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Floral morphs, pollen viability, and ploidy level of *Oxalis corymbosa* DC. in Taiwan

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ABSTRACT. *Oxalis corymbosa*, an exotic species in Taiwan, is a tristylous plant, *i.e.*, with long- (LS), mid- (MS) and short-styled (SS) floral morphs, producing capsules in its native habitat. However, in Taiwan, this species was never observed producing fruits, and it reproduces vegetatively. In this study we investigated floral morphs, observed fruit and seed production of 23 populations, assessed pollen viability, and analyzed the ploidy level of some populations of *O. corymbosa*, in an effort to understand the factors limiting sexual reproduction of this species in Taiwan. No fruit or seed production were observed in any population. The study of morph proportions revealed that ratios of SS, MS, and semi-homostylous (SHS) individuals varied among the populations, and LS individuals appeared to be absent in this region. Furthermore, two types of anthers were observed, yellow anthers with pollen grains and white anthers without pollen grains. In each population, individuals with MS morph and bearing yellow anthers were dominant. SS and SHS individuals were less frequent than MS morph and almost always bore white and male-sterile anthers. The result of fluorochromatic reaction essay revealed that these populations had very low pollen viability (< 4%). Flow cytometry analysis of cell nuclei suggested that individuals with MS and SS floral morph had same ploidy level. These results indicate that absence of LS floral morphs, the unequal proportion of floral morphs, low pollen viability, and the presence of male sterile morphs may all contribute to the absence of sexual reproduction of *O. corymbosa* in Taiwan.

Keywords: Flow cytometry; Heterostyle; Male-sterile; *Oxalis corymbosa*; Sexual reproduction.

INTRODUCTION

Hermaphrodite plants in a population displaying floral morphs with reciprocal differences in style and anther height are called heterostylous (Darwin, 1877). A heterostylous species bears two (distyly) or three (tristyly) floral morphs generally growing in the same population (Barrett, 1992). In distylous plants, a high stigma position is combined with a low anther position in long-styled morphs while short-styled morphs combine a low stigma position with a high anther position. In tristylous species, a stigma and two sets of stamens occupy three levels inside the flower (Darwin, 1877). In short-style morphs (SS), stigmas are located in the lowest position of the flower with the two sets of stamens above the stigmas. In mid-style morphs (MS), the stigmas are located in the middle position between the two whorls of anthers. In long-style morphs (LS), stigmas are located in the highest, with two sets of stamens occupying the middle and lower positions. The floral morphs are genetically controlled (Ganders, 1979). Distyly is found in at least 25 angiosperm families (Lloyd and Webb, 1992), while tristyly is much less common and is reported in only six flowering families, i.e., Oxalidaceae, Lythraceae, Pontederiaceae, Amaryllidaceae, Connaraceae, and Linaceae (Barrett, 1993; Thompson et al., 1996; Barrett et al., 1997).

Heterostylous plants generally combine a strong self- and morph-incompatibility system, and successful pollination (or legitimate pollination) only occurs between anthers and stigmas located at the same level in the flower (Darwin, 1865). Hence, heterostyly is thought to be a modification in the flower morphology and functioning suited to promote outcrossing (Darwin, 1877; Kohn and Barrett, 1992; Lloyd and Webb, 1992). It has been suggested that one of the forces driving the evolution of this morphological adaptation is the avoidance of self-interference between stigmas and anthers within the flowers and the enhancement of accurate pollen transfer between morphs (Lloyd and Webb, 1992). Due to strong self- and morph-incompatibility systems, each floral morph is usually incapable of producing seed after self-pollination and consequently can avoid the deleterious results of self-fertilization (Barrett, 1992; Darwin, 1900). However, species having such breeding systems might not be able to achieve legitimate pollination when introduced into new areas due to the lack or scarcity of compatible

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floral morphs (Barrett and Forno, 1982; Ater, 2005; Castro et al., 2007; Lou et al., 2006).

Oxalis corymbosa DC. (section *Ionoxalis*, Oxalidaceae), a species native to South America (Lourteig, 1980), was introduced into Taiwan as an ornamental plant (Wu et al., 2004). This species belongs to a tristylous genus with strong self-incompatibility and has been reported to have sexual reproduction and to produce capsules in its native environment (Barker, 1965; Lourteig, 1980). In Taiwan, *O. corymbosa* has never been observed to produce fruits, and it reproduces vegetatively by bulbils (Huang and Liu, 1993). The bulbils persist in the soil for many years and are easily dispersed by anthropogenic activities, namely by moving soils for cultivation (Wu et al., 1978). As in Taiwan, this species as been described as reproducing only asexually in other areas in which it has been introduced, like North America, Europe (Denton, 1973; Lourteig, 1980), China (Lou et al., 2006), and Malaysia (Veldkamp, 1971).

Several factors have been suggested for the lack of or low seed production in *Oxalis*, and these include unequal proportions or the absence of reciprocal floral morphs (Barker, 1965; Denton, 1973; Castro et al., 2007), geographical separation between reciprocal floral morphs (Lou et al., 2006), scarcity of pollinators (Marco and Arroyo, 1998), ovule abortion (Guth and Weller, 1986), unviable pollen (Carniel, 1969), and meiotic problems due to polyploidy, odd ploidies, or aneuploidy (Baker, 1965; Castro et al., 2007). For example, in the Mediterranean region, populations of *O. pes-caprae* have long- and short-styled morphs, but the different floral morphs rarely grow in mixed populations and have different ploidies being unable to produce viable offspring (Castro et al., 2007). Previous studies developed in three populations of *O. corymbosa* in a close geographic range in Taiwan revealed that most of the populations were composed by the mid-styled morph (Wu et al., 1978). Additionally, *O. corymbosa* has also been reported with various chromosome numbers, $2n = 14$ (Naranjo et al., 1982; Xu et al., 1992), 28 (Roy et al., 1988; Luo et al., 2006), 35 (Barker, 1965), corresponding to different ploidy levels, i.e., 2x, 4x and 5x, respectively. In light of these observations, it was our objective to understand the factors limiting sexual reproduction of *O. corymbosa* in the exotic range across Taiwan. For this, we expanded the survey and performed a large-scale study across Taiwan in order to (1) investigate the composition and distribution of floral morphs, (2) measure the pollen viability, and (3) assess the ploidy level of wild populations of *O. corymbosa*. Fruit and seed production were also assessed.

MATERIALS AND METHODS

Oxalis corymbosa is a tristylic perennial herb with a tap-root and numerous bulbils. The flower is composed of five sepals, five petals (of a rose-purple color), ten statements in two rounds, and one round of five stigmas displayed in reciprocal heights (i.e., short-styled, SS, mid-styled, MS and long-styled morphs, LS; Figure 2). Furthermore, a semi-homostylous morph (SHS) with a long whorl of anthers and a short whorl of anthers and stigmas coinciding in height (Figure 2C) was also described in Taiwan (Wu et al., 1978). In Taiwan, it generally flowers in late winter to spring. Twenty-three natural populations of *O. corymbosa* in Taiwan were investigated between December 2005 and March 2007. Populations grow in disturbed places such as cultivated ground, roadsides, wasteland, parks and schools. We divided the administrative districts of Taiwan into four regions (northern, central, southern, and eastern regions), and all the populations were randomly selected including twelve populations (no. 1-12) from the northern region (Taipei, and Yilan), four populations (no. 13-16) from the central region (Chiayi), three populations (no. 17-19) from the southern region (Tainan, Kaohsiung, and Pintung), and four populations (no. 20-23) from the eastern region (Hualien, and Taitung) (Figure 1).

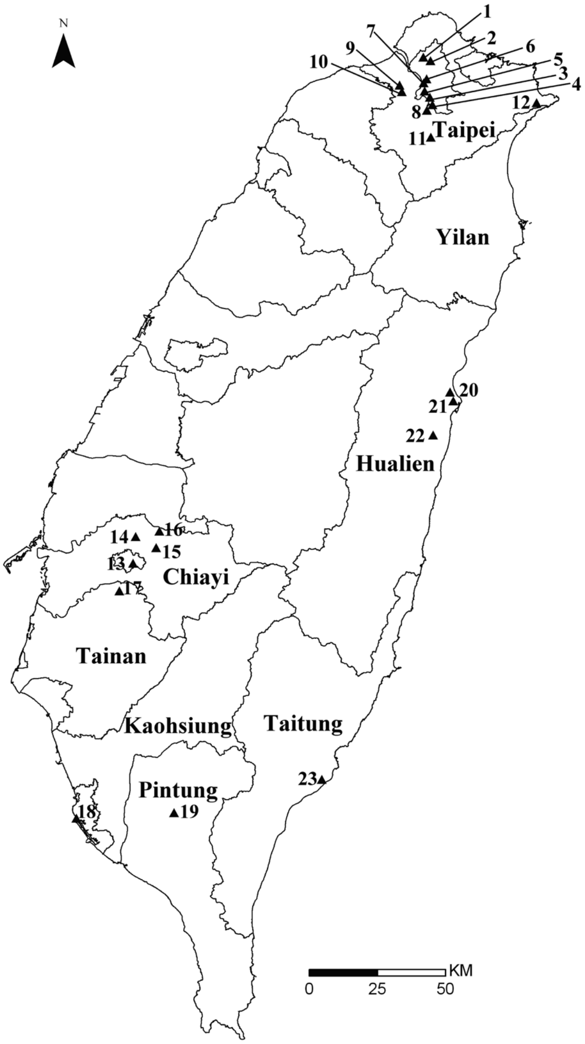

Figure 1. Map of Taiwan showing location of 23 populations of *O. corymbosa* investigated in this study.

In each population, 9-193 individuals were selected randomly and their floral morphs and fruit and seed production were recorded. In a preliminary survey, we found some *O. corymbosa* plants with flowers bearing white anthers (Tsai and Kao, personal observation), and thus, during the survey, this character was also recorded.

Anthers from flowers with different floral morphs were collected to assess pollen viability. We randomly collected 10, 3, 3, and 6 mid-styled individuals from Taipei (population 3), Chiayi (population 13), Kaohsiung (population 18), and Taitung (population 23), respectively, and 7 short-styled individuals from Taipei (population 3) for the analysis (Table 1). As *O. corniculata*, the native congener of *O. corymbosa*, reproduces sexually with success in Taiwan (Huang and Liu, 1993), we examined the pollen viability of *O. corniculata* to provide a male-fertility standard. The fluorochromatic reaction (FCR) was used to determine the vigor of pollen grains (Heslop-Harrison and Heslop-Harrison, 1970; Nepi et al., 2005). Pollen grains, from five mature anthers of an individual, were released into a microslide with a drop of FDA (flurescein diacetate)-sucrose mixture and observed under a fluorescence microscope (Leitz Diaplan, filter wavelength = 459-490 nm) at 200x magnification. Pollen grains showing bright fluorescence under the microscope were denoted as active. The percentage of active pollen (pollen viability) was then calculated as the number of pollen grains with bright fluorescence divided by the total pollen grains observed. Due to varied pollen grain numbers (0-398 pollen grains) in each individual of *O. corymbosa*, we counted all the pollen grains of each microslide.

The DNA ploidy level of MS and SS individuals was assessed using flow cytometry. All individuals were collected from Taipei (population 3) and had three replications. Due to the rarity of SHS morph, no individuals were found during the experiment, and thus we were not able to analyze this floral morph. The fresh young leaves of each plant were chopped in G-buffer (containing 45 mM $MgCl_2 \cdot 6H_2O$, 30 mM Sodium citrate, 20 mM MOPS [3-(N-morpholine)-propanesulfonate], 1% Triton-X 100 and 0.5% β-mercaptoenthanol; pH= 7.0) to release the nuclei and were then filtered by a 30 μm nylon filter. The nuclear suspensions were stained with propidium iodide (PI, 50 μg/ mL), a fluorescent dye, containing RNase in an ice-bath. Samples were then analyzed with a hemacytometer (EPICS Elite ESP Flow Cytometer, Beckman Coulter Inc., USA) with an argon Laser set at 488 nm excitation. The PI fluorescence was collected in a 600-640 nm emission by a PMT4 (photomultiple tube). In each sample at least 6,000 nuclei were analyzed. The WinMDI v.2.8 free software was used to estimate the DNA peak mean using the chicken erythrocyte nuclei (CEN) solution as a standard, with DNA index (= peak mean of sample / peak mean of standard). The analysis was conducted at the Plant Cell Biology Center, Institute of Plant and Microbial Biology, Academia Sinica, Taipei, Taiwan.

One-way ANOVA was used to analyze differences in floral morph and pollen viability among *O. corymbosa* populations. Afterwards, the data was analyzed by Duncan's new multiple range test (SAS Software V8.1, USA). The significant difference was defined as $P < 0.05$.

RESULTS

In the 23 populations of *O. corymbosa* from the areas studied, no fruit or seed production was observed in any population.

In the studied area two floral morphs were observed: MS and SS morphs (Figure 2A and B, respectively). In addition to MS and SS morphs, individuals bearing flowers with a semi-homostylous morphology (SHS) (Figure 2C) were also found in the survey. These flowers had stigmas at the same height as the lower whorl of stamens (Figure 2C). No LS individuals were observed. The proportion of morph for the 23 populations is presented in Figure 3. *Oxalis corymbosa* populations were polymorphic, with each population containing at least two floral morphs. Of the 23 populations investigated, all had MS morphs, 21 had SHS morphs, and 16 had SS morphs. MS morph is always the dominant form.

Both yellow and white anthers were observed within all floral morphs found in Taiwan, despite the fact that they were present in variable proportions (Figure 3). In

Table 1. Percentage of viable pollen of upper and lower stamen in mid- (MS) and short-styled (SS) floral morphs of *Oxalis corymbosa* populations and of homostylic (Homo) *O. corniculata* in Taiwan.

Species	Population no.	Morph (replicates)	Upper stamen	Lower stamen	Average
O. corymbosa	3	SS (7)	0.88 ±0.01^{aB}	0.95 ±0.01^{aB}	0.91 ±0.01^{B}
	3	MS (10)	4.32 ±0.02^{aB}	5.12 ±0.02^{aB}	4.72 ±0.02^{B}
	13	MS (3)	1.29 ±0.00^{aB}	5.61 ±0.03^{aB}	3.45 ±0.01^{B}
	18	MS (3)	6.98 ±0.03^{aB}	3.69 ±0.01^{aB}	5.33 ±0.01^{B}
	23	MS (6)	3.51 ±0.02^{aB}	1.78 ±0.01^{aB}	4.26 ±0.02^{B}
O. corniculata	3	Homo (3)	64.04 ±0.05^{aA}	45.83 ±0.09^{aA}	54.93 ±0.07^{A}

*Values, mean (%) ± s.e., different capital superscripts reveal significant differences within anther level (column) at P = 0.05; different lower-case superscripts reveal significant differences within floral morph (row) at P = 0.05.

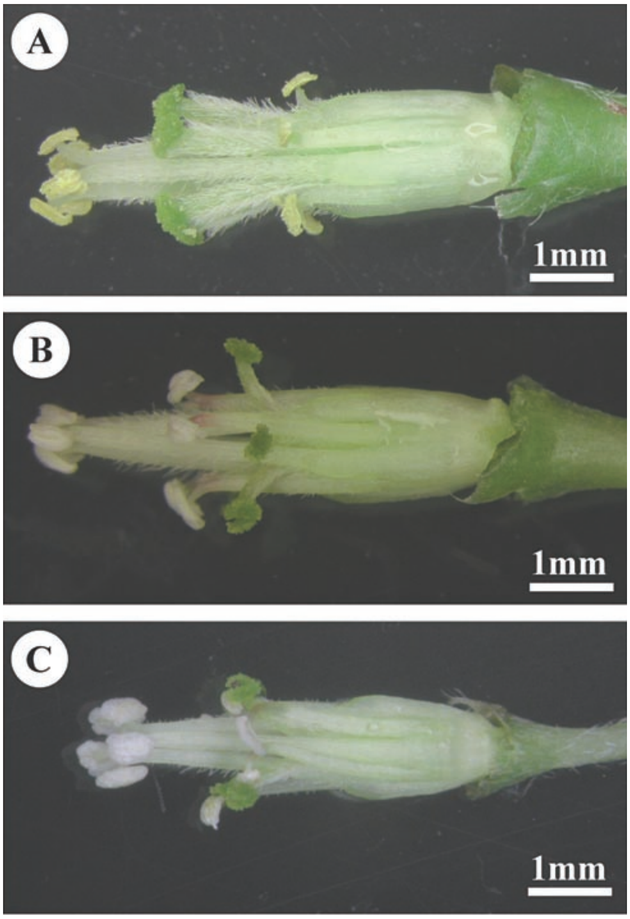

Figure 2. Pictures of flowers, with petals and sepals removed, of a mid-styled floral morph with yellow anther (A), a short-styled floral morph with white anther (B) and a semi-homostylous floral morph with white anther (C) of *O. corymbosa* found in Taiwan.

MS morph, the percentage of individuals with yellow anthers significantly exceeded that of those with white anthers, except in population 14. In contrast, SS and SHS morphs bore only white anthers, with the exception of the populations 3, 9 and 23. Thus, among the 16 populations containing SS morph, 14 bore only white anthers while those in the remaining two populations (3 and 23) had both individuals with yellow and individuals with white anthers. Among the 21 populations containing SHS morphs, 18 bore only white anthers while those in populations 3, 9 and 23 had both individuals with yellow and those with white anthers.

Further observations of the anthers revealed that white anthers did not produce pollen, indicating the complete male sterility of the flowers that bore them. Accordingly, most of individuals with SS morphs or SHS morphs had male sterile flowers. The percentage of viable pollen in yellow anthers from MS and SS morphs of flowers is presented in Table 1. In general, pollen viability was very low for all anther levels and floral morphs. No significant difference was found in the pollen viability between pollen grains from the two sets of anthers. Flowers with MS morph sampled from the four regions had similar pollen viability ranging from 2 to 7%. The percentage of active pollen from the SS morph flower sampled from Taipei in northern Taiwan was even lower (ca. 1%; Table 1). *Oxalis corniculata*, the standard of male-fertile species, had about 55% of active pollen, revealing that the staining technique was working.

Histograms produced by flow cytometric analysis revealed that the DNA ploidy level (given as DNA index) was the same among all the morphs and populations analyzed (Figure 4; Table 2). No significant differences

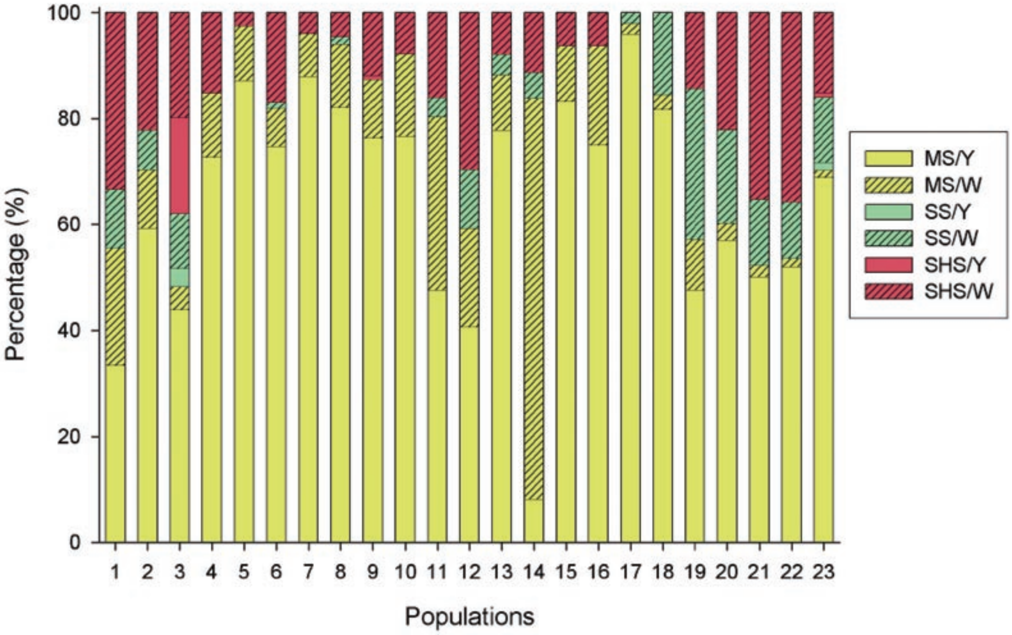

Figure 3. Percentage of individuals carrying mid- (MS), short- (SS) and semi-homo stylous (SHS) floral morph with yellow (Y) or white sterile (W) anther in the 23 populations of *O. corymbosa* in Taiwan.

were observed between the nuclear DNA index of *O. corymbosa* SS and MS individuals, nor between flowers of the same morph with yellow or white anthers (Table 2).

DISCUSSION

This is the first report on the composition and distribution of the floral morphs of *O. corymbosa* in the invasive area of Taiwan. In this survey, flowers of *O. corymbosa* with MS, SS or SHS morphs were observed growing in mixed populations across Taiwan while no LS morph flowers were found on the island. The reason for the absence of the LS genotype in Taiwan is not clear but these observations are in accordance with the information on *O. corymbosa* specimens in Taiwan herbaria where no LS morph flowers have been recorded (Tsai and Kao, personal observation). LS individuals are also absent from North America and China (Denton, 1973; Lou et al., 2006). Accordingly, it is possible that the LS genotype of *O. corymbosa* has not been introduced in these regions. For the tristylous species of the Oxalidaceae, Lythraceae, and Pontederiaceae, a genetic model of floral morph determination has been proposed, in which the diallelic factor S, s interacts epistatically with M, m. The S allele factor controls the expression of short style versus non-short. The M allele factor controls mid-long locus. When S and M are recessive (ssmm), the long morph expresses. This model was put forward by Barlow (1923) and von Ubisch (1926). It was substantiated by Fisher and Mather (1943), and it has been accepted for many other tristylous species (Lewis and Jones, 1992). Therefore, an absence of long morph could be also due to the lack of sexual reproduction which limits the segregation of the LS morph. Alternatively, different genotypes may also have morphological or physiological differences resulting in different survival rates (Ågren and Ericson, 1996), and the LS genotype may not have been able to adapt to the new habitat in Taiwan.

Table 2. DNA index of individuals of mid- (MS) and short-styled (SS) floral morphs with yellow or white anther in *O. corymbosa*. The chicken erythrocyte nuclei (CEN) solution was used as a standard.

Morph/Anther	DNA index	CV%
MS/Yellow	0.90 ± 0.02	5.48
MS/White	0.90 ± 0.02	5.25
SS/Yellow	0.93 ± 0.03	5.51
SS/White	0.92 ± 0.03	6.13
CEN	1	2.76

*Values are Mean ± s.e. (n = 3).

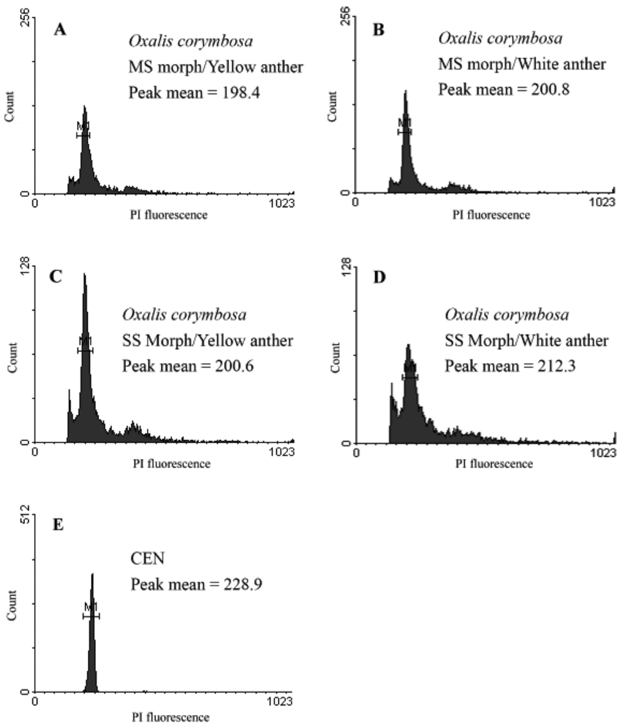

Figure 4. Histograms of mid- (MS) and short-styled (SS) floral morphs with yellow or white anthers in *O. corymbosa* (A-D), and chicken erythrocyte nuclei (CEN) standard solution (E). The peak mean is estimated by WinMDI v. 2.8 to calculate the DNA index in every plant.

No fruit or seed production was observed in any population of *O. corymbosa* from the studied areas, and this result is consistent with previous reports by Huang and Liu (1993). With a strong self- and morph-incompatible system, tristylous plants may have limited sexual reproduction in the habitats in which they are introduced due to the scarcity of reciprocal floral morphs, and thus resort to asexual reproduction under these conditions (Barrett, 1992). This phenomenon has been observed in several heterostylous species, including *Eichhornia carssipes* (Barrett and Forno, 1982), *Nymphoides peltata* (Wang et al., 2005), *O. pes-caprae* (Castro et al., 2007), and *O. corymbosa* (Denton, 1973; Veldkamp, 1971; Lou et al., 2006). *Oxalis corymbosa* populations growing in North America have only SS and SHS flowers, and no sexual reproduction was found (Denton, 1973). Sexual reproduction in *O. corymbosa* is also unknown in China (Lou et al., 2006) and Malaysia (Veldkamp, 1971). In China both MS and SS individuals were detected, but the natural populations were monomorphic, and the spatial separation of floral morphs, together with other factors, leads to no sexual reproduction in this area (Lou et al., 2006). In contrast, Taiwan populations of *O. corymbosa* are polymorphic, and individuals with different floral morphs display no obvious spatial separation. Although the frequencies of the different floral morphs are not equal, there are apparently legitimate mates in the vicinity. The results suggest that other factors are involved the lack of sexual reproduction in *O. corymbosa*.

The occurrence of *O. corymbosa* individuals with white anthers has been previously reported by Wu et al. (1978), and its significance and frequency is studied in detail in the present study. This character occurred in all three morphs of *O. corymbosa* flowers in Taiwan, with most of the SS and SHS morph flowers carrying white anthers. The white anthers proved to be empty with no pollen in the pollen sac. Such unique character confers to the flowers complete sterility for the male function. The factors which might cause a male sterile flower and prevent pollen production are currently under study. Additionally to the presence of anthers lacking pollen, mature yellow anthers revealed very low pollen viability. Although most of MS individuals had yellow anthers with mature pollen, only about 4% of the pollen was viable. Low pollen viability was also found in *O. corymbosa* populations growing in China (Lou et al., 2006). Thus, lack of pollen grains and their poor quality may be considered one of the factors limiting sexual reproduction of *O. corymbosa* in Taiwan.

Different ploidy levels have been shown to play a major role in limited sexual reproductions in other *Oxalis* species (Castro et al., 2007). In this study, no differences in ploidy level were found between SS and MS individuals of *O. corymbosa* in Taiwan. Thus, apparently different ploidy levels between floral morphs are not among the causes responsible for the lack of sexual reproduction in this species at this region. Due to difficulties in staining the chromosomes of *O. corymbosa*, we used the flow cytometry technique to analyze its DNA index, and this was revealed to be an efficient way to rapidly compare ploidy levels among plants. However, future large-scale ploidy screenings are necessary to explore in detail cytotype composition within and between populations of *O. corymbosa*. Furthermore, the possibility of aneuploidy in this species cannot be excluded and needs to be considered in further works as a potential factor in the lack of fruit production.

In conclusion, the absence of LS floral morph, the biased floral morph frequencies, the low pollen viability, and the presence of male sterile morphs may all contribute to the absence of sexual reproduction of *O. corymbosa* in Taiwan.

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紫花酢漿草在台灣的花柱型分布、花粉活性及染色體倍數之調查

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紫花酢漿草（*Oxalis corymbosa* DC.），在台灣為外來種植物，在原生地 (北美地區) 具有花柱三型性 (長花柱、中花柱和短花柱型) 和結實等相關紀錄 ； 引入台灣後，僅採用鱗莖行無性繁殖，並無結實之現象。本研究調查台灣紫花酢漿草族群之花柱型並觀察植株有無結實現象、測量花粉活性和染色體倍數，以探討其不結實的原因。在花柱型調查中，我們並沒有觀察到植株有結實的現象，也沒有發現長花柱型個體 ； 中花柱型個體佔最大比率，且具黃色花藥，而短花柱型和半等高花柱型個體比率低且其花藥多呈現白色。進一步分析發現白色花藥花粉囊內並沒有花粉 (完全雄不孕現象)，而黃色花藥花粉囊內有活性的花粉比率很低，少於 4%。經流測分析短花柱型和中花柱型個體之核 DNA，發現兩者應具有相同染色體倍數。已知紫花酢漿草具自交不親和性且必須經由有效的授粉方式才能成功授粉，因此根據本研究結果推測，台灣目前缺少長花柱型個體、不同花柱型個體數量極端不等、且有活性的花粉比率很低，為影響紫花酢漿草在台灣無法結實的重要原因。

關鍵詞 ： 流測分析 ； 花柱異型性 ； 雄不孕 ； 紫花酢漿草 ； 有性繁殖。