

RESEARCH ARTICLE

Growth responses of Lantana (*Lantana camara* L.) varieties to varying water availability and light conditions

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Abstract: *Lantana camara* L. (Verbenaceae) is an invasive alien species in many countries that causes economic losses and harmful ecological impacts on biodiversity. Its varieties with colourful flowers are being introduced to the horticulture trade in Sri Lanka despite that the orange-red flowered *L. camara* var. *splendens* and yellow-pink flowered *L. camara* var. *camara* introduced to the country in the nineteenth century have been naturalised and considered as invasive alien species of national significance. This study compared drought and shade tolerance abilities of white and purple flowered ornamental *L. camara* varieties with the above two naturalised varieties using statistical analysis. The results provided evidences for significant differences in drought and shade tolerance abilities between naturalised and ornamental *L. camara* varieties in Sri Lanka with regard to growth of the main stem, flowering, fruiting, defoliation, leaf water content and leaf growth rate, leaf area, photosynthetic tissue mass and pigment content, stomatal density, root volume and biomass partition between above and below ground parts. While contributing to fill in the knowledge gap in the biology of 'Lantana group', we report that ornamental *L. camara* varieties are not drought and shade tolerant as the naturalised varieties, and therefore their potential invasiveness may not be as high as the wild varieties that pose a great threat to the biodiversity of Sri Lanka.

Keywords: Growth, lantana, light conditions, soil moisture.

INTRODUCTION

Lantana camara L. (Verbenaceae) was spread across its geographical borders, the islands of West Indies, and Central and South America through deliberate introductions by the Europeans nearly two centuries ago

(Howard, 1970; Cronk & Fuller, 1995) and at present is reported to be naturalised and invasive in many recipient countries (Stirton, 1977; Day *et al.*, 2003). The ecological impacts imposed by *L. camara* on ecosystems by arresting succession (Lamb, 1991), changing structure, composition of communities and disrupting ecosystem functions (Holm *et al.*, 1979; Gentle & Duggin, 1997; Gooden *et al.*, 2009; Aravind *et al.*, 2010; Singh, 2012) reduce productivity of the land and impose high economic costs for control (Howard, 1970; Swarbrick *et al.*, 1998), hence ranked among world's hundred worst invasive alien species (Lowe *et al.*, 2000). Despite these negative impacts, *L. camara* (hereafter referred to as Lantana) has been subjected to intense horticultural modifications mainly through hybridisation to develop new forms or varieties to meet the demand in ornamental plant trade (Smith & Smith, 1982; Graaff, 1986; Li *et al.*, 2004).

Lantana flourish all-year-round in favourable soil, humidity, air temperature and light conditions (Swarbrick *et al.*, 1998) and flower when times of soil moisture, humidity and temperature is high (Holm *et al.*, 1991; Swarbrick *et al.*, 1998). Its successful survival as a woody invasive perennial has been attributed to allelopathy, vegetative propagation, high reproductive output and versatility, and long range seed dispersal capabilities (Sharma *et al.*, 2005). Broad range of tolerance to edaphic and climatic conditions also have been key traits that contributed Lantana to be naturalised and invasive in its introduced environments (Swarbrick *et al.*, 1998; Day *et al.*, 2003; Sharma *et al.*, 2007; Taylor

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et al., 2012). For example it grows as a bush up to 2–4 m height in open unshaded sunny environments (Day *et al.*, 2003), and as a liana up to 15 m when light intensity is low (Lowe *et al.*, 2000) exhibiting very plastic responses to different intensities of sunlight (Carrion-Tacuri & Rubio-Casal, 2011). It thrives in a variety of soil types in which soil moisture is readily available, but also tolerates long period of drought (Munir, 1996). Thus these traits have been widely applied in niche and species modelling to predict potential range expansion of *Lantana* in diverse biogeographic regions as a response to climate change (Taylor *et al.*, 2012). However, *Lantana* has not been successfully controlled in almost all introduced environments probably due to the scarcity of knowledge in plant biology of the ‘*Lantana* group’ (Taylor, 1989; Zalucki *et al.*, 2007).

In Sri Lanka *L. camara* var. *splendens* and *L. camara* var. *camara* have been listed as invasive *Lantana*, which became naturalised following introduction as an ornamental plant (Wijesundera, 2010). Nevertheless, new arrivals of *Lantana* have become popular garden plants which, at present, are propagated and distributed through plant nurseries. As the taxonomy, phenotypes and biology of *Lantana* group in Sri Lanka is poorly explored, we focused our investigations from an ecological-eco-physiological point of view to reveal how these closely related *Lantana* varieties deal with drought (reduced water) and shade (reduced light) conditions, as in most habitats the soil moisture will not be in its field capacity and light conditions in optimum. Hence, this study was aimed at understanding the growth responses of naturalised invasive *Lantana* and ornamental *Lantana* varieties under varying water and light availability levels. It was hypothesised that differences in growth responses were reflected by vegetative and reproductive characteristics, leaf growth rate, water and chlorophyll content, defoliation, stomatal conductance,

photosynthetic tissue mass and biomass partitioning of plant parts of *Lantana* varieties.

METHODOLOGY

Plant material

The two ornamental *Lantana* varieties selected based on public demand (as revealed by nurserymen and plant sellers) included a variety with a straight growing habit producing white flowers (OW) and another with strangling habit producing purple colour flowers (OP). Naturalised (hereafter referred to as wild) *Lantana* varieties were *L. camara* var. *splendens* producing orange-red colour flowers (WR) and *L. camara* var. *camara* producing yellow-pink colour flowers (WY) reported to be invasive (Wijesundera, 2010) (Figure 1). Approximately 20 cm long healthy stem cuttings obtained from the ends of mature branches of plants were planted in pots containing soil mixed with compost and sand (soil pH 5.29 at 30.2 °C, total nitrogen 0.15 %, phosphorous 312.8 ppm, potassium 411.2 ppm) and acclimated for 5 wks in a greenhouse (average temperature 29 °C, humidity 67 %, daylight of 65 kLux) before being subjected to the following two treatments.

Water availability

Eighty *Lantana* plants were arranged according to randomised complete block design in which the *Lantana* varieties ($n = 5$ per variety) were kept as 4 ‘blocks’ under a rain shelter, which received ample sunlight of average 85.5 kLux. Water availability treatments were imposed on *Lantana* plants ($n = 5$ per variety) through addition of 200 mL of tap water daily (W1- control), every 4th (W2), 7th (W3), and 10th (W4) day. Weekly observations were obtained for main stem length, number of flower heads, fruits/berries and fallen leaves from each plant.

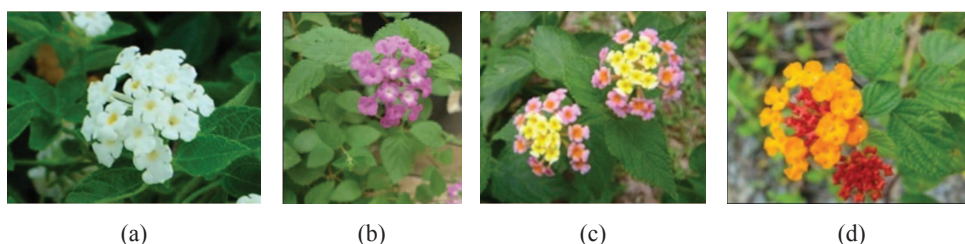


Figure 1: Varieties of *Lantana camara* used for the study. a) ornamental straight growing habit producing white flowers (OW); b) ornamental strangling habit producing purple colour flowers (OP); c) naturalised *L. camara* var. *splendens* producing orange-red colour flowers (WR); d) naturalised *L. camara* var. *camara* producing yellow-pink colour flowers (WY)

Leaf growth rate (LGR) was determined ($n = 10$) as a ratio of leaf extension to the initial length (Ewing *et al.*, 1995), i.e. $LGR = (L2 - L1)/L1$, where $L1$ is the length of the leaf soon after bud break and $L2$ is the length of the leaf after full expansion. Stomatal conductance was measured ($n = 6$) at the 10th wk during midday using a porometer (AP4-UM-3, Cambridge, UK). Stomatal resistance was considered as the reciprocal value of stomatal conductance (Sack & Scoffoni, 2012; Goyal & Sharma, 2015). At the end of 12 wks plants were uprooted carefully and average length and width of cleaned root mass was recorded. The approximate root volume was estimated by $RV = \pi d^2 h/4$, where d is the width of the root mass and h is the height of the root mass. Fresh weight (FW) of leaves, stems, roots and reproductive parts (flower heads and berries) was measured using an electronic scale (PS510/c/2/CT, RADWAG, Poland) and respective dry weights (DW) were obtained following drying in an oven (MOV-112F, SANYO, Japan) at 65 °C for 48 h until a constant weight was obtained. Leaf water content (LWC) [$LWC \% = (FW - DW) / FW \times 100$] was calculated (Sauraa-Mas & Lloret, 2007; Redondo-Gomez *et al.*, 2011). Dry weight of root: shoot ratio and the proportional allocation of biomass in reproductive structures, leaves, stem and root were determined.

Light availability

Eighty Lantana plants were arranged according to randomised complete block design in which four Lantana varieties ($n = 5$ per variety) were kept as 'blocks' in a net house (6 m × 1 m × 2 m) to receive four different treatments of shade conditions, 35 % (S2), 50 % (S3) and 75 % (S4) constructed using standard shade nets. Control (S1) plants were unshaded and received maximum sunlight. All plants were allowed to obtain rain water for their survival. The light intensity of treatments were measured thrice a week between 12 noon – 1.00 p.m. using lux meter (Dw-50512 Heavy Duty Light Meter, Afir, USA). Weekly measurements were obtained for length of the main stem and number of flower heads per plant. At the 12th week, length of petiole, width and length of the oldest leaf of the branch located at the second node from the apex and the length of the first internode of the plant were measured. Leaf area was calculated using the ellipse formula (Carrion-Tacuri & Rubio-Casal, 2011). Photosynthetic pigment content (chlorophyll a, chlorophyll b and carotenoids) of fully expanded leaves were determined by soaking 0.2 g of leaf in 5 mL of 80 % aqueous acetone for 4 h followed by measuring absorbance using a spectrophotometer (G10S UV-Vis, Genesys, USA) at 3 wavelengths (663.2, 646.8 and 470.0 nm), respectively. Concentration of

pigments were calculated using the absorbance value, $A = \alpha cd$, where α is specific absorbance coefficient Lg^{-1} , c is the concentration in mgg^{-1} and d is the path length of the corvette in centimetres (Sims & Gamon, 2002). Photosynthetic tissue mass was measured by obtaining transverse sections of two fully expanded leaves per plant. Length of the palisade parenchyma and spongy parenchyma were measured using a graticule fixed to the light microscope (AxiocamERc 5s, ZEISS, Germany). To identify the stomatal density of abaxial epidermal peels, another two fully expanded leaves were treated with 88 % lactic acid in 100 °C for 30 min. Stomatal density was recorded by counting the number of stomata per microscopic field ($n = 3$) per leaf using the light microscope.

Data analysis

All data on growth parameters were subjected to analysis of variance (ANOVA) using SPSS version 16.0 to compare means, and the significant pairs were identified by least significant differences (LSD) at $p < 0.05$. Regression analysis was conducted to examine the relationships between the leaf water content with soil water content and leaf growth rate in water stress experiment and to examine the relationship between shade level and mean chlorophyll a and b concentrations.

RESULTS AND DISCUSSION

Water availability

The average soil moisture of Lantana pots changed from 39.08 % to 8.16 % across the watering treatments W1-W4 and Lantana varieties responded differently to varying soil water availabilities (Table 1). Treatments W1 and W2 provided favourable conditions for both wild and ornamental Lantana varieties to grow and survive, but further dryness imposed by W3 and W4 treatments negatively impacted on their growth and survival at different scales. Treatment W4 led to the death of all OW ornamental Lantana plants and 80 % of OP by the end of experiment. In contrast, all plants of wild varieties survived.

All Lantana varieties commonly showed a progressive reduction in main stem length, LGR and LWC under reduced water availability, however the responses varied within and between wild and ornamental varieties. Higher LWC was maintained by wild Lantana varieties than the ornamental varieties across the soil moisture gradient and especially at low soil moisture levels (Figure 2a). Moreover it was evident that both wild

Table 1: Effect of water availability on plant growth of wild Lantana varieties *Lantana camara* var. *splendens* (WR), *Lantana camara* var. *camara* (WY), ornamental Lantana varieties producing white (OW) and purple (OP) flowers. Means that do not share same letter are significantly different at $p < 0.05$ significant level. Varietal differences are denoted by superscript letters a, b, c, d and treatments by e, f, g, h (mean \pm SD, $n = 5$).

Plant trait	Watering treatment	Lantana variety			
		WR	WY	OW	OP
Stem length (cm)	W1	55.60 \pm 0.54 ^{ae}	56.76 \pm 0.11 ^{ae}	36.53 \pm 0.12 ^{be}	111.00 \pm 0.15 ^{ce}
	W2	42.60 \pm 4.92 ^{af}	50.18 \pm 0.08 ^{af}	32.00 \pm 0.15 ^{bf}	94.46 \pm 0.11 ^{cf}
	W3	31.20 \pm 2.07 ^{ag}	32.02 \pm 0.11 ^{ag}	0.00 \pm 0.00 ^{bg}	69.54 \pm 0.11 ^{cg}
	W4	27.74 \pm 0.13 ^{ah}	20.48 \pm 0.08 ^{ah}	0.00 \pm 0.00 ^{bh}	25.00 \pm 0.15 ^{ch}
Leaf growth rate	W1	0.55 \pm 0.01 ^{be}	0.73 \pm 0.01 ^{ae}	0.89 \pm 0.01 ^{ce}	0.77 \pm 0.01 ^{de}
	W2	0.35 \pm 0.01 ^{bf}	0.60 \pm 0.01 ^{af}	0.75 \pm 0.01 ^{cf}	0.63 \pm 0.01 ^{df}
	W3	0.23 \pm 0.01 ^{bg}	0.40 \pm 0.01 ^{ag}	0.13 \pm 0.01 ^{cg}	0.11 \pm 0.01 ^{dg}
	W4	0.14 \pm 0.01 ^{bh}	0.34 \pm 0.01 ^{ah}	0.03 \pm 0.01 ^{ch}	0.014 \pm 0.01 ^{dh}
LWC % (Leaf water content)	W1	85.67 \pm 0.01 ^{ae}	89.21 \pm 0.45 ^{be}	85.40 \pm 0.38 ^{ce}	80.36 \pm 0.11 ^{de}
	W2	74.25 \pm 0.49 ^{af}	80.15 \pm 0.14 ^{bf}	68.13 \pm 0.14 ^{cf}	62.07 \pm 0.50 ^{df}
	W3	65.64 \pm 0.45 ^{ag}	42.15 \pm 0.07 ^{bg}	75.23 \pm 0.07 ^{cg}	36.60 \pm 0.10 ^{dg}
	W4	62.68 \pm 0.19 ^{ah}	70.40 \pm 0.47 ^{bh}	12.33 \pm 0.15 ^{dh}	10.16 \pm 0.21 ^{ch}
Cumulative number of leaves fallen	W1	0.00 \pm 0.54 ^{ae}	1.00 \pm 0.75 ^{be}	6.00 \pm 0.41 ^{ce}	5.00 \pm 0.50 ^{de}
	W2	1.00 \pm 0.23 ^{af}	2.00 \pm 0.41 ^{bf}	8.00 \pm 0.15 ^{ce}	5.00 \pm 0.21 ^{de}
	W3	28.00 \pm 0.74 ^{ag}	25.00 \pm 0.51 ^{bg}	8.00 \pm 0.74 ^{ce}	6.00 \pm 0.70 ^{de}
	W4	36.00 \pm 0.12 ^{ah}	37.00 \pm 0.85 ^{bh}	9.00 \pm 0.20 ^{ce}	6.00 \pm 0.72 ^{de}
Stomatal resistance (m ² smol ⁻¹)	W1	20.68 \pm 0.24 ^{ae}	19.73 \pm 0.44 ^{be}	30.79 \pm 0.27 ^{ce}	22.06 \pm 0.33 ^{de}
	W2	32.71 \pm 0.66 ^{af}	30.38 \pm 0.67 ^{bf}	32.97 \pm 0.25 ^{ce}	24.60 \pm 0.32 ^{de}
	W3	74.78 \pm 41.49 ^{ag}	64.97 \pm 1.94 ^{bg}	34.96 \pm 0.099 ^{ce}	26.49 \pm 0.31 ^{de}
	W4	216.67 \pm 40.82 ^{ah}	170.55 \pm 8.78 ^{bh}	28.24 \pm 15.89 ^{ce}	27.93 \pm 0.22 ^{de}
Cumulative number of flower heads/plant	W1	3 \pm 0.83 ^{ae}	4 \pm 0.89 ^{ae}	10 \pm 1.58 ^{be}	9 \pm 2.4 ^{be}
	W2	2 \pm 0.70 ^{af}	2 \pm 0.70 ^{af}	5 \pm 1.14 ^{bf}	5 \pm 1.1 ^{bf}
	W3	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}
	W4	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}
Cumulative number of berries/plant	W1	5 \pm 0.83 ^{ae}	5 \pm 0.54 ^{ae}	3 \pm 0.54 ^{be}	4 \pm 0.85 ^{ce}
	W2	2 \pm 0.54 ^{af}	2 \pm 0.70 ^{af}	1 \pm 0.54 ^{bf}	1 \pm 0.54 ^{bf}
	W3	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}
	W4	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{bg}	0 \pm 0.00 ^{ag}
Root volume (cm ³)	W1	3755.1 \pm 0.08 ^{ae}	8274.33 \pm 0.09 ^{be}	11861.76 \pm 0.03 ^{ce}	24252.35 \pm 0.11 ^{de}
	W2	2503.42 \pm 1.05 ^{af}	13859.74 \pm 0.13 ^{bf}	24252.35 \pm 0.16 ^{cf}	6205.71 \pm 0.05 ^{df}
	W3	6905.01 \pm 0.08 ^{ag}	22752.65 \pm 0.62 ^{bg}	6205.71 \pm 0.06 ^{ag}	10384.75 \pm 0.13 ^{dg}
	W4	10543.76 \pm 0.46 ^{ah}	40595.28 \pm 0.04 ^{bh}	10384.75 \pm 0.27 ^{ah}	17064.42 \pm 0.14 ^{dh}
Root-shoot ratio	W1	0.21 \pm 0.003 ^{ae}	0.14 \pm 0.004 ^{be}	0.085 \pm 0.005 ^{ce}	0.085 \pm 0.001 ^{ce}
	W2	0.22 \pm 0.009 ^{ae}	0.13 \pm 0.006 ^{be}	0.085 \pm 0.001 ^{ce}	0.058 \pm 0.005 ^{df}
	W3	1.10 \pm 0.0250 ^{af}	0.64 \pm 0.034 ^{bf}	0.103 \pm 0.004 ^{cf}	0.064 \pm 0.003 ^{bg}
	W4	2.46 \pm 0.119 ^{ag}	1.34 \pm 0.029 ^{bg}	0.108 \pm 0.006 ^{cg}	0.058 \pm 0.008 ^{dh}
Aboveground biomass allocation (%)	W1	85.02 \pm 0.35 ^{ae}	88.49 \pm 0.07 ^{be}	90.16 \pm 0.12 ^{ce}	88.49 \pm 0.24 ^{be}
	W2	81.15 \pm 0.17 ^{af}	87.56 \pm 0.23 ^{bf}	89.78 \pm 0.14 ^{cf}	90.67 \pm 0.17 ^{df}
	W3	47.69 \pm 0.15 ^{ag}	60.12 \pm 0.32 ^{bg}	89.43 \pm 0.27 ^{cf}	93.54 \pm 0.13 ^{dg}
	W4	49.63 \pm 0.13 ^{ah}	43.80 \pm 0.20 ^{bh}	86.47 \pm 0.14 ^{cg}	91.77 \pm 0.39 ^{dh}

varieties tend to behave in a more or less similar way in maintaining LWC at high soil moisture availability, while the ornamental varieties act *vice versa*. Although LGR was higher in WY than WR, and OW than OP, Lantana varieties exhibited the same trend in changing LGR at varying LWC (Figure 2b, see gradients of regression lines). Defoliation was high in wild Lantana

varieties, especially following exposed to W4 treatment, where WY reported the highest. The two wild Lantana varieties increased their stomatal resistance with water deficit conditions and showed low values under W1 and higher values at W4 treatment (WR showed the highest). Ornamental Lantana varieties did not show a change in stomatal resistance.

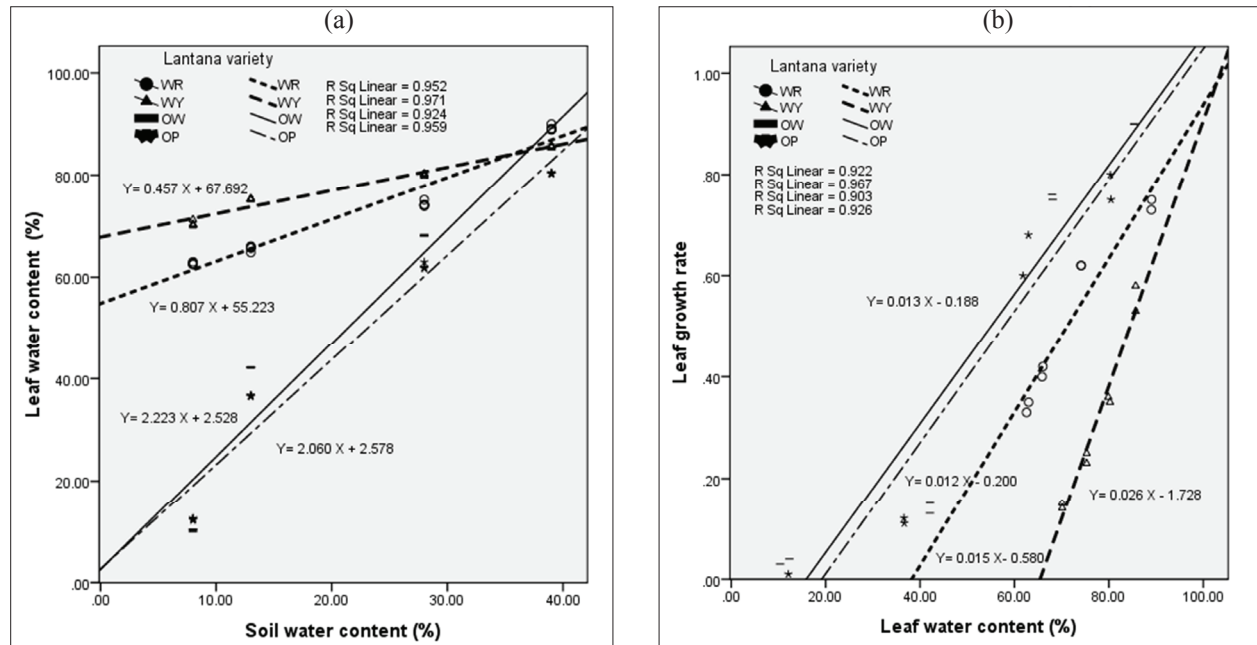


Figure 2: (a) Relationship between soil and leaf water content and (b) leaf water content and leaf growth rate of wild and ornamental Lantana varieties

In all Lantana plants the highest number of flower heads and berries were reported under W1 treatment. Ornamental Lantana varieties produced more flower heads than wild varieties under W1 and W2 treatments.

The root volume of wild Lantana varieties increased with reducing water availability and variety WY reported a higher root volume (approximately a five-fold increase) than that of WR. It was also evident that the proportion allocation of shoot biomass of wild Lantana varieties heavily decreased with low water availability exhibiting a sharp gradual increase in their root: shoot ratio. The results indicated that such consistent growth responses were not reported from ornamental Lantana varieties along with a reduction of soil moisture gradient although significant changes occurred to lesser extents.

The results confirmed that wild Lantana varieties could cope with the dryness of soil much better than ornamental Lantana varieties by overcoming ‘water

stress’ through limiting biomass allocation to above-ground growth. They also showed increased defoliation probably to maintain a high water content of leaves under limited soil water conditions, thus would have had a better osmotic regulation than that of the ornamental varieties. Wild Lantana varieties were also able to adjust stomatal conductance to reduce water loss by making available sufficient water for cellular processes. Munir (1996) reported that Lantana varieties tolerate long drought periods by defoliation and recover during favourable seasons (Baars & Naser, 1999). Our results also revealed that defoliation would have been the more plastic (as well as common) plant response. Increased stomatal resistance by stomatal closure also has been one of the most efficient plastic responses of plants to water stress (Cornic, 2000; Anjum *et al.*, 2011) as water is essential for plant growth, especially for the cell elongation process in leaves and stem. Hence the elongation of main stem and leaf growth rate of Lantana exhibited the same trend in responding to water availability.

Trade-offs in aboveground vs below ground growth, and vegetative vs reproductive growth indicated that wild Lantana varieties allocated more resources to maintain growth functions under water deficit conditions for sustenance in the long run. These observations support the idea that the allocation trade-off mechanism in *L. camara* has been vital for Lantana varieties to be naturalised and become invasive in new environments (Carrion-Tacuri & Rubio-Casal, 2011). As Castillo *et al.* (2007) pointed out, development of a deep root system is also an important trait for the invasiveness and competitive ability of the Lantana taxa.

It has been reported that the photosynthetic stress responses of Lantana were related to surface soil temperatures, thus *L. camara* is unable to survive in areas reaching > 60 °C mid-day temperatures and rainfall < 600 mm year⁻¹ (Fenshan, 1996). Therefore it has been considered not as a drought tolerant, but a drought avoider (Castillo *et al.*, 2007). The existence of functional types such as drought tolerants and drought avoiders within the same genus has been reported by Castillo *et al.* (2007). In this regard, plant morphology of root system, photosynthesis stress levels, hydraulic conduct and stomatal conductance, leaf water potential, and photosynthetic carbon fixation have often exhibited a great plasticity than the other traits (Dickson & Tomlinson, 1996; Nandini, 1999). We also suggest the existence of drought avoidance and intolerance within the Lantana group as exhibited by different varieties of *Lantana camara*. As per the results wild WY Lantana variety reflected more plasticity to low water availability than that of WR. Our observations and personal communications with experts (S. Wijesundara, *Personal Communication*, 2015) have supported the idea that WY is often found in wetter parts and WR in drier parts in Sri Lanka. This could be a possible reason for WY to show higher LWC and LGR compared to WR, and similarly WR to show a higher defoliation and stomatal resistance to low water availability than WY.

Light availability

The un-shaded treatment received full sunlight within a range of 95.5 – 89.5 kLux during midday of the experiment period. Plants under S2 shade level received sunlight within 42.5 – 37.5 kLux range. The range of sunlight of S3 shade level was 27 – 26.3 kLux while plants kept under S4 treatment received 17.8 – 16.4 kLux of sunlight. All Lantana plants except for 40 % of the plants of OW variety exposed to S4 survived throughout the experiment.

Both wild Lantana varieties exhibited progressive increase of the main stem length with decreasing light intensity, while both ornamental varieties recorded to have longer stems with increasing light intensity (Table 2). The strangling Lantana variety OP was much responsive to varying sunlight than the straight growing variety OW except when they were under excessive shade, while no significant difference was observed between the wild varieties. Internodes and petiole lengths of both wild varieties showed a significant increase under shade. Moreover they produced larger leaves (a high leaf area) under shade, whereas leaves of ornamental varieties did not respond in a similar manner. Stomatal resistance of all Lantana plants reported to be high in unshaded conditions (WY reported the highest) and gradually declined with increased shade. The density of stomata of wild Lantana varieties increased with reducing light intensities, while that of ornamental Lantana varieties did not change. The same pattern of response was shown by chlorophyll a and chlorophyll b contents of Lantana leaves along the decreasing sunlight gradient. Wild Lantana varieties exhibited higher contents of chlorophyll a and b at moderate light intensities (particularly S2 and S3), whereas the chlorophyll content of ornamental Lantana varieties at moderate light intensities were almost similar to that of the un-shaded condition (Figures 3a and 3b). Carotenoid content of both wild and ornamental varieties were the same irrespective of the light treatment (Figure 3c). Palisade and spongy parenchyma of both wild Lantana varieties were thinner under shade conditions, while no such difference was reported from ornamental Lantana varieties (Figure 4).

All Lantana plants produced flower heads when they received un-shaded sunlight. The wild varieties produced flowers even at 35 % shade (S2) but beyond further shade they did not produce flowers. Ornamental Lantana variety OP produced more flowers than OW under favourable light conditions. During the study period of the shade experiment fruiting was not reported by Lantana plants.

With decreasing light intensity wild Lantana varieties allocated more biomass to their aboveground parts showing a decrease in root: shoot ratio, while ornamental varieties decreased allocation to the aboveground parts while showing an increase in root: shoot ratio when grown under shade.

While confirming the plastic responses of wild Lantana varieties to become taller or make the stem, internodes and petiole lengths longer to compete with

Table 2: Effect of different light intensities on plant growth of wild Lantana varieties; *Lantana camara* var. *splendens* (WR), *Lantana camara* var. *camara* (WY), ornamental Lantana varieties producing white (OW) and purple (OP) flowers. Means that do not share a letter are significantly different from each other at $p < 0.05$ significant level. Significant different in responses of the same variety to different water stress levels are denoted by superscript letters e, f, g, h and significant different of the responses of different plant varieties to the same treatment are denoted by a, b, c, d (mean \pm SD, $n = 5$)

Plant trait	Treatment	Lantana variety			
		WR	WY	OW	OP
Shoot length (cm)	S1	72.8 \pm 0.83 ^{ac}	71.8 \pm 0.83 ^{ac}	48.4 \pm 0.54 ^{bc}	70.4 \pm 0.54 ^{cc}
	S2	76.0 \pm 1.00 ^{af}	76.6 \pm 0.89 ^{af}	46.0 \pm 0.99 ^{bc}	68.0 \pm 1.00 ^{cf}
	S3	80.8 \pm 0.83 ^{ag}	81.6 \pm 1.14 ^{ag}	42.2 \pm 0.44 ^{bc}	55.4 \pm 0.54 ^{cg}
	S4	88.0 \pm 0.70 ^{ah}	87.0 \pm 0.70 ^{ah}	25.0 \pm 13.98 ^{bf}	52.4 \pm 0.54 ^{bh}
Internode length (cm)	S1	2.54 \pm 0.05 ^{ae}	3.54 \pm 0.11 ^{be}	5.08 \pm 0.08 ^{bg}	2.6 \pm 0.07 ^{de}
	S2	3.08 \pm 0.08 ^{af}	4.12 \pm 0.08 ^{bf}	1.6 \pm 0.07 ^{cf}	2.36 \pm 0.09 ^{df}
	S3	3.5 \pm 0.07 ^{af}	4.08 \pm 0.08 ^{bf}	1.38 \pm 0.08 ^{cf}	2.08 \pm 0.08 ^{df}
	S4	4.48 \pm 0.28 ^{ag}	5.08 \pm 0.08 ^{bg}	1.1 \pm 0.1 ^{cg}	1.6 \pm 0.07 ^{dg}
Petiole length (cm)	S1	0.96 \pm 0.05 ^{ae}	1.46 \pm 0.05 ^{be}	0.58 \pm 0.08 ^{ce}	0.94 \pm 0.05 ^{de}
	S2	1.42 \pm 0.08 ^{af}	1.5 \pm 0.07 ^{bf}	0.46 \pm 0.27 ^{ce}	0.88 \pm 0.08 ^{de}
	S3	2.1 \pm 0.07 ^{ag}	2.24 \pm 0.15 ^{bg}	0.58 \pm 0.08 ^{ce}	0.92 \pm 0.08 ^{de}
	S4	3.12 \pm 0.08 ^{ah}	3.44 \pm 0.05 ^{bh}	0.62 \pm 0.08 ^{ce}	1.06 \pm 0.11 ^{df}
Leaf area (cm ²)	S1	165.45 \pm 0.75 ^{ae}	150.85 \pm 0.12 ^{be}	45.23 \pm 0.12 ^{ce}	97.85 \pm 0.57 ^{de}
	S2	192.35 \pm 0.35 ^{af}	180.65 \pm 0.16 ^{bf}	45.05 \pm 0.15 ^{ce}	97.12 \pm 0.45 ^{de}
	S3	250.78 \pm 0.87 ^{bg}	248.25 \pm 0.78 ^{ag}	44.87 \pm 0.75 ^{ce}	97.05 \pm 0.15 ^{de}
	S4	250.84 \pm 0.12 ^{ag}	250.78 \pm 0.15 ^{bh}	44.05 \pm 0.75 ^{ce}	96.89 \pm 0.18 ^{de}
Stomatal resistance (m ² smol ⁻¹)	S1	100.28 \pm 0.41 ^{bc}	166.95 \pm 0.41 ^{ac}	83.95 \pm 0.87 ^{ce}	70.24 \pm 0.45 ^{de}
	S2	66.91 \pm 0.35 ^{af}	80.37 \pm 0.54 ^{bf}	71.662 \pm 0.33 ^{ce}	62.74 \pm 0.34 ^{de}
	S3	41.65 \pm 0.47 ^{ag}	46.57 \pm 0.40 ^{bg}	53.90 \pm 0.60 ^{cf}	59.23 \pm 0.59 ^{df}
	S4	20.32 \pm 0.46 ^{ah}	21.23 \pm 0.88 ^{bh}	48.95 \pm 0.58 ^{cg}	46.37 \pm 0.71 ^{dh}
Stomatal density	S1	8 \pm 0.01 ^{ae}	8 \pm 0.04 ^{be}	10 \pm 0.07 ^{ce}	11 \pm 0.05 ^{de}
	S2	9 \pm 0.08 ^{af}	8 \pm 0.05 ^{bf}	11 \pm 0.03 ^{ce}	11 \pm 0.07 ^{de}
	S3	12 \pm 0.05 ^{ag}	12 \pm 0.07 ^{bg}	11 \pm 0.07 ^{ce}	12 \pm 0.08 ^{de}
	S4	15 \pm 0.04 ^{ag}	16 \pm 0.08 ^{bg}	11 \pm 0.09 ^{ce}	12 \pm 0.04 ^{de}
Cumulative number of flower heads	S1	6 \pm 0.01 ^{ae}	7 \pm 0.02 ^{bc}	15 \pm 0.07 ^{ce}	18 \pm 0.08 ^{de}
	S2	4 \pm 0.05 ^{af}	3 \pm 0.02 ^{bf}	0 \pm 0.00 ^{cf}	0 \pm 0.00 ^{cf}
	S3	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{af}	0 \pm 0.00 ^{af}
	S4	0 \pm 0.00 ^{ag}	0 \pm 0.00 ^{bg}	0 \pm 0.00 ^{bf}	0 \pm 0.00 ^{bf}
Aboveground biomass allocation (%)	S1	32.43 \pm 0.021 ^{ae}	25.81 \pm 0.044 ^{be}	92.96 \pm 0.14 ^{ce}	92.80 \pm 0.12 ^{de}
	S2	52.22 \pm 0.043 ^{af}	38.02 \pm 0.013 ^{bf}	78.07 \pm 0.15 ^{cf}	85.35 \pm 0.14 ^{df}
	S3	80.59 \pm 0.12 ^{ag}	61.47 \pm 0.012 ^{bg}	44.46 \pm 0.12 ^{cg}	64.36 \pm 0.14 ^{dg}
	S4	89.19 \pm 0.04 ^{ah}	70.58 \pm 0.12 ^{bh}	37.47 \pm 0.12 ^{ch}	11.23 \pm 0.13 ^{dh}
Root: shoot ratio	S1	3.34 \pm 0.05 ^{ag}	3.5 \pm 0.03 ^{bh}	2.90 \pm 1.47 ^{ce}	2.24 \pm 0.65 ^{de}
	S2	3.2 \pm 0.04 ^{ag}	2.97 \pm 0.06 ^{bg}	2.49 \pm 1.7 ^{cf}	1.95 \pm 1.54 ^{df}
	S3	2.55 \pm 0.04 ^{af}	2.52 \pm 0.30 ^{bf}	2.33 \pm 0.32 ^{cf}	1.39 \pm 0.04 ^{df}
	S4	1.78 \pm 0.08 ^{ae}	2.09 \pm 0.23 ^{bc}	1.05 \pm 0.31 ^{cf}	0.85 \pm 2.93 ^{dg}

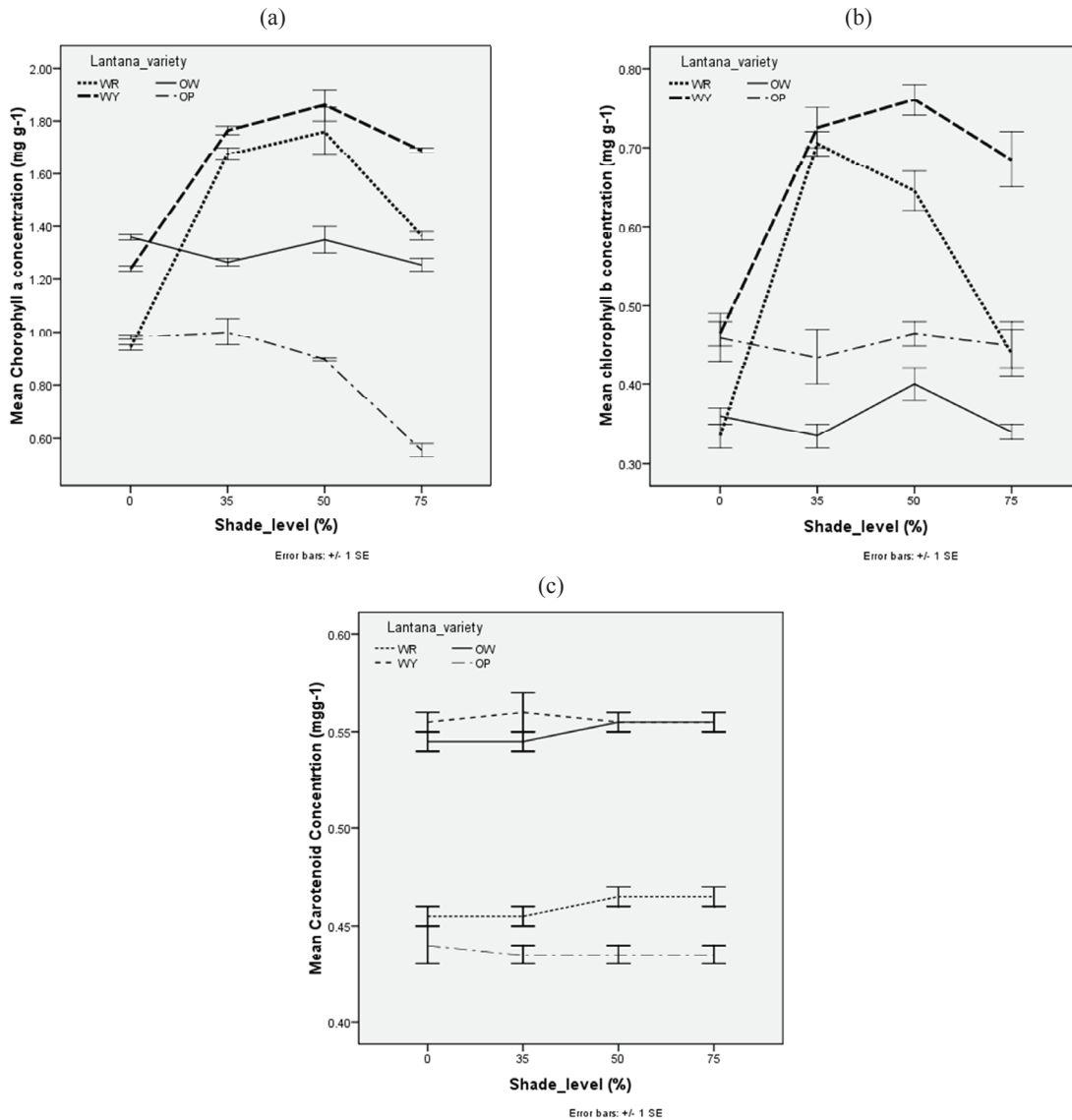


Figure 3: (a) Relationship between the shade level and the concentration of chlorophyll a; (b) relationship between the shade level and the concentration of chlorophyll b; (c) relationship between the shade level and the concentration of carotenoids

neighbouring individuals when growing under shade (Lowe *et al.*, 2000), this study also exhibited that Lantana plants develop larger leaves to capture more light under shade to trap more sunlight. High chlorophyll a and b content at lower light conditions is also a plastic response in many plants so as to increase photosynthetic active radiation (PAR) in shade (Turnbul, 1991; Valladares & Niinemets, 2008) while at high light conditions it tends to reduce by behaving as a photo protective response (Lichtenthaler & Burkart, 1999). The inability of ornamental varieties to respond to different light and shade conditions emphasised that they may not possess plastic responses to successfully challenge shade.

Lantana at low light intensity shows less capacity to produce flowers (Mandal & Joshi, 2015), and similarly in this experiment the wild varieties flowered only in un-shaded and high light intensities and shade conditions hindered them to flower. This was quite clear in ornamental varieties as the trade-off between vegetative growth and reproductive growth under shade would have led the ornamental Lantana varieties to translocate more biomass into aboveground parts, especially to the leaves under shade as they were incapable of adjusting their photosynthetic efficiency by changing leaf area, stomatal resistance, leaf stomatal density, and chlorophyll a and b levels in photosynthetic tissue mass.

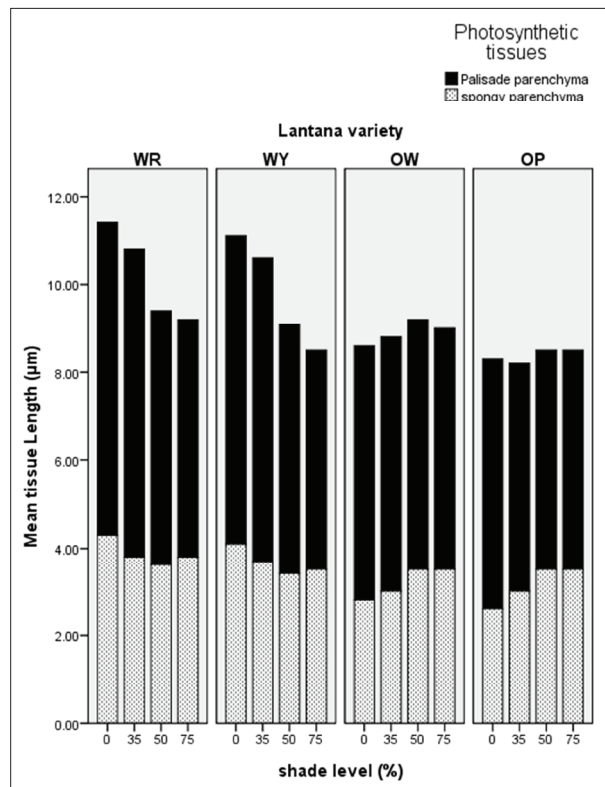


Figure 4: Thickness of photosynthetic tissue mass of Lantana plants under different shade levels

The failures reported in controlling Lantana invasion in more than 60 countries worldwide have been partly attributed to the uncertainties of its taxonomy, biology and ecology (Howard, 1970; Taylor, 1989; Sharma *et al.*, 2005). In most instances growing habit and flower colour have been the primary features that distinguished Lantana varieties and influenced their popularity as ornamental plant varieties without much investigations into eco-physiological differences and related growth responses. Thus the potential of these plants becoming invasive is less discussed. As many plant traits exhibit plasticity with respect to varying levels of exploitation of environmental resources, the favourable conditions for growth and spread of the Lantana taxa, or in other words the degree of tolerance, needs to be understood. In this regard the present study reveals a comprehensive account of growth responses of two commonly grown ornamental Lantana varieties and wild (naturalised and invasive) *L. camara* varieties to varying water and light conditions experienced in Sri Lanka and many tropical environments.

The ornamental varieties would have been probably developed through many steps of hybridisation of

various Lantana varieties and thus may exhibit varying degrees of expression of traits depending on the parental combinations. The intention of hybridisation would have been to improve the habit, blooming and flower colour and not the degree of tolerance to environmental exploitation. The two ornamental Lantana varieties were blooming oriented, short-term survivors in contrast to the long term surviving wild Lantana varieties, which were more growth oriented. This could be proven by the reported reproductive (flower production) and leaf traits in ornamental Lantana varieties (especially OW) even under reduced availability of soil moisture, regardless of the short survival period as indicated by the death of individuals.

The present study provides evidence for the low sustainability and survival of white and purple flowered ornamental Lantana varieties under reduced water and light conditions in contrast to the superior capacity shown by the wild growing (naturalised invasive) varieties; *L. camara* var. *splendens* (WR) and *L. camara* var. *camara* (WY). The low morphological and physiological plasticity observed in ornamental Lantana varieties exhibits their unpreparedness to challenge deficit conditions of water and light, and suggests that the potential invasiveness of these ornamental Lantana varieties could not be as high as the naturalised invasive Lantana taxa in Sri Lanka. However it is important to note that invasive success is considered as a combined outcome of environmental conditions and plant traits (Richardson & Pysek, 2006), thus, the role of species traits is not the only feature that determines biological invasions. Decisive factors such as repeated introductions of species from one or more original ranges into a new environment as well as secondary releases within the new range including cultivation (Mack, 2000), disturbances and cultivated factors (Kowarik, 2003) have acted to promote invasions. The rapid spread of Lantana in India has been also attributed to major land use changes in the country such as habitat degradation, fragmentation, and land conversion creating favourable habitats in terms of higher light availability, moderate soil moisture and other micro environmental parameters (Ray & Ray, 2014). Hence the potential risk of a taxon being invasive may also lie with the spatial and temporal changes of the invisibility of the environment.

CONCLUSION

This study provides evidences for the differences of the level of tolerance to reduced water (drought) and reduced light (shade) between wild and ornamental Lantana varieties. The distinct growth performances of the locally

available white and purple flowered ornamental *Lantana* varieties of horticultural value are incapable to overcome water and shade stress conditions, which threaten their survival, thus is unlikely to become invasive under the present environment conditions in Sri Lanka.

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