

SHORT COMMUNICATION

***Oxalis debilis* in China: Distribution of Flower Morphs,
Sterile Pollen and Polyploidy**

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Received: 25 February 2006 Returned for revision: 28 March 2006 Accepted: 12 April 2006 Published electronically: 30 May 2006

• **Background and Aims** *Oxalis debilis* is a South American tristylous species that is currently naturalizing in China. Based on field observations and herbarium data a report is made on its pollination, morph frequencies, pollen viability, seed set and chromosome number. In addition, a new chromosome count for the species in Africa is provided.

• **Methods** Field observations were conducted in six provinces in south-east China. Flower visitors were recorded and nectar sugar was measured with a refractometer. The species' compatibility system was determined by carrying out experimental self- and cross-pollinations on bagged inflorescences. Stigma receptivity and pollen viability was determined using the MTT test.

• **Key Results and Conclusions** Populations of *O. debilis* in China contain either the mid-style-length morph or the short morph, but not both. Pollination is by nectar- and pollen-foraging bees; pollen viability is low; and seed set in natural and experimentally self- or cross-pollinated flowers is extremely low. Chromosome counts indicate that *O. debilis* contains diploid and tetraploid forms in its native as well as introduced range, which does not support a previous hypothesis that the predominant vegetative reproduction in this species is an escape from pentaploidy.

Key words: Introduced species, *Oxalis*, male sterility, pollen viability, chromosome counts, vegetative reproduction.

INTRODUCTION

Oxalis (Oxalidaceae) is a cosmopolitan genus of perhaps 500 species distributed mostly in Africa and South America (Lourteig, 2000). It includes mostly distylous and tristylous species, with tristylous considered the ancestral system, and distylous or homostylous autogamy thought to have evolved from tristylous (Mulcahy, 1964; Ornduff, 1964, 1972; Denton, 1973; Weller and Denton, 1976; Guth and Weller, 1986; Weller, 1992; Barrett, 1993; Marco and Arroyo, 1998). Several bulbous *Oxalis* species are invasive, perhaps in conjunction with being polyploid and reproducing vegetatively (Baker, 1965; Weller and Denton, 1976; de Azkue, 2000; Lourteig, 2000). An unresolved question is whether polyploidy, vegetative reproduction and loss of heterostyly interact in consistent ways, such that invasive species of *Oxalis* would show similar patterns in different regions of the world. Here, data of relevance to this question are presented using *Oxalis debilis* Kunth, the pink woodsorrel, which appears to be spreading in China.

Oxalis debilis is a tristylous species native to South America and is a member of the bulb-forming section *Ionoxalis* (Denton, 1973; Lourteig, 2000). Easily propagated from bulbils, it is an aggressive weed that has achieved worldwide distribution, including Australia, Hawaii, Fiji, New Caledonia, and the Galapagos Islands (Lourteig, 1980, 2000). In Mainland China, it is naturalized in Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Jiangxi, Sichuan, Yunnan and Zhejiang; it also occurs in Taiwan and Hong Kong. The draft account of the Oxalidaceae by L. Xu in the English-language version

of the *Flora of China* (available online at www.eFloras.org) treats the species as *O. corymbosa* DC., but that name is considered a synonym of *O. debilis* by most specialists [*O. debilis* var. *corymbosa* (DC.) Lourteig (1980, 2000); *O. debilis* subspecies *corymbosa* (DC.) O. de Bolòs & J. Vigo (1990)]. The two varieties of *O. debilis*, var. *debilis* and var. *corymbosa*, are thought to differ in having clusters of oxalate crystals arranged along the leaf margin or spaced evenly throughout the lamina, a difference that frequently breaks down (Lourteig, 2000, p. 567). In South America, the varieties' ranges overlap and both set seeds (Lourteig, 2000), although there are no details on levels of seed set. Both varieties are also frequently cultivated as ornamentals and have become naturalized worldwide (Lourteig, 2000). The minute bulbils can persist for several years in soil clinging to farm products. Besides *O. debilis*, China has six other species of *Oxalis*, most of them introduced, namely the European wood sorrel, *O. acetosella* L., the South African *Oxalis bowiei* Aiton ex G. Don, the South African Bermuda buttercup *O. pes-caprae* L., and the tropical American creeping woodsorrel, *O. corniculata* L.

Denton (1973), in her monograph of section *Ionoxalis*, reports that *O. corymbosa* (*O. debilis* var. *corymbosa*) in North America is self-sterile, but provides no details about how this was tested. She also reports that the species is 'homostylous, infrequently tristylous' (Denton, 1973, p. 508) or 'predominant[ly] semi-homostylous' (Denton, 1973, p. 511), but that the flowers do not self-fertilize. In homostylous flowers, the pollen sacs are at the height of the stigmas while, in semi-homostylous flowers, one set of stamens is at the height of the stigmas, the other lies

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above or below the stigmas (Denton, 1973, fig. 2g and h). In normal tristylous species of *Oxalis*, individuals in each population produce three kinds of flowers (called long-styled, mid-styled and short-styled, hereafter simply referred to as longs, mids and shorts, respectively) that either have long styles and two sets of stamens at two levels below the stigma, or short styles and anthers at two levels above the stigma, or mid-length styles and one set of anthers above the stigma, the other below the stigma (Darwin, 1877). Given Denton's finding of predominantly homostylous flowers (physically capable of automatic selfing), yet absence of seeds, and the known genetic self-incompatibility of many *Oxalis* species, she naturally focused on self-incompatibility as the explanation for the lack of sexual reproduction. Studies of other *Oxalis* taxa, however, demonstrate that some species comprise self-incompatible and self-compatible populations (Ornduff, 1964) and that low seed set can have several causes, including scarcity of pollinators and insufficient pollen deposition (Marco and Arroyo, 1998), problems with gametophyte formation or ovule abortion (Guth and Weller, 1986), unviable pollen due to tapetum malfunction (Carniel, 1969), or meiosis problems in the pollen mother cells after polyploidy or aneuploidy (Baker, 1965).

This study reports on the pollination, morph frequencies, pollen viability, seed set and chromosome number of *O. debilis* in southern China. Also the chromosomes in African material were counted to check for pentaploidy which had been reported by Baker (1965) in African *O. debilis*. Initial observations suggested that this species behaves differently in China than in North America, where it has also been introduced but has become homostylous (above). In initial surveys only mids and shorts were found. This raised several questions: (1) Have longs been introduced to China and what is the geographic distribution of mids and shorts? (2) Are populations polymorphic, suggesting sexual reproduction, or monomorphic, suggesting vegetative propagation? (3) Is there any evidence of seed set, whether sexual or agamospermic? (4) Are there normal, functional pollen grains and ovules? (5) Does the invading entity have the same ploidy level as native South American populations?

MATERIALS AND METHODS

Observations and experiments on *Oxalis debilis* L. were carried out between 26 April 2004 and 20 January 2006 in six natural and two cultivated populations that had between 20 and 100 individuals. The populations were located in the South China Botanical Garden (a 300-ha nature reserve, subsequently referred to as SCBG), Shaojiwo Forest Park (Shaojiwo) and Dinghushan Nature Reserve (Dinghushan), all in Guangdong province; the Campus of Fudan University (Fudan) in Shanghai province; the Campus of China Science and Technology University (CSTU) in Hefei in Anhui province; the Kunming Botanical Garden (KMBG) in Yunnan province; the Xinglong Tropical Botanical Garden (Xinglong) in Hainan province; and the Kadoorie Farm and Botanic

Garden (KFBG) in Hong Kong. The distance from SCBG to Shanghai is approx. 1000 km, to Hefei approx. 700 km, to Kunming 900 km, to Xinglong 400 km and to KFBG 100 km. All study populations were monitored for the presence of shorts, mids and longs, and for the timing and duration of flowering. Also herbarium specimens were examined in the IBSC herbarium, one of the largest in China, to check which flower morphs occur in other parts of China. A voucher specimen from the SCBG population (S. Luo 246) has been deposited in the herbarium of Munich.

Flower visitors at peak flowering were recorded at SCBG on 14 May 2004 and 2005 (0800 and 1800 h), 11 May 2004 (0800–1000 h), 3 June 2004 (1100–1300 h) and 4 June 2004 (1200–1600 h), and nectar sugar was measured with a refractometer (Atago, Japan). The species' compatibility system was determined at the same time by carrying out experimental self- and cross-pollinations on inflorescences bagged with fine nylon mesh or with paper bags. Pollen for outcrossing came from plants several metres away and not only may have involved members of the same clone but indeed always involved plants of the same morph (see Results). Inflorescences were re-bagged following treatments, and fruit set was quantified 10 d later. Controls were netted, but not experimentally pollinated. For hand-pollinations, the anthers of excised stamens were rubbed over the stigmas of freshly opened flowers. A test for agamosperous seed set in emasculated and bagged flowers yielded negative results and was therefore not repeated.

To determine stigma receptivity and pollen viability, the MTT (3-4-5 dimethylthiazol-2-yl-2,5-diphenyl-tetrazolium bromide; Sigma M-2128) test as described in Rodriguez-Riano and Dafni (2000) was used. Field-collected pollen was also germinated in a series of increasing sucrose solutions, starting with 10% sucrose and then supplemented with 7, 9, 15 and 30% sucrose (Dafni, 1992). Germination ratios were recorded after 2, 4, 12, 24 and 48 h. To test the method, pollen of *Oxalis corniculata* was germinated, using the same sucrose solutions; *O. corniculata* was observed at the same sites as *O. debilis* and in both years flowered abundantly from March to August. Ovules were studied at high magnification under a stereoscope (Stemi DV4; Zeiss, Germany). Pollen for the different morphs and stamen whorls was counted under the microscope, using flowers of mids collected at SCBG and of shorts collected and preserved in FAA at CSTU. Pollen was also photographed under a scanning electron microscope (JSM-6360LV, JEOL, USA) to assess size and exine differences. The presence of fat-rich pollenkit was checked with the fat stain Sudan III.

RESULTS AND DISCUSSION

Populations of *Oxalis debilis* in south-east China are monomorphic, containing either mids or shorts, but not both (Fig. 1A and B and Table 1): All individuals at SCBG, Shaojiwo and Dinghushan in Guangdong province, Xinglong in Hainan province, and KFBG in Hong Kong

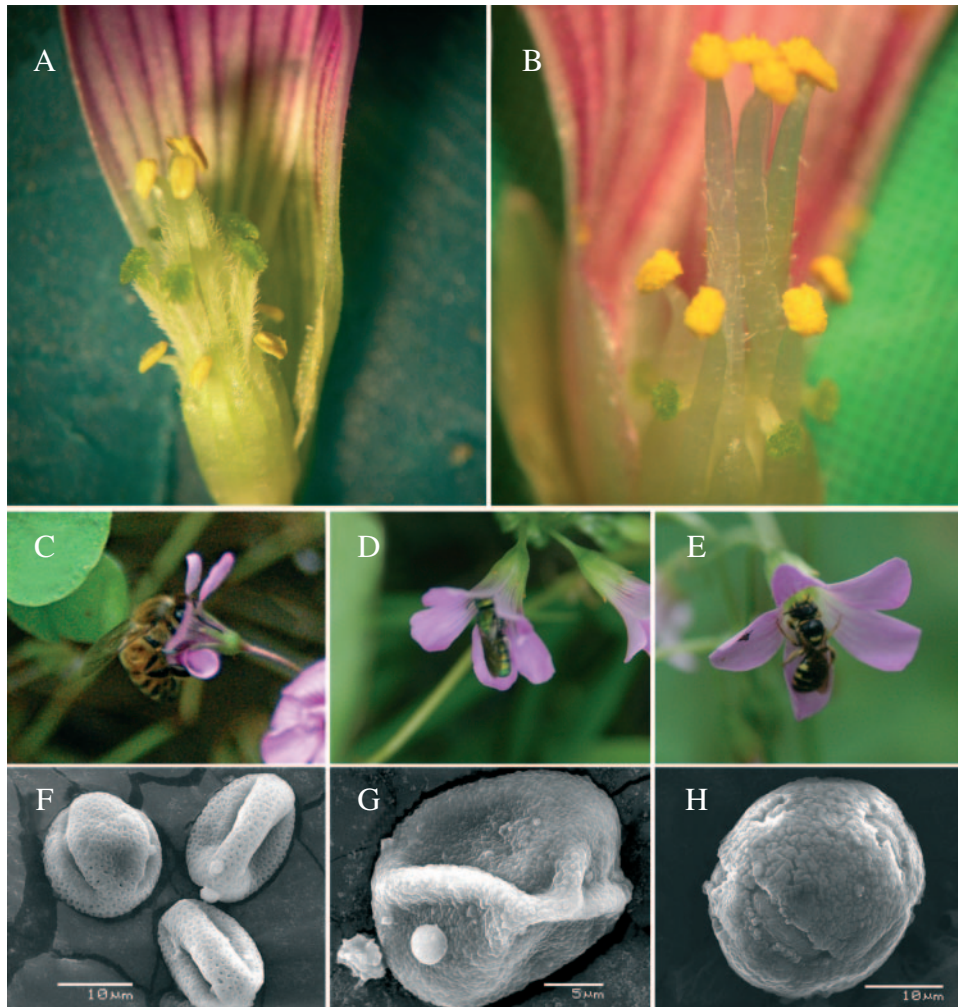


FIG. 1. (A and B) Floral morphs of *Oxalis debilis*: (A) mid-morph with the two sets of stamens, each with just-dehiscent pollen sacs; the five green stigmas are in the middle; (B) short morph, with dehiscent pollen sacs and the five green stigmas below the shorter stamens. (C–E) Flower visitors to *Oxalis debilis*: (C) *Apis cerana*; (D) *Ceratina (Pithitis) smaragdula*; (E) a species of *Ceratina*. (F–H) Scanning electron micrographs of *O. debilis* pollen: (F) one normal and two flattened pollen grains of the short morph; (G) a flattened pollen grain of the mid-morph; (H) a normal pollen grain of the mid-morph.

TABLE 1. *Floral morphs of Oxalis debilis in seven populations in China*

Study sites	Date	Longs	Mids	Shorts
SCBG	26 April 2004	0	402	0
Shaojiwo	30 April 2004	0	100	0
Dinghushan	16 May 2005	0	70	0
Fudan	21 July 2004	0	0	100
CSTU	24 July 2004	0	0	100
KMBG	10 August 2004	0	100	0
Xinglong	28 April 2005	0	50	0
KFBG	20 January 2006	0	20	0

The South China Botanical Garden (SCBG), Shaojiwo Forest Park (Shaojiwo) and Dinghushan Nature Reserve (Dinghushan) are in Guangdong province; the Campus of Fudan University (Fudan) is in Shanghai; the Campus of China Science and Technology University (CSTU) is in Hefei in Anhui province; the Kunming Botanical Garden (KMBG) is in Yunnan province, and the Xinglong Tropical Botanical Garden (Xinglong) is in Hainan province, and the Kadoorie Farm and Botanic Garden (KFBG) is in Hong Kong.

were mids, while all individuals in the populations on the campuses of Fudan University in Shanghai province and CST University in Anhui province were shorts. This fit with the pattern seen in the herbarium: all specimens from south of the Changjiang River were mids ($n = 63$), while all specimens from north of the Changjiang River were shorts ($n = 16$). The Chinese populations are thus neither homostylous (having pollen sacs at the height of the stigmas) like the North America ones (Denton, 1973) nor tristylous like the South American native populations (Lourteig, 1983). Instead, mids and shorts seem to have established and spread vegetatively over large areas, probably from different original introductions.

Each plant produced three to five inflorescences that opened one to three flowers per inflorescence per day ($n = 20$, SCBG site). Flowers opened between 0800 and 0900 h, anthers dehiscent around noon, petals closed between 1800 and 1900 h and reopened the next morning. Stigmas of open flowers were receptive, while those of

buds and withered flowers were unreceptive. Shorts and mids did not differ in the size of their stigma papillae, and the carpels of both contained normal looking ovules [39.5 ± 3.2 s.d. in the carpels of mids ($n = 10$, SCBG) and 37.8 ± 3.9 s.d. in the carpels of shorts ($n = 10$, CSTU)]. Single flowers lasted for 2–3 d ($n = 10$), inflorescences for 11–15 d ($n = 20$), and flowering/plant for about 1 month. Flowers of both morphs secreted nectar throughout anthesis, with the secretion rate of mids peaking between 1200 and 1400 h (that of shorts was not monitored). Nectar sugar concentration was 30–45 %.

Pollination in the present study populations was by hymenoptera. Flowers of shorts on the campuses of Fudan University and CST University were visited by *Apis cerana* (Fig. 1C) foraging for nectar. Flowers of mids at the remaining study sites were visited by *Ceratina* (*Pithitis*) *smaragdula* (Fig. 1D) and an unidentified species of *Ceratina* (Fig. 1E). Visits lasted a few seconds per flower, and bees typically departed after visiting two or three flowers. During 12 h of observation spread out over 4 d throughout the flowering period, 22 bee visits were seen to mids, occurring at a seemingly steady rate (four on 11 May 2004, six on 3 June 2004, eight on 4 June 2004 and four on 23 August 2005). *Ceratina smaragdula* could not reach the nectar with its proboscis and was mainly collecting pollen; staining with Sudan III confirmed that the pollen grains of mids were coated with fat-rich pollenkitt. In North America, *Ceratina* also are important pollinators of *Oxalis*; for example, in Illinois, *C. dupla dupla* pollinates *O. stricta*, *O. corniculata* and *O. violacea* (Robertson, 1929; Hilty, 2005). Based on these observations, a scarcity of pollinators is unlikely to present a problem for the spread of *O. debilis* in China.

Most pollen grains were misshaped (Fig. 1G and Table 2); thus, in mid-styled individuals ($n = 5$), only 11 of 1313 grains from the five upper anthers were normal (Fig. 1F and H). In the lower anthers of these flowers, that ratio was 12 out of 1383. In short-styled plants ($n = 5$), 13 out of 1363 pollen grains from the five upper anthers were normal, and 18 out of 1677 from the lower anthers. As expected in a tristylous species, normal grains of mids were slightly larger than normal grains of shorts (compare F and H in Fig. 1; $28.7 \pm 1.8 \mu\text{m}$ long \times $26.5 \pm 1.7 \mu\text{m}$ wide versus $17.6 \pm 0.6 \mu\text{m}$ long \times $13.7 \pm 2.2 \mu\text{m}$ wide; $n = 5$ for each pollen type), and their exine ornamentation also differed (compare F vs. G and H in Fig. 1).

In spite of abundant application of pollen grains on receptive stigmas, none of the experimentally self- or cross-pollinated flowers set seed (Table 3; note that it is not known whether cross pollinations involved genetically distinct plants, and that crosses involved plants of the same morph), and the *in-vitro* tests showed that pollen germination rates in most study populations were extremely low (Table 4); no pollen from mids germinated and only a few short pollen tubes emerged from shorts. This was in sharp contrast to *O. corniculata*, the populations of which consisted of semi-homostylous individuals (except for one long-styled population in Yunnan; S.L., personal observation). This species had a pollen germination rate of 71.6 % (Table 4), fitting with an

TABLE 2. Number and percentage of normally developed pollen grains in *O. debilis* ($n = 5$ plants per morph)

	Mids		Shorts	
	Upper anthers (5)	Lower anthers (5)	Upper anthers (5)	Lower anthers (5)
Pollen/anther	262.6 ± 46.0	276.6 ± 204.9	272 ± 98.6	335 ± 183.6
Normal	2.2 ± 1.5	2.4 ± 1.8	2.6 ± 3.2	3 ± 4.1
pollen/anther (%)	(0.86 ± 0.59)	(1.1 ± 1.27)	(0.82 ± 1.08)	(0.56 ± 0.77)

Values given are mean \pm s.d.

TABLE 3. Fruit set of *Oxalis debilis* at the SCBG study site in Guangdong province, China

Treatment	Date	Flowers	Fruit set (%)	Fruit set (%)
Natural pollination	26 April–10 May 2004	106	0	0
Insects excluded (netted)	26 April–10 May 2004	68	0	0
Wind excluded (bagged)	26 April–10 May 2004	87	0	0
Hand self-pollination	a.m. on 11 May 2004	16	0	0
Hand cross-pollination	p.m. on 10 May 2004	17	0	0
Hand cross-pollination	a.m. on 11 May 2004	12	0	0
Hand cross-pollination	p.m. on 11 May 2004	12	0	0

Cross-pollinations involved plants of the same morph and probably even the same clone (see Results).

TABLE 4. Pollen germination in *Oxalis debilis*, using *Oxalis corniculata* as a reference

Time after anther dehiscence (h)	<i>Oxalis debilis</i> var. <i>corymbosa</i>			<i>O. corniculata</i>	
	SCBG mids (%)	Shaojiwo mids (%)	Fudan shorts (%)	CSTU shorts (%)	SCBG (%) \pm s.d.
2	0	0	0	0	71.6 ± 1.6
4	0	0	0	5	62.8 ± 1.2
12	0	0	0	2	50 ± 3.3
24	0	0	0	0	25 ± 2.9
48	0	0	0	0	5 ± 2.8

Field-collected pollen was germinated in 10 % sucrose, supplemented with 7, 9, 15 and 30 % sucrose (see Materials and methods).

abundant seed set. This species thus has lost the self-incompatibility that normally characterizes the genus. In *O. debilis*, the lack of seed set we cannot be attributed to either self-incompatibility or sterile pollen because it was not possible to carry out legitimate crosses (because populations were strictly monomorphic). There was also no evidence of agamospermic seed set in netted or bagged flowers (Table 3; although flowers were not emasculated, automatic selfing is precluded by the physical separation of stigmas and anthers; five emasculated flowers also produced no fruits, cf. Materials and methods).

Pollen sterility levels of 20–30 % have been reported from some genotypes of *O. tuberosa*, which was attributed to the species possibly being autoallopolyploid and having

meiosis problems [Gibbs, 1976; Gibbs *et al.*, 1978; Trognitz und Hermann, 2001; Emshwiller and Doyle (2002) concluded that the species is allopolyploid and probably autoallopolyploid]. Meiosis problems have also been assumed for *O. corymbosa* (*O. debilis*) from Ghana, West Africa, with a chromosome count of $2n = 35$ (Baker, 1965), leading Baker to conclude that 'Plants of *Oxalis corymbosa* never form seed for, not only are they pentaploid, but they represent only the short-styled form in a genus where tristily with very strong self-incompatibility is characteristic'. Baker's count, however, is highly unusual in *Oxalis* (de Azkue, 2000), and a new count of material obtained from Tanzania (voucher H. Schaefer 05/314, M) yielded a sporophytic number of $2n = 28$. However, many species of *Oxalis* have extremely small and aggregated chromosomes (de Azkue, 2000), making counts very difficult. In Argentina, *O. debilis* var. *corymbosa* is diploid, with a sporophytic number of $2n = 14$ and a gametophytic number of $n = 7$ (Naranjo *et al.*, 1982), while *O. debilis* var. *debilis* is tetraploid, with $2n = 28$ (de Azkue, 2000). In Himalayan India, the sporophytic number of *O. corymbosa* (*O. debilis*) is $2n = 28$ (Roy *et al.*, 1988), and material from Shanghai has a sporophytic number of $2n = 14$ (Xu *et al.*, 1992). Plants from the SCBG population in Guangdong province gave sporophytic counts of $2n = 28$ ($n = 12$ mitotic cells; photographs available upon request). Populations from the Eastern Himalayas and Darjeeling have been reported to have $n = 15$, with 'meiosis normal', $n = 11$, with 'univalents and multivalents, such as trivalents and tetravalents, [∞] also frequently observed in diakinesis', and $n = 14$, with 'meiosis regular' (Chatterjee and Shamara, 1970). There is no count for North American *O. debilis*.

Based on these counts, *O. debilis* comprise diploid, tetraploid and aneuploid forms in its native range as well as where it has been introduced. The base chromosome number in section *Ionoxalis* is thought to be $x = 7$ (Weller and Denton, 1976; de Azkue, 2000), and the Chinese material, with $2n = 28$, may thus be tetraploid.

The only report on the sexual system of *O. debilis* in its native range appears based on herbarium material and states that southern Brazilian populations contain mostly longs and mids, while shorts are extremely rare (Lourteig, 1983). North American populations are mostly homostylous and set no seed (Denton, 1973; see Introduction); West African populations contain only shorts and set no seed (Baker, 1965); and East African populations contain only mids and also set no seeds (Kabuye, 1971). In Taiwan, most plants (in three populations; Wu *et al.*, 1978) are mids and have yellow anthers and pollen, just as was found in Mainland China (see Fig. 1), which Wu *et al.* (1978) judged to be fertile, based on staining with iodine blue, perhaps not a reliable test (Rodriguez-Riaño and Dafni, 2000). A few of their plants, however, had flowers with white anthers (a character which has never been seen in the plants in the present study), five positioned above the stigmas, the remaining five at the same height as the stigmas, just as in semi-homostylous North American plants (Denton, 1973, p. 511). Pollen from these flowers

did not stain with iodine and was judged unviable (Wu *et al.*, 1978).

The present data, together with the previous studies, confirm the assessment by Baker (1965) that *Oxalis debilis* is conquering the world vegetatively. Vegetative propagation in the Chinese plants, however, does not appear to be an escape from meiosis problems due to pentaploidy as Baker hypothesized for his Ghana populations. Rather, *O. debilis* in China appears to have the same ploidy level as presumably sexual populations karyotyped in Argentina. It was not possible to detect evidence of a possible rejection of self- and same-morph pollen on stigmas because of the extremely low or absent pollen viability in all populations studied. Apparently, prolonged and exclusive reliance on vegetative reproduction has permitted the fixation of male sterility mutations, a process that appears less far along in Taiwan, where mids may still have fertile pollen (Wu *et al.*, 1978). It would be interesting to know whether continued clonal reproduction in invaded areas of North America, Africa and Europe always leads to the spread of male sterility in bulbous *Oxalis*, irrespective of ploidy level, and whether pollen fertility and seed set are ever regained.

To answer the questions raised at the outset of this study, it appears that no long-styled plants have yet been introduced to China, mid-styled plants dominate south of the Changjiang River, shorts north of that river, populations are monomorphic and reproduce vegetatively, seed set is absent, pollen grains are largely sterile, and the invading entity has the same ploidy level as native South American populations, rather than being pentaploid.

ACKNOWLEDGEMENTS

We thank R. Zhang and X. Deng for assistance in the field and S. Li for scanning electron micrographs of the pollen; H. Schäfer for Tanzanian material of *O. debilis*, J. Zoller and M. Vosyka, Department of Biology, University of Munich, for chromosome counts; H. Weiss-Schneeweiss, Department of Systematic and Evolutionary Biology, University of Vienna, and S. Weller, Department of Ecology and Evolutionary Biology University of California, Irvine, for comments on the *O. debilis* karyotype; C. Heibl for comments on the manuscript and Eve Emshwiller for her review. Financial support came from the National Natural Science Foundation of China (30570314, 40332021) and the Natural Science Foundation of Guangdong Province (04002308).

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