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Variation in leaf morphology of the invasive cat's claw creeper *Dolichandra unguis-cati* (Bignoniaceae)

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Abstract. The invasive liana cat's claw creeper *Dolichandra unguis-cati* (L.) L.G. Lohmann (syn. *Macfadyena unguis-cati* (L.) A.H. Gentry) exhibits intraspecific variation in leaf morphology, but this is rarely noted in the published literature. The present study documents variation in leaf morphology in two forms of the species that occur in Australia (long pod and short pod). Leaf morphology is compared between the two forms and the position of the shoots (trunk and ground) at the only two sites in which they co-occur. Leaves were categorised on the basis of leaflet number and the presence or absence of tendrils. Simple leaves were produced mainly on shoots growing along the ground and were more abundant in the short-pod form. Long-pod plants were dominated by bifoliate leaves with tendrils. Cat's claw creeper exhibits considerably wider variation in leaf morphology than recorded previously. Variations in leaf morphology may be linked to differences in the genotype, developmental stage and plastic responses of the plants. Understanding these variations may have implications for taxonomic delimitation and improved management, particularly biological control involving leaf-feeding insects.

Additional keywords: heteroblasty, liana, tendril, weed.

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Introduction

Cat's claw creeper *Dolichandra unguis-cati* (L.) L.G. Lohmann is a liana of neotropical origin in the family Bignoniaceae. It was introduced to Australia as an ornamental plant, and is now regarded in Australia as a significant environmental weed (Batianoff and Butler 2003; Downey and Turnbull 2007). This weed causes considerable damage to native vegetation and man-made structures by growing over them and weighing them down (Raghu *et al.* 2006; Downey and Turnbull 2007). Cat's claw creeper typically invades forested and riparian communities, where its impact is greatest (Downey and Turnbull 2007), and makes these habitats more vulnerable to invasion by other weeds (Floyd 1985; Stockard and Hoyer 1990). Cat's claw creeper also produces extensive ground-covering shoots that inhibit the growth or recruitment of other plants (Downey and Turnbull 2007). The threat that this species poses to the Australian environment has made it the target of much research into biological control (King and Dhileepan 2009; Dhileepan 2012).

Widely known by the synonym *Macfadyena unguis-cati* (L.) A.H. Gentry (Gentry 1973), cat's claw creeper has recently been renamed *Dolichandra unguis-cati* (Hokche *et al.* 2008; Lohmann and Taylor 2013). The species belongs to the tribe Bignonieae, which is characterised by compound leaves, often with leaflets modified into tendrils (Lohmann 2006). The leaf morphology giving rise to the common name 'cat's claw creeper' consists of two leaflets with a three-clawed tendril (Fig. 1). This tendril has been variously interpreted as three separate leaflets (Darwin 1875), as two leaflets on either side of an extended rachis (Sistrunk and Tucker 1974) or as a modification of the terminal leaflet (Lohmann 2006). The hooked tendrils provide the initial anchorage for shoots that grow up vertical surfaces and are later supplemented by aerial roots (Downey and Turnbull 2007). The arrangement of the two unmodified leaflets on either side of the tendril is referred to as bifoliate for the purposes of the present study.

Bifoliate leaves with tendrils are the most commonly documented leaf form of cat's claw creeper, but other leaf



Fig. 1. 'Typical' leaves of cat's claw creeper (*Dolichandra unguis-cati*), consisting of two leaflets and a three-clawed tendril clinging to the support.

types have been observed. Some bifoliate leaves lack tendrils, some have a normal leaflet in place of the tendrils (thus making them trifoliate) or with structures that seem to be intermediate between normal leaflets and tendrils. Also present are simple leaves that do not have tendrils or leaflets. Leaves and leaflets can be of a wide range of shapes and sizes. Different types of leaf have been observed on a single plant, and sometimes at the same node (see also Neubauer 1960).

The variation in leaf morphology within an individual cat's claw creeper plant has been noted previously and attributed to ontogeny, a process termed heteroblasty (Zotz *et al.* 2011). Simple leaves are characteristic of the seedling and juvenile stage that are later replaced by compound leaves with tendrils (Dobbins 1969; Lee and Richards 1991). The first leaves to arise from an axillary bud are frequently simple, even if the main shoot bears compound leaves (Neubauer 1960). Plastic responses to the availability of supporting structures have been suggested as a factor affecting leaf morphology (Gartner 1991; Schweitzer and Larson 1999; Gianoli 2003). In our preliminary field observations, we noted that simple leaves appear mainly on shoots growing horizontally along the ground, rather than those growing vertically on trees. Free-hanging shoots tend to have paired leaflets without tendrils, a trait also observed by Gentry (1983).

Two morphologically different forms of cat's claw creeper have been reported in Queensland (Shortus and Dhileepan 2011). These have been informally called 'long-pod' and 'short-pod', based on differences in the mean length of their fruit, but they can also be distinguished on the basis of flower colour and leaf morphology. Both forms have yellow flowers, with those of the long-pod form being deeper in hue than those of the short-pod form (Dhileepan 2012). The leaves of the long-pod form are usually larger and hairier than those of the short-pod form (Shortus and Dhileepan 2011; Fig. 2). This has given rise to another common name for the long-pod form, namely 'hairy cat's claw creeper' (Navie 2010). Although short microscopic trichomes do occur on the leaves of the short-pod form, their texture and appearance to the naked eye is glabrous (R. Boyne, pers. obs.). The short-pod form is the more common



Fig. 2. A tree trunk covered with the two forms of cat's claw creeper (*Dolichandra unguis-cati*). The larger leaves belong to the long-pod form, whereas the smaller leaves belong to the short-pod form.

of the two forms found in south-east Queensland, and is the one most frequently depicted online and in publications (e.g. Menninger 1970; Sandwith and Hunt 1974; Kleinschmidt and Johnson 1977; Stockard and Hoyer 1990; Lee and Richards 1991; Kleinschmidt *et al.* 1996; Forsyth *et al.* 2000; Downey and Turnbull 2007). Menninger (1970) makes a reference to two forms of this species that differ morphologically, but it is not clear whether these correspond to the long- and short-pod forms.

Cat's claw creeper appears to have variable cytology. There are reports of different chromosome numbers in cat's claw creeper, namely $2n=80$ (Bowden 1940, 1945; Joshi and Hardas 1956; Jullier 1989; Piazzano 1998) and $2n=40$ (Venkatasubban 1945; Simmonds 1954). It is not known at present whether these correspond to the aforementioned morphological forms. A study using haplotype data to trace the origins of Australian cat's claw creepers did not find a corresponding haplotype in the native range for the long-pod form, whereas the majority of the short-pod form in Australia could be traced to a single locality in Paraguay (Sigg *et al.* 2006; Prentis *et al.* 2009). Recent field observations by K. Dhileepan suggest that the long-pod form is widespread in the native range and dominant in Paraguay, Brazil and Argentina.

There are little qualitative or quantitative data concerning leaf variation in cat's claw creeper. The aim of the present study was to document and compare the variation in leaf morphology of cat's claw creeper in south-east Queensland with respect to two morphologically different forms (long and short pod) and positions (trunk and ground) in the field. We discuss the implications of our results on future taxonomic delimitation and improved management, particularly biological control involving leaf-feeding insects.

Materials and methods

Field sites

The short-pod form of cat's claw creeper is the most widespread form, occurring widely in south-east Queensland and northern New South Wales, whereas the long-pod form is known to occur only in seven sites, all of which are in south-east Queensland. Only two sites are known where both forms co-occur (Shortus and Dhileepan 2011). To avoid any site effect, sampling was conducted in the two field sites where both forms were known to co-occur: Oxley (27°60'S, 152°59'E) and Carindale (27°30'S, 152°59'E). The Oxley site was visited between November 2008 and February 2009, and both sites were visited in June 2009. Host trees dominated by only one form of cat's claw creeper were selected for sampling. For each form, five trees from the Carindale site and seven trees from the Oxley site were sampled, making a total of 24 trees.

Leaf sampling

Each infested tree was sampled using two quadrats sized 210 × 297 mm (the size of an A4 sheet of paper). The quadrats were placed vertically on the trunk and horizontally on the adjacent ground, both approximately 1 m from the base of the tree. All leaves within a quadrat were removed (without separating leaflets) and placed into labelled zip-lock bags. Leaves were taken to the Alan Fletcher Research Station or Queensland University of Technology (Brisbane, Qld, Australia), where they were placed into one of the following categories: simple; bifoliate leaves without tendrils; bifoliate

leaves with tendrils; and leaves with more than two leaflets. Simple leaves were distinguished from leaflets of compound leaves by the presence of an axillary bud near the base of the petiole. If tendrils detached from bifoliate leaves while handling, they were still classified as having tendrils.

Five voucher specimens of plants collected from each site have been lodged with the Queensland Herbarium (BRI) with acquisition numbers 862989 (short-pod form) and 822990–862993 (long-pod form).

Leaf data analysis

The percentages of each leaf category were examined with respect to the form of cat's claw creeper (long pod or short pod), the position (trunk or ground) and the sample site (Oxley or Carindale). Data were analysed using SPSS ver. 19.0 (SPSS Inc., Chicago, IL, USA). Non-parametric Mann–Whitney *U*-tests were used to compare the variables between the two forms, positions and sample sites.

Results

Leaf morphology

Leaves, leaflets and tendrils exhibited a range of sizes and shapes, and were predominantly simple (Fig. 3*a–c*) or bifoliate (Fig. 3*d–i*). Leaves with more than two leaflets were diverse in shape and size (Fig. 3*j, k, l*) but, because these were uncommon, they were excluded from subsequent statistical analyses.

Simple leaves, although rare, were recorded mainly from the ground quadrats. Occasionally, simple leaves were observed on

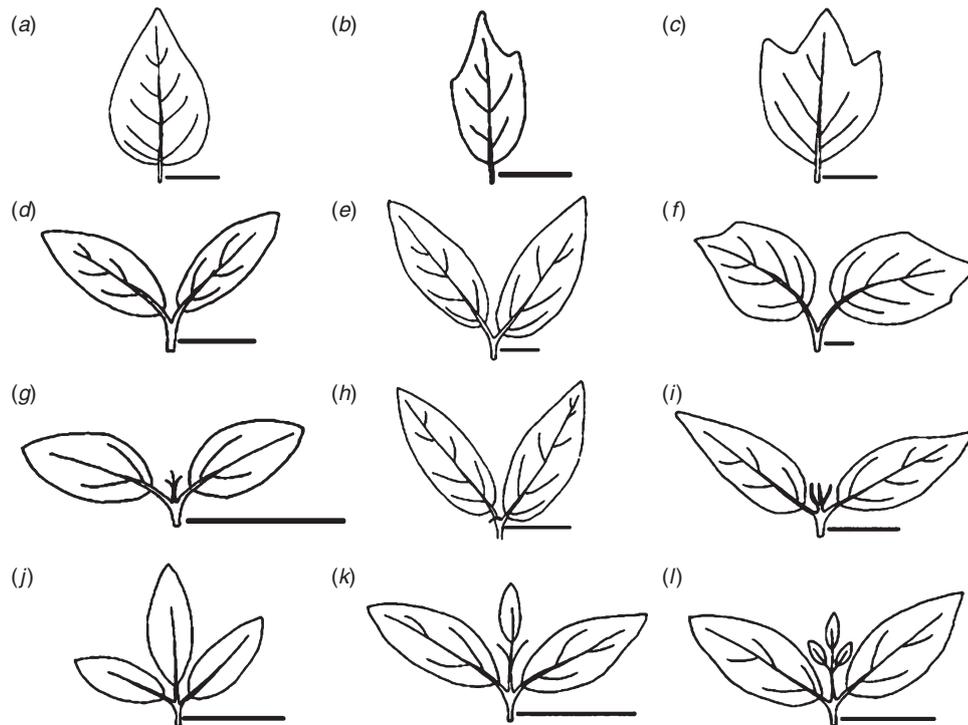


Fig. 3. A selection of different cat's claw creeper (*Dolichandra unguis-cati*) leaf types from different forms and positions. (*a–c*) Simple leaves: short-pod, ground (*a, b*); long-pod, ground (*c*). (*d–f*) Bifoliate leaves with no tendrils: short-pod, trunk (*d*); long-pod, trunk (*e*); long-pod, ground (*f*). (*g–i*) Bifoliate leaves with tendrils: long-pod, trunk (*g, h*); short-pod, trunk (*i*). (*j–l*) Leaves with multiple leaflets: short-pod, trunk (*j*); short-pod, ground (*k, l*), both from the same shoot. Scale bars = 20 mm. All leaves were observed during the field survey in Oxley. Samples in (*b, c, f, i*) were collected from within the quadrats.

Table 1. Percentages of two categories of bifoliate leaves of cat's claw creeper (*Dolichandra unguis-cati*)

Data are the mean \pm s.e.m. All bifoliate leaves are compared between two positions (trunk and ground), two forms (long and short pod) and two field sites (Oxley and Carindale). Long-pod leaves alone are also compared between the field sites

	% With tendrils	% Without tendrils
Position		
Trunk	64.5 \pm 4.7	35.5 \pm 4.7
Ground	52.8 \pm 3.3	47.2 \pm 3.3
Form		
Long pod	64.8 \pm 4.4	35.2 \pm 4.4
Short pod	52.4 \pm 3.8	47.6 \pm 3.8
Site		
Oxley	66.9 \pm 3.9	33.1 \pm 3.9
Carindale	47.8 \pm 3.6	52.2 \pm 3.6
Interactions		
Oxley \times long pod	75.4 \pm 5.8	24.6 \pm 5.8
Carindale \times long pod	50 \pm 2.7	50 \pm 2.7

tree trunks (usually as the first leaf of an axillary shoot), but because they were never found in the study quadrats, they were not sampled or included in the analysed data. Of all the leaves collected from ground quadrats, 38.5% from the short-pod form and 4.3% from the long-pod form were simple, with the remainder being bifoliate. The difference in the percentage of simple leaves between the two forms was significant ($P < 0.001$). There was no significant difference between the field sites.

Within the bifoliate category, leaves with tendrils were more common than leaves without tendrils (Table 1). The Mann–Whitney U -test did not show any significant effect of position ($P = 0.79$) or form ($P = 0.93$). There was a significant site effect for the percentages of each bifoliate category (Table 1), with the Oxley site having significantly more bifoliate leaves with tendrils than the Carindale site ($P = 0.001$). This difference between the sites was most significant when the long-pod form was examined on its own (Table 1; $P = 0.002$). Almost all bifoliate leaves without tendrils had scars in the position where tendrils are normally present.

Discussion

The present study shows that cat's claw creeper displays a wider diversity of leaf morphology than has been reported.

Although simple leaves are associated with the seedling stage of cat's claw creeper (Dobbins 1969; Gentry 1983; Lee and Richards 1991), the present study shows that simple leaves also occur on shoots produced well after the seedling stage and are more commonly found on ground-covering shoots. The leaf morphology of this species appears to be phenotypically plastic with regard to the presence or absence of support. The presence of compound leaves in ground quadrats shows that support is not necessary for the initiation of compound leaves. It is possible that environmental cues affect the timing of different developmental stages, or cause juvenile forms to grow from adult shoots (Lee and Richards 1991). This could be investigated by growing plants from seeds or tubers and recording the sequence of leaf pairs that develop along the shoot under different conditions. The presence of significantly

more simple leaves in the short-pod form than the long-pod form suggests the possibility of genetic variation in the production of different leaf types.

The variation in the size of the tendrils is not coupled with the development of the associated pair of leaflets. Some tendrils were robust and able to provide support while the associated leaflets appeared immature. Other tendrils were filamentous and non-supportive, and the accompanying leaflets were large (Fig. 3*h*). The initiation of tendrils could be a developmental constraint for most leaves, even if the tendrils no longer function and fall off, especially on mature shoots (Downey and Turnbull 2007). This may account for the abscission scars observed on many bifoliate leaves and the absence of tendrils on leaves occurring on free-hanging shoots.

The present study provides further support for the argument that the two forms of cat's claw creepers be regarded as two distinct entities in Australia. It is possible that the long-pod and short-pod forms are only distinct in Australia, or that they represent extremes of a continuum. An examination of herbarium specimens of cat's claw creeper at Kew, Leiden and the Natural History Museum from its native range in the neotropics indicated a much wider variation in leaf forms than that observed in south-east Queensland, which may be related to the greater genetic diversity seen in the native range (Prentis *et al.* 2009). Recent collaboration with researchers in São Paulo, Brazil, suggests that the two forms may be separate species.

The differences in the types and density of hairs can be particularly important for feeding preferences by insects (Kehl and Rambold 2011) or host resistance to herbivory (Sletvold *et al.* 2010). Subsequent research on the establishment, preference and efficacy of potential biological control agents for the control of cat's claw creeper may benefit from incorporating both forms of this weed. It may also be important to consider the effects of environmental conditions on hair density, such as light (Liakoura *et al.* 1997; Dickison 2000).

Conclusion

In summary, cat's claw creeper has highly variable leaf morphology. Some of this may be genotypic (the short- and long-pod forms), and some due to plasticity (the climbing and ground-covering shoots). Ontogeny is an important factor that should be taken into consideration and is worth further investigation. Whether the two forms are truly distinct or whether they represent different ends of a continuous spectrum can only be determined by thoroughly examining the diversity of morphological forms across a wide geographic area in tropical America. Understanding this variation is important for understanding the ecology of this species, and for the development of effective management methods.

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