{-1}) than for shadier treatments (*ca*. 34 cm^2 g^{-1}; *ANOVA*, F = 12.615, p<0.01; *Tukey*'s test, p<0.01; Table 2).

Plant height, cover and number of inflorescences: Plants were taller at darker treatments, varying between 51.0 ± 6.9 cm for T1 and 89.7 ± 3.9 cm for T3 (*Kruskal-Wallis ANOVA*, χ^2 = 8.886, p<0.05; *Mann-Whitney U*-test, p<0.05). Individual plant cover was *ca*. 0.140 m^2, without showing any significant differences between treatments (*ANOVA*, p>0.05). T1 showed much more inflorescences (127 ± 34 inflorescences m^{-2}) than the other three treatments (*ca*. 20–30 inflorescences m^{-2}; *ANOVA*, F = 14.658, p<0.01; Table 2). Finally, the number of fruits per infructescence did not change between treatments, varying between 5 and 15 fruits infructescence^{-1}.

Biomass allocation: Stem and root biomass did not vary between treatments (*ANOVA*, p>0.05). Except T3 showed higher leaf biomass [59.5 ± 12.9 g(DM) m^{-2}] than T1 and T2 [*ca*. 33 g(DM) m^{-2}] (*ANOVA*, F = 5.164, p<0.05; Fig. 3). Above-to-belowground biomass and leaves:stems ratios showed no significant differences between light treatments (*ANOVA*, p>0.05).

Discussion

This work reports that the invasive species *L. camara* is able to acclimate to moderately shaded environments, showing high phenotypic plasticity in the form of a wide variety of morphological and physiologically responses, but its reproductive effort was lower at low light fluxes.

As other plant species, morphological acclimation of *L. camara* to low radiations was typified by increasing leaf size, leaf biomass, LAI and plant height, and by decreasing SD and leaf thickness reflected in a higher SLA (Björkman 1981, Poorter and Perez-Soba 2001). Increment of SLA at low light conditions is due to changes in size, shape, and number of leaf mesophyll cells that reduce leaf thickness (Björkman 1981). A higher SD at more illuminated environments has been described previously, being characterized as a xeromorphic leaf feature (Gyorgy 2009). *L. camara* generally grows from 2 to 4 m high (Auld and Medd 1987, Conn 1992) but to avoid shade conditions it can grow up to 15 m supported by surrounding vegetation (Swarbrick *et al*. 1998). This supports our finding of taller plants at shadier environments with larger but thinner stems. *L. camara* leaves have been reported to be 20–120 mm long and 15–80 mm wide (Holm *et al*. 1977, Conn 1992, Munir 1996, Swarbrick *et al*. 1998, Parsons and Cuthbertson 2001). Our results for plants exposed to full sunlight ranged between those intervals (50–75 mm long and 28–53 mm wide) but our values for shaded plants (84–137 mm long and 64–94 mm wide) were higher than those recorded previously. Van Oosterhout (2004) recorded changes on *L. camara* leaf size as a function of moisture availability. Previous studies for different plant species have described increases in foliar size and LAI as

Table 2. Chlorophyll (Chl) *a*, Chl *b*; carotenoids (Car) contents; Chl *a*:Chl *b* ratio, Chl (*a*+*b*):Car ratio, stomatal density, relative leaf growth rate, leaf area, plant height, occupied areas per plant, inflorescences, leaf area index and specific leaf area for *Lantana camara* in four light treatments (T1 – 100% sunlight; T2 – 55% sunlight; T3 – 37% sunlight; T4 – 23% sunlight). *Different letters* indicate significant difference between treatments. FM – fresh mass. (mean ± SD, $n = 4$).

Variables/Treatments	T1	T2	T3	T4
Chl *a* [mg g^{-1}(FM)]	0.93 ± 0.12^{a}	1.65 ± 0.25^{b}	1.67 ± 0.10^{b}	1.38 ± 0.43^{ab}
Chl *b* [mg g^{-1}(FM)]	0.32 ± 0.06^{a}	0.69 ± 0.12^{b}	0.67 ± 0.05^{b}	0.41 ± 0.27^{ab}
Car [mg g^{-1}(FM)]	0.48 ± 0.05^{a}	0.74 ± 0.12^{b}	0.77 ± 0.07^{b}	0.74 ± 0.10^{b}
Chl *a*:Chl *b*	2.98 ± 0.35^{a}	2.42 ± 0.06^{b}	2.50 ± 0.04^{b}	2.55 ± 0.04^{ab}
Chl (*a*+*b*):Car	2.62 ± 0.41^{ab}	3.19 ± 0.25^{a}	3.07 ± 0.31^{ab}	2.38 ± 0.49^{b}
Stomatal density [stomata mm^{-2}]	283 ± 23^{a}	197 ± 42^{ab}	165 ± 7^{b}	181 ± 25^{b}
Leaf growth rate [mm $week^{-1}$ mm^{-1}]	0.85 ± 0.29^{a}	1.25 ± 0.69^{a}	2.33 ± 1.44^{a}	2.39 ± 0.62^{a}
Leaf area [cm^2]	24.3 ± 3.0^{a}	44.1 ± 11.6^{ac}	66.5 ± 16.7^{bc}	74.0 ± 10.3^{b}
Plant height [cm]	51.0 ± 6.9^{a}	83.3 ± 14.2^{ab}	89.8 ± 3.9^{b}	85.0 ± 10.4^{b}
Occupied area [m^2]	0.15 ± 0.07^{a}	0.15 ± 0.03^{a}	0.14 ± 0.03^{a}	0.14 ± 0.06^{a}
Inflorescences [inflorescences m^{-2}]	127 ± 34^{a}	33 ± 33^{b}	23 ± 8^{b}	23 ± 19^{b}
Leaf area index [cm^2 g^{-1}]	6.4 ± 3.4^{a}	10.4 ± 2.0^{a}	21.4 ± 6.0^{b}	14.6 ± 3.6^{ab}
Specific leaf area [cm^2 g^{-1}]	19.7 ± 3.3^{a}	34.0 ± 5.1^{b}	38.5 ± 4.9^{b}	32.6 ± 4.5^{b}

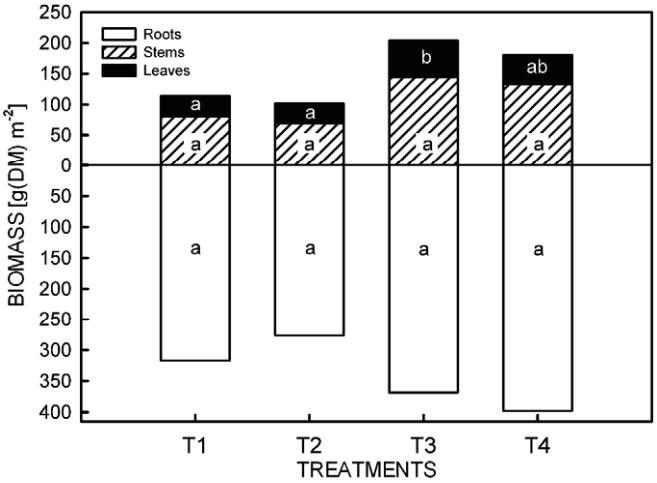

Fig. 3. Biomass allocation in roots, stems and roots [g(DM) m^{-2}] for *Lantana camara* in four light treatments (T1 – 100% sunlight; T2 – 55% sunlight; T3 – 37% sunlight; T4 – 23% sunlight). *Different letters* indicate significant difference between treatments. DM – dry mass. Data are means ($n = 4$).

responses to shady conditions (Lichtenthaler *et al*. 1981, Meziane and Shipley 2001, McAlpine and Jesson 2007).

Above-to-belowground biomass and leaf-to-stem biomass ratios were similar across all light environments. This is not in keeping with optimal partitioning models that predict that some plants optimise growth under different environmental conditions by shifting biomass allocation among tissue types to maximise the capture of limiting resources (McAlpine and Jesson 2007). Thus, *L. camara* seemed to respond to lower radiation levels by changing its growth form rather than by modifying its biomass allocation pattern. Only foliar biomass in conditions of moderate shade was higher than for plants growing at full sunlight. Plants at full sunlight produced a higher number of inflorescences than the shading treatments as reported in other studies (Hampson *et al*. 1996, Matsoukis *et al*. 2001). High temperatures and especially high radiations act as induction stimuli for flowering (Vasconcelos *et al*. 2009). Our results pointed to the existence of an allocation trade–off among vegetative growth and sexual reproduction for *L. camara*, capable of producing relatively large and numerous berries, as has been reported for other species (*e.g*. Thompson and Eckert 2004, Zunzunegui *et al*. 2006).

On the other hand, *L. camara* physiological acclimation to low radiation levels was shown as higher Φ_{PSII}, q_P, and F_v/F_m reflecting higher efficiency of PSII (Bolhàr-Nordenkampf and Öquist 1993). The decrease in F_v/F_m at higher radiation levels was due to lower F_m values with similar F_0, reflecting deactivation of PSII reaction centres at high light (Maxwell and Johnson 2000).

In addition, plants exposed to shadier conditions showed lower NPQ without a clear relationship with Chl (*a*+*b*)/Car ratio, which indicates that the xanthophyll cycle seemed to play an important role in *L. camara* NPQ; this was also supported by the large differences between predawn and midday NPQ recorded for plants exposed to full sunlight (Szabo *et al*. 2005). Moreover, Chl concentration increased at lower light fluxes as an acclimation response to increase radiation absorption (Turnbull 1991). In contrast, a reduction in Chl

concentration at higher radiation levels can be attributed to a photoprotective response against adverse conditions, by reducing the leaf photon absorption capacity, thus preventing over–excitation of photosynthesis (Anderson *et al*. 1992), as reported for invasive *L. camara* subjected to extreme drought at Galapagos Islands (Castillo *et al*. 2007). As a result of the lower concentration of photosynthetic pigments, *L. camara* plants that grow at full sunlight showed a faster saturation of photosynthesis with light and a consequently lower q_P and light saturation point. Photoprotection mechanisms allowed *L. camara* to avoid permanent photodamages as reflected in similar Φ_{PSII}, q_P, and F_v/F_m for every light treatment at predawn.

The capacity of *L. camara* to acclimate to shady environments was also shown as higher P_N, which could be related to very different responses such as a highly efficient PSII and high Chl concentrations. Nevertheless, P_N recorded for *L. camara* was lower than those reported previously for sun leaves [10–15 μmol(CO_2) m^{-2} s^{-1}] following Loach (1967) and Larcher (1995), except for plants exposed to 37% of full sunlight. These plants showed the highest P_N coinciding with the highest g_s. In contrast, *L. camara* plants exposed to full sunlight showed the lowest g_s [*ca*. 100 mmol(H_2O) m^{-2} s^{-1}] even with the highest stomatal density, since stomata closure is regulated by radiation level (Broadman 1977, Smith 1981). The low values of g_s at full sunlight did not limit P_N (C_i dropped just to *ca*. 250 μmol mol^{-1}) in relation to plants at 55% of full sunlight with higher g_s. As a result, *L. camara* at full sunlight showed much higher WUE_i than those exposed to lower radiation levels.

Similar to previous studies of other shade-tolerant species, this plant adjusted physiologically to shading by lower light compensation points and dark respiration rates (Sims and Pearcy 1991, Midgley *et al*. 1992, Hamerlynck and Knapp 1994, Groninger *et al*. 1996, Olsen *et al*. 2002, Aleric and Kirkman 2005), being typified as physiological acclimation to low-light environments (Broadman 1977, Smith 1981). P_{max} increased with increasing light treatment up to intermediate light levels (37% of full sunlight), followed by a decline in P_{max} at full sunlight (Aleric and Kirkman 2005).

L. camara behaves as a facultative shade-tolerant plant, being able to grow on moderately sheltered environments. This result agrees with our field observations of invasive populations in Galapagos Islands and Southwest Iberian Peninsula that are able to colonize unaltered forests. Thus, *L. camara* seems to be capable of invading both open and moderately shaded habitats as are many shade-tolerant invaders (Martin *et al*. 2009) and it must be able to tolerate considerable self-shading in order thrive in dense thickets of its own growth.

Phenotypic plasticity would be particularly advantageous for *L. camara* in disturbed environments where light conditions are highly variable. The degree of phenotypic plasticity has been identified as one of the factors that can be used to predict the plant's invasiveness (Ren and Zang 2009). In fact, phenotypic plasticity of some exotic species grown in different light environments has been found to be greater than for co-occurring native species (Pattison *et al*. 1998, Schweitzer and Larson 1999, Zheng *et al.* 2009). Moreover, invasive populations showed a higher or similar phenotypic plasticity than the same species in their native populations (Bossdorf *et al*. 2005). Pattison *et al*. (1998) showed that invasive species in Hawaii have a higher P_{max} than native species exposed to contrasted radiation levels. According to Pattison *et al*. (1998) and Zheng *et al.* (2009), with a decrease of *ca*. 90% of full sunlight, plant traits such as LCP, P_{max}, relative growth rate and leaf area decreased between *ca*. 50–85% in invasive species and between *ca*. 45–90% in native species. In contrast, *L. camara* showed positive responses by maintaining or increasing between 30–67% those variables following a radiation decrease of 77% of full sunlight. Zheng *et al.* (2009) showed an increase of SLA of *ca*. 55% for invasive and of 50% for native species of *Eupatorium* with 77% of full sunlight while that increment for *L. camara* was 49% with the same shade treatment.

In view of our results, however *L. camara* is able to grow in moderately sheltered habitats, control efforts in patchy environments should be directed first and mainly against individuals invading open areas, especially prior to seed production. This is where the progress of its invasions would be much faster, being able to produce several thousand seeds per square meter every year (Sharma *et al.* 2005). Since *L. camara* shows a high phenotypic plasticity to light changes and positive responses to intermediated light fluxes, its invasion could be limited in very shady habitats such as some well-conserved forests where poor development has been reported (Thakur *et al*. 1992, Fensham *et al*. 1994, Gentle and Duggin 1997).

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