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Morphological and physiological responses of Galapagos endemic tree *Croton scouleri* to site conditions varying through its altitudinal range

Abstract: Galapagos is a natural laboratory offering a great opportunity to study plants functional traits. This study characterises morphological and ecophysiological responses of *Croton scouleri*, an endemic tree that habits from humid and upper elevations to semiarid lowlands, throughout an altitudinal gradient and in a manipulative experiment. *Croton scouleri* trees were gradually smaller with less total leaf area due to a gradual reduction in mean leaf size, and they folded their leaves at lower elevations. These results were also recorded after cutting every deep root. Two physiological traits that allowed *Croton scouleri* to avoid damages to the photosynthetic apparatus were detected between 30 and 150 m a.s.l. Lower variable fluorescence (F_v) and basal fluorescence (F_0) keeping constant maximum photochemical efficiency of PSII (F_v/F_m) denoted a drop in chlorophyll concentration. Concomitantly, the recorded increase in the Quantum efficiency of PSII (Φ_{PSII}) with similar F_v/F_m means that *Croton scouleri* could be using cyclic electron transport as photoprotective mechanism. On the other hand, a deep root system to reach the water table allowed *Croton scouleri* to behave as a drought-avoider, which was reflected in: (1) unvarying water status Leaf Water Content and Relative Water Content were always higher than 69 and 58%, respectively; (2) stable and low photoinhibition levels; and (3) unvarying leaf area index. However, *Croton scouleri* was not able to avoid drought at altitudes lower 30 m a.s.l. where similar responses to those recorded after root cutting were recorded.

Additional Key words: chlorophyll fluorescence; *Croton scouleri*; leaf area index; photosynthetic stress; water content.

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Introduction

Galapagos is a natural laboratory that offers a great opportunity to study plant functional traits since some endemic plant species with wide altitudinal distribution ranges can be found across the whole climatic range from humid highlands to semiarid lowlands (Wiggins and Porter 1971). *Croton scouleri* Hook. f. (Euphorbiaceae) is such a species, a Galapagos endemic tree that is common throughout the archipel-

ago and grows from upper humid forests to semiarid lowlands.

We hypothesized that this endemic tree species that colonises such diverse environments would show a series of adaptive traits (adaptative syndrome) probably related to drought, the most important stress factor at Galapagos lowlands (Hamann 2004). Thus, the main aim of this study was to analyse morphological (root system distribution, leaf morphology, leaf area index and tree architecture) and physiological (water status and photosynthetic stress level) responses of *C. scouleri* to changing abiotic environmental conditions throughout its altitudinal distribution range. In addition, a root-cutting experiment was carried out to explore *C. scouleri* responses to drought and to compare them with the responses recorded throughout its distribution range. There are just a few ecophysiological studies in the Genus *Croton*. For example, Dias de Oliveira et al. (2012) and Duarte et al. (2005) studied *Croton urucurana* Baillon and *Croton compressus* Lam. in Brazil, respectively. In Galapagos, the only ecophysiological study regarding vegetation was carried out by Castillo et al. (2007) working on the responses to drought of the endemic shrub *Lantana peduncularis* Andersson and the invasive *Lantana camara* L. This is the first ecophysiological study of any Galapagos endemic tree.

Methods

Study site and species

The Galapagos are volcanic islands in the Pacific Ocean, approximately 1000 km west of Ecuador. Our study was carried out from August 2005 to May 2006 in Santa Cruz island (90°10'05''–90°32'55''W; 0°28'43''–0°46'23''S) that shows a maximum elevation of 864 m above sea level (a.s.l.). Exploratory fieldwork allowed us to identify suitable study sites. An altitudinal gradient was chosen in the southeast of Santa Cruz between 10–260 m a.s.l. from the lower to the higher altitudinal distribution limit of *Croton scouleri* (point 1 in Fig. 1). In addition, a manipulative experiment was carried out in southeast Santa Cruz, at 25 m a.s.l. close to Puerto Ayora (point 2 in Fig. 1).

During the hot season, from January to June, daytime maximum temperature averages 29°C, mean temperatures are between 25–26°C, and intermittent rains may fall although most days are sunny. During the cool season, from July to December, temperatures are 18–26°C and there is less rain in the lowlands although a mist layer, known locally as 'garua', more frequently occurs during this season at higher elevations, with cloudy days more frequent than sunny days (Alpert 1963, Wiggins and Porter 1971, Ziegler 1995). Based on local climatic data, mean annual precipitation varies between 127 mm ± 144% for the lowlands and 243 mm ± 112% for the highlands. In the cool-dry season when our study was carried out, monthly air temperature and relative humidity varied between 20.9±0.1°C and 89±1% in the highlands, respectively, and 20.0±0.1°C and 87±0% in the lowlands (data coming from meteorological stations located at Bellavista (194 m a.s.l.) and Puerto Ayora (2 m a.s.l.) (90°19'37,20" W – 0°41'46,53" S and 90°50'21,9" W–0°44'37,6" S, respectively).

Vegetation in Santa Cruz island is strongly zoned by altitude, since most rainfall is orographic (Alpert 1963, Wiggins and Porter 1971). The littoral zone includes mangroves and coastal dunes. Semiarid lowlands, where *Croton scouleri* grows at its lower altitudinal distribution limit, are characterised by endemic tree cacti of *Opuntia* and *Jasminocereus* and a shrub layer or by open woodlands, where *C. scouleri* may be co-dominant. The transition zone is characterised by closed mixed forest, where *Croton* is present also. The humid zone above does support *Croton*, representing its higher altitudinal distribution limit (Hamann 1981), especially in open woodland and scrub formations.

Four varieties of *C. scouleri* have been described based on leaf and seed sizes (Wiggins and Porter 1971): var. *brevifolius* grows only at higher elevations in Floreana island. The three other varieties appear all in Santa Cruz and other islands. *C. scouleri* var. *darwinii* is considered rare and appears to prefer lower elevations with leaf width 1.5–6.0 cm and leaf length
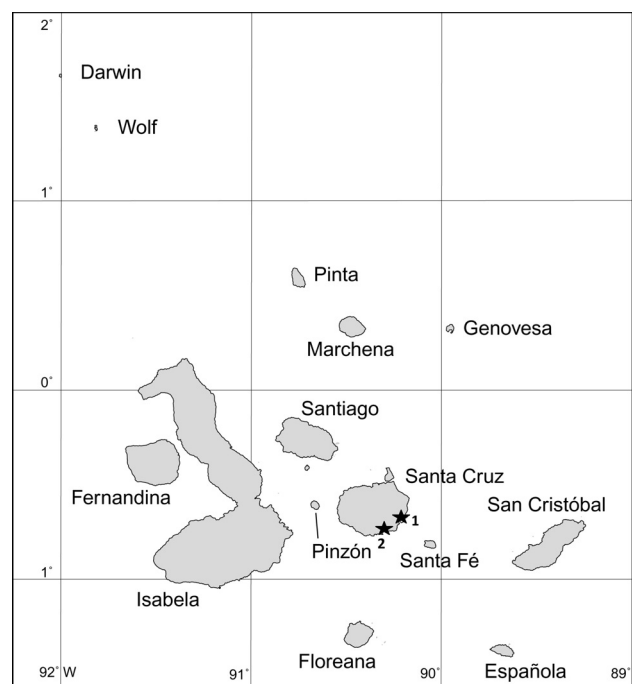

Fig. 1. Map of Galapagos archipelago, indicating the location on Santa Cruz Island of the studied altitudinal gradient (1) and the manipulative experiment site (2)

3.0–7.0 cm, *C. scouleri* var. *grandifolius* occupies typically higher elevations showing leaf width 3.0–8.0 cm and leaf length 6.0–15.0 cm, and *C. scouleri* var. *scouleri* is the most common and colonises mainly lower elevations, with leaf width 0.8–2.3 cm and leaf length 2.0–12.0 cm (McMullen 1999).

Abiotic environmental factors

Measurements of abiotic environmental factors were carried out in parallel with ecophysiological measurements. Height above sea level was measured using a GPS (Garmin model eTrex Vista) with its altimeter adjusted to zero at sea level in the field with 3 m accuracy. Photosynthetic photon flux density (PPFD in μmol m^{-2} s^{-1}) was recorded with a portable photometer (Model LI-189, LICOR Inc., Lincoln, NE, USA). Air temperature (°C) and relative humidity (%) were measured at 1.5 m above soil surface with a portable thermo-hygrometer (Elka FTM–10). Wind speed (m s^{-1}) was measured with an anemometer (Martin Marten TA-6000, Barcelona) at five heights above soil surface (0.5, 1.0, 1.5, 2.0 and 2.5 m; n = 20).

Chlorophyll fluorescence

Photosynthetic stress was measured by chlorophyll fluorescence, which corresponds to variation in the photosynthetic function in response to environmental change (Maxwell and Johnson 2000). Chlorophyll *a* fluorescence was measured in the youngest fully developed leaf of 2–5 stems per plant during the middle part of the day (11–13 h solar time) on frequent cloudy days with a mean PPFD of 1080 ± 93 μmol m^{-2} s^{-1} during September 2005. Measurements were carried out across the altitudinal gradient on southeast Santa Cruz (2–5 plants in each of 15 samples points) and at the area close to Puerto Ayora where the manipulative experiment was carried out (Fig. 1). Selected trees were adult individuals with the maximum height of the population in each sample point.

Light and dark-adapted fluorescence parameters were measured using a portable modulated fluorimeter (FMS-2, Hansatech Instrument Ltd., England). Leaves were dark-adapted for 30 minutes, using leaf–clips. The minimal fluorescence level in the dark-adapted state (F$_0$) was measured using a modulated pulse (<0.05 μmol m^{-2} s^{-1} for 1.8 μs) and the datum stored was an average taken over a 1.6 second period (Schreiber et al. 1986). Maximal fluorescence (F$_m$) was measured after applying a saturating actinic light pulse of 15000 μmol m^{-2} s^{-1} for 0.7s and its value was recorded as the highest average of two consecutive points. Variable fluorescence (F$_v$ = F$_m$ – F$_0$) and maximum photochemical efficiency of PSII (F$_v$/F$_m$) were calculated. F$_v$/F$_m$ correlates with the number of functional PSII reaction centres and can be used to quantify photoinhibition (Maxwell & Johnson 2000). 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. A saturating actinic light pulse of 15000 μmol m^{-2} s^{-1} for 0.7 was then used to produce the maximum fluorescence yield (F$_m$') by temporarily inhibiting PSII photochemistry. Quantum efficiency of PSII was calculated as: $\Phi_{PSII} = (F_m' - F_s)/F_m'$, and non-photochemical quenching as: NPQ $= (F_m - F_m')/F_m'$ (Schreiber et al. 1986).

Tree morphological analysis and leaf area index

Maximum length and width were recorded for ten adult leaves of five adult individuals of *C. scouleri* used for chlorophyll fluorescence at each of twelve different elevations throughout the altitudinal gradient. Measurements were carried out using a Vernier calliper in October 2005. Mean leaf area was calculated as the area of an ellipse.

Height, number of stems and cover of the same trees (n = 36; three trees per elevation) were recorded on May 2006. The length and number of leaves per stem was also recorded for two stems in every individual tree. The total number of leaves per tree was calculated as the product of the mean number of leaves per stem by the number of stems per tree. Total leaf area at every elevation was estimated as the product of the total number of leaves and the mean leaf area per every tree. Finally, leaf area index (LAI) was calculated as the total leaf area divided by the cover for every individual tree.

Leaf water content

Adult apical leaves (n = 10–15) from seven trees individuals throughout the whole altitudinal gradient were harvested in the field during the middle part of the day and stored in sealed plastic bags at 5°C. On return to the laboratory, ten punched circular pieces (0.7 cm diameter) per plant were taken. Leaf water content was calculated as:

$$LWC\ (\%) = (FW - DW)/FW \times 100$$

where FW is the fresh weight and DW is the dry weight after oven-drying samples at 80°C for 48 h (Medrano and Flexas 2004). Relative water content (RWC) was calculated as:

$$RWC\ (\%) = (FW - DW)/(TW - DW) \times 100$$

where TW is the turgid weight after rehydrating samples for 24 h.

Root system distribution and manipulative experiment

The root system of four plants of *C. scouleri* was explored in southeast Santa Cruz at 25 m a.s.l. close to Puerto Ayora (point 2 in Fig. 1) on 8 September 2005. Exploration was carried out by digging manually using a shovel around isolated adult individuals to a depth of 30–40 cm until the bedrock appeared and the root system close to the main stem was free of soil, taking care not to break any main root. Any deep roots penetrating into the bedrock were noted. Then, deep roots of two individuals were cut while the other two were left intact. Finally, the root system of all individuals was reburied using the original soil. Leaf chlorophyll fluorescence was recorded, as described above, in cut and uncut individuals after 12 days. Leaf morphology and the number of leaves per tree were recorded eight months after the beginning of the experiment (April 2006). Survivorship of every tree was followed until July 2006.

Statistical analysis

Statistical analysis was carried out using SPSS v 12.0 (SPSS Inc.). Pearson coefficients were calculated to assess correlation between different variables. Data were tested for normality with the Kolmogorov-Smirnov test, and homogeneity of variance with the Brown-Forsythe test. Data were transformed, using the functions $1/x$, $\ln(x)$ and when homogeneity of variance was not reached. Differences between two means were compared by the Student t-test.

Results

Altitudinal gradient

 Air temperature during the middle part of the day varied between 25 and 30°C and relative humidity between 48 and 63%, both parameters being independent of elevation. Wind speed was lower at higher altitudes ($r = -0.70$, $P < 0.01$, $n = 14$), varying from 1 to 5 m s^{-1} (Fig. 2).

F_v/F_m was independent of atmospheric conditions and elevation, being c. 0.810. However, it showed a significant decrease to values c. 0.700 at elevations below 30 m a.s.l. (*t*-test, $t_{77} = -7.64$, $P < 0.0001$) due to a higher decrease in F_m than in F_0 (Fig. 3).

Mean F_v and F_0 varied together ($r = 0.93$, $P < 0.0001$, $n = 14$), both decreasing at lower elevations ($P < 0.0005$) with a marked drop below 140 m a.s.l (F_0: from c. 215 r.u. to c. 120 r.u.; F_v: from c. 900 r.u. to c. 400 r.u.) (Fig. 3).

Mean Φ_{PSII} varied between 0.500 and 0.700, being also independent of atmospheric conditions. Maximum values were recorded between 30 and 150 m a.s.l., decreasing at lower and higher elevations. The
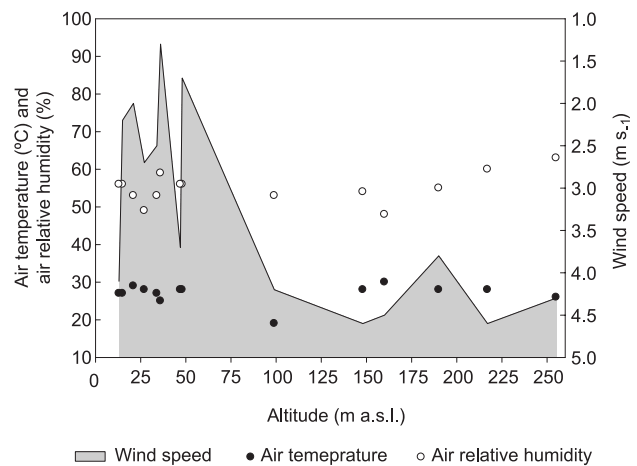

Fig. 2. Air temperature, air relative humidity and wind speed recorded together with fluorescence measurements of *Croton scouleri* during the middle part of the day across an elevational transect (13–255 m above sea level) on southeast Santa Cruz Island, Galapagos

increase in Φ_{PSII} at elevations between 30 and 150 m a.s.l. was due to a higher decrease in F_s (c. 64%) than in F_m' (c. 41%), whereas at elevations lower than 30 m a.s.l. the decrease in F_m' (c. 53%) was higher than in F_s (c. 25%). Maximum differences between F_v/F_m and Φ_{PSII} (c. 300) were recorded at elevations upper 140 m a.s.l. due to a decrease in Φ_{PSII} with constant values of F_v/F_m. Mean NPQ was independent of elevation during the middle part of the day, but maximum values (c. 1.4) were recorded at lower elevations (Fig. 3).

Mean leaf area decreased gradually with elevation ($r = 0.97$, $P < 0.0001$, $n = 12$), due to significant reduction in both width (from 3.8 to 0.4 cm; –10.5%) and length (from 9.6 to 5.0 cm; –52.1%). Mean leaf area ranged from 28.7 ± 2,6 cm^2 at 255 m a.s.l. and 1.4 ± 0.1 cm^2 at 21 m a.s.l. Furthermore, mean leaf area increased with F_0 and F_v ($r = 0.80$, $P < 0.005$, $n = 12$). Mean stem length, height, cover, number of stems and estimated total leaf area of individual trees increased at higher elevations ($P < 0.01$). However, the number of leaves per tree (varying between 173–3127), and the LAI were independent of elevation. Mean LAI was 0.64 ± 0.07, varying between 0.15 and 1.67 (Fig. 4). The folding of leaves across their main axis was observed at elevations lower than 150 m a.s.l. and leaves with a reddish colouration were noted at elevations lower than 30 m a.s.l.

On the other hand, LWC varied between 69 and 76% and RWC between 58 and 73%, both parameters being independent of elevation between 31 and 250 m a.s.l.

Root system distribution and manipulative experiment

The *C. scouleri* root system included two to four vertical deep roots penetrating rock fissures, below the more superficial horizons of the soil, which was c. 15
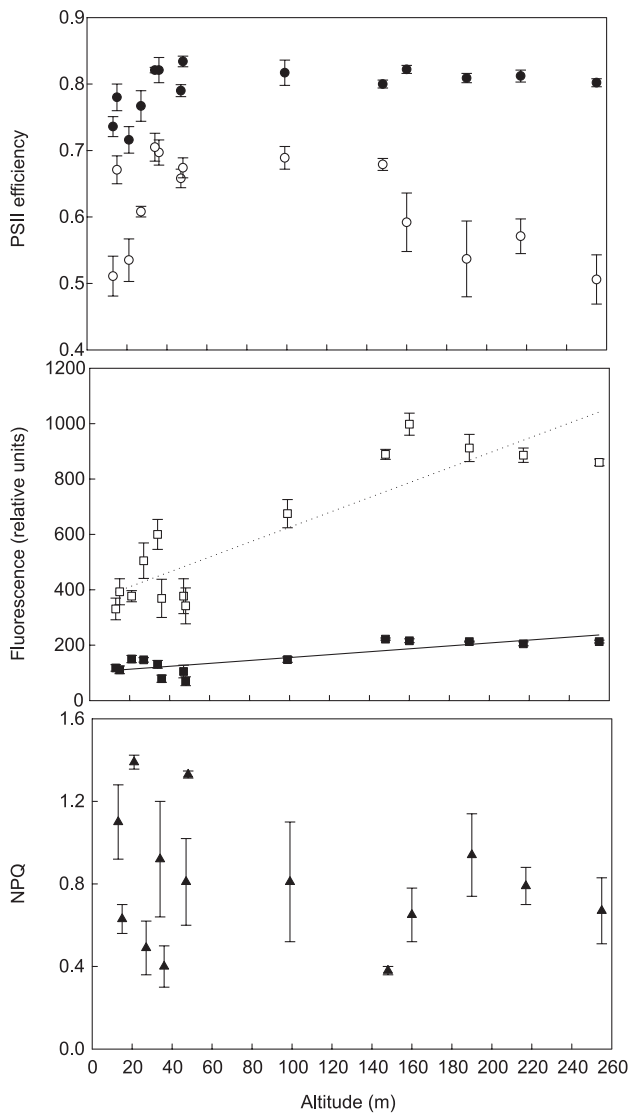
Fig. 3. Relationships between altitude (m) and potential photochemical efficiency (F_v/F_m; ●), quantum efficiency of PSII (ΦPSII; ○), basal fluorescence (F_0; ■), variable fluorescence (F_v; □) and non-photochemical quenching (NPQ; ▲) for *Croton scouleri* across an altitudinal gradient on southeast Santa Cruz (Galapagos). Data are mean ± SE (n = 5–10). Regression equations: F_0 (—): y = 102,76 + 0,53 x; F_v (·····): y = 356,67 + 2,69 x
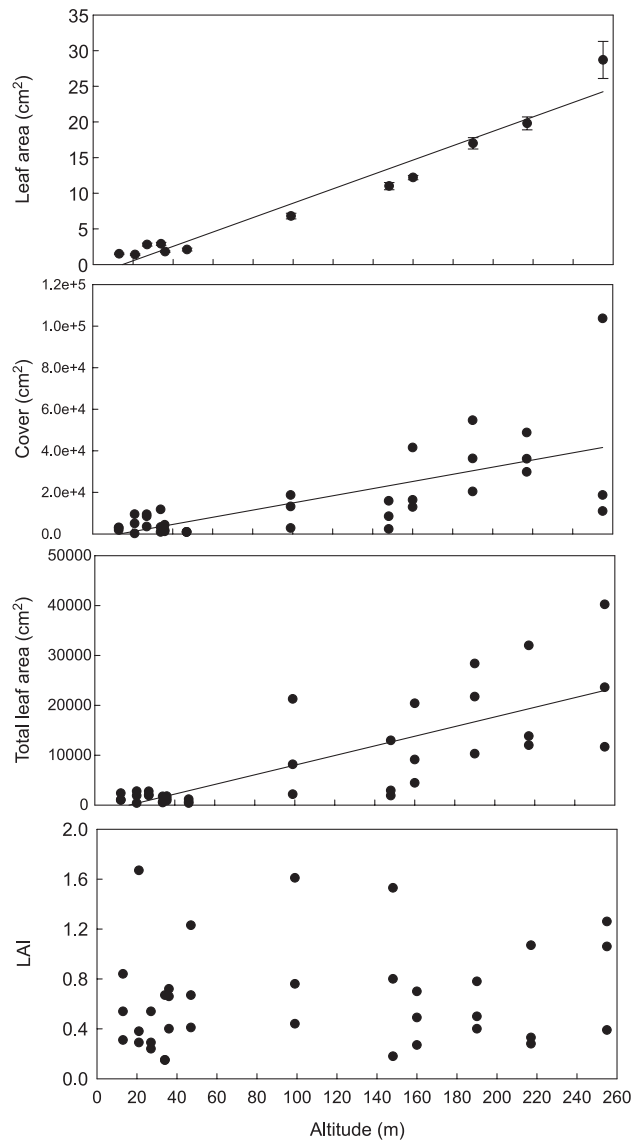

Fig. 4. Relationship between altitude (m) and leaf area (cm^2), Cover (m^2), total leaf area (cm^2) and LAI for *Croton scouleri* throughout an altitudinal gradient in southeast Santa Cruz (Galapagos). Data are mean ± SE (n = 50). Regression equation: y = −1.48 + 0.10 x

cm deep in the semiarid lowland where the experiment was carried out. There were also many smaller roots close to the soil surface.

F_v/F_m and Φ_{PSII} were lower 12 days after cutting every deep root (*t*-test, $P < 0.05$). The drop in F_v/F_m was due to a higher decrease in F_m than in F_0. NPQ increased from 0.39 ± 0.04 in control plants to 1.12 ± 0.21 in treated plants (Table 1). Folded and reddish leaves were observed in treated plants from one week after beginning the experiment. Eight months after beginning the experiment, total leaf area was lower for treated trees, due to a reduction in individual leaf size (10.1 ± 0.5 cm^2 for controls and 4.7 ± 0.3 cm^2 af-

Table 1. Potential photochemical efficiency (F_v/F_m), quantum efficiency of PSII (Φ_{PSII}), basal fluorescence (F_0), variable fluorescence (F_v) and non-photochemical quenching (NPQ) for four *Croton scouleri* trees with intact and cut deep roots in a manipulative experiment on southeast Santa Cruz (Galapagos) (n = 10; 5 measurements per tree)

	Intact roots	Cut roots
F_v/F_m**	0.764 ± 0.05	0.682 ± 0.02
Φ_{PSII}**	0.651 ± 0.023	0.475 ± 0.03
F_0*	218 ± 9	158 ± 14
F_v**	706 ± 28	349 ± 42
NPQ*	0.39 ± 0.4	1.12 ± 0.21

Student *t*-student: *$P < 0.01$, **$P < 0.001$

ter treatment; t-test, t_{38} = 11,15, P < 0.0001) with similar leaf numbers. Both uncut trees were still alive, but one treated individual was dead within eleven months of cutting every deep root and the other was alive after producing new deep roots.

Discussion

The immediate atmospheric environment around midday throughout the altitudinal distribution range of *Croton scouleri* (characterised by wind speed, air temperature and relative humidity) did not explain the variations of any of its recorded physiological and morphological responses. This was probably due to the dominant southeast winds coming directly from the ocean at the study site, homogenising atmospheric conditions throughout the altitudinal gradient, from semiarid lowlands at 30 m a.s.l to the humid *Scalesia* zone at 255 m a.s.l. Wind speed decreased at higher altitudes probably due to the friction of the oceanic southeast winds with the surface of the island.

C. scouleri trees were progressively smaller with less total leaf area at lower elevations, due to a gradual reduction in mean leaf area (maximum reduction c. 95%). Furthermore, *C. scouleri* responded by folding its leaves across their main axis at elevations below 150 m. In addition to these morphological traits, we detected two foliar physiological traits that allowed *C. scouleri* to avoid damage to the photosynthetic apparatus between 30 and 150 m a.s.l. The recorded increase in Φ_{PSII} with similar F_v/F_m (with Φ_{PSII} as high as 0.705 ± 0.021 at 1090 μmol m^{-2} s^{-1}) in comparison with higher elevations means that *C. scouleri* could be using cyclic electron transport as a photoprotective mechanism (Fryer et al. 1998). This pathway can lead to an additional consumption of reducing equivalents and can thus function as a sink for excessive excitation energy (Asada 1996). Concomitantly, lower F_v and F_0 while keeping constant F_v/F_m may denote a drop in chlorophyll concentration, which did not result from severe photoinhibitory damage.

The recorded variations in morphological and physiological traits in *C. scouleri* seem to be functional responses to deal with water shortage throughout its altitudinal distribution range; drought in Galapagos increases from the humid upper elevations to the lowlands where it is the most important stress factor (Hamann 2004). Thus, the reduction in leaf area has been described as a mechanism to decrease water losses through transpiration, for example in the Ethiopian *Croton macrostachyus* Hochst. ex Delile (Gindaba et al. 2004), and the folding of leaves across their main axis would decrease solar radiation interception, thereby reducing photoinhibition and dehydration (Muraoka et al. 1998, Bolger et al. 2005). These results were supported by the experiment where a re-

duction in leaf area (–53%) and increased leaf folding were recorded after cutting deep roots. As well, both responses of PSII recorded in *C. scouleri* through its altitudinal distribution range (cyclic electron transport and a drop in chlorophyll concentration) have been described previously for other species as adaptive photoprotective mechanisms against excess radiation under drought (Kyparissis et al. 1995, Bukhov and Carpentier 2004). *Lantana camara*, an invasive weed in Galapagos, showed a reduction in chlorophyll contents to cope with drought (Castillo et al. 2007). Thus, these physiological responses dissipated excess energy for photosynthetic apparatus between 30 and 150 m a.s.l., since the unchanging NPQ indicated that there was not an increase in thermal dissipation in the PSII antennae (Maxwell and Johnson 2000). Furthermore, *C. scouleri* had a deep root system to reach the water table, keeping LWC and RWC always higher than 69 and 58%, respectively, according with the responses showed by drought-avoiding species (Nardini et al. 1999).

However, *C. scouleri* was not able to avoid damages to its photosynthetic apparatus at elevations lower 30 m a.s.l. Thus, although *C. scouleri* increased dissipation of excess excitation energy by heat emission, reflected in maximum NPQ values and reddish leaves probably related to an increase in the carotenoids/chlorophyll ratio. This photoprotection was not enough to avoid PSII damage, and the decrease in F_m was higher than in F_0, which provoked a slight but significant drop in F_v/F_m and Φ_{PSII} due to a deactivation of PSII reaction centres (Maxwell and Johnson 2000). Our results showed that F_v/F_m and Φ_{PSII} were ecophysiological parameters very tolerant to drought in *C. scouleri* leaves, dropping only at very extreme conditions, as reported by Epron and Dreyer (1993) for *Quercus* species. The responses recorded at the lowest elevations were similar to those recorded in the manipulative experiment for individuals with cut deep roots, which could be due to a situation where even adult individuals in semiarid lowlands close to the coast were not able to reach a very low water table. The water stress could be provoking even the observed death of *C. scouleri* in the field, especially in dry years. In this sense, populations of native Galapagos species with deep root systems in semiarid lowlands, such as *C. scouleri*, could be negatively impacted by overexploitation of water table resources for urban use in inhabited islands.

Leaf area index (LAI) of *C. scouleri* was independent of environmental variations, since cover increased together with mean leaf area and the number of leaves was independent of altitude. Such a reduction in LAI has been recorded in many deciduous (drought-tolerating) species, such as *C. macrostachyus* (Gindaba et al. 2004), as a response to drought, prompting a reduction in solar radiation interception (Brison and Casals

2005, Pettigrew 2004, Ares and Fownes 1999). However, other tropical trees retain all leaves during abnormal droughts (Borchert et al. 2002). Observed constant and relatively low LAI in *C. scouleri* (0.64 ± 0.07) would be in equilibrium with changing environmental conditions throughout the its altitudinal distribution range to maximize carbon assimilation in relation to tree size and water transpiration. In drier areas, trees were smaller so leaves were more packed. In this situation, packed leaves should be smaller to avoid self shading (Falster and Westboy 2003) and reduce water loss through transpiration as discussed above.

The gradual reduction in leaf size recorded across the altitudinal gradient, from large leaves corresponding to variety *grandiflorus* at higher elevations to leaf sizes similar to those of varieties *darwinii* and *scouleri* at lower elevations, together with the leaf area reduction observed in the root-cutting experiment, suggest that phenotypical differences described as varieties for *C. scouleri* are actually ecophenes, phenotypic responses to variation in environmental conditions. Thus, leaf area and seed size variation as seen in the four *C. scouleri* varieties may reflect water supply (Li et al. 2006, Valencia-Diaz and Montana 2005). However, a genetic component influencing these traits cannot be excluded and more detailed studies to identify the determinants of growth form are needed to clarify whether ecotypes have developed through genetic differentiation as a response to drought in *C. scouleri*, as has been described in an endemic shrub from Crete (Syros et al. 2006).

Acknowledgements

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