

Comparative growth and biomass allocation of two varieties of cat's claw creeper, *Dolichandra unguis-cati* (Bignoniaceae) in Australia

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Abstract. Introduced as an ornamental vine, cat's claw creeper *Dolichandra unguis-cati* (syn. *Macfadyena unguis-cati*) has invaded coastal and subcoastal areas of subtropical eastern Australia. Two varieties have been indentified, one of which ('short-pod') is found throughout south-eastern Australia, while the other ('long-pod') appears to be restricted to several sites in south-eastern Queensland. We compared the growth and biomass allocation patterns of the two varieties in the field over a 22-month period to determine if a higher growth rate and/or more efficient allocation of biomass may contribute to this disparity in distribution. The long-pod variety produced greater aboveground and total biomass than the short-pod variety in both riparian and non-riparian zones. Belowground the two varieties produced a similar number of tubers and overall biomass, though the long-pod variety allocated a smaller portion of its carbon belowground. High growth rates and greater biomass allocation aboveground are characteristic of invasive species, allowing them to outcompete and crowd out existing vegetation. There was no significant site by variety interaction, an indication of consistency in variety performance across riparian and non-riparian sites. Results from our study suggest that differences in growth and biomass allocations are unlikely to have contributed to the disparity in distribution of the two varieties. Despite currently occupying a relatively small range, the long-pod variety may be a more adept invader than the short-pod variety, and could become more prevalent in the future.

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Introduction

Invasive vines and lianas are some of the most destructive invasive plants, significantly impacting the ecosystems they invade (Harris and Gallagher 2010). As they are not self-supporting, vines can allocate a greater proportion of their resources to stem elongation and leaf production compared to tree and shrub species, allowing them to rapidly smother existing vegetation (Putz and Mooney 1991). Due to their rapid growth, vines are able to monopolise available light in the canopy, reducing the amount of photosynthetically active radiation reaching both the host plant and the forest floor, further reducing the growth of host trees and suppressing regeneration of native species (Putz and Mooney 1991; Harris *et al.* 2007). Dense infestations can also cause the total collapse of the vegetation canopy. Exotic vines are often referred to as 'transformer' weeds due to their ability to alter abiotic conditions (Vivian-Smith and Panetta 2002). They are particularly problematic in rainforests (Harris and Gallagher 2010). In the subtropical rainforests of eastern Australia 70% of the invasive species are vines (Grice and Setter 2003), including three Weeds of National Significance (<http://www.weeds.org.au/WoNS/>, accessed 28 September 2012).

Recently renamed *Dolichandra unguis-cati* (L.) L.G. Lohmann (Bignoniaceae; Nuevo Cat. Fl. Vasc. Venezuela

273. 2008), cat's claw creeper [formally known as *Macfadyena unguis-cati* (L) Gentry] is a perennial woody vine native to tropical Central and South America, including Trinidad and Tobago (Everett 1980; Howard 1989). Dispersed as an ornamental vine, it now has a pan-tropical distribution and has become naturalised in Australia, New Zealand, numerous Pacific Ocean nations (including Hawaii), southern USA, China, India, southern Africa, Mauritius, Bermuda and St Helena (GISD 2008). Cat's claw creeper was first reported as naturalised in Australia in the 1950s (Batianoff and Butler 2002). Populations have expanded and the weed is now widespread in coastal and subcoastal areas of southern Queensland and northern New South Wales, where it poses a significant threat to biodiversity in rainforest and riparian communities (Csurhes and Edwards 1998; Downey and Turnbull 2007). In 2012 cat's claw creeper was recognised as a Weed of National Significance (<http://www.weeds.org.au/WoNS/>).

Cat's claw creeper is a vigorous climber (Csurhes and Edwards 1998). It can climb structures of 20 m or higher, smothering trees and causing their collapse. In areas without standing vegetation, the vine forms dense mats that inhibit the growth of understorey vegetation. Cat's claw creeper also has a vigorous root and tuber system and reproduces vegetatively from tubers and stolons (Vivian-Smith and Panetta 2004). In Australia

two varieties have been observed in the field, differing most notably in leaf, flower and seed-pod traits (Shortus and Dhileepan 2011). Dubbed 'long-pod' and 'short-pod' (the long-pod variety is also known as 'hairy cat's claw creeper' or 'bat's claw creeper'; Technigrow 2010), the two varieties have both been identified as the same species, *D. unguis-cati* (Shortus and Dhileepan 2011). As the name suggests, the long-pod variety has significantly longer seed pods than the short-pod variety (an average of 71 cm compared to 32 cm; Shortus and Dhileepan 2011). Long-pod plants also have larger mature leaves compared to short-pod plants (66 mm² compared to 13 mm²).

The short-pod variety is found throughout south-eastern Australia, while the long-pod variety appears to be restricted to several sites in south-eastern Queensland (Shortus and Dhileepan 2011). The long-pod variety is believed to have a propensity to invade different vegetation types to the short-pod variety and may become a serious weed of non-riparian vegetation (Technigrow 2010). In view of the disparity in the distribution of the two varieties and potential preference for different vegetation types, we compared the growth and biomass allocation of the two varieties at several field sites with the aim of determining whether higher growth rate and/or more efficient allocation of biomass may contribute to the wider distribution and greater abundance of the short-pod variety and how vegetation type (riparian and non-riparian) affects the two varieties. High biomass production and low allocation of biomass to roots are traits that have been linked to invasive species (e.g. Grotkopp *et al.* 2002; Zheng *et al.* 2009). Four study sites were selected; two in riparian communities (a zone where cat's claw creeper has become particularly prevalent; Dhileepan *et al.* 2010) and two in non riparian communities. This study will provide an insight into possible future changes in the comparative prevalence of the two cat's claw creeper varieties in Australia.

Materials and methods

Study sites

Four sites in south-eastern Queensland with existing cat's claw creeper infestations were selected for this study (Table 1). Nerang and Canungra were both riparian sites and will be referred to as riparian A and B, respectively. Carindale and Bardon were non-riparian sites and will be referred to as non-riparian A and B, respectively. Cat's claw creeper was a dominant species at all

study sites, smothering the majority of trees, shrubs and forming dense mats on the ground. The short-pod cat's claw creeper variety was present at all sites. The long-pod variety was initially present at Carindale (non-riparian A) only.

Experimental design

To ensure there were an adequate number of similar sized tuberlings for the study, tubers were collected from the field (Fort Bushland Reserve in the Brisbane suburb of Oxley (-27.534S, 152.967E), where both varieties occur) and grown under glasshouse conditions. Two-hundred each of long-pod and short-pod field-collected subterranean tubers (devoid of leaves and other plant material) were measured (diameter at the widest point and wet biomass) and then planted in black plastic pots (15 cm diameter) containing commercial grade potting mix. Plants were grown in a glasshouse for 2 months and were watered daily.

At each site, 40 similar sized glasshouse-grown tuberlings (20 each of long-pod and short-pod) were randomly planted in pairs (one long-pod and one short-pod), with a minimum of 5 m distance between each pair. Individuals within each pair were planted with the potting mix from their pot, ~80 cm apart on either side of a 1.2 × 0.9 m (height × width) trellis, which was erected to encourage vertical growth. Plants were watered 1 week after planting. Due to the removal of numerous plants by wallabies and bandicoots, replacement glasshouse-grown plants were planted 6 weeks after the initial planting (one at Canungra, three each at Nerang and Bardon, and 11 at Carindale).

Shoot length, number of shoots, basal stem diameter (BSD), and number of leaves were recorded one week before planting in the field (mid September 2008) and then at quarterly intervals (early January, mid April, mid July, mid October 2009). The final recording took place at the time of harvesting (late May 2010) – 22 months after the trial began. Tuber fresh weight was also recorded at this time. The average amount of growth per week was determined by dividing the change in each parameter by the number of weeks between recordings. Plants were separated into roots, stems and leaves and dried in an oven at 50°C for 2 weeks. Dry weights were recorded on two occasions, several days apart (with samples returned to the drying oven in between), to ensure that no moisture remained. Root, leaf and stem weights were recorded and then divided by total weight to determine root, leaf and stem mass fractions.

Table 1. Field site details

Site	Nerang	Canungra	Carindale	Bardon
Site ID	Riparian A	Riparian B	Non-riparian A	Non-riparian B
Location	-28.017S, 153.300E	-28.0336S, 153.117E	-28.017S, 153.300E	-27.402S, 152.983E
Existing CCC variety	Short-pod	Short-pod	Long-pod and short-pod	Short-pod
Land tenure	Riparian zone abutting a golf course	Riparian zone abutting farmland	Private property abutting a bushland reserve	State government land
Vegetation ^A	Remnant open eucalypt forest	Remnant open eucalypt forest	Remnant open dry eucalypt forest	Remnant open eucalypt forest
Aspect	n.a.	n.a.	West	South
Site size	~10 ha	~10 ha	~5–10 ha	~5 ha

^AVegetation classification as defined by Specht (1970, cited in Specht and Specht 1999).

Statistical analysis

The impact of Variety and Site on the growth of the two varieties was analysed. Growth in the two varieties was compared using two-way ANOVA. Pairings were used as a blocking variable for data collected after the field trial commenced. Aboveground, belowground and total biomass were \log_e transformed and mass fractions were square-root transformed before analysis. The relationship between both root mass fraction (RMF) and leaf mass fraction (LMF) (both \log_e transformed) and total biomass (square-root transformed) was examined using linear regression. All analyses were conducted using GENSTAT Release 11.1 (Payne *et al.* 2008).

Results

Growth patterns

The long- and short-pod tuberlings that were selected for planting in the field were all of similar size (Table 2). The only exception was BSD, which was significantly greater for long-pod tubers.

Growth patterns were similar for the two varieties (Fig. 1), increasing during the warmer months and slowing or declining during the cooler months. Leaf number in particular dropped markedly during the cooler months (Fig. 1). During the final 6 months of the study, stem length increased substantially.

Varietal differences in growth were evident for shoot length and number of leaves; both being greater for long-pod (Fig. 2). The change in tuber weight for tubers and the number of tubers per plant were similar for both varieties (Fig. 2).

Differences between sites were evident for all parameters measured (Table 3). Plants at site non-riparian B had significantly greater growth compared to plants grown at riparian A for all parameters measured, including number of tubers (Fig. 2). Growth parameters at riparian B and non-riparian A were intermediate between riparian A and non-riparian B. There was no significant interaction between site and variety for any of the parameters.

Biomass

Aboveground biomass and total biomass gained were significantly greater for long-pod plants than short-pod plants at all sites (Table 4; Fig. 3). Long-pod plants also produced more belowground biomass, but due to a high level of variation, the difference was not statistically significant. Site had a significant effect on the amount of biomass produced. Plants grown at the two non-riparian sites produced significantly more biomass than those planted at riparian A. The amount of aboveground biomass produced by plants at riparian B was also significantly higher than for riparian A. Underground biomass on the other hand, was

similar between the two sites. The location of plant pairs within sites had a significant effect on the amount of aboveground biomass and belowground biomass produced, and thus total biomass (Table 4). There was no significant site by variety interaction, an indication of consistency in variety performance across different sites.

Biomass allocation differed significantly between the two varieties (Table 4; Fig. 3). LMF and shoot mass fraction were higher and RMF lower for long-pod plants than short-pod plants (i.e. less carbon is devoted towards the root in the long-pod variety). Average proportions for the two varieties were 0.29, 0.32 and 0.40 (long-pod), and 0.20, 0.25 and 0.56 (short-pod) for leaf, stem and root, respectively. Site did not significantly affect shoot mass fraction or RMF, but did affect LMF, with plants at riparian A and non-riparian A having lower values than the other two sites.

There was no linear relationship evident between total biomass and LMF for either variety (long-pod: $F_{1,57} = 0.68$, $P = 0.412$; short-pod: $F_{1,41} = 0.03$; $P = 0.863$). A negative relationship was found between total biomass and RMF for long-pod plants [$F_{1,57} = 31.70$, $P < 0.001$; $\sqrt{(\text{total dry weight}_{\text{LP}})} = 3.781\text{--}3.304$ (RMF)] but not short-pod plants ($F_{1,43} = 0.03$, $P = 0.863$).

Discussion

To our knowledge, this is the first published study of the growth of cat's claw creeper in the field. It confirms observations that the main growing period is between spring and autumn (Downey and Turnbull 2007). Growth also occurs during the cooler months but is greatly reduced. The long-pod variety had a higher growth rate, producing greater aboveground and total biomass than the short-pod variety at all study sites. High growth rates are characteristic of many invasive species, allowing them to outcompete and crowd out other species (Pattison *et al.* 1998; Grotkopp *et al.* 2002; Grotkopp and Rejmánek 2007). Several studies have demonstrated a positive association between RGR and invasiveness for closely related species (Burns 2004; Garcia-Serrano *et al.* 2005; Grotkopp and Rejmánek 2007). For example, Grotkopp *et al.* (2002) found seedling RGR to be the most important feature associated with invasiveness for *Pinus* spp. (under optimal conditions). In their analysis of studies dealing with invasive tree species, Lamarque *et al.* (2011) found growth rate to be the most efficient predictor of invasiveness for invasive trees and also invasion success once established. The ability of long-pod plants to grow more rapidly than short-pod plants suggests that they could be more successful invaders than the short-pod variety by outcompeting and crowding out existing vegetation more rapidly.

Table 2. *F*-ratios and *P*-values from two-way ANOVA comparing the growth parameters for short-pod and long-pod plants planted at four field sites in south-east Queensland, before the commencement of the trial
Residual df for: growth parameters, 136; tuber wet weight, 150

Factor	df	Basal stem diameter (mm)		Number of stems		Stem length (cm)		No. of leaves		Tuber weight (g)	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Variety	1	179.49	<0.001	0.56	0.457	0.91	0.341	0.35	0.552	3.62	0.059
Site	3	0.68	0.565	0.37	0.772	0.29	0.829	1.10	0.353	2.00	0.116
Variety × site	3	0.72	0.543	0.69	0.562	0.01	0.998	0.10	0.958	0.11	0.956

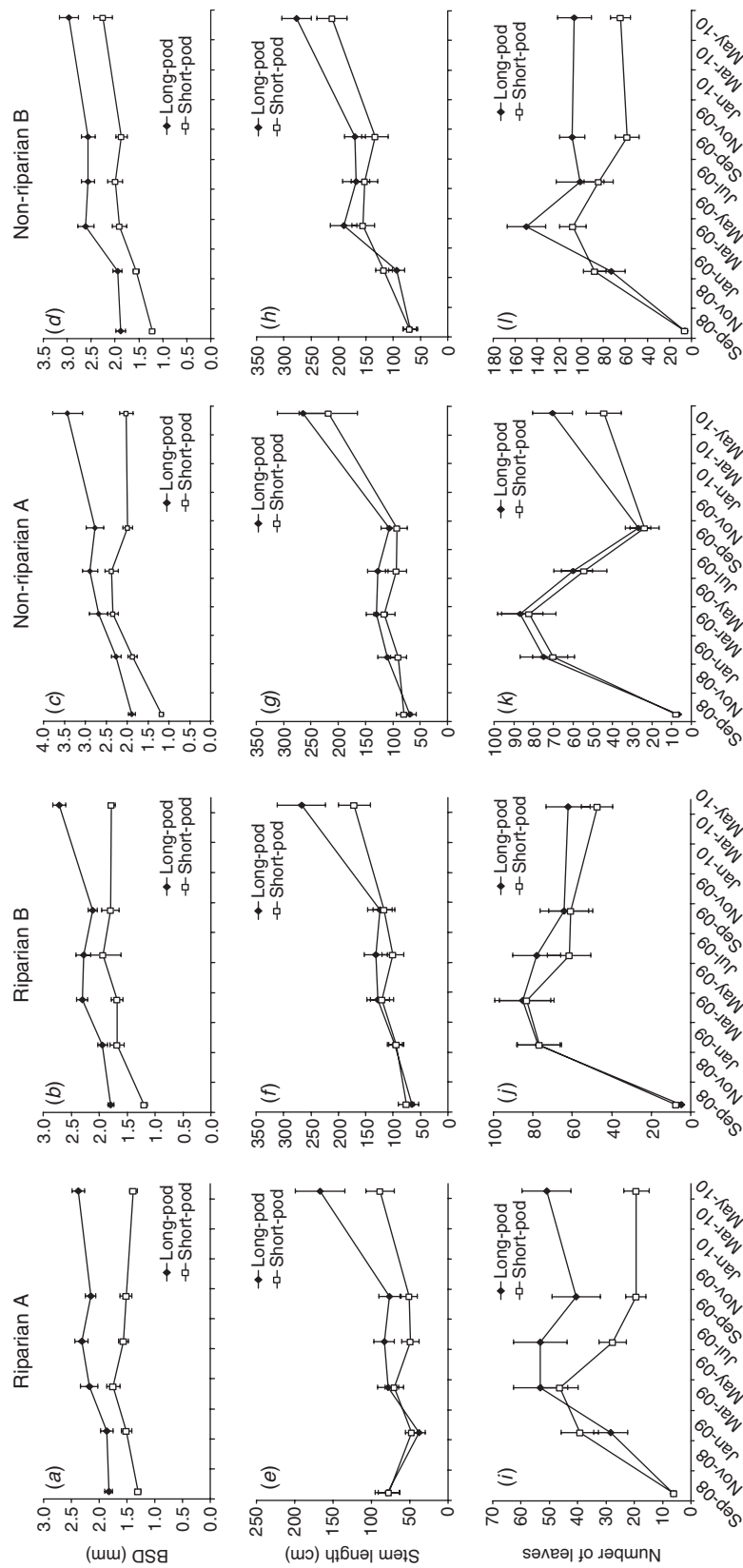


Fig. 1. Growth pattern of short-pod and long-pod cat's claw creeper plants planted at four field sites in south-east Queensland (mean \pm 1 s.e.). (a–d) Basal stem diameter – BSD (mm); (e–h) maximum stem length (cm); (i–l) number of attached leaves.

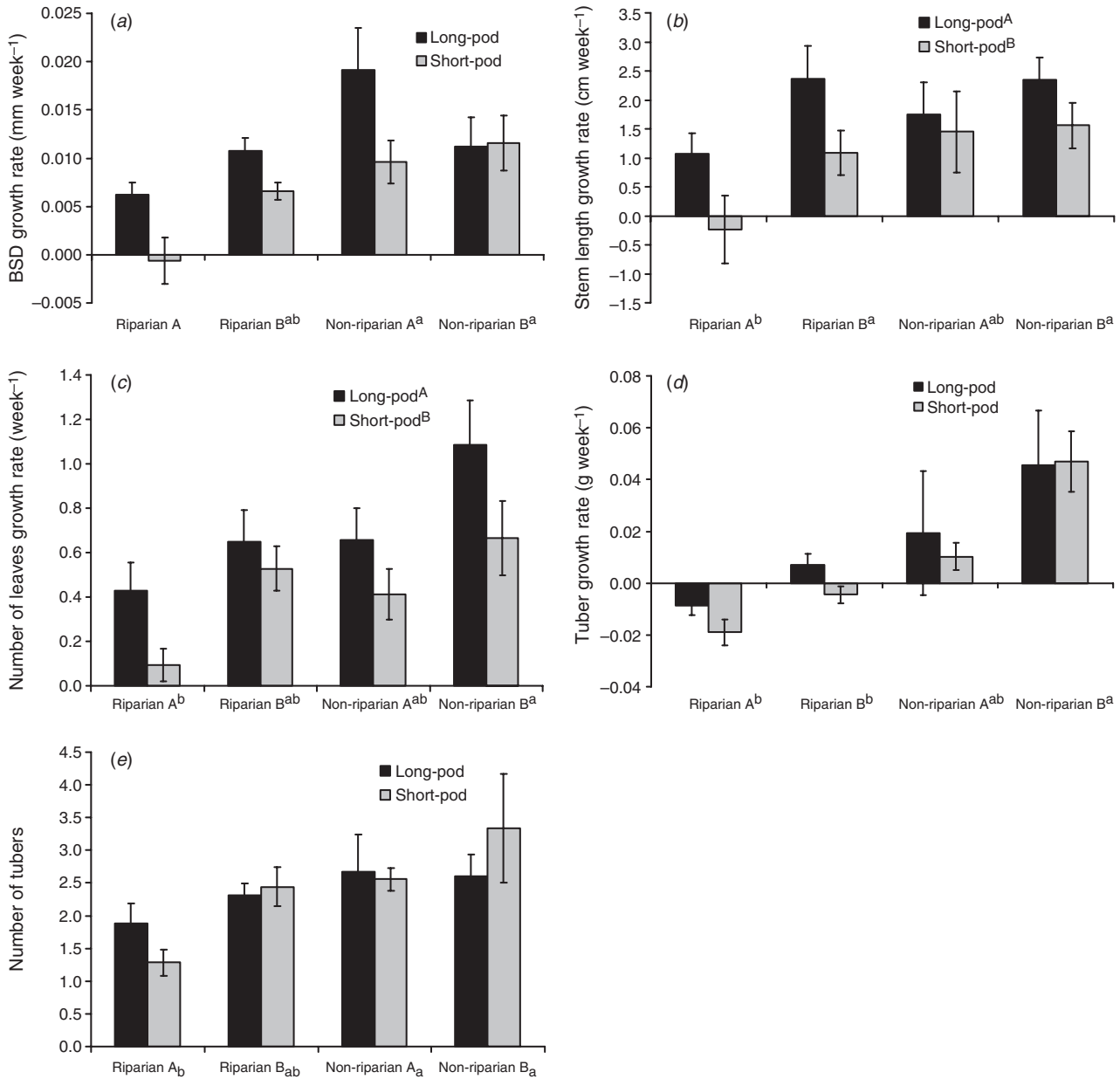


Fig. 2. Growth parameters for short-pod and long-pod plants planted at four field sites in south-east Queensland (mean \pm 1 s.e.). (a) Change in basal stem diameter (BSD) per week; (b) change in stem length per week; (c) increase in number of leaves per week; (d) change in tuber weight per week; (e) number of tubers. Significant differences (at $P < 0.05$) between varieties or sites are indicated by different letters.

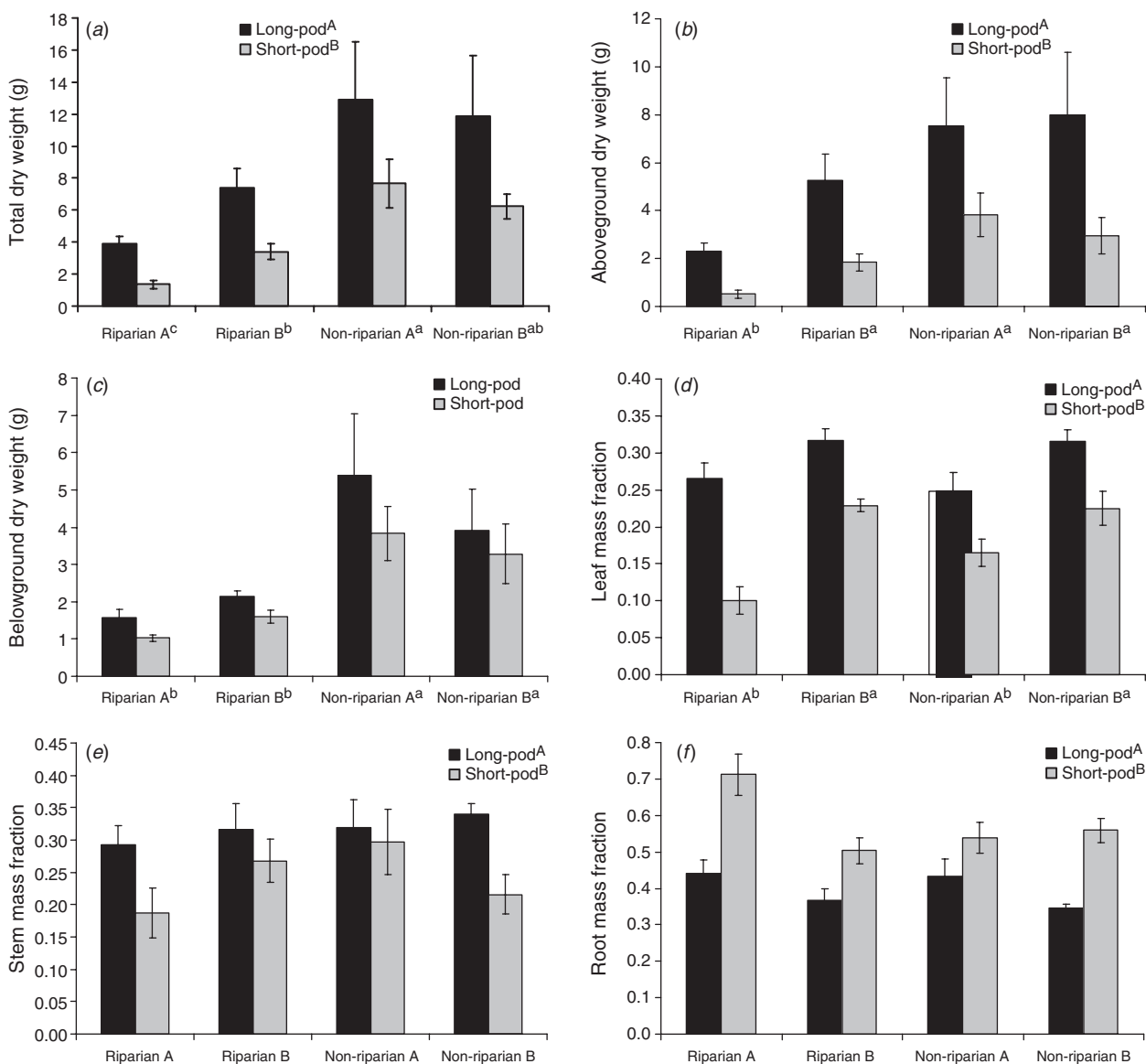
Table 3. *F*-ratios and *P*-values from two-way ANOVA comparing the growth parameters for short-pod and long-pod plants planted at four field sites in south-east Queensland

Residual df for: growth parameters, 81; tuber wet weight, 79

Factor	df	Growth per week									
		Basal stem diameter (mm)		Stem length (cm)		No. of leaves		Tuber weight (g)		Number of tubers	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Pair (blocking variable)	19	0.56	0.924	0.84	0.655	1.46	0.198	1.29	0.215	1.18	0.295
Variety	1	3.38	0.070	5.13	0.026	5.46	0.035	0.13	0.721	0.84	0.363
Site	3	6.09	<0.001	3.31	0.024	5.01	0.002	7.20	<0.001	3.93	0.011
Site \times variety	3	1.60	0.289	0.43	0.733	0.39	0.791	0.15	0.931	0.91	0.438

Table 4. *F*-ratios and *P*-values from two-way ANOVA comparing the log_e transformed dry weight data for short-pod and long-pod plants planted at four field sites in south-east Queensland

Factor	df	Aboveground biomass		Belowground biomass		Total biomass		Leaf mass fraction		Stem mass fraction		Root mass fraction	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
		Residual df=82											
Pair (blocking variable)	19	1.83	0.032	1.98	0.018	1.95	0.020	0.98	0.494	1.40	0.149	1.15	0.322
Variety	1	26.254	<0.001	1.93	0.168	26.50	<0.001	46.38	<0.001	6.94	0.010	36.68	<0.001
Site	3	9.66	<0.001	18.58	<0.001	9.79	<0.001	6.03	<0.001	0.09	0.967	2.13	0.103
Site × variety	3	0.47	0.702	0.21	0.890	0.12	0.948	1.97	0.125	0.72	0.545	0.82	0.487

**Fig. 3.** Biomass production and allocation for short-pod and long-pod plants planted at four field sites in south-east Queensland (mean \pm 1 s.e.). (a) Total dry weight; (b) aboveground dry weight; (c) belowground dry weight; (d) leaf mass fraction; (e) stem mass fraction; (f) root mass fraction. Significant differences (at $P < 0.05$) between varieties or sites are indicated by different letters.

Higher growth rates are generally associated with lower biomass allocations to roots [due to higher allocations to leaves and stems (Zheng *et al.* 2009)]. For example, lianas of

Bauhinia spp. with relatively high growth rates also had lower RMF than more slowly growing *Bauhinia* species (Cai *et al.* 2007). In a similar fashion, the long-pod variety in this study also

allocated (on average) 20% less biomass to roots compared with the short-pod variety. Further, RMF was negatively related to total biomass for long-pod plants. There was a negative trend for short-pod plants, though the relationship was not statistically significant due to the effect of an outlier.

Despite differences between varieties in biomass allocation to roots, there were no significant differences in tuber growth rate, or number of tubers, between varieties. This is in contrast to a previous study which suggested that long-pod plants produced a greater number of tubers than short-pod plants (Osunkoya *et al.* 2009). This suggestion was an extrapolation from a comparison of soil samples from sites with one (short-pod only) or both varieties and did not involve specific measurements of each variety. Due to their larger overall size, long-pod plants generally produced more belowground biomass, though this was not statistically significant.

The allocation of biomass to leaves in our study was 1.5 times greater for long-pod plants (compared to short-pod plants). They also produced more than 3 times the dry weight of leaf material. This might suggest that the higher growth rate of the long-pod variety is facilitated by the greater biomass allocation to leaves and thus greater ability to photosynthesise. However, several studies examining the specific factors that correlate with growth rate, have found that LMF does not have a strong association; parameters such as leaf area ratio (LAR) and specific leaf area (SLA) being better predictors (Poorter and Remkes 1990; Poorter and Lambers 1991; Grotkopp *et al.* 2002; Daehler 2003; Shipley 2006; Grotkopp and Rejmánek 2007). Consistent with the purported lack of association, we found no relationship between LMF and total biomass for either variety. Neither LAR nor SLA were recorded during this study, though SLA has been reported elsewhere to be similar for the two cat's claw creeper varieties (Shortus and Dhileepan 2011). LAR, which is the product of SLA and LMF, is therefore likely to be higher for the long-pod variety (as LMF is higher for long-pod).

Without the need to support themselves, vines can afford to allocate a greater proportion of biomass to leaves than other life forms such as trees (Putz 1983). Invasive vines such as *Anredera cordifolia* (Ten.) Steenis, *Celastrus orbiculatus* Thunb. and *Lonicera japonica* Thunb. ex Murray allocate 40–50% or more of their biomass to leaves (Sasek and Strain 1991; Ellsworth *et al.* 2004; Osunkoya *et al.* 2010). Other invasive vines, including cat's claw creeper, have smaller allocations (Osunkoya *et al.* 2010). Under low-light glasshouse conditions Osunkoya *et al.* (2010) determined the LMF for cat's claw creeper to be 31%. This is comparable to the 29% LMF we found for long-pod plants, but greater than the 18% determined for short-pod plants. Though not stated, it is likely (given their prevalence) that Osunkoya *et al.* (2010) used short-pod plants in their study. The variation in results between our studies may be attributed to the growing conditions (i.e. field versus glasshouse). With the exception of light, conditions for growth would have been optimal in the study by Osunkoya *et al.* (2010) allowing plants to allocate more biomass to leaf construction and thus energy production.

Leaf level traits for cat's claw creeper such as low LMF and SLA are not typical of invasive vine species (Harris and Gallagher 2010; Osunkoya *et al.* 2010), yet cat's claw creeper is a fast

growing and highly invasive species (e.g. Godfrey 1988; Swarbrick and Dreier 1990; King *et al.* 2011). A prolonged juvenile stage allows the species to devote more resources to roots and tubers when young, aiding stem growth and leaf production (Downey and Turnbull 2007). Cat's claw creeper is a structural parasite (Stevens 1987). Increases in stem diameter are slow, whereas stem elongation towards light is rapid (Francis undated). Tubers also promote the persistence of cat's claw creeper and readily form new plants if separated from the parent plant (Vivian-Smith and Panetta 2004). Tuber density in mature infestations can be as high as $\sim 1000\text{ m}^{-2}$ (Achilles 2003). Asexual reproduction is an adaptation common to many invasive vine species, particularly the production of tubers and adventitious roots (Harris and Gallagher 2010). Cat's claw creeper stems produce adventitious roots when in contact with bark or soil, and can form new plants (Vivian-Smith and Panetta 2004).

Seed production was not examined in this study as cat's claw creeper plants do not begin flowering until well established and the seedbank is relatively small and short-lived (Vivian-Smith and Panetta 2004). The long-pod variety produces significantly more seeds per pod than the short-pod variety (Shortus and Dhileepan 2011). However, there is currently little information regarding comparative pod production between the biotypes, other than anecdotal evidence suggesting that the short-pod variety flowers more regularly than the long-pod variety (in south-eastern Queensland; Shortus and Dhileepan 2011). Although seeds facilitate the spread of plant species, they are not essential for successful invasion (Harris and Gallagher 2010). The exotic vine blue morning glory [*Ipomoea indica* (Burm.f.) Merr.] does not produce viable seed in Australia (Muyt 2001) and Madeira vine [*Anredera cordifolia* (Ten.) Steenis] rarely produces seed (Vivian-Smith *et al.* 2007), yet both are among the most widespread and destructive exotic vines in the country (Harris and Gallagher 2010).

Variation between sites

Cat's claw creeper typically invades riparian communities (Dhileepan *et al.* 2010). The high level of disturbance experienced by riparian communities makes them particularly susceptible to plant invasions and they often act as corridors for the rapid movement of exotic species (Ede and Hunt 2008). Indeed, cat's claw creeper seeds are adapted for dispersal by water (as well as air). Vegetative fragments are also effectively dispersed and establish as new individuals. Yet although infestations of cat's claw creeper are prevalent in riparian communities, we found biomass production to be higher in the non-riparian (and drier) sites used in our study. Both varieties performed particularly poorly at riparian site A. Dry weights were up to 5 times lower at the two riparian sites compared to the non-riparian sites. Tuber size also showed the same pattern. Riparian A site which bordered a river, was subject to at least two major flood events during the study period, causing most of the plants to be submerged and/or waterlogged for an extended period. This most likely adversely affected plant biomass production (Mommer and Visser 2005). The riparian B site, which bordered a creek, experienced minor flooding. The negative impact of inundation on the growth of cat's claw

creeper is not unexpected. Inundation has been demonstrated to have a negative impact on other riparian invaders (e.g. Vandersande *et al.* 2001; Vreugdenhil *et al.* 2006). For example, the relative growth rate of the serious riparian weed *Salix nigra* Marshall is negatively affected by inundation; the highest growth rate recorded for plants experiencing no inundation (Stokes 2008). Although flooding of riparian areas is to be expected, the February 2010 flood was an atypical event. The Gold Coast hinterland (where the two riparian sites were located) received up to 360 mm over a 24-h period, which is greater than the average rainfall for the entire month (Bureau of Meteorology 2010).

Light may have also contributed to differences in biomass production at riparian versus non-riparian sites; canopy cover at the two riparian sites was notably greater than at non-riparian site A. However, light levels were not measured during this study. Cat's claw creeper is moderately shade tolerant and can grow under forest canopies (Francis undated; Osunkoya *et al.* 2010). The high RMF for cat's claw creeper reflects its shade tolerance and has been demonstrated for other shade-tolerant species (e.g. Kitajima 1994; Paz 2003). For example, a similar RMF was found by Cai *et al.* (2007) for the shade-tolerant liana *Bauhinia aurea*, which was higher than the RMF of its light-demanding congeners. Shade tolerance allows the juvenile cat's claw creeper plants to establish under the forest canopy. Growth is slower than for plants growing in full sun (see also Floyd 1989; Osunkoya *et al.* 2010), and shoot tips are positively phototropic (Raghu *et al.* 2006).

The location of plant pairs within sites had a significant effect on the amount of biomass produced. This is likely an artefact of the heterogeneous distribution of resources (e.g. sunlight, soil nutrients, moisture) (Kelly and Canham 1992). Differences in belowground parameters across sites can be attributed overall plant size as the allocation of biomass belowground was similar across the sites.

Plants at the Nerang site (riparian site A) had different biomass allocation to those at other sites. The LMF for plants at Nerang was notably lower than at the other sites. This was particularly evident for short-pod plants and may also be an artefact of the flooding events. When leaves of terrestrial plants become submerged, CO₂ enters leaves predominantly via diffusion across the cuticle (Mommer and Visser 2005). Thinner leaves, characteristic of long-pod plants (Shortus and Dhileepan 2011), are thus more conducive to underwater gas exchange, which may explain why the long-pod variety fared the better of the two varieties at this site.

Shortus and Dhileepan (2011) considered that the higher leaf dry matter content and smaller leaf area of short-pod plants would make them more resilient, contributing to their wider distribution. Indeed, smaller leaves have a lower boundary layer resistance, allowing for better convective cooling of leaves and higher water-use efficiency (WUE), and a lower LMF means less area from which to lose water (Parkhurst and Loucks 1972; Ackerly *et al.* 2002). Results from a preliminary glasshouse study suggest that short-pod plants do indeed have a higher WUE than long-pod plants (D. Taylor, unpubl. data). However, we found no significant site and species interaction, indicating that site conditions did not affect the growth responses of the varieties differently. The observation that the long-pod

variety prefers non-riparian communities [in contrast to the short-pod variety; Technigrow (2010)] is thus not supported by our results.

The ability of long-pod plants to grow more rapidly than short-pod plants suggests that they could be more successful invaders than the short-pod variety. Indeed, at the three sites where both the long-pod and short-pod varieties have naturalised, the long-pod variety appears to dominate. Yet the long-pod variety is only known to occur at a small number of sites in south-eastern Queensland, whereas the short-pod variety occurs throughout coastal and subcoastal areas of southern Queensland and northern New South Wales (Technigrow 2010; Shortus and Dhileepan 2011). The scarcity of the long-pod variety relative to the short-pod variety could be due to its infrequent and/or more recent use as an ornamental compared to the short-pod variety. Several studies have demonstrated a positive association between residence time (the time an exotic species has been present in its introduced area) and invasion success (e.g. Rejmánek 2000; Hamilton *et al.* 2005). Harris *et al.* (2007) found that the longer that an exotic vine species has been present in Australia, the more widespread it will be. Propagule pressure (the number of times a species is introduced to a new area), has also been found to play an important role in invasion success (e.g. Rejmánek 2000; Mulvaney 2001; Dehnen-Schmutz *et al.* 2007; Bucharová and van Kleunen 2009), though sourcing such information is often difficult or impossible (Pyšek and Richardson 2006). Cat's claw creeper is known to have been used as an ornamental species in Australia since the 1860s (Mulvaney 1991) and the short-pod variety is a feature of many gardens around Brisbane. Photos of cat's claw creeper from the 1930s in Brisbane appear to be of the short-pod variety, though this cannot be stated conclusively. Anecdotal observations around Brisbane suggest that the use of the long-pod variety is much rarer than the short-pod variety and is associated with more recently established gardens. Only 11 sites with the long-pod variety have been identified to date, all in south-eastern Queensland (K. Dhileepan, unpubl. data). An ornamental planting of the long-pod variety occurs less than 500 m from the Carindale site, the only site in this study to have a pre-existing population of the variety. A shorter residence time and lower propagule pressure may also explain why the long-pod variety appears to prefer different vegetation communities to the short-pod variety as long-pod may not have had the opportunity to invade all suitable communities. As no information could be found regarding the historical use of different cat's claw creeper varieties in Australia (or elsewhere), this suggestion remains speculative.

Conclusions

Results from this study suggest that the long-pod variety may be a more successful invader than the short-pod variety, despite currently occupying a relatively small range. The long-pod variety produced greater aboveground and total biomass than the short-pod variety at all field sites including riparian and non-riparian locations. It also had a higher LMF, and smaller RMF. It will likely become more prevalent in the future. However, we found no evidence to suggest that the long-pod variety prefers non-riparian over riparian communities.

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