

Leaf trait co-ordination in relation to construction cost, carbon gain and resource-use efficiency in exotic invasive and native woody vine species

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- **Background and Aims** Success of invasive plant species is thought to be linked with their higher leaf carbon fixation strategy, enabling them to capture and utilize resources better than native species, and thus pre-empt and maintain space. However, these traits are not well-defined for invasive woody vines.
- **Methods** In a glass house setting, experiments were conducted to examine how leaf carbon gain strategies differ between non-indigenous invasive and native woody vines of south-eastern Australia, by investigating their biomass gain, leaf structural, nutrient and physiological traits under changing light and moisture regimes.
- **Key Results** Leaf construction cost (CC), calorific value and carbon : nitrogen (C : N) ratio were lower in the invasive group, while ash content, N, maximum photosynthesis, light-use efficiency, photosynthetic energy-use efficiency (PEUE) and specific leaf area (SLA) were higher in this group relative to the native group. Trait plasticity, relative growth rate (RGR), photosynthetic nitrogen-use efficiency and water-use efficiency did not differ significantly between the groups. However, across light resource, regression analyses indicated that at a common (same) leaf CC and PEUE, a higher biomass RGR resulted for the invasive group; also at a common SLA, a lower CC but higher N resulted for the invasive group. Overall, trait co-ordination (using pair-wise correlation analyses) was better in the invasive group. Ordination using 16 leaf traits indicated that the major axis of invasive-native dichotomy is primarily driven by SLA and CC (including its components and/or derivative of PEUE) and was significantly linked with RGR.
- **Conclusions** These results demonstrated that while not all measures of leaf resource traits may differ between the two groups, the higher level of trait correlation and higher revenue returned (RGR) per unit of major resource need (CC) and use (PEUE) in the invasive group is in line with their rapid spread where introduced.

Key words: Construction cost, leaf physico-chemical properties, plant invasion, photosynthesis, resource-use efficiency, specific leaf area, woody vines, *Anredera*, *Araujia*, *Cardiospermum*, *Macfadyena*, *Pandorea*, *Parsonsia*.

INTRODUCTION

In a novel environment, invasive alien organisms may disrupt the delivery of ecosystem services and goods (Batianoff and Butler, 2003; Hulme, 2006). Consequently, for understanding and management of biological invasion, the search for functional traits associated with invasiveness has been the focus of many empirical studies and reviews, especially in plants (e.g. Rejmánek and Richardson, 1996; Daehler, 2003; Funk and Vitousek, 2007; Leishman *et al.*, 2007, 2010; Pyšek and Richardson, 2007; Kleunen *et al.*, 2010). Reported diagnostic leaf traits for invasive plant species when compared with co-occurring native species, include greater morphological and physiological plasticity, higher specific leaf area (SLA), higher maximum photosynthesis (A_{\max}), and higher nitrogen (N) content but decreased allocation to defence and shorter leaf life span (Pattison *et al.*, 1998; Grotkopp *et al.*, 2002; Grotkopp and Rejmánek, 2007; Drenovsky *et al.*, 2008). Most of these traits are believed to be strongly linked with greater nutrient, water or light resource-use efficiency (RUE), consequently

resulting in higher relative growth rate (RGR) and rapid biomass gain. However, not all these diagnostic traits have been fully accepted by ecologists as equivocal findings have been reported, notably those relating to greater trait plasticity across resources, higher RGR and higher RUE for the invasive species (see Williams and Black, 1994; Baruch and Goldstein, 1999; Leishman *et al.*, 2007, 2010; McAlpine *et al.*, 2008; Osunkoya *et al.*, 2004, 2010). Richards *et al.* (2006) argued that plasticity of morphological and physiological traits enhances niche breadth but is unlikely to have any effect on invasiveness unless that plasticity is adaptive and thus contributes to fitness such as reproduction and survival. Examples of plant adaptive traits likely to contribute to fitness include RGR, total biomass and SLA; the first two traits can influence niche pre-emption and occupation while the last drives carbon assimilation per unit energy invested (Reich *et al.*, 2003; Wright *et al.*, 2004). Thus it is expected that plasticity of these traits, amongst many others, is likely to increase fitness in multiple environments, with invasives exhibiting higher values than native or non-invasive exotics.

Expressing plant activities in terms of efficiencies gives good indications of resource capture (i.e. revenue stream) per unit investment (McDowell, 2002; Wright *et al.*, 2004). For example, A_{\max} can be limited by low N or water availability. Therefore maximizing A_{\max} relative to N and moisture cost may be one mechanism of invasive plant success (Baruch and Goldstein, 1999; McDowell, 2002; Funk and Vitousek, 2007; Feng *et al.*, 2008). Also low resource requirements for photosynthesis, as evidenced by low leaf construction cost [CC; defined as grams of glucose (+ minerals) required to synthesize 1 g of carbon skeleton (Poorter *et al.*, 2006)] often increase the competitive ability of a plant species as more of the fixed carbon (C) is left for growth and reproduction. Thus low tissue density (i.e. high SLA) and low CC have been advocated as important traits contributing to the runaway success of introduced plants in their novel environment (see Nagel and Griffin, 2001, 2004; Funk and Vitousek, 2007; Song *et al.*, 2007; Feng *et al.*, 2008). However, there is a dearth of studies linking the two performance measures of SLA and CC to fitness (e.g. seed production) or other traits closely associated with fitness itself such as RGR or biomass accumulation (but see Grotkopp *et al.*, 2002; Poorter and Bongers, 2006; James and Drenovsky, 2007), especially so in woody vines.

Vines are an enigmatic group of plants with greater growth and energy investment in leaves at the expense of other biomass parts (Putz and Mooney, 1991). In coastal Queensland and New South Wales, Australia, many introduced woody vine species have become major environmental weeds affecting riparian habitats, disturbed rainforest communities and remnant natural vegetation, where they displace native tree and vine species (Batianoff and Butler, 2003). In densely infested areas, they smother standing vegetation, including large trees and shrubs, causing mechanical damage, reduction of resources available to their hosts and eventually host canopy collapse (Batianoff and Butler, 2003; Osunkoya *et al.*, 2009). In the habitats mentioned above, these exotic vines also deplete water courses especially during periodic and long-term drought events (Osunkoya *et al.*, 2009), but there is no information on their long-term water-use efficiency (WUE) in comparison to co-occurring native species.

In an earlier work in south-east Queensland, Australia (Osunkoya *et al.*, 2010) on comparative ecophysiology of four exotic invasive versus their phylogenetically equivalent native woody vines, it was shown that certain whole plant (e.g. leaf area ratio) and leaf level physiological traits [e.g. quantum use efficiency (AQE), dark respiration, light compensation point and SLA], rather than plasticity of these traits, consistently differed between the two groups. However, the explanatory power of these combined traits on the dichotomy was only moderate (approx. 31%) as some native vine species were found to possess trait ranking similar to those of the invasives. We then hypothesized that perhaps other leaf traits such as tissue CC, leaf chemistry and RUEs, especially integrated as opposed to instantaneous WUE, might explain the dichotomy better. Herein, data on leaf chemistry, including the stable carbon isotope (a measure of long-term WUE) and CC of the same group of invasive and native vines species responding to changes in light and moisture regimes, are presented. Then these primary data are

combined with the groups' leaf structural and physiological responses reported in Osunkoya *et al.* (2010). We hypothesized the following: (a) the invasive group of plants will exhibit lower resource needs (e.g. tissue density/SLA, N, CC) but higher returns in terms of revenue stream (e.g. A_{\max} , biomass and RGR) due to higher RUE and greater level of trait co-ordination when compared with the native group; and (b) the invasive species, due to niche pre-emption capability, will show greater trait plasticity.

MATERIALS AND METHODS

Four highly invasive (introduced) and four native vines species were investigated (see Table 1). These invasive vines and their phylogenetically paired natives are *Macfadyena unguis-cati* (L.) A.H.Gentry (cat's claw creeper vine; Bignoniaceae) vs. *Pandorea jasminoides* (Lindl.) K. Schum. (bower of beauty vine; Bignoniaceae), *Anredera cordifolia* (Ten.) Steenis (Madeira vine; Bassellaceae) vs. *Hibbertia scandens* (Willd.) Dryand (climbing guinea vine; Dilleniaceae), *Araujia sericifera* Brot. (white moth vine; Asclepiadaceae) vs. *Parsonsia straminea* (R.Br.) F.Muell (monkey rope vine; Apocynaceae) and *Cardiospermum grandiflorum* Sw. vs. *C. halicacabum* L. (both with the common name of balloon vine; Sapindaceae). Young plants of these focal species were grown either from seeds (the two *Cardiospermum* species), field-collected stem cuttings (*Anredera* and *Araujia*) and seedlings (*Macfadyena*) or from young seedlings procured via a nursery (*Hibbertia*, *Pandorea* and *Parsonsia*) in a glasshouse setting during the warmer months of November 2007 to April 2008 at Alan Fletcher Research Station, Brisbane, Australia (27°31'S, 152°58'E, 50 m a.s.l.). Here, in a factorial experiment, individual plants were exposed for 14 weeks in 20-L pots to either 30% ($645.72 \pm 26.21 \mu\text{mol m}^{-2} \text{s}^{-1}$) or 2–5% ($44.93 \pm 26.21 \mu\text{mol m}^{-2} \text{s}^{-1}$) full sunlight (high and low) and three moisture regimes of either 200 mL of water every other day, twice weekly or once weekly (low, medium and high). At the end of each watering cycle, moisture regimes were assessed using a moisture probe attached to an LI-8100 machine (LI-Cor, Lincoln, NE, USA), and corresponded to 62.5%, 27.2% and 11.1% soil volumetric water content, respectively (O. O. Osunkoya, unpubl. res.). There were eight replicate potted plants of each species in two light \times three moisture regimes (i.e. a total of 48 plants per species; for further details of experimental protocols, see Osunkoya *et al.*, 2010).

Leaf gas exchange (carbon gain)

At the end of 14 weeks of growth, and for each species \times light \times moisture treatment, leaf photosynthetic response to increasing and saturated light (PAR) (i.e. 0, 5, 10, 20, 30, 40, 50, 60, 90, 100, 200, 250, 300, 400, 500, 600, 1000, 1500 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was determined with an LI-6400 portable photosynthesis system (LI-Cor) using mature leaves from at least four individuals. From these primary data, various gas exchange parameters were derived, including light-saturated net assimilation rate, maximum photosynthetic rate, leaf conductance and transpiration rates, quantum efficiency, dark respiration, light compensation and

saturation points (for details of measurement protocols and associated equations, see Osunkoya *et al.*, 2010).

Leaf structural and total biomass traits

Following gas exchange measurements, plants were harvested and the roots washed free of soil. Plants were separated into leaves, roots and shoots. Leaf samples were scanned and computer image analysis software (ImageJ 1.31v; Rasband, 2004) was then used to estimate leaf area (in cm²). Plant parts were then dried at 70 °C for at least 4 d before weighing. A number of growth parameters were calculated from the primary data collected. These included total biomass, leaf area, specific leaf area (SLA = leaf area/leaf mass) and relative growth rate [RGR = (ln W₂ - ln W₁)/(t₂ - t₁), where ln W is the natural logarithm of biomass, t is the time (in months), and the subscript refers to initial and final biomass]. The initial biomass values were obtained from eight set-aside plants of each species grown at the high light regime prior to treatment applications.

Leaf chemistry and derivation of RUEs

At the end of the growth period, the following analyses were carried out on dried leaf samples collected per plant per treatment (n = 8) per species. Total N and C (% dry mass) were determined by the Dumas micro-combustion technique (Eurovector EA 3000, Milan, Italy). Ash content (g g⁻¹) was determined in triplicate by incinerating 1 g samples of the dried leaves in a muffle furnace at 500 °C until a white-grey residue remained (3–4 h). Heat of combustion (HC) was measured in triplicate per plant using 1 g, with a Gallenkamp bomb calorimeter (model CRA-305, UK) calibrated against benzoic acid pellets of known energy value.

Leaf CC was calculated using a formula based on the growth efficiency of leaf tissue, heat of combustion, ash and nitrogen content according to Williams *et al.* (1987):

$$CC = [(0.06968HC - 0.065)(1 - \text{ash}) + 7.5(k \times N/14.0067)]/E_g$$

where HC = ash free heat of combustion (kJ g⁻¹), N = total Kjeldahl nitrogen (g g⁻¹), k is the oxidation state of the nitrogen source (+5 for nitrate, or -3 for ammonium), and E_g is the growth efficiency (the fraction of cost required to provide reductant that is not incorporated into biomass) (see Williams *et al.*, 1987; Poorter *et al.*, 2006). The value of E_g used in this study was 0.87 (see Williams *et al.*, 1987). In the calculation it was assumed that the nitrogen source was both nitrate and ammonium for all species and hence CC is calculated using both k = +5 and -3, and the average values are reported.

Photosynthetic nitrogen-use efficiency (PNUE) was calculated as the ratio of instantaneous A_{max} to N on area basis. Photosynthetic energy-use efficiency (PEUE) was calculated as the ratio of instantaneous A_{max} to CC on an area basis. Instantaneous WUE was calculated as the ratio of A_{max} to transpiration for PAR > 300 μmol m⁻² s⁻¹. The carbon isotope ratio (δ¹³C) of leaves indicates the long-term WUE integrated

over the lifetime of a leaf (Farquhar *et al.*, 1989), reflecting both stomatal opening and carboxylation rate. Plants with less negative δ¹³C values generally display higher time-integrated WUE (Farquhar *et al.*, 1989). The leaf ¹³C: ¹²C ratio was analysed by mass spectrometry (GV Isoprime, Manchester, UK) at Griffith University, Brisbane, Australia, and δ¹³C (‰) calculated as:

$$\delta^{13}\text{C}(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R_{sample} is the ¹³C: ¹²C ratio of a sample and R_{standard} is the ¹³C: ¹²C ratio of the international PeeDee Belemnite standard. Analytical precision was ± 0.3 ‰.

Data analysis

Where required, area-based estimates for individual × species × treatment data were obtained by dividing mass-based values by their corresponding SLA data. Excluding the invasive *Cardiospermum grandiflorum* because of lack of some data for the equivalent native *C. halicacabum* (see Table 1) did not affect trends or significance of tests carried out and hence their data, where available, were included in all analyses. Leaf photosynthetic response, structural and chemical parameters as well as whole-plant biomass data were analysed using a linear mixed ANOVA model with fixed terms for light (high vs. low), moisture (low, medium and high), and species origin group (invasive vs. native), and random term for individual species pair (taxonomic grouping: four levels) and their two-way interaction effects. Interactions were limited to two-way effects to maintain power of the tests ≥ 80 %. The last term (i.e. taxonomic group) helps to correct/reduce the influence of phylogenetic membership on the dataset (see Harvey and Pagel, 1991). Moisture effects were minimal (see Results), and hence species mean values at each light treatment were used to carry out correlations and regressions between pairs of measured variables. For correlation, a critical level of P = 0.02 was selected to exert table-wise alpha control yet avoid the unduly harsh effect a full Boniferroni alpha adjustment of P = 0.05/n (where n is the number of pair-wise comparison being made). To examine overall differences, including level of trait co-ordination between invasive and native vine species, as well as to explore which traits were most influential in separating the two groups, ordination following normalization and using principal component analysis (PCA) was carried out on the species mean values of all traits, except RGR and biomass. All the above analyses were done using SPSS ver. 16.0, except where otherwise stated.

Across multiple resources of light and moisture, the plastic response of the invaders relative to the native species was estimated using the point-based plasticity index of Valladares *et al.* (2006) (see also Funk, 2008), calculated for each species as the difference between the minimum and maximum mean value divided by the maximum mean value (per trait). The index ranges between 0 (no plasticity) and 1 (maximum plasticity). The difference between the two species origin groups in the median for the plasticity index was then determined by the Wilcoxon paired signed rank test. To explore how adaptive traits of RGR, total biomass

TABLE 1. Mean trait performance of invasive and native vine species of south-east Queensland, Australia. Only data on light treatment effects are presented as moisture effects were minimal and hence data were pooled. The superscript number besides each species name identifies the invasive and ecologically/phylogenetically equivalent native pair

Species	Light cond.	Leaf chemistry						Leaf resource need			Leaf resource use efficiency						Plant fitness		
		N_{mass}	N_{area}	C	C : N	Ash	HC	SLA	CC_{mass}	CC_{area}	$A_{\text{max,area}}$	$A_{\text{max,mass}}$	AQE	WUE	$\delta^{13}\text{C}$	PNUE	PEUE	Biomass	RGR
Invasive (I)																			
¹ <i>Macfadyena</i>	High	5.14	0.032	41.19	8.11	11.7	17.65	161.09	1.254	78.17	11.35	0.184	0.079	7.31	-28.86	36.52	146.70	16.25	1.06
<i>unguis-cati</i>	Low	5.52	0.017	52.67	9.53	11.7	16.96	439.12	1.212	32.06	6.68	0.29	0.076	5.69	-29.16	34.23	183.68	0.87	0.21
² <i>Anredera</i>	High	4.79	0.016	37.00	7.77	17.5	16.66	310.55	1.147	37.31	7.54	0.229	0.058	10.79	-28.65	48.65	199.96	34.79	0.84
<i>cordifolia</i>	Low	7.41	0.009	33.00	4.46	30.0	13.02	867.88	1.081	9.94	3.83	0.331	0.055	3.27	-33.22	44.42	383.56	2.35	0.09
³ <i>Araujia</i>	High	4.87	0.021	43.62	8.95	11.2	18.89	245.33	1.348	57.40	5.70	0.132	0.049	8.99	-28.09	27.28	97.71	31.23	0.96
<i>sericifera</i>	Low	5.29	0.006	39.02	7.37	14.9	17.30	623.81	1.199	18.51	5.26	0.333	0.045	5.84	-33.11	57.07	283.30	0.90	-0.13
⁴ <i>Cardiospermum</i>	High	2.82	0.011	43.82	16.08	6.6	18.58	203.29	1.361	67.61	9.91	0.201	0.085	9.39	-26.59	74.76	147.63	64.65	1.07
<i>grandiflorum</i>	Low	4.98	0.007	42.40	8.59	13.5	17.11	672.70	1.204	17.89	6.27	0.422	0.088	5.08	-31.76	85.26	351.31	2.90	0.16
Native (N)																			
¹ <i>Pandorea</i>	High	3.17	0.020	46.39	14.85	7.9	20.03	198.40	1.457	112.46	10.34	0.206	0.033	8.69	-26.66	65.47	141.98	26.45	1.25
<i>jasminoides</i>	Low	3.61	0.011	46.22	12.83	9.3	19.64	335.34	1.42	44.79	5.60	0.199	0.051	6.1	-26.87	54.48	139.94	1.46	0.40
² <i>Hibbertia</i>	High	2.91	0.020	43.64	15.04	10.6	18.37	146.74	1.314	89.86	5.28	0.078	0.025	10.36	-29.07	26.79	59.62	33.31	0.66
<i>scandens</i>	Low	3.16	0.009	40.68	12.85	13.5	17.27	336.90	1.215	36.25	7.65	0.259	0.035	3.93	-31.49	81.78	213.42	3.79	-0.08
³ <i>Parsonsia</i>	High	5.42	0.033	39.45	7.41	10.3	19.10	167.77	1.369	123.37	6.40	0.107	0.066	8.58	-31.55	20.01	78.48	8.28	1.27
<i>straminea</i>	Low	6.1	0.011	37.76	12.83	10.9	17.76	588.45	1.306	26.05	3.79	0.225	0.058	7.18	-32.16	26.70	113.19	0.94	0.58
⁴ <i>Cardiospermum</i>	High	5.85	0.019	-	-	9.6	19.51	315.37	1.405	44.50	-	-	-	-	-	-	-	-	-
<i>halicacabum</i>	Low	5.61	0.007	-	-	15.7	18.48	823.76	1.273	15.50	-	-	-	-	-	-	-	-	-
Summary of ANOVA																			
Light		*	***	NS	NS	**	***	***	***	***	**	***	NS	***	**	*	***	***	***
Moisture		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	**	NS	NS	*	NS
Group		***	NS	NS	***	***	***	**	***	**	NS	*	*	NS	NS	NS	**	*	NS
Light x Group		*	NS	NS	NS	*	**	*	**	NS	NS	NS	NS	NS	**	NS	NS	NS	*
Light x Moisture		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Moisture x Group		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS
Direction of group difference																			
High		I > N			I < N	I > N	I < N	I > N	I < N	I < N		I > N	I > N				I > N	I > N	NS
Low		I > N			I < N	I > N	I < N	I > N	I < N	I < N		I > N	I > N				I > N	NS	I < N
Overall mean performance																			
Invasive	High	4.94	0.022	40.60	8.28	13.4	17.73	238.19	1.25	61.02	8.21	0.182	0.06	9.16	-28.53	37.42	148.12	27.42	0.95
Invasive	Low	6.31	0.010	41.74	6.42	19.3	15.53	643.60	1.08	18.46	5.25	0.318	0.058	4.92	-31.61	45.25	272.34	1.37	0.06
Native	High	3.81	0.024	43.16	12.44	9.6	19.17	170.97	1.38	89.35	7.34	0.131	0.038	9.62	-29.09	37.42	93.36	22.68	1.06
Native	Low	4.12	0.012	40.72	11.96	10.9	18.42	420.23	1.31	34.04	5.68	0.228	0.049	6.01	-30.46	62.56	171.22	2.06	0.30
	LSD	0.05	0.004	2.98	2.65	1.85	0.44	53.56	0.04	8.40	1.1	0.04	0.01	1.04	0.81	12.92	38.90	2.88	0.09

*, $P < 0.05$; **, $P < 0.02$; ***, $P < 0.001$; n.s., not significant; LSD, least significant difference.

SLA, A_{max} , biomass and RGR values were extracted from Osunkoya et al. (2010) and are presented here for ease of comparison of trait-pair relationships.

Abbreviations and units: N_{mass} = mass-based nitrogen concentration (mg g^{-1}); N_{area} = area-based nitrogen content (mg cm^{-2}); C = carbon concentration (mg g^{-1}); Ash = mineral ash (mg g^{-1}); SLA = specific leaf area (cm g^{-1}); HC = heat of combustion (Kj g^{-1}); CC_{mass} = mass-based construction cost (g g^{-1}); CC_{area} = area-based construction cost (g m^{-2}); $A_{\text{max,area}}$ = area-based maximum photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$); $A_{\text{max,mass}}$ = mass-based maximum photosynthesis ($\mu\text{mol g}^{-1} \text{s}^{-1}$); AQE = quantum (light)- use efficiency ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photon); WUE = instantaneous water-use efficiency ($\mu\text{mol CO}_2 \text{mmol}^{-1} \text{H}_2\text{O}$); $\delta^{13}\text{C}$ = isotopic carbon (%); PNUE = photosynthesis nitrogen use efficiency ($\mu\text{mol CO}_2 \text{mol N}^{-1}$); PEUE = photosynthesis energy-use efficiency ($\mu\text{mol CO}_2 \text{g}^{-1}$); Biomass = total biomass accumulated by 14 weeks of growth (g); RGR = relative growth rate ($\text{g}^{-1} \text{g month}^{-1}$).

and SLA varied across the light and/or moisture environments for each group, these traits were regressed against log-transformed measured structural, physiological, nutrient and resource-use traits using standardized major axis (SMA) regression as implemented in SMATR software (Warton *et al.*, 2006), and used the value of the scaling (slope) and intercept parameters as an index of C economy (revenue stream per unit investment; see also Leishman *et al.*, 2010). SMA estimates of lines summarizing the relationship between two variables are superior to ordinary least square linear regression and have been advocated in the literature because residual variance is minimized in both x and y dimensions rather than in the y dimension only (Falster *et al.*, 2003; Warton *et al.*, 2006). When comparing regressions, differences can occur in either the exponent of a (y intercept) and/or b (regression slope). If b (slope) differs amongst species, species with larger b will show greater increase in y per increment of x . If a differs, but b does not, species with larger a will have a consistently larger amount of y at any given value of x (Warton *et al.*, 2006).

RESULTS

General trends

Light had a greater effect on species and group performance than moisture (mixed model ANOVA; Table 1). Light availability had a significant effect on all measured leaf variables, except C, the C : N ratio and AQE, whereas the moisture availability appeared only to influence instantaneous and long-term WUE and biomass accumulated. Light \times group interaction effects were significant for many of the traits examined, suggesting that group performance varied depending on the light condition, especially for HC, CC_{mass} and long-term WUE (Table 1). In contrast, the light \times moisture and group \times moisture interaction effects were minimal, indicating consistency of moisture effect on traits under changing light regimes. Hence in most cases, except where the moisture effect was significant, data on moisture level effects were pooled. Consistent, significant differences were found, irrespective of the light condition, in the following traits (a) N_{mass} , total ash, SLA, A_{max} (mass-based), AQE and PEUE, in which invasive > native group values; and (b) the C : N ratio, HC, CC_{mass} and CC_{area} in which invasive < native group values. In the high light condition only, total biomass but not RGR was significantly higher in the invasive species group; the converse was the case at low light, with the invasive species exhibiting a significantly lower value for RGR but not total biomass.

Resource conservation, usage and efficiency

Of the six resource traits examined, three (WUE, isotopic C and PNUE) did not show significant differences between invasive and native groups of species (Table 1). On both area and mass bases, CC was lower in the invasive group, while PEUE and AQE showed the opposite trend, being higher in the invasive relative to the native species (Table 1). WUE and isotopic C were similar under high light, but differed significantly between the two groups under the low light regime where

the natives have a better water conservation strategy as indicated by the group's higher WUE and higher isotopic C signature (i.e. less negative value; Table 1).

Trait plasticity, co-ordination and correlation

There was no evidence of a difference in individual trait plasticity between the two groups (data not shown). However, across light regimes, a significantly higher level of trait correlations existed within the invasive group compared with the native group. Of the 153 leaf trait pairs (from 18 traits) examined, 17 and 29 of the relationships were significant at $P < 0.02$ and $P < 0.05$, respectively, for the native group (mean $R^2 = 0.85, 0.65$) compared with 37 and 59 for the invasive group (mean $R^2 = 0.92, 0.76$) (see also Osunkoya *et al.*, 2010). The difference between the two groups in the strength of these relationships was significant ($t = 3.77, P = 0.001, n = 17$; match-paired t -test). The trends between SLA and leaf resource traits are given in Fig. 1. In general and across light regimes, thinner leaves (i.e. higher SLA) had significantly lower N_{area} , lower CC and higher PNUE and PEUE but demonstrated low water conservation. SMA regression analyses indicated that the slopes did not differ significantly between the two groups in any of the relationships tested (Table 2). However, assuming slope homogeneity, significant differences existed in the intercepts of the SLA relationships with N_{area} , with CC (mass- and area-based) and with PEUE (Table 2 and Fig. 1B–D and F). Thus the analyses indicated that at a common (given) SLA value, significantly lower CC but higher N content were achieved by the invasive relative to the native species (Fig. 1 and Table 2). Mean distance along the common slope for PEUE vs. SLA relationship also differed between the two groups; natives were at the lower end while the invasives had a much wider distribution on the spectrum.

The trends between RGR and leaf resource traits are given in Fig. 2 and Table 2. Across groups and light regimes, RGR increased significantly with increasing N_{area} , CC_{area} and WUE (Fig. 2A, B and D), but decreased with increasing PEUE and SLA (Fig. 2C and F). The RGR relationships with PNUE and N_{mass} were not clear (i.e. not significant), due to different and often conflicting directions of the trends at each of the two light regimes. Slope values were also homogenous for the two groups for all the RGR and leaf resource traits examined (Fig. 2 and Table 2). However, evidence was found that the intercepts differed significantly between the two groups for RGR relationships with CC (mass- and area-based) and PEUE, such that at a common investment, a higher RGR often resulted for the invaders.

In summary, of the 17 pair relationships between SLA or RGR vs. leaf resource traits examined there was no evidence of slope heterogeneity between invasive and native groups (Table 2). However, there appeared to be some incidence of differences in intercept and/or in distance along a common slope value, mainly with CC or its derivative of PEUE.

Ordination of species

Data on leaf physico-chemical and resource traits were used in multivariate analyses. Ordination of the species based on all

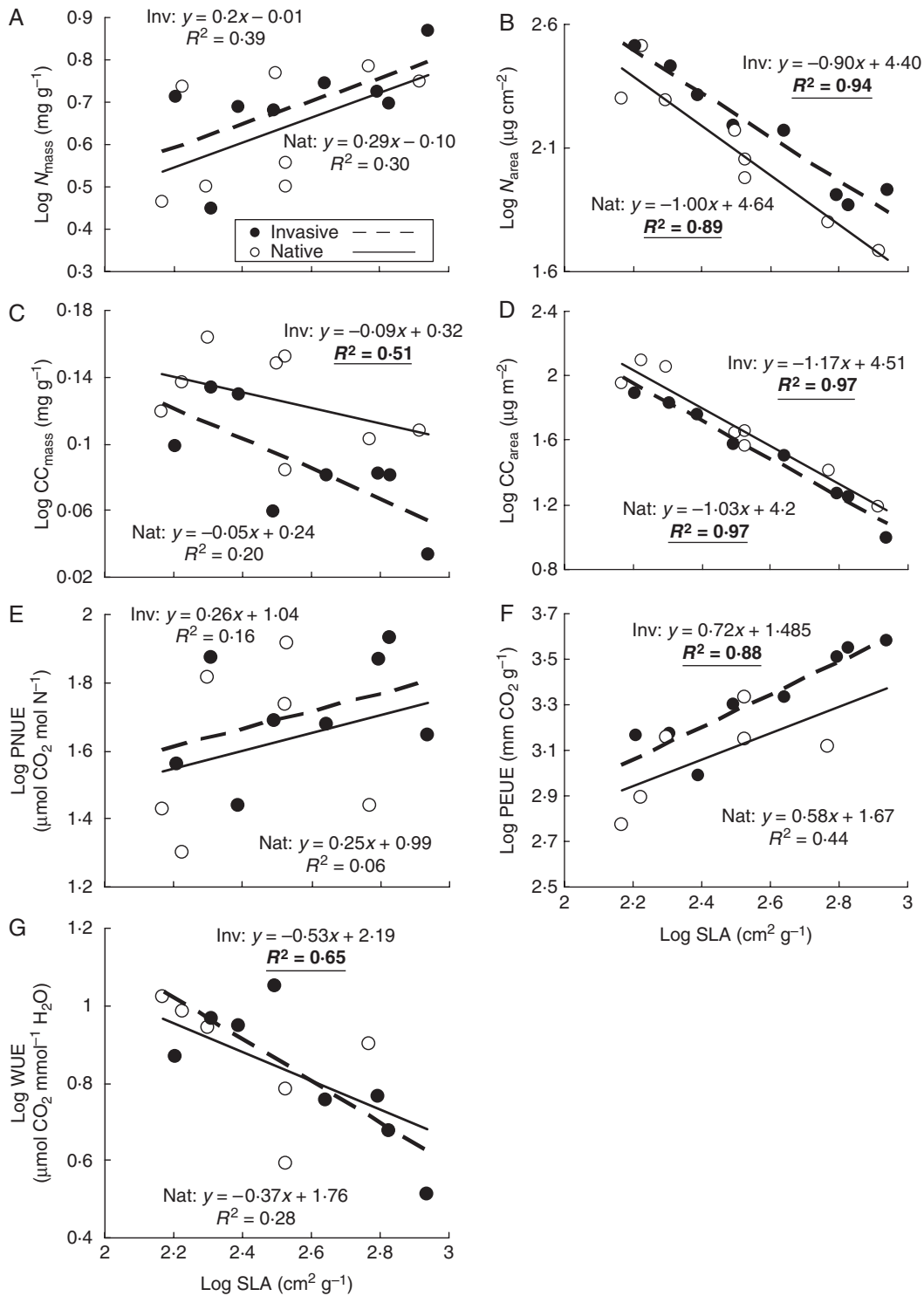


FIG. 1. The relationships across light regimes between SLA and various leaf resource traits for invasive and native vines, as indicated. Each point is a mean of species value from four to eight plants per light (high and low) treatment. Significant trends (R^2 value) are in bold and underlined. See Table 2 for tests of differences between the two groups in slope, intercept and distance along a common slope.

traits (except RGR and total biomass, see Table 1) indicated that the first three axes explained close to 90% of variation in the data set. A plot of species positions on ordination space of axes I and II is shown in Fig. 3. Axis 1, which explained 65.3% of the variation in the data set, was

influenced in decreasing order by CC (mass- and area-based), HC, ash, SLA and PEUE and, to a limited extent, by N_{mass} . This axis correlated significantly ($P < 0.05$; $n \geq 14$) with RGR ($r = 0.74$), and especially more so for invasive than native species (Fig. 4). The second axis (with 17% capture

TABLE 2. Test of differences in coefficients of the scaling (slope), the intercept and shift along a common slope of bivariate relationships between invasive and native species across two light regimes using standardized major axis regression analyses as implemented within SMATR software

Trait pair (y vs. x)	Test of plant group difference in:		
	Slope	Intercept	Distance along a common slope
N_{mass} vs. SLA	n.s.	n.s.	n.s.
N_{area} vs. SLA	n.s.	*	n.s.
CC_{mass} vs. SLA	n.s.	*	n.s.
CC_{area} vs. SLA	n.s.	*	n.s.
PNUE vs. SLA	n.s.	n.s.	n.s.
PEUE vs. SLA	n.s.	*	*
WUE vs. SLA	n.s.	n.s.	n.s.
$\delta^{13}\text{C}$ vs. SLA	n.s.	n.s.	n.s.
RGR vs. N_{mass}	n.s.	n.s.	n.s.
RGR vs. N_{area}	n.s.	n.s.	n.s.
RGR vs. CC_{mass}	n.s.	*	n.s.
RGR vs. CC_{area}	n.s.	*	n.s.
RGR vs. PNUE	n.s.	n.s.	n.s.
RGR vs. PEUE	n.s.	*	n.s.
RGR vs. WUE	n.s.	n.s.	n.s.
RGR vs. $\delta^{13}\text{C}$	n.s.	n.s.	n.s.
RGR vs. SLA	n.s.	n.s.	n.s.

n.s., non-significant; *, $P < 0.05$.

See Figs 1 and 2 for equations describing each of the ends and Table 1 for meaning of trait abbreviations.

of data variation) was a mixed bag of traits (N, C:N ratio, A_{max} , PNUE) but was not significantly linked to RGR ($P > 0.05$). The third axis (with 8% capture of data variation) was a physiological axis of AQE, A_{max} and N_{area} and was also not correlated with RGR. Separate analyses for each group indicated that the vector loading (as % variance) of axis I (which correlated significantly with RGR) was higher for the invasive species (60.7%) compared with the natives (43.4%), again confirming greater trait co-ordination in the invasives.

DISCUSSION

Plant adaptive and fitness traits such as growth, defence or reproduction are expected to be influenced by synthesis costs and resource availability, to the extent that lower CC as found in this study for the invasive group has been associated with plants with higher RGR (Daehler, 2003; Pyšek and Richardson, 2007; Kleunen et al., 2010). Overall, no difference in RGR could be detected between the two groups (see Table 1). Probable reasons for the lack of a difference in RGR between exotic invasive and native species have been fully discussed in Osunkoya et al. (2010), including (a) the fact that some of the native species chosen are common, widespread components of the local flora (especially *Pandorea jasminoides* and *Parsonsia straminea*) with invasive potential elsewhere and thus may have RGRs that overlap with those of the invasive exotic species investigated, and (b) RGR is known to decrease with age, being maximal when seedlings are young and then to decrease over time (Hunt, 1982). Nonetheless, the SMA regression analyses indicated that at a common CC, a higher intercept (i.e. higher RGR) value was

obtained for the invasive group relative to the native group (Fig. 2 and Table 2). This suggests that the invasives utilize essential growth resources more efficiently than their native counterparts by investing less energy per unit of RGR or leaf structure (SLA). This observed trend is increasingly being reported in invasive plant biology work (Baruch and Goldstein, 1999; Grotkopp and Rejmánek, 2007; Song et al., 2007; Feng et al., 2008).

The cost of constructing leaves in the invasive group was lower and, consequently, one can expect leaf payback time to occur rapidly (in terms of revenue stream through higher carbon fixation potential per investment) and leaf longevity to be shorter (Wright et al., 2004; Poorter et al., 2006; Osunkoya et al., 2008) compared with the natives. Indeed, a shorter duration of leaf retention was observed in members of the invasive group investigated in the course of the experiment, though the trend was not documented. No doubt rapid replacement of older leaves by new ones photosynthesizing at a greater rate will be an adaptive advantage for the invasive over the native species. The invasive species have lower CC_{mass} despite higher N_{mass} , though N is used in the derivation of the CC currency (Table 1). The relatively higher mass-based leaf N but low mass-based leaf CC of the invasive group (especially *Anredera cordifolia*) suggests that this group has a low energetic expense per unit N, thus contributing to its greater photosynthetic capacity at minimal costs.

Contrary to one of our hypotheses, a difference in instantaneous PNUE between the two groups, expressed both on a mass and an area basis, was not detected. This is in contrast with most studies (Baruch and Goldstein, 1999; McDowell, 2002; Funk and Vitousek, 2007; Feng et al., 2008), but similar to findings reported by Feng et al. (2007) and Leishman et al. (2007, 2010). Thus, though there was a moderate and significant increase in A_{max} of invasive compared with native species (approx. 20%; see Table 1), it seems a higher N content in the invasive group more than offset any expected higher PNUE. Taken in isolation, this observation for the investigated invasive vines will make them no more efficient in N use than the natives. On the other hand, the lower resource need (CC) and shorter leaf life span when combined with the instantaneous PNUE may still lead to a higher long-term PNUE for the invasive group (Nagel and Griffin, 2004), thus contributing to the field-observed runaway success of this group.

Higher N content in leaves of the invasives is in line with the group's preference for disturbed habitats commonly associated with high pulses of nutrient input (Funk et al., 2008; Vasquez et al., 2008). A significantly lower leaf C:N in the invasive group (Table 1) could indicate a reduced level of herbivory in their novel environment (Nagel and Griffin, 2001; Pyšek and Richardson, 2007; Feng et al., 2008), the consequence of which is low CC as a result of reduced need for structural and/or defence carbon compounds, such as cellulose and lignin which have higher energetic costs (Osunkoya et al., 2008). In fact, Onoda et al. (2004) and Feng et al. (2008) have shown that allocation of large proportions of N to structural cell wall toughness and chemical defence may be selected for more strongly in the native range where consumer pressure is intense, but this allocation strategy may be selected against

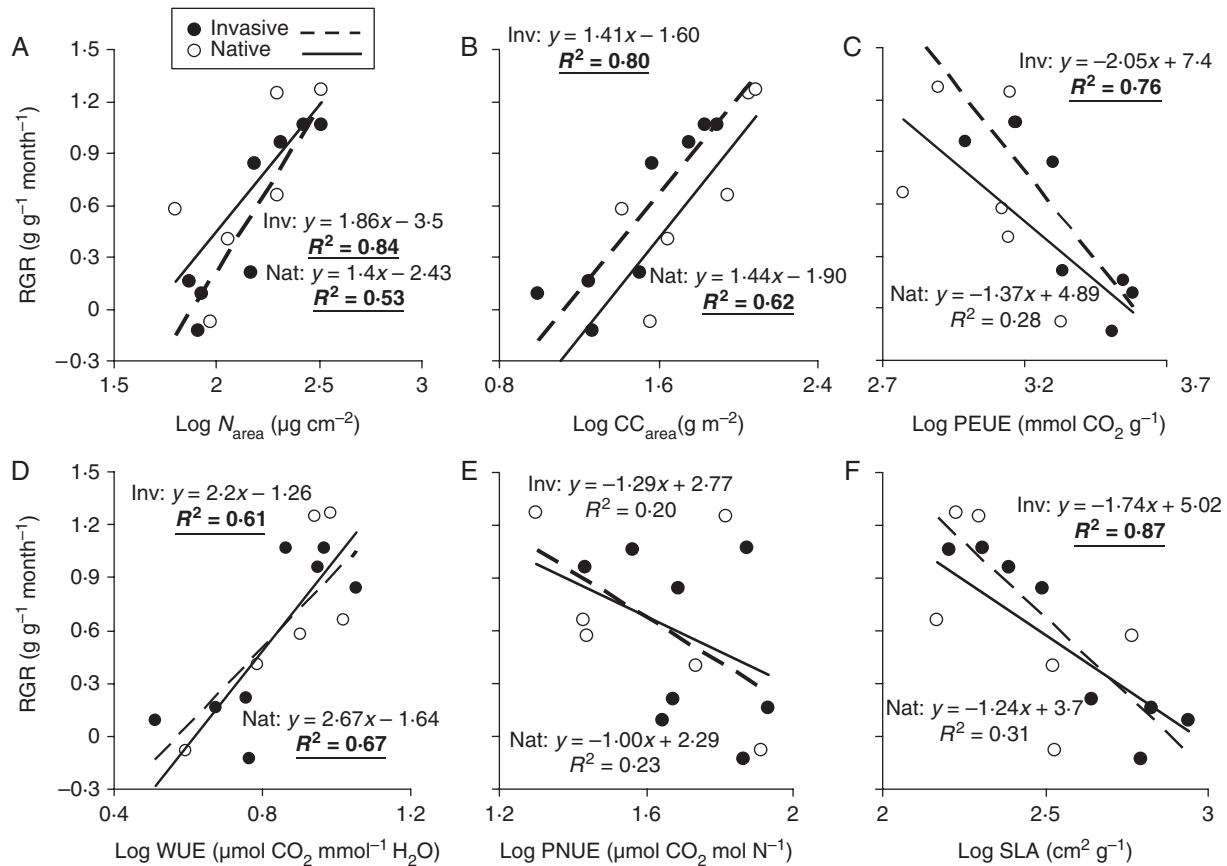


FIG. 2. The relationships across light regimes between biomass RGR and various leaf resource traits for invasive and native vines, as indicated. Mass-based traits gave weaker trends of the relationships and hence are not presented. Each point is a mean of species value from four to eight plants per light (high and low) treatment. Significant trends (R^2 value) are in bold and underlined. See Table 2 for tests of differences between the two groups in slope, intercept and distance along a common slope.

in the absence of strong consumer selective pressure in the introduced range. Thus it would be interesting to explore the C:N composition of the tested invasive vine species in their native range compared with values obtained in the present study.

Across light availabilities, a greater number and higher level of trait-pair correlations were found in the invasive group relative to the natives. This pattern was also supported by the results of the multivariate PCA in which axis I for the invasive group data captured more of the dichotomy as well as correlated more with RGR than did the same axis for the native group data. Though correlation does not necessarily imply causation, traits within and between traits categories are frequently causally related or associated though trade-offs, especially if they contribute to a common adaptive function (Shipley *et al.*, 2000; Grotkopp *et al.*, 2002; Westoby *et al.*, 2002). Thus a greater trait correlation in the invasives may favour a better, more mechanistic exploitation and adaptation to the changing environment as resources that are captured are tightly coupled and are efficiently utilized in some major dimensions (e.g. CC, SLA and PEUE in this work). This may allow excess resources captured to be diverted to major fitness components of carbon balance, reproduction or biomass growth (see Shipley *et al.*, 2000; Reich *et al.*, 2003; Westoby and Wright, 2006).

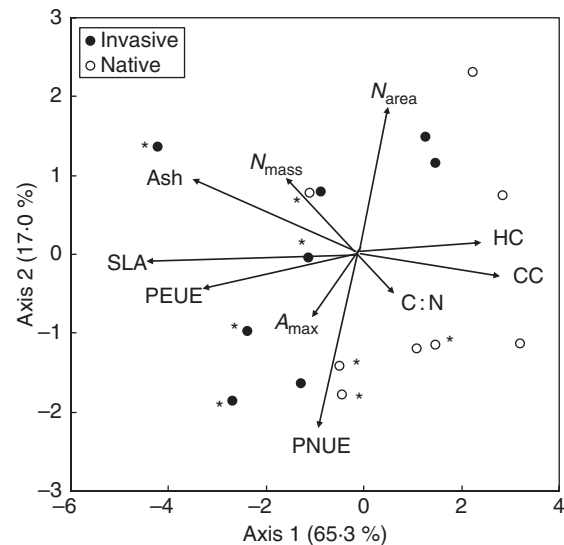


FIG. 3. Ordination of invasive and native woody vine species grown at two light regimes and based on 16 leaf eco-physiological and chemical traits. The 16 leaf traits are listed in Table 1. The directions and magnitudes of traits that load significantly and hence separate the invasive from the native group are indicated as well as the proportion of variation captured by each axis. The asterisk "*" denotes the low light regime.

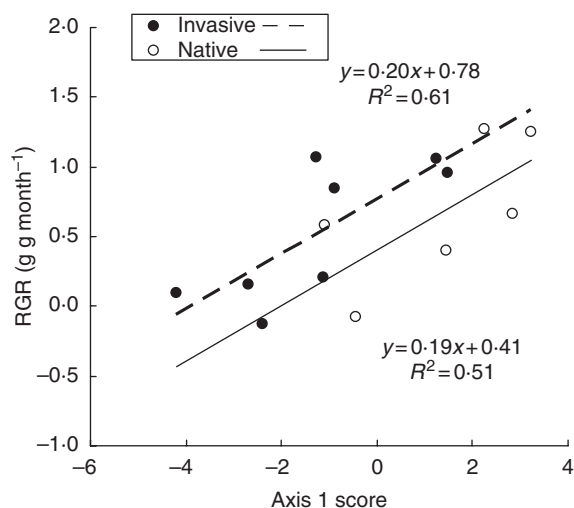


FIG. 4. Plot of the axis I score from PCA against RGR for invasive and native species, as indicated. Each trend is significant at $P \leq 0.05$.

Management implications

Amongst the 16 leaf physico-chemical traits measured, including six resource requirements, capture and use (A_{max} , AQE, PNUE, SLA, WUE, CC), through summarizing data using PCA, consistent and diagnostic differences were found between the invasive and native groups in five (SLA, CC, HC, ash, PEUE; Fig. 3). Only axis I of the PCA which captured most of the variation in these traits correlated significantly with adaptive trait of RGR. This is further evidence that these are indeed syndromes of traits that could serve as determinants of plant invasiveness and is in line with the findings of Pattison *et al.* (1998), Nagel and Griffin (2001) and Funk *et al.* (2008). Although many of these measures require expensive technical equipment, leaf SLA and ash which correlate significantly with the above-mentioned diagnostic traits (see Fig. 1), can quickly and easily be measured to screen for plant species with invasive potential and possibly to assist in choice of replacement species in restoration work (see Funk *et al.*, 2008; Osunkoya *et al.*, 2010). The latter will involve selecting native species with traits whose magnitudes and direction are similar to the diagnostic traits of the invaders.

Conclusions

As in previous work (Osunkoya *et al.*, 2010), limited evidence of differences in trait plasticity was found between exotic invasive and native vines at singular and trait-pair (relationship) levels. Slope homogeneity in all of the trait pairs examined also confirmed this observation which is in line with the assertion by Leishman *et al.* (2010) that the two groups may not have fundamentally different carbon-capture strategies. However, this study took a step further and included tissue CC, a functional trait which summarizes inorganic mineral content, calorific value and N need of a leaf carbon economy, but is rarely investigated in studies of trait-pair relationship across multiple habitats in plant invasion work. At the same resource requirement (e.g. at a

common SLA), intercept tests indicated that the invasive species have lower CC and higher energy utilization efficiency (PEUE), partly in line with the hypotheses raised in the Introduction. These test results, coupled with the PCA patterns, are indicative that for a given investment (CC or SLA), the return was likely to be much higher in the invasive group than in their native counterparts. Water usage/conservation strategy as quantified both by instantaneous (WUE) and integrated measures (C isotopic ratio) did not differ between the two groups, a pattern consistent with some previous studies (e.g. Leishman and Thomson, 2005; Funk and Vitousek, 2007) but at variant with others (e.g. Daehler, 2003; McAlpine *et al.*, 2008). The inconsistency in WUE difference between the two groups and across studies indicates limited utility of this measure as a diagnostic trait. Equally, the lack of a significant difference between the groups for PNUE is at odds with many published works, but all these studies are based on different life forms to the one investigated herein. Thus more studies using woody vines and integrating leaf life-span are needed to clarify further the role of PNUE in invasiveness within this life form.

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