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What lies beneath? The pattern and abundance of the subterranean tuber bank of the invasive liana cat's claw creeper, *Macfadyena unguis-cati* (Bignoniaceae)

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Abstract. Cat's claw creeper, *Macfadyena unguis-cati* (L.) Gentry (Bignoniaceae) is a major environmental weed of riparian areas, rainforest communities and remnant natural vegetation in coastal Queensland and New South Wales, Australia. In densely infested areas, it smothers standing vegetation, including large trees, and causes canopy collapse. Quantitative data on the ecology of this invasive vine are generally lacking. The present study examines the underground tuber traits of *M. unguis-cati* and explores their links with aboveground parameters at five infested sites spanning both riparian and inland vegetation. Tubers were abundant in terms of density (~1000 per m^2), although small in size and low in level of interconnectivity. *M. unguis-cati* also exhibits multiple stems per plant. Of all traits screened, the link between stand (stem density) and tuber density was the most significant and yielded a promising bivariate relationship for the purposes of estimation, prediction and management of what lies beneath the soil surface of a given *M. unguis-cati* infestation site. The study also suggests that new recruitment is primarily from seeds, not from vegetative propagation as previously thought. The results highlight the need for future biological-control efforts to focus on introducing specialist seed- and pod-feeding insects to reduce seed-output.

Introduction

Cat's claw creeper, *Macfadyena unguis-cati*, is a climbing woody vine native to tropical America, from Mexico through Central America to tropical South America, including Trinidad and Tobago (Everett 1980; Howard 1989; Rafter *et al*. 2008). *M. unguis-cati*, originally introduced as an ornamental plant, has since become invasive in several countries including Australia, South Africa, India, Mauritius, China, USA (Hawaii and Florida) and New Caledonia (Holm *et al*. 1991; Langeland and Burks 1998; Meyer 2000; Downey and Turnbull 2007). In Australia, it is a major environmental weed in coastal Queensland and New South Wales (Quirico 1992; Batianoff and Butler 2003) where it poses a significant threat to biodiversity in riparian areas, rainforest communities and remnant natural vegetation (Csurhes and Edwards 1998; Batianoff and Butler 2003). *M. unguis-cati* is a high-climbing woody vine, with stems up to 6 cm in diameter and roots becoming elongated and tuberous with age. Upright branches and horizontal runners can develop adventitious roots. In densely infested areas, *M. unguis-cati* covers standing vegetation, including large trees and shrubs, eventually causing canopy collapse (Sparks 1999). In areas without standing vegetation or man-made structures (e.g. fences), the vines grow along the forest floor and form dense mats.

Macfadyena unguis-cati can propagate both from seeds and vegetatively from belowground tubers. Stems trailing along the ground are also capable of producing roots at the nodes. Seeds are dispersed by wind and water and the species does not have a persistent seed bank, suggesting that although its mechanism of spread is through seeds, its mechanism of persistence is through the tuber bank (Vivian-Smith and Panetta 2004). The tuber bank is an important but, as yet, poorly understood life-history component of *M. unguis-cati* (Vivian-Smith and Panetta 2004). Very limited information is available on the incidence and abundance of tuber banks in the field and it is not known whether the existing tuber banks are produced through seed germination (genet) or branching from existing tubers (ramet). This information is vital to understanding the mechanism of colonisation and expansion of the weed and how these processes could be affected through various control efforts.

The management objectives for this weed are to reduce the rate of shoot growth to limit the vine's ability to climb and smother native vegetation, as well as to reduce the tuber bank

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(Raghu *et al*. 2006). Chemical-control options for managing *M. unguis-cati* are available, although often not used because of the sensitive ecosystems (riparian vegetation and rainforest) where it occurs (Dhileepan *et al*. 2005). Mechanical control of aboveground growth provides only temporary relief, as regeneration from subterranean tubers can continue over many years. Biological control is considered the only viable long-term management option for this weed (Dhileepan *et al*. 2005, 2007*a*; Downey and Turnbull 2007). If spread is primarily through seeds, a seed-feeding insect would be desirable as a biocontrol agent. However, if new plants arise from existing tubers, then identifying an agent that can reduce the density and size of tubers could be of priority.

In general, the effects of various management options on aboveground vegetation are easier to quantify, although their influence on subterranean tubers are difficult to assess. Currently, the only method to quantify the abundance and biomass of *M. unguis-cati* subterranean tubers is through destructive belowground sampling, which is very labour intensive and may not be possible in sensitive riparian areas. Hence, there is a need to develop a non-destructive sampling strategy to quantify the abundance and biomass of subterranean tubers through sampling the aboveground parameters.

In the present study, we investigate the possible source of new plants (i.e. from seeds or from the existing tuber bank) and explore whether any of the aboveground plant parameters can be used to predict the prevalence and abundance of subterranean tubers so as to provide quantitative information on *M. unguis-cati* tuber banks.

Materials and methods

Study species

Macfadyena unguis-cati is capable of climbing significant heights with the aid of its claw-like tendrils. The roots can become elongated and develop tubers with age. The stems can also develop adventitious roots, which can become tuberous. The leaves are compound and opposite (Downey and Turnbull 2007) with some leaflets modified to form pronged, claw-like tendrils, with deciduous horny hooks, that enable the plant to climb almost any structure, be it natural or man-made (Raghu *et al*. 2006; Downey and Turnbull 2007). Shoot tips have been found to be positively phototropic, whereas the tendrils, as in most tropical vines, are skototropic (a form of negative phototropism in which initial growth is towards the dark shadow cast by trees blocking light) (Raghu *et al*. 2006). The fruits (15–45 cm long), which may contain up to 200 seeds, are flattened linear capsules that mature in late summer to early autumn (February–May in Queensland, Australia). Seeds (2–4 cm long) are also flattened and oblong in shape, and are papery with two wings (Downey and Turnbull 2007). The seeds are dispersed by wind and water, and do not persist in the seed bank for a long period of time (Vivian-Smith and Panetta 2004; Raghu *et al*. 2006). *M. unguis-cati* can grow successfully in varying light and soil conditions (Raghu *et al*. 2006). These features, combined with the phototropic shoot tips and the skototropic tendrils, enable the plant to be successful as a structural parasite.

In south-eastern Queensland, two varieties (short- and long-pod type) of the invasive vine are known. The short-pod variety, which has a smaller pod size (30–45 cm long), small glabrous leaves (3.96 ± 0.32 cm^2, $n = 100$) and yellow flowers, is more widespread than the long-pod variety (pod size: 40–85 cm long; large pubescent leaves: 20.03 ± 2.46 cm^2, $n = 95$; yellowish-orange flowers), which is restricted to a few sites in south-eastern Queensland (R. Boyne and K. Dhileepan, unpubl. data). The two varieties co-exist, although one often predominates at a given infestation site (K. Dhileepan, pers. obs.).

Study sites

Five study sites (Oxley, Bardon, Carindale, Nerang and Boonah) were chosen on the basis of known *M. unguis-cati* infestations in the Brisbane region, south-eastern Queensland. Distances between the sites are at least 10 km. *M. unguis-cati* infestation sites in Oxley (27°60′S, 152°59′E), Bardon (27°30′S, 152°60′E) and Carindale (27°30′S, 152°59′E) are ~5–10 ha each and are within the Brisbane City Council forest parks. These three sites all occur in gentle undulating topography. Nerang (27°60′S, 153°20′E) and Boonah (27°60′S, 152°41′E) are linear forest sites (~10 ha each) along riparian zones, with the former located in the Gold Coast hinterland, ~60 km south of Brisbane city, whereas the latter is in the Esk Shire, ~120 km west of Brisbane. At all these sites, *M. unguis-cati* dominates the landscape, with many of the scattered trees (mainly *Eucalyptus* species) and much of the ground cover smothered by the invasive vine.

Sampling method

In November 2007, through to January 2008, five soil-sampling points (each 25 cm × 25 cm in area and 20 cm in depth) were established at each infestation site. Where possible, samples were taken every 15–20 m along a linear transect. However, because of the sporadic nature of infestations within some of the sites (e.g. Carindale, Nerang and Boonah), some samples were taken from individual *M. unguis-cati* patches within the site, although in all cases, keeping distance between sampling plots to at least 20 m. Plot areas to be sampled were delineated by red spray paint around the periphery of specially made metal frames of the size specified above. Wide sharp-edge shovels and spades were used to dig down to 20-cm depth, followed by careful removal and transfer of the cut-soil plot, including the aboveground vegetation, into heavy duty plastic bags for transportation back to Alan Fletcher Research Station at Sherwood (Brisbane, Australia). In the laboratory, samples were sorted through, carefully removing established plants and seedlings, and ensuring that any underground (rhizome) connections between plants were maintained. Various morphometric measurements were then taken, including (1) the form of *M. unguis-cati* (long or short pod, as determined by the size of the leaves), (2) whether the established plant was singular (genet) or was connected to another plant via an underground rhizome/runner (ramet), (3) leaf number, stem diameter at the root–stem junction, (4) stem length and number of stems per plant and (5) the number and size of tubers per plant. Because of the ellipsoidal

shape of the *M. unguis-cati* tuber, the size was determined in two directions: longitudinally, i.e. length (one measurement), and transversely, i.e. diameter (three measurements at the distal end and middle points of the longer axis of the tuber). It is recognised that some of the plants described as genets may previously have had connections and technically should be classified as ramets; however, at the point in time when soil sampling took place, if obvious connections were not evident, the plants were classified as genets. To improve precision in biomass estimation, 10 plants were randomly selected from each sampled plot and dried at 80°C for several days to a constant weight.

Data analysis

The data were analysed with SPSS software (ver. 16.0: SPSS Inc., Chicago, IL, US). The data were confirmed for homogeneity of variances and hence there was no need for transformation before parametric analyses (ANOVA, correlation and linear regression). Frequency data (number of tubers per plant, stems per plant and level of clonality) were analysed with goodness-of-fit (χ^2) test. Within (and across) site, correlations were carried out among all measured variables by using the mean value within each replicate plot (and in some cases within each site). Regressions were also made to quantify the extent to which the aboveground traits (e.g. stand density) could predict belowground parameters (e.g. tuber density and biomass).

Results

The number of root tubers per individual plant varied between zero and four, with most plants (81.4%) excavated having one tuber (Fig. 1). About 10% of the plants sampled did not display any underground tubers; rather, they had vestiges of their photosynthetic cotyledons still attached, an indication that these were seedlings, possibly from the current year's seed cohort (Fig. 1). These seedlings were observed mainly in the riparian sites (i.e. Boonah and Nerang) (Fig. 1). Many plants also appeared to be genets (i.e. arising from seeds) because lateral, belowground connections (rhizomes) among the tubers excavated were infrequent; ramet values ranged between 5 and 15% at all sites, except in Boonah where ~30% of the tubers displayed the ramet trait (Fig. 2*a*). About 7% of the plants examined exhibited multiple stems, with the long-pod variety (Carindale and Oxley populations) displaying significantly more of this trait (20%) than the short-pod variety (Boonah, Bardon and Nerang populations) (4%) ($\chi^2 = 9.41$, $P < 0.05$; Fig. 2*b*). Pattern and level of clonality did not vary significantly between the long- and short-pod varieties ($\chi^2 = 0.84$, $P = 0.44$).

Average values for the traits examined at each site are given in Table 1. Most parameters examined varied significantly among sites. The Oxley and Carindale populations, which are predominantly of the long-pod variety, generally tended to have plants with larger values for average stem length, stem diameter, tuber length, tuber diameter and, consequently, individual plant biomass. The Oxley and Carindale populations exhibited the lowest aboveground stem and belowground tuber densities, although these do not necessarily translate to reduced below- and/or aboveground biomass.

Across infestation sites, of the 36 pairwise bivariate relationships examined, 17 appeared significant at $P \leq 0.05$ (Table 2). Analysis and examination of the significant trends at the individual-site level indicated that only four of these relationships remained consistent and significant and hence may have predictive value for the purpose of estimation, modelling and management of *M. unguis-cati* infestations

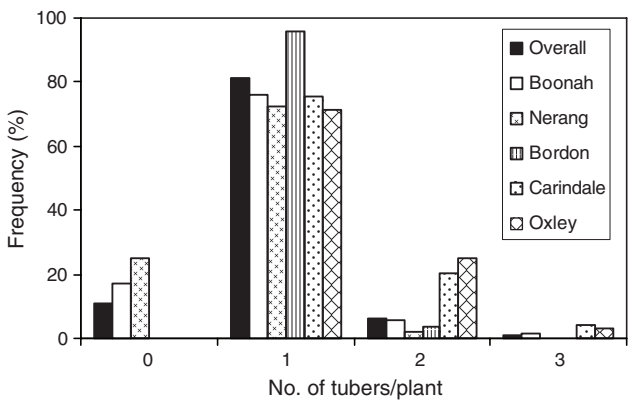

Fig. 1. Frequency distribution of the number of root tubers per plant of *Macfadyena unguis-cati.* Note the exclusive occurrence of young seedlings (i.e. plants with no tubers) in the two riparian zones of Boonah and Nerang.

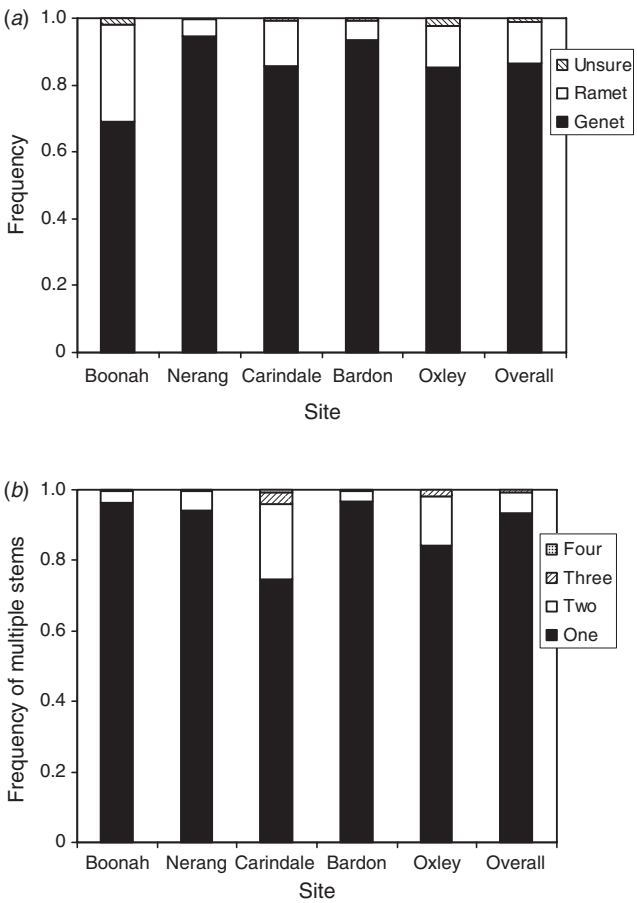

Fig. 2. Frequency of occurrence of (*a*) ramets *v.* genets and (*b*) multiple stems per plant in *Macfadyena unguis-cati* at each of the five sites surveyed.

Table 1. Average (± s.e.) values of morphometric measurements on *Macfadyena unguis-cati* collected at each of the five sites investigated
Summary ANOVA refers to 1-way ANOVA of test of differences among sites, with error degrees of freedom (d.f.) of 4 and 20. Across sites (i.e. within a row) means with the same superscripts are not significantly different at $P \leq 0.05$, using the l.s.d. multiple-comparison procedure. $^{**}P < 0.02$, $^{***}P < 0.001$; n.s., not significant

Trait	Site					Pooled data	Summary ANOVA	
	Boonah[B]	Nerang[B]	Bardon	Carindale	Oxley		*F*-ratio	Significance
Stem height (cm)	17.52a ± 1.37	10.92b ± 1.79	8.84b ± 1.60	27.26c ± 1.69	22.72c ± 1.52	17.45 ± 3.49	23.41	***
Stem diameter (mm)	1.83b ± 0.13	1.07a ± 0.08	1.70b ± 0.13	2.57c ± 0.18	3.07d ± 0.12	2.05 ± 0.34	36.02	***
Root tuber diameter (mm)	6.23b ± 0.42	3.96a ± 0.20	5.64b ± 0.45	8.44c ± 0.43	11.38d ± 0.63	7.13 ± 1.24	40.78	***
Root tuber length (mm)	24.76a ± 0.89	17.08b ± 0.53	19.19b ± 1.18	27.69a ± 1.88	35.06c ± 2.44	24.76 ± 3.24	21.32	***
Tuber density[A]	104.00a ± 9.58	105.20c ± 23.12	132.00c ± 17.33	30.20b ± 6.83	24.60b ± 2.20	79.20 ± 23.61	12.09	***
Stand (stem) density[A]	108.40a ± 10.24	111.60a ± 24.61	133.20a ± 16.77	39.40b ± 8.80	31.20b ± 2.27	84.76 ± 23.14	9.95	***
Individual-plant biomass (g)	1.61a ± 0.22	0.52b ± 0.06	0.85b ± 0.12	3.74c ± 0.77	3.97c ± 0.58	2.14 ± 0.78	13.05	***
Total aboveground biomass[A] (g)	276.88a ± 31.97	244.03a ± 31.97	92.82b ± 28.6	205.42a ± 28.6	190.38a ± 28.6	196.81 ± 28.8	5.45	**
Total belowground biomass[A] (g)	139.48a ± 6.91	70.5a ± 27.81	39.20b ± 9.38	78.66a ± 11.49	76.5a ± 10.71	78.77 ± 9.09	5.41	**
Total (below + above) mass[A] (g)	456.12a ± 45.44	381.26ab ± 87.22	140.48d ± 15.43	321.47ac ± 16.89	306.57ac ± 29.56	321.18 ± 29.82	6.18	**
Root mass fraction	0.34a ± 0.07	0.19a ± 0.09	0.32a ± 0.20	0.27a ± 0.08	0.28a ± 0.04	0.28 ± 0.13	1.066	n.s.

[A]Plot dimension: 25 cm (length) × 25 cm (breadth) × 20 cm (depth); [B]riparian site.

Table 2. Across sites ($n = 5$, and hence d.f. = 3) matrix of correlation coefficients as indices of level of association between measured below- and aboveground traits of *Macfadyena unguis-cati*
Significant trends ($P \leq 0.05$) across the five sites investigated are in bold. Underlined trends indicate bivariate relationships that remained significant within each of the five sites and hence of predictive value for estimation, modelling and management purpose

	Stem height	Stem diameter	Tuber diameter	Tuber length	Tuber density	Stand (stem) density	Individual-plant mass	Belowground mass	Aboveground mass
Stem height	1.00	0.86	0.79	0.83	**–0.91**	**–0.91**	**0.94**	0.35	0.28
Stem diameter		1.00	**0.98**	**0.96**	**–0.88**	**–0.89**	**0.97**	0.08	–0.11
Tuber diameter			1.00	**0.98**	**–0.88**	**–0.89**	**0.94**	0.04	–0.09
Tuber length				1.00	–0.86	**–0.88**	**0.93**	0.25	0.09
Tuber density					1.00	**0.99**	**–0.96**	–0.09	–0.17
Stand (stem) density						1.00	**–0.97**	–0.09	–0.15
Individual-plant mass							1.00	0.12	0.04
Belowground mass								1.00	0.84
Aboveground mass									1.00

(Fig. 3). These are positive trends between (a) underground tuber density and aboveground stand density, and (b) aboveground individual plant biomass and tuber size (diameter or length), (c) a negative trend between aboveground individual plant biomass and tuber density and (d) a marginally significant positive trend between above- and belowground biomass per unit area (Fig. 3*a–d*). However, within each of the five sites, the last relationship holds only in the Oxley population and hence is of limited predictive value.

Discussion

This exploratory work has shown that in riparian zones (Boonah and Nerang), recruitment of *M. unguis-cati* is from both the seed bank as well as from vegetative propagation (Fig. 1). In general, floodplain, and hence riparian, vegetation will be more prone to invasion by exotics than the surrounding landscape (e.g. Carindale, Oxley and Bardon) because of (i) increased opportunities for propagule dispersal in water followed by germination and seedling establishment, and (ii) increased physical disturbances created by water movement and inundation of the floodplain (Thomas *et al*. 2006). It is also most likely that the unusual, and extended, drought experienced in south-eastern Queensland before our survey could have contributed to lack of opportunities for dispersed *M. unguis-cati* seeds to germinate in the surrounding landscapes of the three non-riparian sites. The year 2006–2007 was an exceptionally dry year in south-eastern Queensland, with rainfall ~20% lower than the long-term average (see http:\\www.bom.gov.au/climate/averages). Vivian-Smith and Panetta (2004) have shown that *M. unguis-cati* does not have a persistent seed bank (<1 year) and hence we can conclude

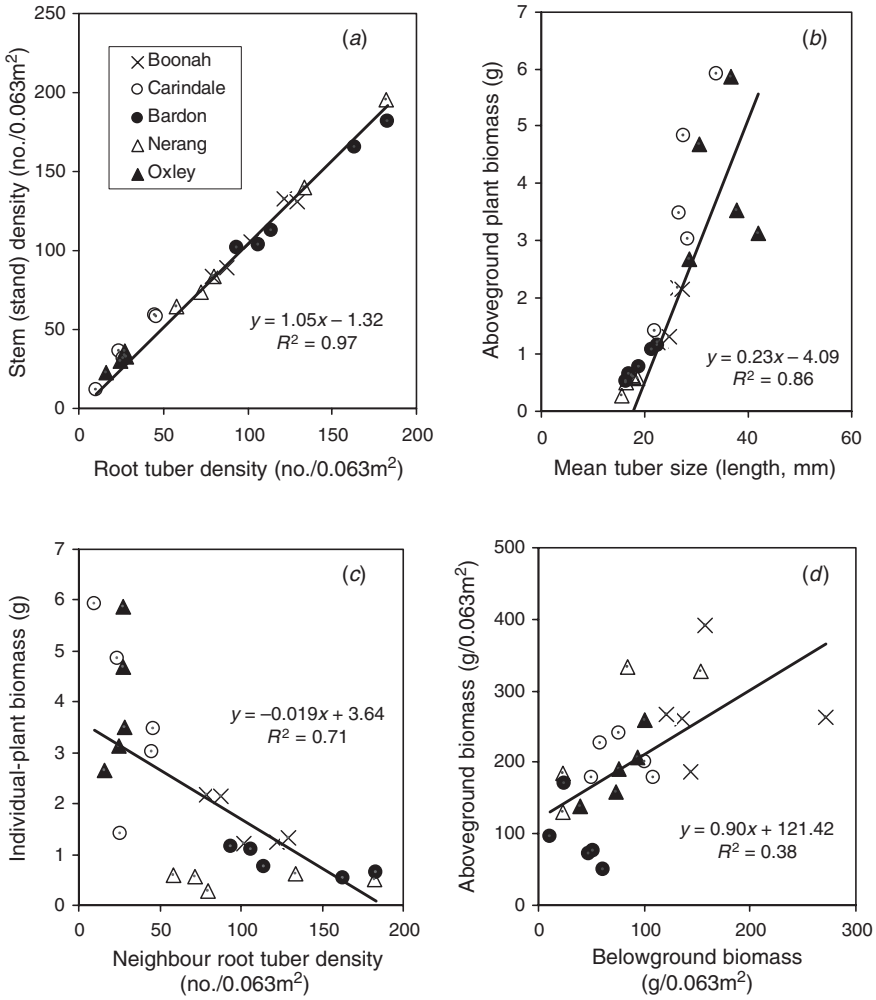

Fig. 3. Patterns of relationships between above- and belowground ecological traits of *Macfadyena unguis-cati.* In all cases $P < 0.01$. Each point represents mean value derived from a sampled area of 25 cm × 25 cm. Only bivariate relationships that show consistent and significant ($P < 0.05$) links at each of the five sites surveyed are drawn. See Table 2 for across-site correlation among all measured traits.

that seedlings observed in the riparian floodplains of Boonah and Nerang are likely to be recruits from a recent seed-dispersal event. This finding is also in agreement with the assertion by Silvertown (2008) that sexual reproduction (genets) should be favoured over clonal (ramets) reproduction in disturbed environments and clones should increase in frequency with the time elapsed since the last disturbance.

The present study found that the roots (including tubers) constitute 17–37% of the dry weight of the total biomass of the samples (Table 1). This is much lower than that documented for underground tubers of other invasive vines, such as *Asparagus asparagoides*, *A. scandens* and *Rumex sagittatus*, which contribute 87–94% of their plant biomass (Raymond 1996; Timmin and Reid 2000). Nonetheless, given the tuber density and volume (~1000 tubers per m^2; Table 1, see also Achilles 2003), *M. unguis-cati* probably also alters the biota of the soil and litter, changing rates of litter decomposition and nutrient cycling. We currently lack data on this, and suggest that it will be interesting to document and compare changes in soil-ecosystem properties, including micro-invertebrate diversity and microbial CO_2 fluxes at sites with and without *M. unguis-cati* infestation.

The general belief is that tubers in *M. unguis-cati* are massive in size and are highly interconnected (see Downey and Turnbull 2007, and references therein). Our findings suggest this may not be all encompassing; close to 90% of the plants excavated had a rather small number of tubers (1 or 2 tubers per plant), with an average length of 2.5 cm (range 0.5–10 cm) and there was a greater number of genets rather than ramets. Whether this is mainly because we sampled away from, rather than underneath, nearby host trees remains to be seen. Time (age) since invasion could also determine the extent of subterranean connections and tuber size; however, we lack data on the history of our investigated sites, and hence cannot explore this line of argument further. Nonetheless, it is noteworthy that one of our five sites, the riparian floodplain in Boonah, shows evidence of extensive (~30%) regeneration via ramets (clonality) (Fig. 2*a*).

In line with the observations of Vivian-Smith and Panetta (2004), 3–21% (depending on sites) of plants, including seedlings, examined exhibited multiple stems (individuals)

(Fig. 2*b*). This suggests (i) the initiation of vegetative/clonal reproduction via tillering and/or (ii) the possible occurrence of facultative apomixy (asexual seed production), although flower bagging and emasculation are required to confirm the latter. Polyploidisation tests on *M. unguis-cati* in its native range have confirmed that this plant has both diploid ($2n = 40$) and tetraploid ($2n = 80$) populations (Gentry 1983; Liogier 1995). The polyploidy trait protects apomicts from the expression of recessive mutations that accumulate in asexual genomes (Archetti 2004; Whitton *et al*. 2008) and could potentially contribute to the runaway invasive success of the vine.

The two varieties of the *M. unguis-cati* appeared to differ significantly in morphometric data. We found that sites that are predominantly dominated by the long-pod variety (Oxley and Carindale) exhibit larger plant parts (including root tubers) and a significantly lower density of tubers (Table 1). They also appear to have a larger proportion of ramets (12–14%) and exhibit higher level of multistem production (22%) than that found at sites dominated by the short-pod variety (3–8%) (Fig. 2). These differences in the proportion of ramets *v.* genets and the level of multiple-stem production will no doubt affect the ecology of the two varieties, including growth and reproductive capacity and plasticity, although there is a dearth of data to substantiate this claim. For example, does clonal fragmentation rather than sexual reproduction (seed input) account for most of the recruitment of new plants into these sites? DNA analyses using dominant inter-simple sequence repeat (ISSR) (also known as microsatellite DNA) and codominant allozyme markers to identify genetic individuals and measure genetic diversity can help to resolve this question.

Conclusions

The study revealed that *M. unguis-cati* vine recruitment is both from seed and vegetative propagation, although the occurrence of a higher frequency of genets rather than ramets in the study plots suggests that reproduction occurs primarily from seeds, not from vegetative propagation as previously thought. For rapid survey and management purposes (e.g. gauging the efficacy of biocontrol efforts), very few significant and consistent links among many of the traits examined were apparent. Ground stem density appeared to be a good predictor of belowground tuber density, but not of its biomass. Also, although to a more limited extent, aboveground individual-plant biomass can provide a reasonably good estimate of its tuber size and neighbouring or surrounding tuber density.

Because of the economic and ecological constraints of chemical and mechanical methods of control, biological control is the more attractive viable option for managing *M. unguis-cati*. Simulated herbivory studies suggest that the vine is susceptible to defoliation (Raghu and Dhileepan 2005; Raghu *et al*. 2006), and hence ongoing biological-control efforts are being focussed on using specialist leaf herbivores (Dhileepan *et al*. 2007*a*, 2007*b*). These specialist leaf-herbivores, through reduction of photosynthetic leaf surfaces and hence assimilates, could be effective in reducing the existing tuber bank (Conrad and Dhileepan 2007), although they may have limited impact on the weed spread or the establishment of new tubers from seed inputs. Hence, future biological-control efforts should equally focus on reducing seed-production by targeting fruit pods or mature seeds by using specialist pod-and seed-feeding insects.

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