

# Incidences and ecological correlates of dioecious angiosperms in Taiwan and its outlying Orchid Island

Yu-Hsin TSENG, Chang-Fu HSIEH, and Jer-Ming HU\*

*Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan 106*

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**ABSTRACT.** Sexual systems, particularly dioecy, and the habit correlations were examined for 3052 native angiosperms in Taiwan and 689 species from its outlying Orchid Island, and compared among different vegetation types. The majority of angiosperms in Taiwan are hermaphrodites (74.4%,  $N = 2272$ ), followed by monoecious taxa (11.2%,  $N = 341$ ), and then dioecious taxa (7.9%,  $N = 240$ ) and polygamous taxa (6.5%,  $N = 199$ ). The incidence of dioecy in Taiwan (7.9%) and Orchid Island (11.9%,  $N = 82$ ) exceeded world averages, but was lower than that of most tropical oceanic islands. Dioecy in Taiwan and Orchid Island is strongly associated with woodiness, and is over represented in trees and climbers, but not in shrubs. In woody taxa, 175 of 1,005 (17.4%) taxa are dioecious while only 65 of 2,047 (3.2%) herbaceous taxa are dioecious in Taiwan. The percentages of dioecy decrease with increasing altitude in Taiwan. The percentages of dioecy varied among the six selected vegetation types in Taiwan, from 14.1% in the Linkou Laterite Terrace secondary forest to 23.9% in the Nanjenshan plot, the highest percentage ever found in a forest plot.

**Keywords:** Dioecy; Flora; Orchid Island; Sexual system; Taiwan.

## INTRODUCTION

The ecological correlates and the potential driving forces for the evolution of dioecy in plants have been debated intensively over the past decades. The traditional view suggests that dioecy has evolved mainly because it guarantees outcrossing to avoid the drawback of inbreeding depression (Charlesworth and Charlesworth, 1978; Lewis, 1941; Thomson and Barrett, 1981). Other studies indicate that sexual specialization, resource reallocation, and/or other ecological factors may also be behind the evolution of dioecy, under which males and females can have higher fitness than their hermaphroditic counterparts (Bawa, 1980; Brunet and Charlesworth, 1995; Freeman et al., 1997; Givnish, 1980; Thomson and Brunet, 1990). Despite the advantages of having separate sexes, dioecious plants are not common, and estimates as low as 3-4% (Yampolsky and Yampolsky, 1922) or 6% (Renner and Ricklefs, 1995) in angiosperms. However, the actual incidents of dioecy in the local flora are variable, ranging from 2.8% in California (Fox, 1985) to as high as 14.7% in Hawaii (Sakai et al., 1995b).

The evolution and maintenance of dioecy has been associated with several ecological and life history attributes. Among these are: woodiness (Bullock, 1985;

Conn et al., 1980; Flores and Schemske, 1984; Fox, 1985; Freeman et al., 1980b; Givnish, 1980; Sakai et al., 1995b; Webb et al., 1999), climber growth (Renner and Ricklefs, 1995), small, inconspicuous, or greenish flowers (Fox, 1985; Ibarra-Manriquez and Oyama, 1992), unspecialized pollinators (Baker and Cox, 1984; Ibarra-Manriquez and Oyama, 1992), wind pollination (Freeman et al., 1980b; Renner and Ricklefs, 1995), fleshy fruits (Flores and Schemske, 1984; Givnish, 1980; Ibarra-Manriquez and Oyama, 1992; Webb et al., 1999), tropical floras (Bawa and Opler, 1975; Givnish, 1980; Sobrevila and Arroyo, 1982), and island habitats (Abe, 2006; Baker and Cox, 1984; Bawa, 1980; Sakai et al., 1995a, b). Many of these ecological traits are not necessarily the causal factors of dioecy, and some have only been studied in a small local flora, and the validity of these correlations has been questioned (Fox, 1985; Renner and Ricklefs, 1995; Steiner, 1988). Recent studies using phylogenetic analysis to examine the correlations between dioecy and those ecological attributes have shown that although many dioecious clades are species poor, they are strongly associated with traits like tropical distribution, woody growth form, abiotic pollination, small inconspicuous flowers and inflorescences, and fleshy fruits (Vamosi et al., 2003). In addition, dioecious lineages with more of these traits showed a higher relative species richness upon sister-group phylogenetic analysis, particularly those that had a tropical distribution or fleshy fruits (Vamosi and Vamosi, 2004).

\*Corresponding author: E-mail: jmhu@ntu.edu.tw; Tel: +886-2-33662472; Fax: +886-2-23686750.

Furthermore, dioecy has been demonstrated to be more frequent in certain plant community types, such as tropical forests (Bawa and Opler, 1975; Bawa et al., 1985; Matalana et al., 2005; Momose et al., 1998), mountain cloud forest in Venezuela (Sobrevila and Arroyo, 1982), tropical semi-deciduous forest in Mexico (Bullock, 1985), and some communities of the semiarid Intermountain West in California (Freeman et al., 1980b). However, a high incidence of dioecy has not been found associated with certain community types in other tropical floras, such as Puerto Rico (Flores and Schemske, 1984), palm swamps in Venezuela (Ramirez and Brito, 1990), or dry forests in Caatinga, Brazil (Machado et al., 2006). Most studies of dioecy incidents were conducted for tropical floras, particularly in the New World, and little has been studied in Asia or subtropical regions.

Taiwan is a subtropical island on the western edge of the Pacific Ocean about 200 km east of Fujien Province on the Chinese mainland and 360 km north from Luzon Island in the Philippines (Hsieh and Shen, 1994). The dry land mass of Taiwan was formed during the Miocene as an island, but is generally believed to have been connected to mainland China during four glacial periods of the late Quaternary and then disconnected permanently at the end of the last glacial period around 0.01 million years ago (Shen, 1994). The flora of Taiwan is then largely comprised of taxa originating from mainland China and also from Japan and the Philippines (Hsieh et al., 1994). According to the comparison of nonendemic species in seed plants among Taiwan and adjacent areas, 48.2% of total nonendemic species in Taiwan are also spread throughout China, which is higher than those in Japan (27.9%), Korea (9.6%), India (15.8%), or in the Philippines (16.4%) (Ying and Hsu, 2002). Taiwan is a high mountain island of about 35,800 km<sup>2</sup>, and 30% of the landmass is 1,000-3,000 m above sea level. Due to complex landscapes and the influence of monsoons, the vegetations of Taiwan contain elements from tropic, temperate, and even sub-arctic climates (Hsieh et al., 1994). Therefore, predicting the incidence of dioecy in the flora of Taiwan based on the overall habitat and without considering the history of the flora is difficult.

It is reasonable to assume the plants that migrated through a land-bridge between Taiwan and the Eurasia landmass are mostly temperate components because the weather was cold during these glacial periods when the two lands were connected. These plants eventually retreated to the higher altitudes of Taiwan as the weather warmed around 10,000 years ago, the sea level rose, and the 'land-bridge' disappeared (Shen, 1994). As a result, the majority of the lowland flora of Taiwan likely migrated to Taiwan without any available land-bridge, i.e. they came through long distance dispersal later than 10,000 years ago. If the incidence of dioecy is associated with long-distance dispersal and/or tropical elements, then the lowland flora of Taiwan should have a higher percentage of dioecious plants.

The sexual systems in Taiwan's flora have never been

extensively studied, and most of the data are only present in taxonomic description from the Flora of Taiwan. Here we provide the first synopsis of sex expression data of native angiosperms in Taiwan based on the species list from the second edition of the Flora of Taiwan (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003) and the recent literature. We also conducted a separate analysis for Orchid Island (Lanyu), a subsidiary islet about 90 km to Taiwan's southeast, for comparison. Furthermore, seven plots of different vegetation types in Taiwan were selected and compared to other studies, to examine incidences of dioecy and the correlations to plant habit.

## MATERIALS AND METHODS

### Data sources

The species list for this study was based on the second edition of the Flora of Taiwan (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003) and recent taxonomic revisions (supplementary data 1). Only native angiosperms in Taiwan were recorded. Gymnosperms, naturalized plants, and cultivars were excluded in this study. To reduce double counts at the infraspecific level, only one record will be used for those with more than one variety, subspecies, and forma because there is usually no variability in the category of the sexual system within species (Sakai et al., 1995a).

### Sexual systems

Characterization of sexual expression for these taxa was based largely on the descriptions in the Flora of Taiwan (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003) and reports mentioned in the previous section. Plant sexual systems in our study were divided into four categories: hermaphroditic, dioecious, monoecious, and polygamous. Species were recorded as hermaphroditic when they had bisexual flowers (definitions *sensu* Bawa, 1980). Species described as monoecious or dioecious were considered monoecious since 'dioecious' records sometimes reflect dichogamous expression of unisexual flowers, i.e., male and female flowers open at different times. Species listed as 'dioecious or rarely monoecious,' and 'functionally dioecious' were treated as dioecious. Species described as andromonoecious, gynomonocious, androdioecious, polygamo-dioecious, polygamous-monoecious, 'dioecious or hermaphrodites', 'dioecious or polygamous', 'monoecious or polygamous', 'dioecious or hermaphrodites or polygamous', and 'dioecious or monoecious or polygamous' were all recorded as polygamous. The exclusion of that information is necessary to maintain consistency in counting since only a few taxa have been studied quantitatively for floral types in Taiwan, and the majority of the species in Taiwan's flora have no detailed sexual system information.

Twenty-five species with uncertain sexual systems in Taiwan and Orchid Island were excluded due either to the absence of a description or to one that is controversial (see supplementary data 2). The species list and sexual expression for the flora of Taiwan and Orchid Island were treated separately.

Growth forms were categorized into four types: trees, shrubs, herbs, and climbers based on the description in the Flora of Taiwan of each species' predominant mature morphology. Plants listed as small trees and large trees were both recorded as trees while those listed as shrub or shrublet were recorded as shrubs. Both herbaceous and woody vines were scored together as climbers in habit analysis or scored separately in the analysis for woodiness. The herbs in our analysis included annual and perennial herbs, regardless of whether they were parasites, epiphytes, or aquatic plants. Trees, shrubs and woody vines were grouped together as 'woody,' and herbaceous plants and herbaceous vine were grouped as 'herbaceous' accordingly.

In comparison with the dioecy percentage in Taiwan and other areas, we reviewed the data from different islands and continental areas. We also compared the sexual systems among different vegetation types from tropical and temperate areas, including seven plots with detailed vegetation information in Taiwan and Orchid Island. Two of the seven study sites in Taiwan, Nanjenshan plot I (Hsieh et al., 1992) and Nanjenshan plot II (Hsieh et al., 1996), are at the Nanjenshan Long-Term Ecological Research (LTER) site in southern Taiwan. The former is a subtropical evergreen broad-leaved/seasonal forest of 3 hectares at an altitude of 300 to 340 m. Nanjenshan plot II is a tropical seasonal forest about 2.1 hectares at an altitude of 225-275 m. The third, a 25-hectare Fushan Forest Dynamics Plot, is another LTER plot in northern Taiwan, categorized as a subtropical rain forest. The fourth transect at Lopeishan is a warm temperate forest, and its altitude ranges from 650 m in the Manyuehyuan to 1270 m on the hillsides of a *Fagus*-dominated forest (Hsieh et al., 1998). The fifth plot is the Kwangin Coastal Nature Reserve located in the *Ficus-Machilus* zone of a subtropical rain forest (Huang et al., 1991). Although this reserve plot is near the coast, the number of seashore plants is relatively small because it contains steep rocky slopes and does not have a wide beach. The sixth is Linkou Laterite Terrace Secondary Forest, which is composed of natural forests, secondary forests, and a few plantations, categorized as a semi-evergreen forest (Li and Huang, 1987). We included Orchid Island, which is a 45 km<sup>2</sup> volcanic island off the southeastern coast of Taiwan in the Pacific Ocean, and it is considered to have the most tropical elements anywhere in Taiwan or in its adjacent islands (Hsieh et al., 1994). We recorded all angiosperm species from Orchid Island as a whole based on their description in the Flora of Taiwan (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003).

In order to further elucidate the correlations between

sexual systems and climatic zones, the sexual systems in different climatic zones of Taiwan were recorded. On basis of the definition by Su (1984), we analyzed six climatic zones equivalent to vegetation zones in Taiwan: tropics, subtropics, warm-temperate, temperate, cool-temperate, and cold-temperate.

### Data analysis

The distributions of sex expressions according to life-forms were compared by chi-square tests with Yates's correction factor. The analyses were performed for different sexual systems on each of the categories of life forms in corresponding columns. The null hypothesis was that the frequency distribution of sexual systems was not significantly different among different life-forms compared to those of the entire flora.

## RESULTS AND DISCUSSION

### Sexual systems in Taiwan and Orchid Island

Our analysis is the first to examine the frequency of sexual systems among angiosperms in Taiwan and Orchid Island. Of the 3052 native species surveyed in this study of Taiwan, 240 (7.9%) are dioecious, 341 (11.2%) are monoecious, 199 (6.5%) are polygamous, and 2272 (74.4%) are hermaphrodite. At the family level, 9 of the 181 families (5.0%) in Taiwan's flora contain only dioecious taxa; two of them (*Daphniphyllaceae* and *Salicaceae*) are exclusively dioecious worldwide while the other seven (*Aquifoliaceae*, *Dioscoreaceae*, *Ebenaceae*, *Icacinaceae*, *Menispermaceae*, *Pandanaceae*, and *Smilacaceae*) have mixed sex expression types within the family although dioecy is usually the most common type for those families. Eighteen of the 181 families (9.9%) contain only monoecious taxa; five of them are exclusively monoecious worldwide (*Betulaceae*, *Ceratophyllaceae*, *Sparganiaceae*, *Theligonaceae*, and *Typhaceae*) while the other 13 (*Aceraceae*, *Begoniaceae*, *Buxaceae*, *Callitrichaceae*, *Eriocaulaceae*, *Fagaceae*, *Juglandaceae*, *Lardizabalaceae*, *Lemnaceae*, *Musaceae*, *Najadaceae*, *Passifloraceae*, and *Zosteraceae*) have mixed sex expression types elsewhere. For the rest of the families, 99 of them are exclusively hermaphroditic, and the other 55 families have two or more mixed sex expression systems within the family.

At the genus level, 85 of the 1120 genera (7.6%) in Taiwan's flora contain one or more dioecious species, and 63 of them (74.1%) contain exclusively dioecious taxa in Taiwan. In addition, since the majority of them (52 genera) contain only three or fewer species in Taiwan, dioecy seems unassociated with diversification of the flora. The most species-rich genera with exclusively dioecious species are *Ilex* (21 spp.), *Dioscorea* (11 spp., *Dioscoreaceae*), *Litsea* (10 spp., *Lauraceae*), *Smilax* (18 spp., *Smilacaceae*), and *Eurya* (13 spp., *Theaceae*). In contrast, 87 of the 1120 genera in Taiwan contain exclusively monoecious taxa, and the most speciose

**Table 1.** The incidence of dioecy in seed plants without introduced and naturalized species (unless noted) from various floras of continental areas and islands.

Flora	Dioecy (%)	No. of species	Reference
CONTINENT AREAS			
Portugal	2.0	2183	(Pires, 1947 in Baker and Cox, 1984)
California, USA	2.8 <sup>a</sup>	5421	(Freeman et al., 1980b)
Carolina, USA	3.5 <sup>b</sup>	3274	(Conn et al., 1980)
South Australia, Australia	3.9	2102	(Black, 1922-1952 in Parsons, 1958)
British Isles	4.3 <sup>c</sup> , 4.4 <sup>d</sup>	1377 <sup>c</sup> , 1380 <sup>d</sup>	(Kay and Stevens, 1986)
Alaskan arctic slope, USA	5.8	411	(Fox, 1985)
Cape flora, South Africa	6.6 <sup>c</sup> , 6.7 <sup>d</sup>	8497 <sup>c</sup>	(Steiner, 1988)
ISLANDS			
San Clemente Islands, USA	2.0	221	(Raven, 1963 in Baker and Cox, 1984)
Galápagos	3.0	439	(Wiggins and Porter, 1971 in Baker and Cox, 1984)
Réunion, Indian Ocean	4.0	838	(Cordemoy, 1985 in Baker and Cox, 1984)
Puerto Rico and the Virgin Islands	6.1 <sup>d</sup>	2037	(Flores and Schemske, 1984)
Taiwan	7.9 <sup>e</sup>	3052	This study
Seychelles, Indian Ocean	8.0 <sup>e</sup>	237	(Summerhayes, 1926 in Baker and Cox, 1984)
Barro Colorado Island, Panama	9.0 <sup>e</sup>	1212	(Croat, 1979 in Steiner, 1988)
Mauritius, Indian Ocean	11.0	682	(Baker, 1877 in Baker and Cox, 1984)
Orchid Island, Taiwan	11.9 <sup>e</sup>	689	This study
Ogasawara Islands, Japan	13.0 <sup>e</sup>	269	(Abe, 2006)
New Zealand	12-13 <sup>c</sup>	1813	(Godley, 1979)
Hawaii Islands, USA	14.7 <sup>c</sup>	971	(Sakai et al., 1995b)
Tonga, Pacific Ocean	16.0	404	(Yuncker, 1959 in Baker and Cox, 1984)
Samoa, Pacific Ocean	17.0	539	(Setchell, 1924 in Baker and Cox, 1984)

<sup>a</sup>Including introduced species.

<sup>b</sup>Including naturalized species.

<sup>c</sup>Without gymnosperms.

<sup>d</sup>With gymnosperms.

ones are *Begonia* (11 spp., Begoniaceae), *Chamaesyce* (10 spp., Euphorbiaceae), *Cyclobalanopsis* (13 spp., Fagaceae), *Pasania* (13 spp., Fagaceae), and *Pilea* (13 spp., Urticaceae).

The chi-square test of the correlations between sexual systems and life forms showed that dioecy is associated with woodiness ( $P < 0.001$ ) and hermaphroditism is associated with an herbaceous habit ( $P < 0.001$ ) (Table 2A). When analyzed with four life forms, the sexual systems show significant correlations with all of them (Table 2,  $N = 3052$ ,  $df = 9$ ,  $\chi^2 = 422.3$ ,  $P < 0.001$ ). Dioecy is significantly associated with trees, shrubs, and climbers, and is strongly under-represented in the herbaceous taxa in Taiwan (Table 2B,  $N_{obs} = 24$ , compared with expected

$N_{exp} = 150.0$ ). In comparison, monoecy is significantly associated with trees (89 vs. expected 50.7), but negatively associated with other life forms. Among 199 taxa listed as 'polygamous', the association to life forms is less extreme, but still significant ( $\chi^2 = 11.7$ ,  $P = 0.01$ , Table 2). Overall, nearly half of the trees (42.3%) have unisexual flowers, and very few herbaceous taxa are dioecious or monoecious (11.9%). It is interesting to see that herbaceous vines have a higher proportion of dioecious taxa than woody vines. This is likely due to the inclusion of *Smilax* and *Dioscorea* in the herbaceous vine category, both genera are species rich and account for ~21% (29 species) of herbaceous vines in Taiwan.

A strong correlation was found between dioecy and



**Table 2.** Frequencies of sexual systems in Taiwan's flora and the associations with different life forms to (A) Woodiness and (B) Habit, and to (C) Total flora. The observed ( $N_{obs}$ ) and expected ( $N_{exp}$ ) numbers of species under different categories of life forms are shown. The percentage corresponding to total species numbers are shown in parentheses.

**(A)**

Woodiness		Sexual system							
		Dioecy		Monoecy		Polygamy		Hermaphrodite	
Life form	No. species	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$
Woody	1005	175 (5.7%)	79.0	126 (4.1%)	112.3	55 (1.8%)	65.5	649 (21.3%)	748.2
Herbaceous	2047	65 (2.1%)	161.0	215 (7.0%)	228.7	144 (4.7%)	133.5	1623 (53.2%)	1523.8
		$\chi^2 = 172.0, P < 0.001$		$\chi^2 = 2.3, P = 0.11$		$\chi^2 = 2.3, P = 0.11$		$\chi^2 = 19.4, P < 0.001$	

**(B)**

Habit		Sexual system							
		Dioecy		Monoecy		Polygamy		Hermaphrodite	
Life form	No. species	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$
Trees	454	103 (3.4%)	35.7	89 (2.9%)	50.7	29 (1.0%)	29.6	233 (7.6%)	338.0
Shrubs	350	38 (1.2%)	27.5	29 (1.0%)	39.1	9 (0.3%)	22.8	274 (9.0%)	260.6
Herbs	1908	24 (0.8%)	150.0	204 (6.7%)	213.2	142 (4.7%)	124.4	1538 (50.4%)	1420.4
Climbers	340	75 (2.5%)	26.7	19 (0.6%)	38.0	19 (0.6%)	22.2	227 (7.4%)	253.1
		$\chi^2 = 323.9, P < 0.001$		$\chi^2 = 41.4, P < 0.001$		$\chi^2 = 11.3, P = 0.01$		$\chi^2 = 45.7, P < 0.001$	

**(C)**

Total	Sexual system			
	Dioecy	Monoecy	Polygamy	Hermaphrodite
No. species	$N_{obs}$	$N_{obs}$	$N_{obs}$	$N_{obs}$
3052	240 (7.9%)	341 (11.2%)	199 (6.5%)	2272 (74.4%)

climbers (woody or herbaceous) in Taiwan, a point rarely mentioned in the literature (Renner and Ricklefs, 1995). This association can be explained by a differential selection for resource allocation to sexual functions (Renner and Ricklefs, 1995). For example, females of a dioecious climber, *Dioscorea japonica* Thunb. (Dioscoreaceae) tend to pay a higher reproductive cost than males, which implies a tradeoff between sexual and vegetative reproduction (Mizuki et al., 2005). In order to support heavy fruits, it is necessary to produce a thicker, more slowly growing stem; in contrast, male plants with pollen dispensing flowers would prefer to grow on more exposed plant body (Renner and Ricklefs, 1995). In addition, long life spans in woody vines are another likely explanation for the correlation with dioecy because long-lived plants are favored for selection by

outbreeders compared with short-lived ones (Stebbins, 1950; Steiner, 1988; Matallana et al., 2005). Furthermore, the distribution and frequency of dioecy in herbaceous vines may also support this view, based on the fact that 40 out of 41 dioecious herbaceous vines in Taiwan are perennial plants, including tuber or rhizomatous perennials in Dioscoreaceae.

In comparison, Orchid Island has a higher percentage of dioecious taxa (82 spp., 11.9%) than Taiwan (Table 3). There are 72 monoecious, 45 polygamous, and 490 hermaphroditic taxa on Orchid Island. Two families, Cecropiaceae (1 sp.) and Myristicaceae (2 spp.), are not found in Taiwan, and all three species are dioecious. The incidence of dioecy in both Taiwan (7.9%) and Orchid Island (11.9%) exceeds the estimates from most of the continental floras (Table 1). The dioecy percentage in

**Table 3.** Frequencies of sexual systems in Orchid Island's flora and the associations with different life forms to (A) Woodiness and (B) Habit, and to (C) Total flora. The observed ( $N_{obs}$ ) and expected ( $N_{exp}$ ) numbers of species under different categories of life forms are shown. The percentage corresponding to total species numbers are shown in parentheses.

## (A)

Woodiness		Sexual system							
		Dioecy		Monoecy		Polygamy		Hermaphrodite	
Life form	No. species	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$
Woody	308	71 (10.3%)	36.7	30 (4.4%)	32.2	15 (2.2%)	20.1	192 (27.9%)	219.0
Herbaceous	381	11 (1.6%)	45.3	42 (6.1%)	39.8	30 (4.4%)	24.9	298 (43.3%)	271.0
		$\chi^2 = 56.5, P < 0.001$		$\chi^2 = 0.2, P = 0.60$		$\chi^2 = 1.9, P = 0.13$		$\chi^2 = 5.8, P = 0.014$	

## (B)

Habit		Sexual system							
		Dioecy		Monoecy		Polygamy		Hermaphrodite	
Life form	No. species	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$	$N_{obs}$	$N_{exp}$
Trees	158	49 (7.1%)	18.8	18 (2.6%)	16.5	11 (1.6%)	10.3	80 (11.6%)	112.4
Shrubs	82	5 (0.7%)	9.8	10 (1.5%)	8.6	2 (0.3%)	5.4	65 (9.4%)	58.3
Herbs	348	2 (0.3%)	41.4	41 (6.0%)	36.4	29 (4.2%)	22.7	276 (40.1%)	247.5
Climbers	101	26 (3.8%)	12.0	3 (0.4%)	10.6	3 (0.4%)	6.6	69 (10.0%)	71.8
		$\chi^2 = 104.6, P < 0.001$		$\chi^2 = 6.4, P = 0.095$		$\chi^2 = 5.8, P = 0.12$		$\chi^2 = 13.5, P = 0.004$	

## (C)

Total	Sexual system			
	Dioecy	Monoecy	Polygamy	Hermaphrodite
No. species	$N_{obs}$	$N_{obs}$	$N_{obs}$	$N_{obs}$
689	82 (11.9%)	72 (10.4%)	45 (6.5%)	490 (71.1%)

Taiwan's flora is within that of tropical and temperate islands and a bit lower than that of other subtropical islands like Norfolk island (12%) and New Zealand (12-13%) (Baker and Cox, 1984).

The association of sexual systems with different life forms in Orchid Island resembles what has been observed in Taiwan (Table 3). Dioecy is associated with woodiness ( $N = 71, P < 0.001$ ), and hermaphroditism is associated with herbs ( $N = 298, P = 0.014$ ) (Table 3A). In comparison with the plants of Taiwan, the sexual systems only show significant correlations with dioecism and hermaphroditism in Orchid Island (Table 3B). Dioecy is significantly associated with trees and climbers, and is strongly under-represented in shrubs and herbaceous taxa (Table 3B).

A strong correlation has been demonstrated between the level of dioecism and both proximity to the equator and maximum island height, which is an indicator of potential habitat diversity (Baker and Cox, 1984). Our result shows that the percentage of dioecy in Taiwan's flora follows this rule since Taiwan is at the Tropic of Cancer and the highest point is near 4,000 m. However, Taiwan is a continental island and may show a different pattern from that of other oceanic islands listed in Baker and Cox (1984). The plants in oceanic islands, islands that separated from the landmass more than 45 million years ago, are mostly comprised of colonists of long distance dispersal regardless of whether they are at lowland or mountain regions of the island (Sakai et al., 1995b). This is the reason why the proportions of dioecy for the woody plants of lowland and montane Hawaii are very similar

(Sakai et al., 1995a). In contrast, the flora of a continental island is highly influenced by the plants that have migrated from an adjacent landmass. The migration of plants will be substantial if the island has been connected to a continent through a 'land bridge,' and no long-distance dispersal is required for plant establishment on the island.

Sexual systems were analyzed among different climatic zones in Taiwan, and the results showed a general trend toward decreasing dioecy as altitude increased (Table 4). The incidence of dioecy in the tropics, subtropics, and temperate regions (8.2-8.8%) was similar, and it was lowest in the cold temperate area (2.0%). A similar trend can be observed for monoecious taxa. In comparison, the incidence of polygamy was nearly constant among all regions while hermaphroditism was highest in the cold-temperate area, but remained the same in other regions (Table 4). This data, however, should be viewed with caution since the counting of species numbers is not exclusive among different climatic zones. The climatic zones are only roughly classified, and many plants are found in more than one zone. Therefore, chi-square statistics cannot be readily applied.

### Sexual systems among different vegetation types

The sexual systems of seven sites from Taiwan and Orchid Island are compared with data from the literature (Table 5). It is not easy to compare different vegetation types since some studies only used tree data while others used data for all plants. In general, dioecy percentages are higher in the tropics than in the subtropics or other regions, except for dry or semi-dry forests, a trend that has been previously documented (Bawa and Opler, 1975; Givnish, 1980). The Nanjenshan II plot of Taiwan had the highest dioecy percentage (23.9%) of all the studies with all floras analyzed. However, when only tree data were used in the analysis, the percentage (27.2%) fell below those from several other studies like the 40.0% from the Okomu Forest Reserve, South Nigeria (Table 5). The flora of Orchid Island is counted as one site and has 31.0% dioecious plants among its trees, the highest among the

seven study sites of Taiwan/Orchid Island. Interestingly, all seven sites we analyzed have a significantly higher incidence of dioecy (11.9-23.9%) than the total flora (7.9%). However, the dioecy among trees of the seven sites is similar to the dioecy based on the total flora (18.7-31.0% vs. 22.7% of the total trees, Table 5). The two tropical communities in this study, Nanjenshan II and Orchid Island, have similar proportions of sexual systems to other tropics forests; on the other hand, the incidence of dioecious species among the four subtropical and one warm temperate forest is higher than that in the temperate regions and some tropical forests.

We have to point out that estimates of sexual systems in the flora of Taiwan have several problems, one of which is the definition of native plants. Taiwan is one of the world's most heavily populated countries, and even though over 52% of Taiwan is covered with forests (Hsieh et al., 1994), many are highly fragmented or have suffered human disturbance in lowland areas. Many plants adapted to this disturbed environment are then found in the flora of Taiwan, including many herbaceous plants. The herbaceous taxa comprise a large portion in Taiwan's flora (62.5%), but contain only 24 dioecious taxa. The herbaceous species are mostly found in the five largest families—Gramineae, Orchidaceae, Compositae, Cyperaceae, and Leguminosae—which comprise nearly 33.4% of Taiwan's seed plant species (Hsieh, 2003). All five families are predominant at lower altitudes and are dioecy-poor. Except for orchids, the other four families are well known for their spreading ability and adaptation to disturbed areas. The Linkou Laterite Terrace and Kwangin Coastal Nature Reserve are the most disturbed plots sampled in our study. They contain 20-21% of taxa from those four 'weedy' families: 87/411 from Linkou and 62/305 taxa from Kwangin. This is probably why these two regions have the lowest dioecy percentages (14.1% and 14.8%, respectively).

Another problem that influences values for the incidence and correlation of dioecy is the criterion for assignment of sexual systems. In fact, the categorization of sexual expression among species poses certain

**Table 4.** Frequencies of sexual systems of Taiwan in six climatic zones. The percentage corresponding to total species numbers in each climatic zone are shown in parentheses.

Climatic zone	No. species	Sexual system			
		Dioecy	Monoecy	Polygamy	Hermaphrodite
Tropics	2029	167 (8.2%)	231 (11.4%)	137 (6.8%)	1494 (73.6%)
Subtropics	1233	102 (8.3%)	152 (12.3%)	77 (6.2%)	902 (73.2%)
Warm-temperate	799	70 (8.8%)	85 (10.6%)	59 (7.4%)	585 (73.2%)
Temperate	555	47 (8.5%)	59 (10.6%)	33 (5.9%)	416 (75.0%)
Cool-Temperate	324	21 (6.5%)	24 (7.4%)	23 (7.1%)	256 (79.0%)
Cold-Temperate	201	4 (2.0%)	10 (5.0%)	14 (7.0%)	173 (86.1%)

**Table 5.** Proportions of plant sexual systems in seven study sites in Taiwan compared to other plant communities. Data including all species (A) and trees only records (T) are separated in different column for comparison.

Forest types and locations	No. species <sup>a</sup>	Sexual system (%)								Reference
		Dioecy		Monoecy		Polygamy		Hermaphrodite		
		A	T	A	T	A	T	A	T	
<b>TROPICS</b>										
Deciduous forest										
Secondary deciduous forest, Venezuela	51/-	4.0	-	14.0	-	-	-	82.0	-	(Jaimes and Ramirez, 1999)
Semi-deciduous forest										
Tropical semi-deciduous forest, Mexico	708/-	12.3	-	13.0	-	4.6 <sup>b</sup>	-	70.2 <sup>c</sup>	-	(Bullock, 1985)
Dry Forest										
Caatinga, Brazil	147/26	2.7	11.5	9.5	3.8	4.8 <sup>d</sup>	3.8 <sup>d</sup>	83.0 <sup>c</sup>	80.8	(Machado et al., 2006)
Evergreen Forest										
Western Ghats, India	-/656	-	20.0	-	5.0	-	16.0	-	57.0	(Krishnan and Ramesh, 2005)
Mountain forest										
East Usambara mountain forest, Tanzania	262/-	12.6	-	6.9	-	7.3	-	73.3	-	(Rodgers and Homewood, 1982 in Krishnan and Ramesh, 2005)
Rain Forest										
Okomu Forest Reserve, South Nigeria	NA	-	40.0	-	13.0	-	-	-	47.0	(Jones, 1955 in Bawa and Opler, 1975)
Lowland rain forest, Costa Rica	-/333	-	23.1	-	11.4	-	-	-	65.5	(Bawa et al., 1985)
Tropical palm swamp, Venezuela	128/-	3.1	-	19.5	-	-	-	77.3	-	(Ramirez and Brito, 1990)
Lowland mixed dipterocarp forest, Malaysia	270/-	14.1	-	8.9	-	0.7 <sup>e</sup>	-	76.3	-	(Momose et al., 1998)
Lowland mixed dipterocarp forest, Malaysia	-/711	-	26.0	-	14.0 <sup>f</sup>	-	-	-	60.0	(Ashton, 1969)
Nanjenshan II, Taiwan	222/103	23.9	27.2	10.8	15.5	5.4	5.8	59.9	51.5	This study
Orchid Island, Taiwan	689/158	11.9	31.0	10.4	11.4	6.5	7.0	71.1	50.6	This study
Cloud forest										
Montane cloud forest, Venezuela	-/36	-	30.6	-	-	-	-	-	69.5 <sup>g</sup>	(Sobrevila and Arroyo, 1982)
Marine influenced vegetation										
Restinga de Jurubatiba National Park, Brazil	566/-	14.0 <sup>h</sup>	-	11.0 <sup>i</sup>	-	-	-	75.0	-	(Matallana et al., 2005)
<b>SUBTROPICS</b>										
Nanjenshan I, Taiwan	171/92	18.1	22.8	12.9	18.5	5.3	4.3	63.7	54.3	This study
Fushan, Taiwan	235/83	15.7	24.1	11.9	16.9	4.3	3.6	68.1	55.4	This study



**Table 5.** (Continued)

Forest types and locations	No. species <sup>a</sup>	Sexual system (%)								Reference
		Dioecy		Monoecy		Polygamy		Hermaphrodite		
		A	T	A	T	A	T	A	T	
Kwangin coastal nature reserve, Taiwan	305/86	14.8	30.2	11.5	18.6	8.9	7.0	64.9	44.2	This study
Linkou laterite terrace secondary forest, Taiwan	411/101	14.1	24.8	10.9	15.8	7.8	11.9	67.2	47.5	This study
WARM TEMPERATE										
Lopeishan, Taiwan	207/91	16.9	18.7	11.6	14.3	4.3	3.3	67.1	63.7	This study
TEMPERATE										
Gallipolis, Ohio	-/17	-	11.0	-	83.0	-	-	-	6.0	(Braun, 1950 in Bawa and Opler, 1975)
Campbellsville, Kentucky	-/20	-	15.0	-	70.0	-	-	-	15.0	(Braun, 1950 in Bawa and Opler, 1975)
Hueston's Woods, Ohio	-/15	-	13.0	-	60.0	-	-	-	27.0	(Braun, 1950 in Bawa and Opler, 1975)
Pisgah Mountain, New Hampshire	-/13	-	6.0	-	81.0	-	-	-	13.0	(Braun, 1950 in Bawa and Opler, 1975)

<sup>a</sup>The first value is the species number of all life forms and the second value is the number of trees. NA: data non available.

<sup>b</sup>Including 1.6% gynomonocious, 2.0% andromonoecious, 0.3% polygamomonocious, 0.6% gynodioecious, 0.1% androdioecious species.

<sup>c</sup>Including heterostylous species.

<sup>d</sup>Andromonoecious species only.

<sup>e</sup>Androdioecious and andromonoecious species only.

<sup>f</sup>Including some protandrous and some protogynous, hermaphroditic species.

<sup>g</sup>Including heterostylous and monoecious species based on the original paper.

<sup>h</sup>Including gynodioecious and androdioecious species.

<sup>i</sup>Including gynomonocious and andromonoecious species.

difficulties especially when a species has been observed with more than one sexual type, such as species with 'monoecious or dioecious' or 'dioecious or monoecious or polygamous.' In our study, we included polygamous species that contain sexual dimorphic (polygamodioecious, gynodioecious, or androdioecious), monomorphic systems (polygamomonocious, gynomonocious, or andromonoecious) (definitions given by Sakai et al., 1995b) and species having two or more sexual expressions (except for species described as 'monoecious or dioecious'). In some other studies, sexual systems were simply classified as dioecy, monoecy, or hermaphrodite (Bawa et al., 1985; Ramirez and Brito, 1990; Abe, 2006). These diverse sexual systems are indeed very important for elucidating the actual evolutionary pathway to dioecy in specific taxa (McComb, 1966). For example, dioecy might have originated via the developmental transitions from monoecy (e.g., Renner and Ricklefs, 1995; Dorken et al., 2002; Harrison and Yamamura, 2003; Dorken and Barrett, 2004), gynodioecy (e.g., Charlesworth and Charlesworth, 1978; Ashman, 1999; Charlesworth, 1999; Weiblen et al., 2000), androdioecy (e.g., Bawa, 1980; Charlesworth,

1999; Pannell, 2002), heterostyly (e.g., Ornduff, 1966; Muenchow and Grebus, 1989), and dichogamy (e.g., Dommee et al., 1990; Pendleton et al., 2000; Pannell and Verdu, 2006). Thus, incomplete analysis not only results in sampling errors, it neglects the useful information behind these sexual systems.

Another potential problem in studying the general patterns of sexual systems is plasticity. Plasticity in gender and sexual systems among individuals has long known in plants (Lloyd, 1980; Lloyd and Bawa, 1984). Sex changes can even occur in the same individual over different years (Freeman et al., 1980a; Lloyd and Bawa, 1984; Nanami et al., 2004). Plants can be monoecious or hermaphroditic, but the male and female phases of the flowers can mature dichogamously (Lloyd and Webb, 1986). Furthermore, fitness measured by the gender functions is complicated since they are quite variable in different plants, and thus obscure the inference of dioecism (Delph and Wolf, 2005). Despite of these difficulties, we hope to provide a synopsis for the sexual systems in the flora of Taiwan for future studies.

In this study, we present the most species-rich (3052 species) survey of an island flora for its sexual systems. This is also the first comprehensive report on the sexual systems of continental islands. The high incidence of dioecy in Taiwan (7.9%) is possibly due to a combination of tropical and/or oceanic components, woodiness, and long distance dispersal, all of which have been suggested to be associated with dioecism (Bawa, 1980, 1984). However, current understanding of sexual systems in Taiwan's flora is heavily influenced by the limited data, such as insufficient data on pollination and dispersal modes. Therefore, further detailed investigation on reproduction biology is required to elucidate the ecological correlation with the richness of dioecy in Taiwan. Data from adjacent continental regions like Southeastern China and Indo-China are also required for comparison.

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## 台灣與蘭嶼原生被子植物雌雄異株生殖系統與生活型關係之初探

曾好馨 謝長富 胡哲明

國立臺灣大學 生態學與演化生物學研究所

本研究整理 3052 種台灣和 689 種蘭嶼原生被子植物之生殖系統，特別是雌雄異株型，對其與生活型的關聯進行討論。結果發現台灣本島大部份的被子植物都是兩性花（74.4%，N = 2272），其次為雌雄同株異花（11.2%，N = 341），雌雄異株（7.9%，N = 240），以及雜性花（6.5%，N = 199）。不論是台灣本島（7.9%）或是蘭嶼（11.9%）的雌雄異株植物，比例都高於世界平均值，但低於大部份的熱帶海洋性島嶼。台灣和蘭嶼的雌雄異株植物都顯示和木本生活型有顯著相關，而在喬木和藤本中所佔的比例都相當的高。在台灣本島 1,005 種木本被子植物中，有 175 種為雌雄異株植物（17.4%），而在 2,047 種草本植物中，則僅有 65 種（3.2%）為雌雄異株。雌雄異株植物的比例也隨著海拔升高而遞減。另外本研究在檢視了六個森林樣區中之所有原生被子植物資料，發現其中雌雄異株植物的比例有相當的變異，從林口紅土台地次生林的 14.1%，到南仁山熱帶森林的 23.9% 不等，後者甚至為目前所有發表樣區資料中雌雄異株比例最高的地區。

**關鍵詞：**雌雄異株植物；植物相；蘭嶼；生殖系統；台灣。



**Supplementary data 1.** References of recent taxonomic revisions referred in this paper for census, in addition to the Flora of Taiwan, 2nd edition.

Acanthaceae (Hsieh et al., 1999), Apiaceae (Chen and Wang, 2001; Shan et al., 1985), Araceae (Li, 1979), Araliaceae (Hoo and Tseng, 1978), Arecaceae (Pei et al., 1991), Asteraceae (Boufford and Peng, 1993; Chen, 1999; Chung and Peng, 2002; Chung et al., 2008; Ling et al., 1979), Begoniaceae (Peng and Sue, 2000; Peng et al., 2005), Brassicaceae (Al-Shehbaz and Peng, 2000), Boraginaceae (Wang and Shen, 2001; Wang et al., 1989), Burmanniaceae (Yang et al., 2002), Celastraceae (Liu and Yang, 2000), Commelinaceae (Chen, 1998), Convolvulaceae (Liao et al., 2000), Cornaceae (Yang and Liu, 2002), Elaeagnaceae (Huang, 2002), Elatinaceae (Huang, 1994), Euphorbiaceae (Chen, 2000; Chen and Wu, 1997; Hsu, 2003; Kiu et al., 1996; Li, 1994), Gentianaceae (Chen and Wang, 2000; Chen et al., 2006; Chen et al., 2008; Hsieh et al., 2007), Gesneriaceae (Wang and Wang, 2000; Wang et al., 1990), Hydrocharitaceae (Sun and Wang, 1992), Icacinaceae (Chuang, 1981), Labiatae (Huang et al., 2003), Liliaceae (Chen et al., 1980; Peng et al., 2007), Loranthaceae (Tam, 1988), Lythraceae (Huang et al., 1989), Malpighiaceae (Chen and Chen, 1997), Malvaceae (Cheng and Tsai, 1999), Menyanthaceae (Li et al., 2002), Melastomataceae (Yang and Liu, 2002), Meliaceae (Chen, 1997a), Moraceae (Tzeng, 2004), Mysinaceae (Chen, 1979), Nyctaginaceae (Zhou, 1996), Haloragaceae (Li and Hsieh, 1996), Oleaceae (Chang et al., 1992), Orchidaceae (Chung, 2002; Ormerod, 2002, 2003, 2004; Su, 2002), Poaceae (Kuoh, 2003), Polygalaceae (Hsieh et al., 1995), Polygonaceae (Kuo, 1997), Rhamnaceae (Chen and Chou, 1982; Liu et al., 1990), Rhizophoraceae (Lu et al., 1999), Rosaceae (Hsieh and Chaw, 1996; Hsieh and Huang, 1997; Lu et al., 2005; Yang and Liu, 2002), Rubiaceae (Lo et al., 1999a; Lo et al., 1999b), Rutaceae (Ho, 1995; Huang, 1997), Scrophulariaceae (Chen and Chou, 2008; Hsieh, 2000; Hsieh and Yang, 2002), Simaroubaceae (Chen, 1997b), Staphyleaceae (Hsu, 1981), Sterculiaceae (Hsu, 1984), Theaceae (Wu et al., 2003), Theligonaceae (Huang et al., 1989), Ulmaceae (Chen and Tang, 1998), Urticaceae (Hsu et al., 2003; Shih, 1995; Shih and Yang, 1998; Shih et al., 1995a; Shih et al., 1995b), Vitaceae (Hsu, 1999; Hsu and Kuoh, 1999; Hsu and Wu, 2000), and Zygophyllaceae (Huang and Hsieh, 1994).

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**Supplementary data 2.** List of species with uncertain sexual system in Taiwan and Orchid Island according to the Flora of Taiwan (Huang and Editorial Committee of the Flora of Taiwan, 1993, 1996, 1998, 2000, 2003).

Family	Species	Note
Anacardiaceae	<i>Rhus ambigua</i>	Description of the genus is polygamous but 3 out of 5 species in this genus are dioecious. Sexual system undescribed for the species.
	<i>Rhus hypoleuca</i>	Description of the genus is polygamous but 3 out of 5 species in the genus are dioecious. Sexual system undescribed for the species.
Apiaceae	<i>Peucedanum japonicum</i>	Description of the genus is polygamous. Sexual system undescribed for the species.
	<i>Peucedanum formosanum</i>	Description of the genus is polygamous. Sexual system undescribed for the species.
	<i>Torilis japonica</i>	Flowers' illustration show staminate flower and perfect flower. Sexual system undescribed for the species.
	<i>Torilis scabra</i>	Sexual system undescribed for the species.
Aponogetonaceae	<i>Aponogeton taiwanensis</i>	Flowers usually bisexual or rarely unisexual by abortion in the family. Sexual system undescribed for the species.
Araliaceae	<i>Dendropanax dentiger</i>	Description of the genus is bisexual or polygamous. Sexual system undescribed for the species.
	<i>Dendropanax trifidus</i>	Description of the genus is bisexual or polygamous. Sexual system undescribed for the species.
	<i>Eleutherococcus trifoliatus</i>	Description of the genus is perfect or polygamous. Sexual system undescribed for the species.
	<i>Pentapanax castanopsicola</i>	Description of the genus is bisexual or polygamous. Sexual system undescribed for the species.
Asteraceae	<i>Anaphalis nepalensis</i>	Description of the genus is dioecious or polygamo-dioecious. Sexual system undescribed for the species.
	<i>Anaphalis royleana</i>	Description of the genus is dioecious or polygamo-dioecious. Sexual system undescribed for the species.
	<i>Pterocypsela x mansuensis</i>	Sexual system undescribed for the species.
Clusiaceae	<i>Calophyllum blancoi</i>	Description of the species is flower (bisexual?).
Cyperaceae	<i>Hypolytrum nemorum</i>	Description of the genus is bearing a monandrous staminate flower. Sexual system undescribed for the species.
	<i>Rhynchospora rugosa</i> subsp. <i>brownii</i>	Other species in this genus are monoecious or polygamous or hermaphroditic. Sexual system undescribed for the species.
	<i>Rhynchospora malasica</i>	Other species in this genus are monoecious or polygamous or hermaphroditic. Sexual system undescribed for the species.
Icacinaceae	<i>Gomphandra luzoniensis</i>	Description of the genus is dioecious. Sexual system undescribed for the species.
Loranthaceae	<i>Korthalsella japonica</i>	Description of the genus is unisexual. Sexual system undescribed for the species.
Malpighiaceae	<i>Ryssopterys timoriensis</i>	Description of the genus is androdioecious in flora of Taiwan and usually unisexual in flora of China. Sexual system undescribed for the species.
Nyctaginaceae	<i>Pisonia umbellifera</i>	Description of species is unisexual in the Flora of Taiwan, polygamous in the Flora of China.
Oleaceae	<i>Chionanthus coriaceus</i>	Description of the genus is polygamous or dioecious. Sexual system undescribed for the species.
Rutaceae	<i>Phellodendron amurense</i> var. <i>wilsonii</i>	Description of the genus is dioecious in flora of Taiwan, dioecious or polygamous in (Ho, 1995). Sexual system undescribed for the species.
Simaroubaceae	<i>Brucea javanica</i>	The description of the genus is dioecious, but flower's illustration shows hermaphroditic.