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Eco-physiological performance may contribute to differential success of two forms of an invasive vine, *Dolichandra unguis-cati*, in Australia

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Abstract

Invasive plant species are hypothesized as being more efficient at resource acquisition and use, resulting in faster growth than co-occurring non-invasive plant species. Nonetheless, some findings suggest that trait differences between invasive and non-invasive species are context dependent. In this study, two forms of an invasive vine species, *Dolichandra unguis-cati*, were used to test the context-dependent hypothesis. *Dolichandra unguis-cati* is a weed of national significance in Australia with two different forms: the 'long pod' (LP) and 'short pod' (SP). The two forms have different levels of distribution on the eastern Seaboard of the continent, with the SP form occurring extensively in both States of Queensland and New South Wales while the LP form is found only in isolated sites in South-East Queensland. This study examines whether differences in eco-physiological performance could be responsible for differential success of the two forms. A partially factorial experiment was set up in controlled conditions where potted plants of both forms were grown under two levels of light, water and nutrient resources (high and low) for 15 months. We measured several traits that are known to correlate with plant performance and resource use efficiency (RUE). The SP form exhibited higher values of carbon assimilation, RUE, number of subterranean tubers and leaf nitrogen than the LP form. However, the LP form produced greater biomass than the SP form, with the difference driven mainly by high resource conditions. The LP form displayed significantly higher phenotypic integration (number of traits significantly correlated) than the SP form in response to all treatments while the SP form exhibited higher phenotypic integration than the LP form in response to high resource conditions only. The SP form displayed traits that are well suited for successful colonization, possibly explaining its increased success in Australia, while the LP form possessed traits of opportunistic plants. Overall, we find that the two forms of the weedy vine deploy different carbon economies in response to resource conditions, which is evidence of the context-dependent trait hypothesis.

Keywords

Cat's claw creeper, disturbance, functional traits, resource use efficiency, invasiveness, Bignoniaceae

Introduction

A key component of invasion ecology is to understand traits that enable introduced species to colonize and thrive in novel environments (Richardson and Pyšek 2006; Reichmann et al. 2016). Comparative trait-based frameworks involving congeneric introduced invasive and native species are often used to compare and understand the traits that may lead to varying levels of success (Daehler 2003; Bradley et al. 2010; Finerty et al. 2016; Hui et al. 2016). Although trait-based studies have advanced the state of knowledge of how functional traits drive plant community assemblages, results have been equivocal (Palacio-López and Gianoli 2011; Oduor et al. 2016). For example, several pairwise studies found that invasive and non-invasive species had comparable traits under similar environmental conditions (Meiners 2007; Palacio-López and Gianoli 2011; Jo et al. 2016). A review of plant ecological strategies revealed that significant trait differences are sometimes detectable within a species, indicating intraspecific trait variability (Funk et al. 2016). Thus, while there may be differences between some invasive and congeneric non-invasive species, this pattern is not universal (Leishman et al. 2010; Parker et al. 2013). These conflicting outcomes of trait-based pairwise studies may indicate context-dependence of trait differences (Leishman et al. 2010; Leffler et al. 2014; Li et al. 2016). Therefore, comparisons of multiple forms/varieties of an introduced species that both occupy similar niches but exhibiting different levels of invasion success could yield informative insights into invasion success (Kolar and Lodge 2001).

Invasive plants often display faster growth strategies than non-invasive species in the same environments (Davies et al. 2000; Firn et al. 2012). They explore limiting resources more efficiently than co-occurring species in the same environment (Vitousek et al. 1996). Invasive species display higher carbon assimilation rates (A_{max}) and higher relative growth rates (RGR) than non-invasive species (Pattison et al. 1998; Grotkopp et al. 2002; Feng et al. 2007; van Kleunen et al. 2010b). Significantly higher values for these traits and other resource use efficiency (RUE) indices including water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE) are directly linked with faster growing plants (Wright et al. 2004; Firn et al. 2012).

Other studies have demonstrated that invasive species show higher trait integration than non-invasive ones (Osunkoya et al. 2014; Luo et al. 2015). Trait integration (or trait coordination) is an estimation of the number of trait pairs that are significantly correlated in their response to changes in environmental conditions. The higher the number of correlated trait pairs, the more integrated or coordinated a species is considered to be (Pigliucci 2003). More integrated traits may allow organisms to adapt better to the environment (Waitt and Levin 1993; Godoy et al. 2012).

Many studies have tried to identify the key traits that explain successful colonization and establishment by invasive plants, but results have shown that context matters more than any one trait and disturbance seems to frequently matter too (MacDougall et al. 2014). Disturbed plant communities are more susceptible to invasion because of unused resources e.g. pulses in light gaps and nutrient load (Davis et al. 2000). In addition, most invading species have heightened capabilities for niche pre-emption (Baruch and Goldstein 1999; Stratton and Goldstein 2001), even in low resource environments such as canopy understories and arid environments (Abrams 1983; Stubbs and Bastow Wilson 2004; Schwilk and Ackerly 2005). Invasive species that are adapted to low resource environments often show traits associated with resource conservation such as slow growth and high RUE (Funk and Vitousek 2007; Firn et al. 2012; Ens et al. 2015). Thus, mechanisms allowing successful colonization of low resource habitats will be different from those driving invasion of high resource habitats (Funk et al. 2013). These two ends of a continuum of invasiveness strategy agree with the leaf economic spectrum (LES), which proposes a trade-off in the traits held by plant species growing in productive versus unproductive environments (Wright et al. 2004).

Cat's claw creeper, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) (Bignoniaceae) is an invasive vine in Australia. Two morphologically distinct forms of this species occur in Australia ('long' and 'short' pod – in reference to the average length of fruit pods produced by each form) (Shortus and Dhileepan 2011). The two forms of *D. unguis-cati* show different prevalence or abundance. The short pod (SP) form is more abundant, occurring extensively in the states of Queensland and New South Wales (Dhileepan 2012), while the long pod (LP) form occurs in ~15 isolated sites in southeast Queensland (Liz Snow, personal communication, 07/03/2016). Where the LP form is present, it usually co-occurs with the SP form (Dhileepan 2012). The cause of variation in abundance and prevalence between the two forms is not known, but we hypothesised that differences in eco-physiological responses to environmental resources could offer a potential explanation (Buru et al. 2016a, 2016b). The SP form exhibited higher RGR, stem length, specific leaf area (SLA) and tuber abundance than the LP form in glasshouse conditions (Buru et al. 2016a). However, in a field study it was shown that the LP form accumulated more biomass and had higher RGR than the SP form (Taylor and Dhileepan 2012). The more abundant SP form has rapid and higher germination rates and a greater prevalence of poly-embryonic seeds (40%) than the less abundant LP form (Buru et al. 2014, 2016b).

To understand the eco-physiological mechanisms that underpin colonization success, it is vital to investigate potential links between plant growth and physiology, including photosynthetic traits (Osunkoya et al. 2010b). In this study, we compared eco-physiological traits of the two forms of *D. unguis-cati* to gain a better understanding of the mechanistic reasons for the SP form being more successful in its invaded range than the LP form. We measured and compared photosynthetic capacity and biomass accumulation under varying environmental resources of water, light and nutrient (low vs. high) and examined shifts in these traits in response to changes in resource conditions. Specifically, we examined traits related to carbon gain including maximum carbon assimilation (A_{max}), transpiration, C: N ratio, total biomass, SLA, LDMC and tuber density. We correlated assimilation rates, SLA, resource use efficiency traits and tuber abundance with total biomass to ascertain whether physiological performance resulted in differences of fitness and growth in the two forms. We hypothesised that SP, the more abundant form of *D. unguis-cati* in Australia, would show higher photosynthetic capacity, higher RUE and perform better under disturbance scenarios of high nutrients and light levels than the less abundant LP form.

Methods

Study species

Cat's claw creeper, *Dolichandra unguis-cati* (L.) Lohmann (syn. *Macfadyena unguis-cati* (L.) Gentry) (Bignoniaceae) is a native of the Greater and Lesser Antilles, Mexico, South and Central America, Argentina and Trinidad and Tobago (Gentry, 1976). This species was introduced into Australia for ornamental purposes from South America in the 1800s (Downey and Turnbull 2007). *Dolichandra unguis-cati* presents a serious threat to native biodiversity, especially in riparian and rainforest plant communities as a structural parasite (Raghu et al. 2006; Dhileepan 2012; Ewers et al. 2015). Where there is standing vegetation, it smothers tree canopies, and the biomass can build to a point where it causes the collapse of canopy structures (Batianoff and Butler 2003). In the absence of vertical support, it readily grows along the ground, forming dense mats that preclude recruitment, growth and germination of indigenous understory vegetation. This growth pattern transforms natural habitats into monospecific stands, resulting in loss of floral biodiversity and changes in soil biota and physico-chemical properties (Osunkoya et al. 2009). As a result, this invasive vine is classified as an ecosystem transformer. *Dolichandra unguis-cati* regenerates both asexually (vegetatively), by production of subterranean tubers, as well as sexually, with production of numerous papery seeds (Downey and Turnbull 2007; Osunkoya et al. 2009). The two forms of *D. unguis-cati* that occur in Australia have been informally referred to as long pod (LP) and short pod (SP) based on their average (± SE) fruit length at maturity (LP form: 70.024 ± 2.35 cm; SP form: 30.089 ± 8.96 cm). The LP and SP forms have been shown to carry an average of 120 ± 10.67 and 60.89 ± 23.17 seeds per pod at maturity, respectively. Seeds of both forms are two-winged, papery and flattened/oblong in shape, 10–18 mm long, 4.2–5.8 mm wide (Shortus and Dhileepan 2012). These two forms appear to prefer similar habitats, although there is general lack of research on the ecology of this species (Osunkoya et al. 2009).

Experimental design

This study was carried out in temperature-controlled glasshouse and shade-house facilities at the Queensland Department of Agriculture and Fisheries (DAF) in Brisbane, Australia. During the 15-month experiment, average temperature during the warmer months (October–April) ranged from 18 °C to 35 °C, and between 10 °C and 23 °C during the cooler months (May–September). Relative humidity ranged between 50–70% during this study.

Fruits containing seeds of the LP and SP forms were collected from various sites around the greater Brisbane area in South East Queensland (SEQ) and parts of New South Wales (NSW), Australia. Seeds of both forms were germinated in plant growth chambers, (model ADAPTIS A1000; Conviron Ltd., USA). For further germination details see Buru et al. (2016a). After two weeks of germination, seedlings were transferred into small 0.8 L plastic pots (dimensions: Diameter = 200mm, Height = 190mm) filled with locally available commercial potting mix (Osmocote) to establish the plants. Plants were watered every two days for two months without addition of extra nutrients. After two months of growth, plants of both forms were transferred into bigger 13.5 L plastic pots (dimensions: Diameter = 300 mm, Height = 290 mm) filled with a multi-purpose potting mix containing a wetting agent and trace elements (Osmocote). After two weeks in the bigger pots, these plants were then subjected to different treatments as described below.

Light x nutrients experiments

A factorial experiment of light and moisture was set up in a shade-house. For each form of *D. unguis-cati*, growth and physiology under two light resource levels were investigated i.e., (a) High light (HL) in which plants received ~35–40% of full sun (870 -1100 µmol m^{-2} s^{-1}); and (b) Low light (LL) in which plants received ~1–2% of full sun (25–50 µmol m^{-2} s^{-1}). LL conditions were achieved by creating a shade using 2–3 layers of locally available Coolaroo 1.83m Charcoal 90% shade cloth. These two light levels were chosen as approximations of irradiance levels encountered in disturbed habitats and open spaces (HL), and in rainforest understories (LL) where *D. unguis-cati* usually occurs. Light levels were measured using a LICOR 6400 portable photosynthesis system (LICOR, Inc., Lincoln, NE). Both forms were grown under HL and LL conditions with plants in each light level receiving either of two nutrient regimes. High nutrient (HN) condition was obtained by adding granules of a slow-release all purpose fertiliser (Osmocote, NPK 21:2:6 plus trace elements) to the growth medium every two weeks. No additional fertilizer was added to the growth media to create the low nutrient (LN) condition. The two nutrient levels (HN, LN) were chosen to mimic habitats of high nutrients (e.g., following fertilizer discharge) and low nutrient pulses respectively. All plants were watered to pot capacity by the addition of ~ 300 ml of water every two days using an automated watering system. The combinations of treatments were as follows: HLHN, HLLN, LLHN and LLLN.

Water x nutrients experiments

These experiments were set up in a temperature-controlled glasshouse facility with temperatures ranging from 22–28 °C during the experiment. The mid-day photosynthetically active radiation (PAR) in the glasshouse was 800–1500 µmol m^{-2} s^{-1}. These light conditions are comparable to the HL conditions described above for the light x nutrient experiment. Two water regimes were applied, reflecting the riparian and non-riparian environments where *D. unguis-cati* occurs: (i) a well-watered or high water (HW) condition in which soil moisture level was maintained at 100% pot capacity by the addition of ~ 300 ml of water every two days, and (ii) a low water (LW) condition in which moisture was maintained at 5% pot capacity by adding ~ 15 ml of water once every two weeks. Pot water capacity was determined at the beginning of the experiment by filling four replicate 13.5 L plastic pots with the commercial potting mix (Osmocote Multi-Purpose). The potting mix was oven dried using a Thermolite Scientific + 6100 Model oven for 48 hours at 80 °C and weighed to determine dry weight (DW). The potting mix was then saturated with water and excess water allowed to drain freely for 2-3 hours until no more water drained out. The pots were weighed again to determine saturated weight (SW). Pot capacity was calculated as the difference between SW and DW (Frosi et al. 2013). The two water treatment levels were further factored by two levels of nutrient application as described above. Thus, the combinations of treatments were as follows: HWHN, HWLN, LWHN and LWLN.

Data collection

The light and water treatments, at two nutrient levels, were replicated seven (7) times for both the LP and SP forms. Thus, there were 112 total number of plants for this experiment. Physiological and growth traits were measured at the end of the experiment after 15 months of plant growth.

Physiological traits

Assimilation rates were measured using an open-path portable gas exchange system (LI-6400; LICOR, Inc., Lincoln, NE, USA). For each treatment, five replicates (plants) of each form were randomly selected, and for each plant, two recently matured leaflets were identified and tagged for measurements. Photosynthetic rate (A, µmol m^{-2} s^{-1}), transpiration rate (E, mol m^{-2} s^{-1}) and stomatal conductance (g_s, mol m^{-2} s^{-1}) were measured at a constant CO_2 concentration of 400 µL L^{-1}. The relative humidity within the leaf chamber ranged between 50–65% while the temperature was kept at 23–25 °C. To investigate the response of the leaflets to changes in PAR, instantaneous assimilation A and transpiration measurements were taken at 50, 500, 1500 and 2500 µmol m^{-2} s^{-1}. Leaves were kept at the respective PAR levels for ~ 10 minutes until they were stabilised. From the primary physiological data collected, the instantaneous water-use efficiency (WUE) was calculated as follows:

WUE = *Asat*/*E*, where *Asat* was assimilation rate at 2500 µmol m^{-2} s^{-1}

Leaf chlorophyll content (measured in SPAD units) was estimated using a chlorophyll meter (Konica-Minolta SPAD-502, Spectrum Technologies, IL, USA). The same leaves tagged for physiological measurements were used to determine chlorophyll content, taking three random measurements from each leaf. Physiological data could not be obtained for HWLN and LWLN combinations because the plants under these treatments developed very few leaves.

After measurement of physiological data, the tagged leaflets were harvested, weighed (fresh weight) and photographed against a graduated background using an IPAD camera (Apple Inc., CA, USA) for leaf area estimation. The open access software, Image J 1.47v (www.imagej.nih.gov/ij) was used to calculate the leaf area (cm^2) from the images. The harvested leaflets were thereafter dried at 65 °C for 72 hours, and their dry weight measured. The data collected were used to estimate specific leaf area (SLA = leaf area/leaf dry mass) and leaf dry matter content (LDMC = leaf dry mass/leaf fresh mass).

The dried leaf samples were analysed for total carbon (C) and nitrogen (N) concentrations using Plant CN Dumas combustion method (Jung et al. 2003). All chemical components of this study were analysed at the Chemistry Centre, Queensland Department of Science Information, Technology and Innovation (DSITI), Brisbane, Australia. After collection of the leaf chemical data, the following parameters were calculated:

Photosynthetic nitrogen use efficiency (PNUE) =
= A_{max}/leaf N, where assimilation rate was at 2500 µmol m^{-2} s^{-1}

Leaf Carbon to leaf Nitrogen ratio (C: N) = Leaf C / leaf N

Leaf Chlorophyll to leaf Nitrogen ratio (Chl: N) = Leaf Chl / leaf N

Growth and biomass traits

At the end of the experiment (i.e. at 15 months growth), all plants were harvested and separated into above-ground (shoots) and below-ground (roots and tubers) tissues. The number of subterranean tubers per plant was recorded per treatment and per plant form. All plant tissues were dried at 65 °C for three weeks before weighing to determine total dry mass (g) and shoot/root ratio.

Statistical analyses

All data were tested for normality and homoscedasticity using the Shapiro-Wilks test. Data that violated the ANOVA assumptions of normality and homogeneity of variance were either $\log_{10}$ transformed (A_{max}, WUE), square-root transformed (shoot/root ratio) or Box-Cox power transformed (basal stem density [BSD], number of tubers, root and shoot dry mass, total dry mass, and all leaf traits). Values presented in this paper were back-transformed data, unless otherwise stated.

Mean differences for all traits were analysed using a two-way analysis of variance (ANOVA + an error structure of replicate/leaf number/or treatment) with treatments (HLHN, HLLN, LLHN, LLLN, HWHN, HWLN, LWHN, LWLN) and plant form (LP or SP) as fixed effects. When significant differences were detected, a Tukey LSD post-hoc test was performed to check differences between specific means. Pearson correlation coefficients were generated to determine the linear association among traits and how they compare between the LP and SP forms, and they were also used to test for the extent of trait integration within each of the two forms. A multivariate method of principal components analysis (PCA) based on Euclidian distances was used to explore how the two forms were separated by traits on an ordination space. Principal components smaller than 15% were discarded. All statistical tests were conducted using R version 3.1.0 (R Development Core Team 2014) and graphics were created using SPSS (version 22.0; IBM SPSS Statistics; Armonk, NY, US).

Results

Biomass production and resource allocation patterns

Biomass production and allocation traits were not consistent within each form in response to high and low resources as shown by significant interactions between form and treatment for many of the traits examined ($F_{1,7}$ = 3.184, P<0.005; Table 2). The two forms differed significantly in biomass accumulation in the HLHN and LWHN treatments (Fig. 1a. b). Under the HLHN scenario, the LP accumulated more biomass, suggesting opportunist traits or a specialised micro-climate for this form. On the other hand, the SP form accumulated more biomass in the LWHN treatment, which suggests resource substitution. Overall (i.e., across treatments), SP and LP total biomass levels differed significantly at the end of the 15 months growth period ($F_{1,7}$ = 8.124, P<0.006; Table 1), with the LP individual plants showing more biomass. Light intensity, amount of nutrient and water supplied to the plants all had significant effects on all biomass allocation traits of the two forms ($F_{1,7}$ = 12.195, P<0.0001), and was of the order: HLHN>HWHN>HLLN>LWHN>LLHN>LLLN=LWLN (Table 2). Both the SP and LP forms accumulated more biomass in response to light x nutrient treatments than in response to water x nutrients treatments (Fig. 1a, b).

The SP form developed more tubers than the LP form in high light (HLHN and HLLN) and high nutrient (HWHN and LWHN) conditions ($F_{1,7}$ = 46.459, P<0.001; Fig. 1c, d; Table 1 and 2). However, the LP form showed significant differences in response to light × nutrients (HLHN > HLLN = LLHN > LLLN) and when both water and nutrients were abundant (HWHN > HWLN = LWHN = LWLN) (Fig. 1c, d; Table 2). There were no significant differences in total biomass and tuber development between the two forms under the most stressful conditions of low light, low water and

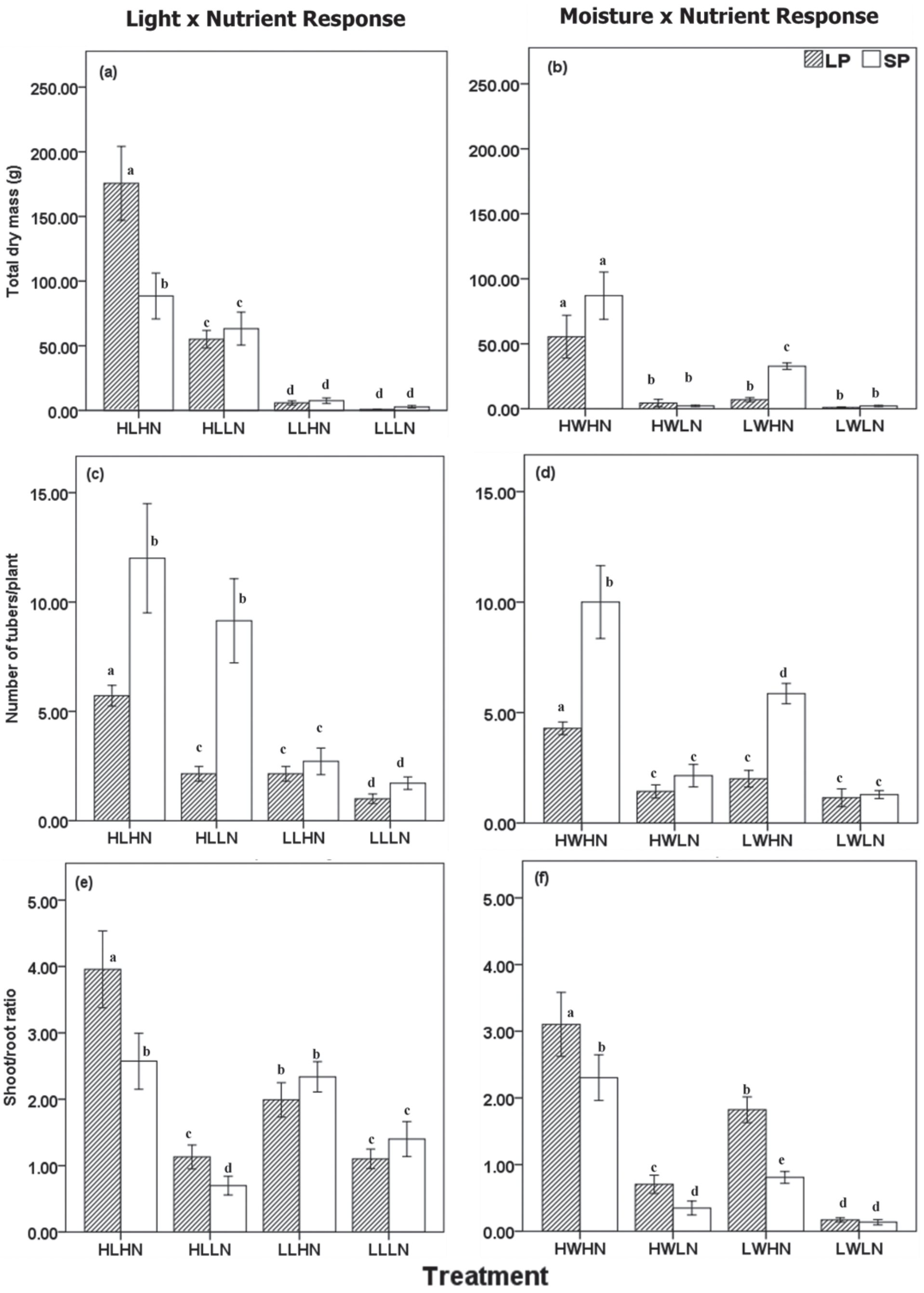

Figure 1. Trait response of the LP and SP forms to varying levels of light, water and nutrient conditions. Total biomass accumulated (**a, b**); Average number of tubers per plant (**c, d**); Shoot/root ratio (**e, f**). The legend in the graph (**b**) applies to all graphs. Graphs on the left (**a, c, e**) show traits responses to light x nutrient experiments and those on the right (**b, d, f**) show trait responses to water x nutrients experiments. Bars represent standard error of the mean (SEM). Differences across treatments are denoted by letters.

Table 1. Mean (± SE) growth, physiological and leaf chemical traits of both forms, long pod (LP) and short pod (SP) of *D. unguis-cati*. Summary ANOVA refers to F- and P-values of a two-way ANOVA (+ an error structure) of log transformed performance traits and physiological traits for both forms, with a fixed effects structure of form (LP and SP) and treatments (HLHN, HLLN, LLHN, LLLN, HWHN, LWHN). NS = not significant.

Traits	**Form**		**Summary ANOVA**		**Direction of difference**
	LP	**SP**	***F*-value**	***P*-value**	
Total biomass (g)	38.11 ± 0.25	35.75 ± 5.89	8.12	0.0060	LP>SP
Leaf area (cm^2)	26.27 ± 2.14	11.74 ± 0.80	54.52	0.0001	LP>SP
SLA (cm^2 g^{-1})	3.95 ± 0.19	4.08 ± 0.27	0.45	0.60	NS
LDMC (mg g^{-1})	296.94 ± 14.11	293.04 ± 9.88	0.16	0.694	NS
No. of tubers $plant^{-1}$	2.48 ± 0.24	5.61 ± 0.69	46.46	0.0001	LP<SP
Root dry mass (g)	11.35 ± 2.13	15.23 ± 2.54	2.54	0.122	NS
Shoot dry mass (g)	26.76 ± 6.76	20.90 ± 3.90	0.01	0.912	NS
*Shoot/root ratio (SRR)	1.78 ± 0.19	1.31 ± 0.15	1.99	0.20	NS
A_{max} (μmol m^{-2} s^{-1})	3.48 ± 0.27	3.97 ± 0.34	4.07	0.05	LP<SP
WUE (μmol $CO_2$$mol^{-1}$ H_2O)	4.03 ± 0.21	4.53 ± 0.31	30.29	0.001	LP<SP
PNUE (μmol mol s^{-1})	1.27 ± 0.15	1.21 ± 0.08	0.14	0.71	NS
C (g m^{-2})	43.82 ± 0.26	43.28 ± 0.24	6.28	0.018	LP>SP
N (g m^{-2})	3.45 ± 0.26	3.73 ± 0.19	5.31	0.03	LP<SP
C: N	14.63 ± 1.38	12.37 ± 0.82	7.29	0.01	LP>SP
Chl. (SPAD units)	41.00 ± 0.85	57.24 ± 0.03	58.52	0.0001	LP<SP
Chl: N	13.29 ± 0.38	15.74 ± 0.77	1.60	0.22	NS

*Root biomass includes tuber biomass

low nutrients: biomass (LLLN: *P* = 0.365; LWLN: *P* = 0.424) and tuber abundance (LLLN: *P* = 0.856; LWLN: *P* = 0.836) (Fig. 1a-d).

Response of leaf traits to light, water and nutrient availability

Overall, both the SP and LP forms differed in terms of SLA depending on treatments ($F_{1,4}$ = 257.845, *P*<0.0001; Table 2). Both forms invested significantly less biomass in their leaves in the LLHN condition compared to the HLHN condition (Table 2), indicating the importance of light intensity in determining resource allocation strategies.

Across treatments, the LP form accumulated significantly higher total leaf carbon (C) than the SP form ($F_{1,4}$ = 6.282, P<0.018). Conversely, the SP form showed higher area based total leaf nitrogen (N) ($F_{1,4}$ = 5.310, *P*<0.03) (Table 1). Thus, the LP form exhibited significantly higher C: N ratio ($F_{1,4}$ = 7.289, *P*<0.02) than the SP form (Tables 1 and 2). However, variations in leaf nutrient concentrations were best explained by treatment and its interactions with form (Table 1). Total leaf N concentrations were significantly higher in HLHN than HLLN treatments, but there was no significant difference in leaf N between LLHN and LLLN for either forms (Table 2). This pattern indicates a strong effect of light intensity in determining resource acquisition and use efficiency.

Table 2. Mean trait performance and summary of ANOVA of the SP and LP forms in different light, water and nutrient treatments. *, *P*<0.05; **,*P*<0.02; ***, *P*<0.001; NS, not significant. Treatments: HL, high light; LL, low light; HN, high nutrient; LN, low nutrient; HW, high water; LW, low water.

Form	Treatment	N, g m^{-2}	C, g m^{-2}	C: N	Chl., spad units	Chl: N	$A_{max,}$ µmol m^{-2} s^{-1}	WUE, µmol CO_2mol^{-1} H_2O	PNUE, µmol mol s^{-1}	SLA, cm^2 g^{-1}	LDMC, mg g^{-1}	Total dry mass,g	No. of tubers	S/R ratio	BSD, cm
SP	HLHN	4.27	43.74	10.24	62.24	14.59	5.79	5.68	1.36	4.63	354.89	105.08	15.0	2.94	3.14
LP	HLHN	4.14	44.76	10.87	42.01	10.19	5.41	4.36	1.33	3.83	341.39	140.41	6.00	3.91	5.53
SP	HLLN	2.21	42.47	19.47	41.02	18.69	2.50	4.49	1.10	3.67	394.25	69.23	10.0	0.55	3.30
LP	HLLN	1.87	42.72	22.96	33.51	17.82	3.67	4.83	1.94	7.35	458.48	60.95	2.20	0.95	5.25
SP	LLHN	3.96	42.95	10.83	59.36	14.99	3.78	3.35	0.96	5.74	308.15	7.97	2.75	2.47	2.03
LP	LLHN	4.08	42.66	10.46	55.04	13.49	2.44	2.94	0.59	4.67	332.58	4.55	2.33	1.91	2.79
SP	LLLN	3.42	42.13	12.34	60.09	17.59	4.60	3.24	1.35	–	–	2.99	1.33	1.55	1.71
LP	LLLN	2.64	44.05	19.38	52.42	23.00	3.16	3.20	1.38	–	–	1.33	1.00	0.86	1.77
SP	HWHN	4.41	44.40	10.07	61.80	13.99	5.55	5.10	1.26	3.32	361.79	87.04	8.60	1.68	4.59
LP	HWHN	4.27	44.56	10.64	34.47	7.86	3.75	3.88	0.89	3.85	363.97	41.74	4.20	3.16	3.99
SP	HWLN	–	–	–	–	–	–	–	–	–	–	2.19	2.14	0.35	1.53
LP	HWLN	–	–	–	–	–	–	–	–	–	–	4.40	1.43	0.70	1.78
SP	LWHN	4.28	44.68	10.45	61.14	14.30	2.07	4.68	0.49	4.34	405.94	30.93	6.00	0.782	2.73
LP	LWHN	–	–	–	–	–	2.45	4.52	–	4.54	334.41	6.93	2.00	1.82	2.43
SP	LWLN	–	–	–	–	–	–	–	–	–	–	2.16	1.29	0.14	1.24
LP	LWLN	–	–	–	–	–	–	–	–	–	–	0.97	1.14	1.58	0.97
								Summary of ANOVA							
Form		*	*	NS	***	*	*	***	NS	NS	NS	**	***	NS	**
Treatment		***	**	**	*	***	***	***	*	***	***	***	***	NS	***
Form x Treatment		.	.	*	NS	NS	**	*	*	***	*	**	*	NS	***
Direction of form difference		LP<SP	LP>SP	LP=SP	LP<SP	LP<SP	LP<SP	LP<SP	LP=SP	LP=SP	LP=SP	LP>SP	LP>SP	LP=SP	LP>SP

Carbon assimilation rate and resource use efficiency in response to variations in light, water and nutrients

The SP form showed a significantly higher rate of carbon assimilation (*A*) than the LP when compared across all resource treatments ($F_{1,\,5}$ = 4.067, *P*<0.05) (Table 1). The significant interaction effect of form x treatment suggests that response patterns of two forms were not consistent under changing environmental resources ($F_{1,\,5}$ = 4.499, *P*<0.001; Table 2). The two forms were not different in carbon assimilation (*A)* in the HLHN condition. The SP form had slightly higher *A* in low light (LLHN and LLLN), whereas the LP form had slightly higher *A* under HLLN (Fig. 2a; Table 2).

The SP form showed a significant shift in carbon assimilation in response to light levels as there was nearly a two-fold difference in *A* between low light (LLHN) and high light (HLHN) conditions (P<0.0001; Fig. 2a) when nutrient level was high. In contrast, in the LP form, *A* only increased by a factor of 0.5 from low light (LLHN) to high light (HLHN) (P<0.001). When nutrient level was low, the SP form still increased its *A* two-fold from high light (HLLN) to low light (LLLN) conditions (P<0.0001) while there was no significant change in *A* in the LP form (P > 0.05; Fig. 2a; Table 2). This trend suggests a better plasticity and hence acclimation for the SP form to a decreasing light condition. *A* was measured for only two treatments under the moisture experiments, i.e. HWHN

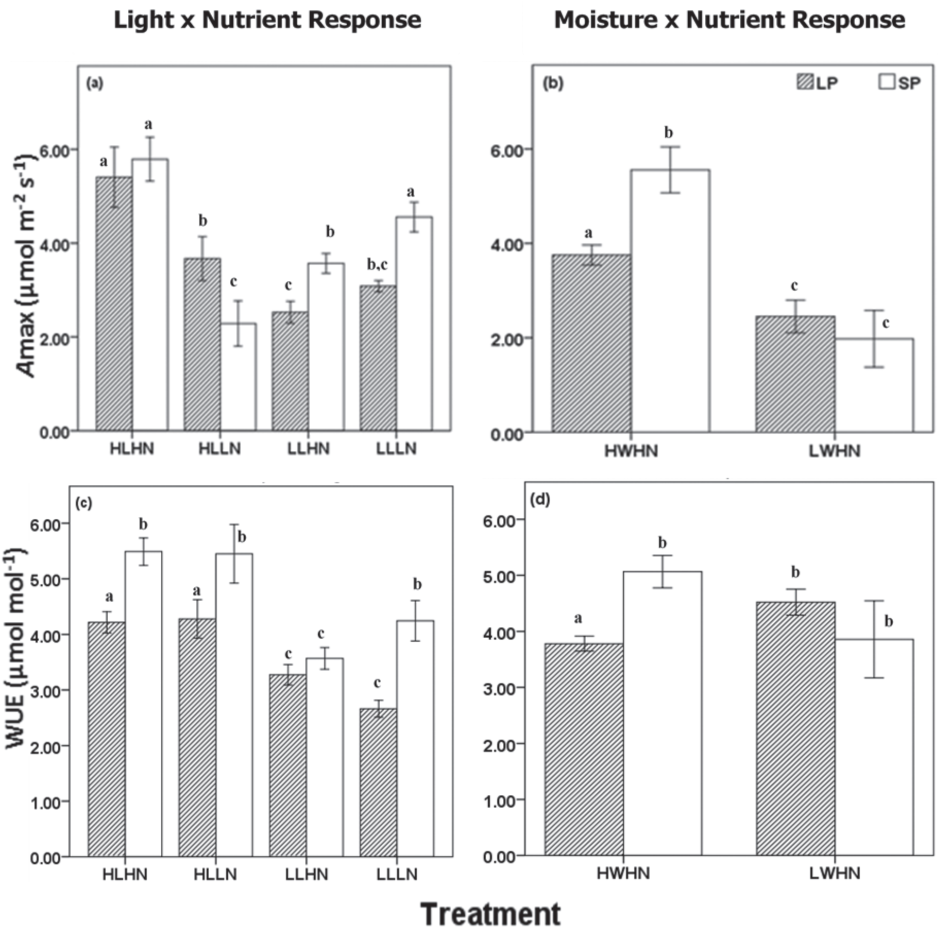

Figure 2. Carbon assimilation rates and water use efficiency of the LP and SP forms in response to light, water and nutrient resources. Maximum carbon assimilation, A_{max} (**a, b**); water use efficiency, WUE (**c, d**). The legend in the graph **b** applies to all graphs. Graphs on the left (**a, c**) show traits responses to light x nutrient experiments and those on the right (**b, d**) show trait responses to water x nutrients experiments. Bars represent standard error of the mean (SEM). Differences across treatments are denoted by letters.

and LWHN. The response did not vary significantly between the SP and LP forms (Fig. 2b) under LWHN but did so under HWHN (Table 2). In both forms *A* declined significantly with a reduction in water availability (from HWHN to LWHN) but the SP form had significantly higher *A* with abundant water and nitrogen (HWHN) (Fig. 2b).

The SP form showed higher water use efficiency (WUE) than the LP form in response to different treatments ($F_{1,5}$ = 30.294, *P*<0.001; Table 1). Water loss in the SP form was more restrained in the order HLLN > HLHN > LLLN. This resulted in significantly higher WUE for SP in these treatments than LLHN (P<0.01; Fig. 2c). This is so because both *A* and WUE were large under the HLHN and LLLN conditions (Fig. 2a, c), i.e., HLLN is the only treatment where WUE in the SP form did not follow the same pattern as for *A*. WUE in the LP form was significantly higher in high light than in low light in the order HLHN = HLLN > LLHN = LLLN (P<0.001; Fig. 2c; Table 2). WUE in the SP form did not differ significantly between water treatments (HWHN and LWHN) (P >0.05) but WUE for the LP form was significantly lower in the HWHN treatment than the LWHN treatment (Fig. 2d; Table 2). There was no difference between LP and SP in terms of photosynthetic nitrogen use efficiency (PNUE) ($F_{1,7} = 0.138$, $P<0.712$; Table 1). Both forms exhibited lower *A* and RUE (WUE, PNUE) in stressful conditions (LL, LN and LW) than non-stressful conditions (HL, HN and HW) (Fig. 2; Table 2). Physiological data could not be obtained for treatments receiving HWLN and LWLN because the plants under these treatments developed few leaves. This suggests the importance of nutrient availability (N) in leaf development for both forms of the invasive vine.

Differences in trait coordination and trait correlations between the LP and SP forms

Across treatments, all performance traits examined changed in response to changes in biomass accumulated, although the trends were not significant for the SP form in terms of assimilation rate (*A*) and leaf chlorophyll content. It is instructive to see that at a given plant biomass, higher trait values were obtained for the SP form relative to the LP form (Fig. 3; Table 2). It is also interesting that SLA, a trait that facilitates photosynthetic capture, was significantly linked to carbon assimilation and biomass accumulation only in the SP form, but not in the LP form (Table 3; Fig. 3c).

Considering all possible bivariate relationships for the traits measured in the study (i.e. 45 pairwise comparisons), the number of significant correlations were higher for the LP form (23) than the SP form (17) (Table 3). To test whether there was a difference in level of trait integration or coordination between the two forms in response to high resources, eco-physiological traits were correlated with SLA and total biomass (two important performance and/or fitness traits) for (a) high light intensity (HL) and (b) enhanced nutrients (HN) scenarios separately. Under high light conditions, more traits were significantly correlated with biomass gained for the SP form (5 out of 12) than the LP form (3 out of 12). Two physiological traits, *A* and leaf N were significantly linked to SLA in the SP form while only one trait (PNUE) was linked to SLA in the LP form (Suppl. material 1: Table S1).

In the high nutrient scenario, more traits (4) were correlated with SLA in the SP form (biomass gained (negative), A_{max} (positive), WUE (negative) and total leaf N (negative). In contrast, only two traits (leaf N and leaf Chl.) were positively associated with SLA in the LP form. In the same high nutrient condition regardless of light and moisture condition, a slightly higher number of traits (compared to the high light scenario) were linked to biomass gained for the LP form (5 out of 12), but more traits were significantly correlated with total biomass for the SP form (7 out of 12) in the high nutrient scenario (Suppl. material 1: Table S2). Thus, it is safe to conclude that there was more trait integration in the SP form than in the LP form under high resource conditions of light and nutrients (Suppl. material 1: Table S1 and Table S2), while there was more trait integration in the LP than SP form when considering all the resource conditions investigated in the study (Table 3). Hence, context is key when considering the trait integration in the two forms of *D. unguis-cati*.

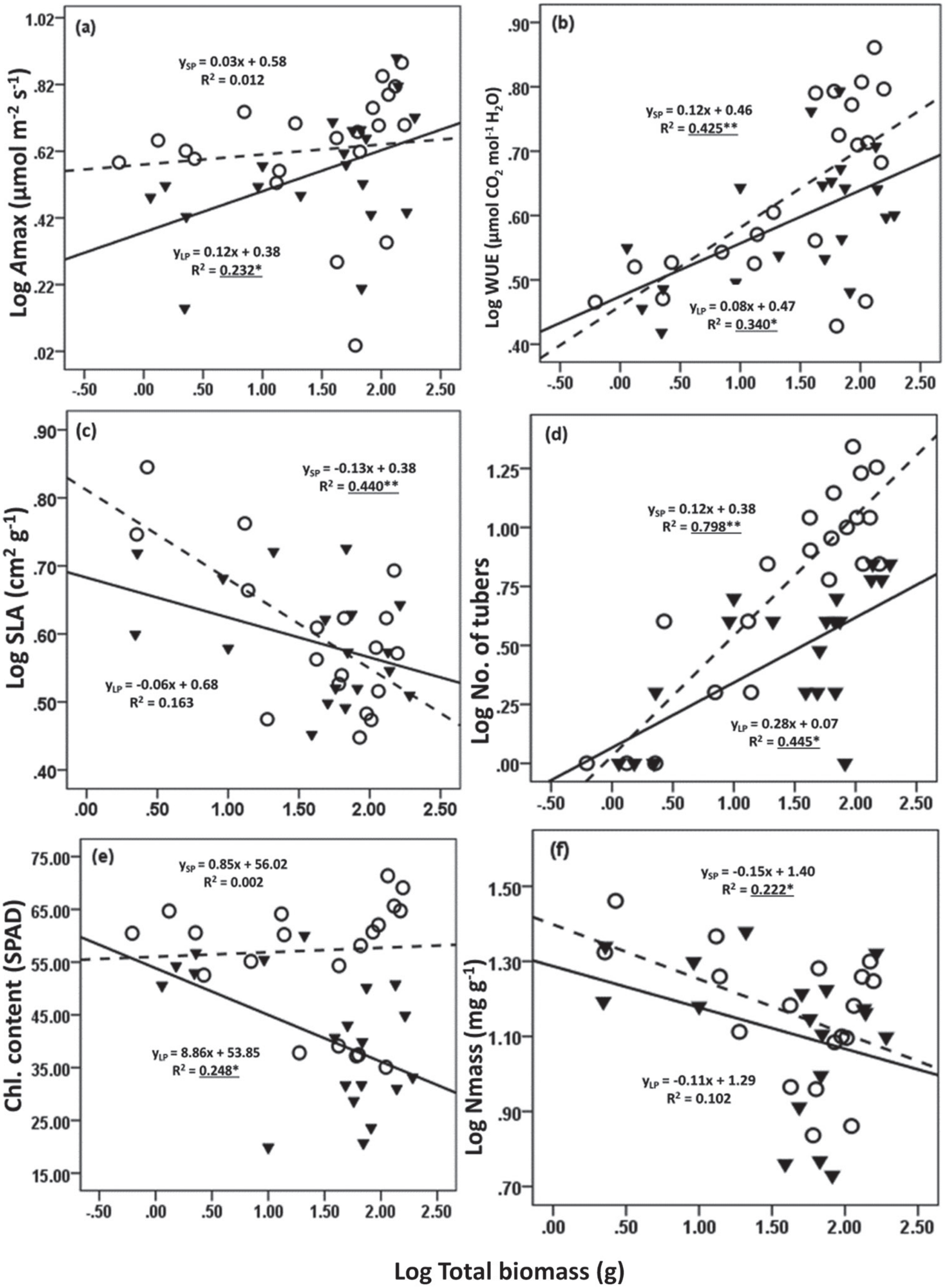

Figure 3. Trait relationships across light, water and nutrient regimes between total biomass accumulated versus A_{max}(**a**), WUE (**b**), SLA (**c**), number of tubers (**d**), chlorophyll content (**e**) and leaf N concentration (**f**). The LP form is represented by triangles (▲) and a solid line (—) while the SP form is represented by open circles (○) and dotted lines (---). Significant relations (P<0.05) are shown by underlined R^2 values, **, P < 0.0001; *, P < 0.05.

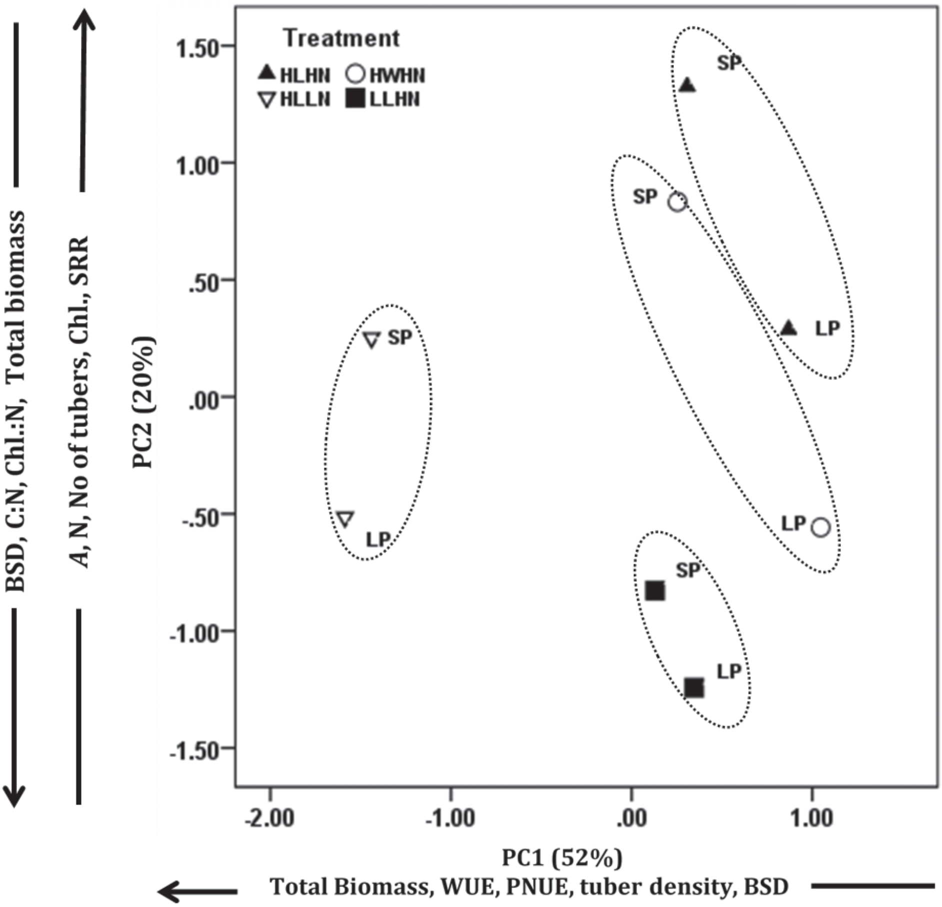

Figure 4. Principal component analysis of LP and SP across four treatments (HLHN, HWHN, HLLN, and LLHN) based on 13 eco-physiological traits projected on the first two axes. The traits on each axis are the main drivers of the variation explained by that axis. The percentage of the variance explained by each principal component is shown in brackets. There was no determination of leaf chemistry for treatments that are not included in this PCA because of insufficient leaf materials. Dotted lines connect the LP and SP forms under similar treatments for the sake of comparison.

A graphical representation of a principal component analysis (PCA) of the LP and SP forms based on 10 traits under four resource treatments (HLHN, HLLN, HWHN and LLHN) is shown in Figure 4. The remaining treatments (LLLN, LWHN, HWLN and LWLN) were not included because not all physiological and chemical traits were measured in those treatments. The PCA shows that the first two axes explained 72% of the total variation in the data. The first axis explained 52% of the data variation and was strongly correlated with RUE traits (WUE, PNUE), SLA and total biomass. The second axis explained 20% of the total variation in the data and was strongly linked to C: N ratio, shoot/root ratio, assimilation rate (*A*) and total leaf N per mass (Fig.

Table 3. Matrix of Pearsons correlation coefficients (r) for functional traits of the LP and SP forms (SP shown in brackets). Data have been pooled across light, water and nutrient treatments. Significant correlations ($P<0.05$) are shown by bold font and asterisks (**, $P < 0.001$; *, $P < 0.05$); n = 18-20.

	SLA LP (SP)	**Total biomass LP (SP)**	**No of tubers LP (SP)**	**WUE LP (SP)**	**PNUE LP (SP)**	**N LP (SP)**	**C: N LP (SP)**	**Amass LP (SP)**	**A_{max} LP (SP)**	**Chl. LP (SP)**
SLA	1									
Total biomass	0.403(-**0.663****)	1								
No of tubers	-0.073(**-0.519***)	**0.667****(**0.893****)	1							
WUE	-0.383(-0.424)	**0.583****(**0.652****)	**0.474***(**0.515***)	1						
PNUE	**-0.570***(-0.213)	0.352(0.163)	0.069(0.161)	**0.688****(-0.094)	1					
N	**0.588***(**0.684****)	-0.319(**-0.471***)	0.404(-0.383)	**-0.472***(-0.120)	**-0.736****(0.097)	1				
C: N	-0.237(-0.083)	-0.018(0.039)	**-0.519***(0.037)	0.318(-0.183)	**0.657****(-0.293)	-**0.924****(**-0.782****)	1			
Amass	-0.107(0.392)	0.426(-0.142)	**0.715****(-0.069)	**0.515***(-0.117)	**0.552***(**0.659****)	0.157(**0.812****)	-0.215(**-0.781****)	1		
A_{max}	**-0.533***(-0.099)	**0.482***(0.111)	**0.593****(0.109)	**0.595****(0.069)	**0.679****(**0.821****)	-0.126(**0.521***)	-0.108(**-0.785****)	**0.898****(**0.877****)	1	
Chl.	**0.564***(0.027)	**-0.498***(0.045)	-0.254(-0.097)	-0.380(0.421)	-0.401(0.314)	**0.568***(0.446)	-0.310(**-0.569****)	0.034(**0.529***)	-0.239(**0.545***)	1

4; Suppl. material 1: Table S3). The two forms of *D. unguis-cati* clustered together on the first axis, meaning that traits correlated with this axis have low explanatory power in differentiating the two forms. Separation on the first axis only increases slightly for treatments other than HLLN, but especially for HLHN and HWHN (Fig. 4). However, the two forms were significantly separated along the second axis (see the separation shown by dotted shapes comparing the two forms under similar experimental treatments). The separation on the second axis was strongly driven by varying responses to treatments of HWHN, HLHN and HLLN as noted for shoot-root allocation pattern, leaf N content, C: N ratio, root tuber abundance and *A*. In all cases, the SP form exhibited a higher combination of the above-named traits compared to the LP form (Suppl. material 1: Table S3).

Discussion

The two forms of *D. unguis-cati* in Australia were found to display significant differences in traits suggesting they likely occupy different positions in the LES (also see Penuelas et al. 2010; Wright et al. 2004), with the SP form positioned more towards the faster growing, high return on investment end. The observed stronger trait correlation in the SP form implies that this form exhibits a higher level of phenotypic integration than the LP form. High phenotypic integration (Luo et al. 2015) or coordination (Osunkoya et al. 2014) is a trait associated with invasiveness. Phenotypic integration is considered a phenomenon that could constrain non-adaptive phenotypic plasticity in plants (Pigliucci 2003), thereby increasing fitness in heterogeneous environments (Wanderley et al. 2016). As the two forms clearly separated along the 2nd axis in the ordination space of a PCA, our study shows that the two forms have varying patterns of resource acquisition, biomass allocation and carbon assimilation in response to treatments.

The LP form accumulated more biomass when grown under high light and high nutrient resource conditions while the SP form did so under low resource conditions. This suggests that the LP form exhibits traits of an opportunistic invader that effectively exploits extra resources in the environment while the SP form does not. The theory of fluctuating resource availability holds that species that can exploit excess resources have a higher chance to successfully colonize disturbed habitats (Davis et al. 2000). From a performance perspective, our results partly concur with Taylor and Dhileepan (2012) that the LP form has the potential for further spread, particularly under disturbed conditions where increased resource conditions such as light and soil nutrients is common. However, adaptation to low resources has also been shown to be a trait of some invasive species (Funk and Vitousek 2007). Thus, our results imply that the SP form has potential to perform better than the LP form in low resource habitats like undisturbed forest understories. This could partly explain the current extensive distribution of this form when compared to the LP form.

Biomass production and allocation patterns in response to resources

This study supports the context-dependent hypothesis of trait differences (Leffler et al. 2014) as shown by significant interactions of form and treatment in explaining biomass accumulation and tuber development differences between the SP and LP forms. Because biomass production is closely linked to RGR in plants (Malhi et al. 2015), it is often used as an indicator of performance (Luo et al. 2015) or fitness (Osunkoya et al. 2010a). Species with a propensity to be invasive may have similar carbon capturing strategies with less invasive species, but could exhibit trait differences in response to disturbances (Leishman et al. 2010). In our study, the LP form accumulated more biomass than the SP form in response to resources (Table 1 and 2), but this was largely driven by the HLHN condition, suggesting an opportunistic strategy for this form or a plant that has a specialised micro-climate. The SP form developed more biomass than the LP under resource poor conditions of LWHN, which indicates resource substitution by the SP form (Wright et al. 2001; Taylor and Eamus 2008). This finding is in agreement with Taylor and Dhileepan (2012) who reported that the LP accumulated more biomass than SP in a field experiment. This implies that the LP form performs better when growing in disturbed sites with high light and nutrient availability (e.g. river banks) (Davis et al. 2000; Melbourne et al. 2007), whereas the SP form can persist in both stressed (e.g. under canopies) and resource rich conditions (e.g. along exposed river banks). This buttresses the observed greater distribution of the SP form relative to the LP form in SE Australia because it is more capable of pre-empting and occupying varying niches of resource-rich and poor habitats.

Interestingly, another study showed that SP accumulated more biomass under low nutrient scenarios (Buru et al. 2016a), a trend also supported in this study (see Fig. 1a, treatment HLLN). This context-dependence of trait differences between the SP and LP forms and the significant differences of carbon assimilation between the two forms could explain their differential levels of invasiveness observed in the field (see also Burns 2004; Daehler 2003; Drenovsky et al. 2008). Other studies (reviewed in Funk et al. 2016) have demonstrated that different varieties of a species can exhibit significant trait differences, which is consistent with our findings.

The SP form developed a significantly higher number of tubers than the LP form (Fig. 3), which could have contributed to its reduced shoot/root ratio (Table 1 and 2). This is in agreement with Buru et al. (2016a) who found the SP form to produce more tubers earlier in its development (3-5 months following germination) than the LP form. Tubers act as a sink or storage organs for moisture and photo-assimilates, and they may also regenerate, producing new plants (Janeček and Klimešová 2014; Orthen 2001; Schubert and Feuerle 1997). Apart from seed germination (Vivian-Smith and Panetta 2004), *D. unguis-cati* propagates vegetatively through tubers (Downey and Turnbull 2007; Osunkoya et al. 2009). Horizontal stems and branches trailing along the ground develop adventitious roots at nodes (Vaughn and Bowling 2011), which penetrate the soil and develop more tubers (Osunkoya et al. 2009). If new plants regenerating at the nodal tubers are severed from the mother plant, they grow independently as genets (Osunkoya et al. 2009). Tubers can also remain dormant for extended periods below-ground as a stress tolerance strategy (Orthen 2001). Thus, this finding of greater linkage between tuber density and biomass gained for the SP form suggests a greater niche pre-emption strategy leading to domination of invaded landscapes by this form (Ashton et al. 2010).

Leaf-level traits response to light, water and nutrients

Although the LP form is known to have broader leaves than the SP form (Shortus and Dhileepan 2011; Boyne et al. 2013), our study indicates that the SP form invested more biomass in leaf tissues as indicated by similar specific leaf area (SLA = LA/Leaf dry mass) between the two forms. Heavy investment in constructing leaf tissue (thicker leaves) (Lambers and Poorter 1992) is a trait often associated with slow growing plants (van Kleunen et al. 2010a). High specific leaf area (SLA) facilitates greater capture of light and is often associated with invasive species (but see Garcia-Serrano et al. 2005; Osunkoya et al. 2010a,b). Higher SLA indicates thinner leaves which are cheaper to produce quickly when compared to thicker leaves for the same surface area (Poorter and Remkes 1990). With thinner and broader leaves, the LP form appears to perform better than the SP form in this regard. If we consider the SP form to be the more successful colonizer than the LP form based on current abundance and distribution, then our study does not associate SLA with colonization success for this invasive species.

Developing thicker leaves by the SP form could be a strategy to compensate for less surface area by way of increasing photosynthetic apparatus (palisade parenchyma). Indeed, the SP form has significantly thicker palisade mesophyll tissue than the LP form (JC Buru, unpublished data). This trend also follows suit with our other findings that this form accumulates more biomass in undisturbed conditions where resources are lower. Thicker mesophyll tissues are known adaptations to low light conditions (Chabot and Chabot 1977). The most likely vines to be successful colonizers are those that are adaptable to low light conditions (Baars and Kelly 1996). These are traits exhibited by the SP form.

Physiological responses to light, water and nutrient resources

We found differences in carbon economy between the two forms with the SP form exhibiting higher assimilation rates (*A*) and WUE than the LP form. In the low nutrient scenario, carbon assimilation was two-fold higher under low light than high light for the SP form. This was accompanied by a greater leaf N concentration at the low light level. The leaf economic spectrum suggests that high *A* needs more leaf N to drive rapid growth (Wright et al. 2004). Thus, the observed higher *A* under low light conditions could be a strategy by the SP form to increase growth to reach greater heights for more light acquisition. Faster growing plants have a larger demand for nutrients (Luo et al. 2015), therefore low C: N ratios found for the SP form may be a consequence of a higher N need.

The LP and SP forms were found to use resources in similar ways, at least under same and/or fluctuating light, water and nutrient resources, as no significant difference was found in their photosynthetic nitrogen use (PNUE). When light conditions were considered separately, a negative relationship between PNUE and biomass gained was obtained for the LP form, an indication of less RUE in this form. However, considering nutrient conditions separately, both forms show a positive relationship between PNUE and biomass gained. Correlation coefficient (r) values were greater in the SP form suggesting that at a given PNUE, a higher biomass was always attained for the SP form relative to the LP form, also indicating less RUE in the LP form.

Previous studies have found non-native invasive species to have higher RUE than native non-invasive congeners (Firn et al. 2012; Funk and Vitousek 2007). In the high light scenario, only the SP form showed positive (albeit marginally significant) relationship between PNUE and biomass gained, while in the LP form the relationship was not significant. This is yet again an indication of better RUE by the SP form than the LP form (Osunkoya et al. 2010b). However, Funk (2008) argues that traits such as PNUE and WUE may not correlate with fitness measures on a short time scale or may reflect a context-dependence of traits differences. Considering all resource conditions, the SP form exhibited better WUE than the LP form (Fig. 3). However, because this trait was significantly associated with biomass accumulation in both forms, it does not necessarily explain their difference in prevalence.

Trait coordination and ordination in response to resources

The traits measured in this study were correlated for each form to assess the extent of covariance among them, which gives an indication of phenotypic integration (Luo et al. 2015; Osunkoya et al. 2014). Consistent with the context-dependence theory, we found significant differences in trait correlations across resource conditions, with the LP form showing significantly higher integration than the SP form (Table 3). This relationship could indicate greater phenotypic integration for the LP form when considering all possible interactions. We thus reject our hypothesis that the SP form would exhibit more trait coordination than the LP form. However, it is interesting that SLA, a trait that facilitates photosynthetic capture was significantly linked to carbon assimilation and biomass accumulation only in the SP form, but not in the LP form.

There was a significant shift of trait integration in favour of the SP form in response to high light and nutrients resources, a result similar to findings of Osunkoya et al. (2010b) while working on a suite of invasive vs. native vines in Queensland including *D. unguis-cati*. This means that the SP form exhibited a higher level of phenotypic integration than the LP form in response to elevated resources only. Some previous studies have suggested that when traits respond to environmental fluctuations in a coordinated fashion, it enhances plant performance (Reich et al. 2003; van Kleunen and Fischer 2005). A well-coordinated response to environmental heterogeneity enables plants to adapt better to abiotic changes in their habitat (Luo et al. 2015; Osunkoya et al. 2010b; Osunkoya et al. 2014). Based on this argument, the SP form could be expected to perform better than the LP form under similar environmental conditions.

Management implications of study findings

As both forms of *D. unguis-cati* were found to thrive in high resource environments, care must be taken to ensure that disturbances are minimised, especially along sensitive habitats like riparian corridors that the weed invades. Effluent discharge into creeks and riparian habitats of QLD should be monitored and minimised as this might encourage proliferation of this species, especially the opportunistic LP form (see Davis et al. 2000). Current control and management options of both forms include chemical, mechanical and biological control strategies (Dhileepan et al. 2013).

The biological control agents that have been released to control this weedy vine include a leaf mining beetle, *Hylaeogena jureceki* and leaf sucking tingid, *Carvalhotingis visenda* (Dhileepan et al. 2010; Dhileepan et al. 2013). These agents have shown evidence of success in controlling the populations of both the LP and SP forms (Dhileepan et al. 2013). Their feeding behaviour significantly reduce foliage and thus minimise photosynthetic capacity of the weed. Thus, concerted efforts must be prioritised to continually release these agents in large numbers to reduce the rate of shoot growth for both forms, thus keeping their populations within acceptable limits. We suggest that biological control agents that attack tubers in combination with the agents currently in use would be appropriate for this species, especially for the SP form which was found to produce significantly higher number of tubers than the LP form in this study (also see Raghu et al. 2006).

Conclusion

Overall, the results provide support for the context-dependent hypothesis (Leffler et al. 2014). This is at odds with some of our hypotheses in the Introduction section, as we had expected that the SP form would exhibit higher values for most of the traits we measured. The LP form performed better than the SP form when grown under high resource conditions (e.g. high light, high nutrient) whereas the SP form performed well in both high and low resource conditions. Both forms obviously underperformed at low resources, but the negative effects of such stressed conditions were more pronounced on the LP form than the SP form. This indicates that the LP form exhibits traits of an opportunistic plant that is likely to be restricted to disturbed areas characterised by high resource pulses, whereas the SP form can cope more with habitats of both low and high resources. This might explain the greater prevalence of the SP form in Queensland, Australia.

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Supplementary material 1

Supplementary tables

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Data type: occurrence

Explanation note: The Supplementary Material for this article consists of three Tables showing traits coordination under high light and high nutrients (Table S1 and S2) and PC loadings for traits used in the PCA that is shown in Figure 4 (Table S3).

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