

Gender variation and the evolution of dioecy in *Wurmbea dioica* (Liliaceae)

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Abstract

A major obstacle for empirical tests of hypotheses concerning the evolution of dioecy in flowering plants is the limited number of species that possess both cosexual and dioecious populations. *Wurmbea dioica* (Liliaceae) is a diminutive, fly-pollinated geophyte native to temperate Australia. Marked geographical variation of floral traits is evident, particularly with respect to sex expression. A survey of phenotypic gender in 45 populations from Western Australia (WA), South Australia (SA), Victoria (Vic) and the Australian Capital Territory (ACT) revealed two contrasting patterns. Populations in SA, Vic, and ACT were uniformly dimorphic for gender, containing female and male plants, whereas populations in WA were either monomorphic or dimorphic. In most dimorphic populations varying numbers of male plants produced hermaphrodite flowers (male inconstancy). There was a significant negative relationship between female frequency and the proportion of inconstant male plants. Depending on region and population, male plants produced more flowers of larger size than females. In WA monomorphic populations often occurred on rich, moist soils at high density, whereas dimorphic populations were more commonly found at lower density on shallow soils in drier areas. In an area of sympatry, plants with contrasting sexual systems flowered at different times and were ecologically differentiated. The patterns of gender variation in *W. dioica* indicate that dioecy has evolved via the gynodioecious pathway. The spread of females in monomorphic populations may be favoured where ecological conditions result in increased selfing and inbreeding depression in hermaphrodites.

Introduction

The evolution of dioecy, the presence of male and female plants within populations, has attracted much attention in recent years (reviewed in Thomson & Brunet,

1990). A variety of hypotheses have been proposed concerning the ecological and genetic conditions that favour selection of this form of gender dimorphism (Charlesworth & Charlesworth, 1978; Willson, 1979; Bawa, 1980; Givnish, 1980; Thomson & Barrett, 1981; Charnov, 1982; Lloyd, 1982; Muenchow, 1987). A major obstacle for empirical tests of these hypotheses has been the difficulty of finding plant groups that possess wide intraspecific variation in gender. Among the many dioecious taxa distributed among 37 orders of flowering plants, few are known in which different populations of a single species display both cosexual and dioecious sexual systems (e.g. as in *Ecballium elaterium*, Galán, 1946; Westergaard, 1958; *Isotoma fluviatilis*, McComb, 1968; *Sagittaria latifolia*, Wooten, 1971; *Cotula* spp., Lloyd, 1972). In common with other breeding system changes in flowering plants (see Baker, 1961; Barrett, 1989), the evolution of dioecy has usually been accompanied by reproductive character divergence and speciation restricting opportunities for microevolutionary investigations. Because of this difficulty, workers have resorted to comparative surveys in an effort to determine the ecological and life-history correlates associated with the origin of dioecy (see Thomson & Brunet, 1990). While these approaches have provided useful information on the associations between dioecy and various traits (e.g. fleshy fruits, small unspecialized flowers, woodiness) they often suffer from the difficulties of distinguishing between similarity, owing to convergent evolution, and that due to common ancestry (Felsenstein, 1985; Pagel and Harvey, 1988; Donoghue, 1989).

Another problem for empirical studies of the evolution of dioecy is the paucity of accurate information on the nature of variation in plant sex. Descriptions of the sexual systems of most plant species are notoriously unreliable and are based on a bewildering array of botanical terms (see Frankel and Galun, 1977, Pg. 11; Richards, 1986, Pg. 285 for examples), many of which were originally coined by Linnaeus (1737) and Darwin (1877). These typological descriptions are often based on limited sampling of herbarium material and can frequently give misleading information on the true extent of variation in gender within and among populations. In an effort to provide a quantitative approach for studies of plant sexual systems, Lloyd (1979a, 1980a) introduced methods for measuring the magnitude of gender variation in natural populations. The methods, discussed in detail in Lloyd and Bawa (1984), highlight the great variation that can occur in the performance of individuals as male or female parents. In addition, they also emphasize the basic dichotomy in plant sexual systems, between populations that are monomorphic for gender, with a unimodal distribution of gender values, and those that display a bimodal distribution and are dimorphic for gender. Application of gender measures provides the necessary quantitative basis for documenting the pathways of evolutionary change in sexual systems (Lloyd, 1980b) and, in conjunction with ecological and genetic studies, offer population biologists better opportunities for understanding the forces responsible for the evolution of gender dimorphism in plants.

Wurmbea dioica (R.Br.) F. Muell (Liliaceae) is a diminutive, fly-pollinated geophyte of widespread distribution throughout temperate Australia (Fig. 1). Populations occur in a wide variety of habitats including open rocky slopes in grasslands and pastures, granite outcrops, seepage slopes, stream edges and

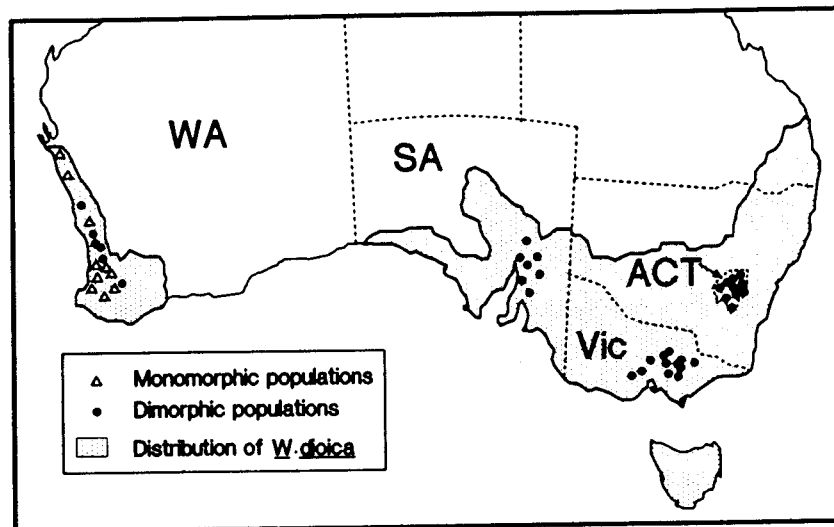


Fig. 1. Distribution of populations of *Wurmbea dioica* in temperate Australia sampled in the study. Populations were either monomorphic or dimorphic for gender. The distribution of *W. dioica* follows Macfarlane (1980). WA-Western Australia, SA-South Australia, Vic-Victoria, ACT-Australian Capital Territory. Populations of *W. dioica* in Western Australia are referred to as subsp. *alba*; populations from the remainder of the range are subsp. *dioica* (Macfarlane, 1980).

Eucalyptus woodlands. Populations are conspicuous in early spring (July–October, depending on region) and are among the first to flower in many communities, giving rise to the plant's common name Early Nancy. Botanical observations of the floral morphology of *W. dioica* populations suggest considerable variation in their sexual systems. In a recent monographic treatment of *Wurmbea* in Australia, Macfarlane (1980) described *W. dioica* as either dioecious, polygamodioecious, hermaphrodite or androhermaphrodite, whereas Ornduff (1985) described a population from Western Australia as a "mixed monoclinal-andromonoecious population containing two morphs". These reports indicate that sex expression in *W. dioica* is complex and that botanical terminology alone is likely to provide an incomplete description of gender variation in the species. To clarify the complex nature of sex expression in *W. dioica* I initiated a quantitative study of intraspecific variation in gender patterns in different parts of the geographical range of the species. Here I report on the results of this work and discuss their relevance for studies of the evolution of dioecy.

Methods

To investigate patterns of gender in *Wurmbea dioica* a total of 45 natural populations was sampled during the springs of 1983–84 in four regions of Australia: Western Australia (WA), South Australia (SA), Victoria (Vic), and the Australian Capital Territory (ACT). Localities of populations are given in the Appendix and mapped in Figure 1. In each population a random sample of flowering plants was obtained. Sampling is straightforward in *W. dioica* since clonal

propagation is absent and most mature individuals in populations are reproductive. The following attributes were recorded on each plant: 1) the total number of flowers. Most individuals produce a single inflorescence per season; 2) the sexual condition of each flower (e.g. hermaphrodite, female or male) and its position on the indeterminate spicate inflorescence (basal flower 1 opens first, next 2 etc.). The sexual condition of flowers is easily determined in *W. dioica*. Female flowers most commonly lack stamens; where present they possess short filaments and lack viable pollen. Male flowers possess shrunken non-functional gynoecia with non-elongated styles. Controlled hand-pollinations confirmed the absence of female function in male flowers with shrunken gynoecia.

In a subset of 12 populations (WA1,2,5,6,7,8; Vic2,5,11; ACT2,3,9) the diameter of two fully open flowers per plant (flower positions 1 and 2) were measured to compare flower size among gender classes and populations. Estimates of pollen production, ovule number, and open pollinated seed set were made for three populations (WA3, ACT2,3). Data on pollen and ovule numbers were obtained by preserving unopened flower buds in fixative (FAA) and following methods outlined in Barrett and Helenurm (1987). Sample sizes and details of ANOVAs used for comparisons of reproductive traits are provided in the appropriate tables and figures.

To quantify patterns of gender at the individual and population levels two methods were used. Within each population simple tallies of the relative frequencies of the three possible sex conditions (hermaphrodite, female and male) of flowers and individuals were made based on data collected from censuses of individual flowers. A second approach used data on the sexual condition of flowers and employed standardized measures of phenotypic gender (Lloyd, 1979a; Lloyd and Bawa, 1984). The method records the expenditure a given plant makes on pollen (l_i) and ovules (d_i) (or seeds) relative to the average ratio of expenditure in the population. In this study data on the number of ovule-bearing flowers (d_i) and polliniferous flowers (l_i) were used to estimate G_p , the standardized phenotypic femaleness of individual plants in each population by the formula:

$$G_p = \frac{d_i}{d_i + l_i E}$$

where E is an equivalence factor that measures the ratio of ovule-bearing to polliniferous flowers in the population as a whole:

$$E = \frac{\sum d_i}{\sum l_i}$$

A G_p value of 1.0 represents plants that produce only ovules and 0.0, plants that produce only pollen. Values of G_p were calculated for plants sampled in all populations and rank-gender plots portrayed for populations displaying representative patterns.

Results

Sex phenotypes

Populations of *Wurmbea dioica* exhibit complex patterns of sex expression within individuals, populations and geographical regions of Australia. A range of sex phenotypes was observed, with individual plants possessing different combinations of hermaphrodite, female or male flowers (Fig. 2). Patterns of sexual variation in *W. dioica* can be grouped into the two fundamental population-level gender patterns that occur in flowering plants. Here I follow the terminology established for these different gender patterns (Lloyd & Bawa, 1984) and refer to plants in monomorphic populations as cosexual, and plants in dimorphic populations as either female or male. Deviations from strict hermaphroditism and unisexuality occur in *W. dioica*; the nature of this variation is illustrated in Fig. 2 and discussed in detail below.

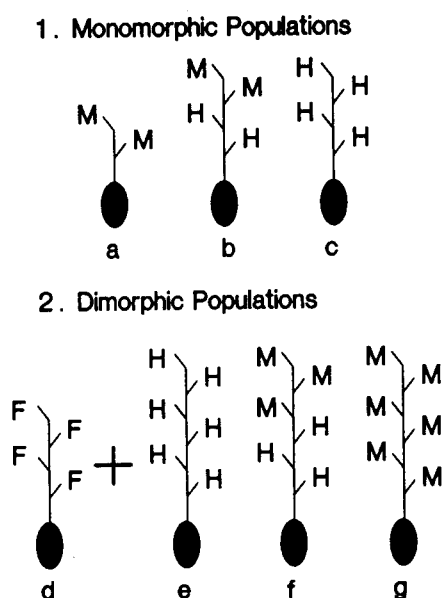


Fig. 2. Range of sex phenotypes that occur in Australian populations of *Wurmbea dioica* that are monomorphic or dimorphic for gender. Monomorphic populations exhibit continuous variation in gender with phenotypes (a–c) possessing different numbers of hermaphrodite (H) and male (M) flowers. Dimorphic populations display discontinuous variation in gender with two distinct classes of plants; females (d), with only female (F) flowers and males with continuous variation in the number of male and hermaphrodite flowers (e–g). Male plants bearing hermaphrodite flowers are referred to as inconstant males (Lloyd, 1976).

Geographical patterns

All populations of *W. dioica* surveyed in SA, Vic, and ACT were dimorphic for gender, whereas populations in WA were either monomorphic or dimorphic (Fig. 1). The frequencies of sex conditions within populations are listed in the Appendix

Table 1. The mean frequencies of female and male plants in 35 dimorphic populations of *Wurmbea dioica* sampled in four regions of Australia during 1983–4. See Appendix for data for individual populations.

Region	N		female	Mean frequency	
	populations	plants		constant	male inconstant
Western Australia*	6	1025	0.420	0.475	0.105
South Australia	7	633	0.474	0.525	0.001
Victoria	11	830	0.481	0.483	0.036
Australian Capital Territory	11	2196	0.358	0.522	0.120

* An additional 10 sexually monomorphic populations were sampled in WA.

and summarized by region in Table 1. Of the 16 populations sampled in WA, ten were monomorphic for gender, and the remaining six were dimorphic. Although no clear separation was evident in the geographical distribution of monomorphic and dimorphic populations in WA (Fig. 1), the former were more commonly encountered at moist sites on rich soils, whereas the latter frequently occurred in more arid sites on shallow soils.

Monomorphic populations

Variation between plants in sex expression was evident in all monomorphic populations of *W. dioica* sampled from WA. The commonest phenotype possessed only hermaphrodite flowers (Fig. 2c). A second phenotype (Fig. 2b) with hermaphrodite and male flowers occurred at varying frequencies in all populations sampled (mean frequency 0.31, range 0.02–0.70); such plants have been referred to as androhermaphrodite (McFarlane, 1980) or andromonoecious (Ornduff, 1985). Male flowers of this phenotype are always borne at distal positions in the inflorescence and hermaphrodite flowers at basal positions. The mean frequency of male flowers sampled on all plants in monomorphic populations was 0.15, range 0.01–0.33 (Appendix). In four populations a small number of plants possessed a third phenotype (Fig. 2a), with only male flowers (WA1 1 plant, WA2 3 plants, WA7 2 plants, WA16 12 plants). Plants of this phenotype were smaller on average than plants with hermaphrodite flowers, with 14 of the 18 plants sampled producing a single flower only. It seems likely that these plants may be relatively immature (or occur in stressful conditions, see below) and with subsequent growth may be capable of producing hermaphrodite flowers. If this is true the variation in sex expression of cosexual plants in monomorphic populations represents a continuum involving different combinations of hermaphrodite and male flowers.

Dimorphic populations

Male plants in dimorphic populations displayed patterns of gender variation similar to that observed in monomorphic populations (Fig. 2e–g). In 29 of the 35 populations surveyed, male plants bearing hermaphrodite flowers were observed. These plants are referred to as inconstant males (Lloyd, 1976). The probability of floral hermaphroditism declined from basal to distal positions within inflorescences of male plants (Fig. 2f). The average frequency of inconstant males within all dimorphic populations was 0.07, range 0–0.33. Among male plants sampled in dimorphic populations the average proportion bearing hermaphrodite flowers was 11.1%, range 0–50%. Male sex inconstancy was extremely rare in SA (a single plant in SA3), infrequent in Vic, but was commonly observed in WA and ACT (Table 1).

The fundamental difference between monomorphic and dimorphic populations of *W. dioica* resides in the presence of female plants in dimorphic populations (Fig. 2d). Sex inconstancy was not observed in female plants. In only five of the 35 dimorphic populations sampled was the frequency of female plants higher than that of males. Female frequencies averaged 0.43, range 0.22–0.61, with small but significant differences in average frequency evident among geographical regions (Table 1). Differences in female frequency among regions were associated with the magnitude of sex inconstancy in male plants. In regions with moderate levels of sex inconstancy (WA and ACT) female frequencies were lower on average than in regions with little sex inconstancy (SA and Vic). Overall there was a weak but significant negative relationship between female frequency and the frequency of male plants with sex inconstancy within populations (Fig. 3).

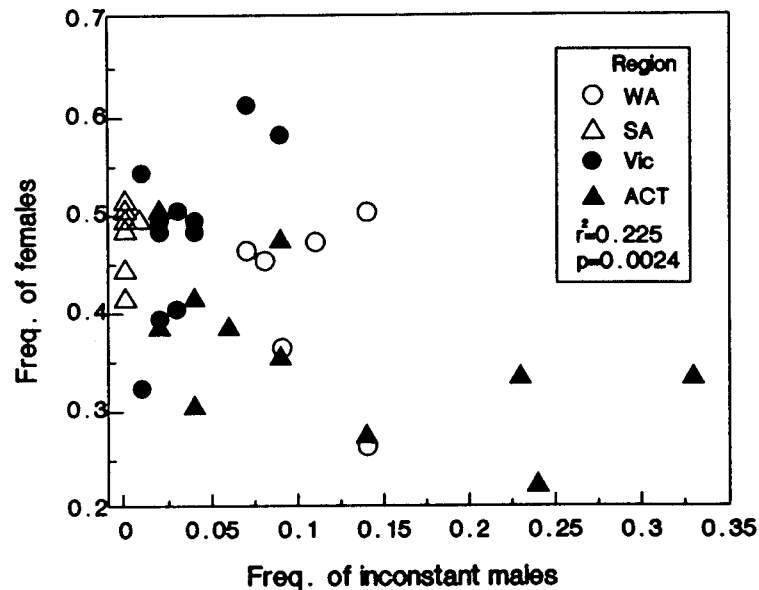


Fig. 3. The relationship between the frequency of females and the frequency of inconstant males in 35 Australian populations of *Wurmbea dioica* dimorphic for gender.

Collectively, the data on the frequencies of sex phenotypes in dimorphic populations indicate a continuum of gender variation among populations ranging from gynodioecy (populations with male sex inconstancy), to strict dioecy, with no male sex inconstancy (six populations in SA). Quantitative estimates of gender (see below) confirm the presence of near continuous variation among the dimorphic sexual systems of *W. dioica*.

Quantitative measures of gender

Rank distributions of standardized measures of phenotypic gender (G_p) for plants in six populations of *W. dioica* from different regions of Australia are illustrated in Fig. 4. The populations were chosen to represent the range in patterns of gender observed in *W. dioica*. Populations WA15,1,16 are monomorphic for gender with increasing numbers of plants bearing male flowers. Field observations suggested that part of this increase in phenotypic maleness of plants in the populations sampled was associated with a decrease in the moisture status of soils and more stressful growing conditions. Population WA16 was exceptional among monomorphic populations in containing a significant number of plants producing only male flowers. Mean flower number per plant in this population (1.9, range 1–3) was the second lowest (after WA7, mean 1.6 range 1–3) observed in the entire survey (see Appendix).

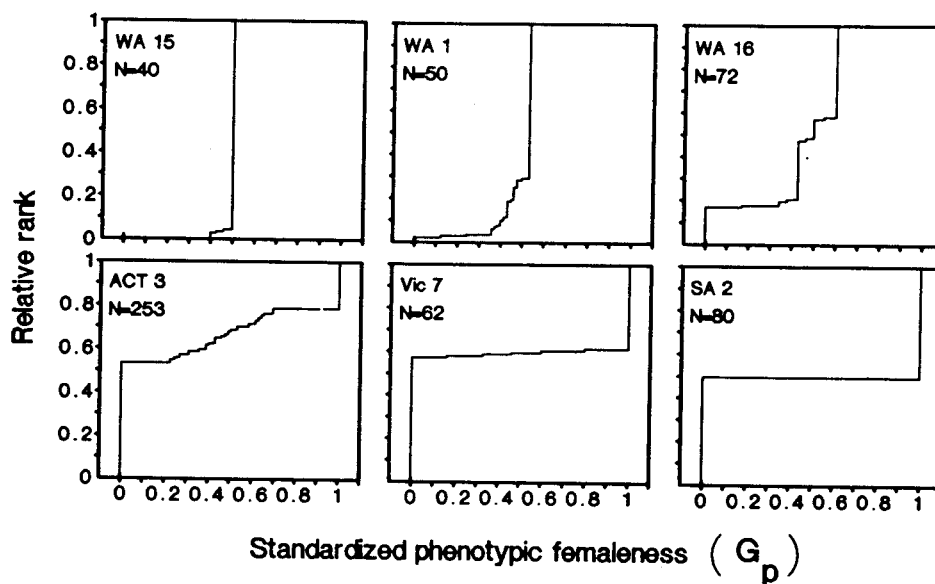


Fig. 4. Variation in phenotypic gender among six populations of *Wurmbea dioica* from Australia. Each distribution is the relative rank (rank divided by sample size) of standardized phenotypic femaleness (G_p) for samples of plants obtained from each population. See text for method of calculation of G_p . Populations WA15,1,16 are monomorphic for gender, populations ACT3, Vic7, SA2 are dimorphic. Plants with a G_p value of 0 and 1 are strictly male and female, respectively.

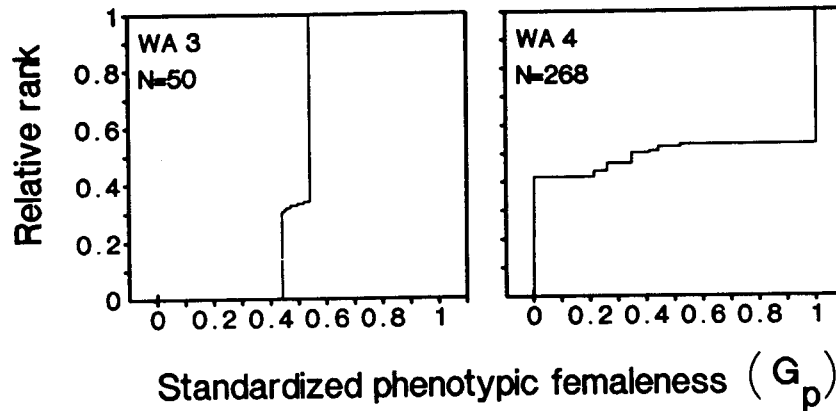


Fig. 5. Contrasting patterns of phenotypic gender in two sub-populations of *Wurmbea dioica* growing in close proximity on a hillside in the Darling Range, near Gosnells, S.W. Australia. Sub-population WA3 is monomorphic for gender whereas WA4 is dimorphic. The two sub-populations were ecologically segregated and differed in plant density and flowering time (see text for details).

Rank distributions of phenotypic gender for three dimorphic populations (ACT3, Vic7, SA2) are also illustrated in Fig. 4. The populations differ in female frequency and in the degree of male inconstancy. Population SA2 is strictly dioecious with equal frequencies of female and male plants. Populations with low female frequencies (e.g. < 0.20) and high levels of seed set in male plants were the only part of the continuum in gender not represented among the dimorphic populations surveyed.

In Western Australia monomorphic and dimorphic populations of *W. dioica* occasionally occur in the same area. At a locality on the Darling Range near Perth (Mills Road, Gosnells), two sub-populations displaying different patterns of gender were found on the same hillside growing within 10 metres of one another. Gender plots for the two sub-populations are illustrated in Fig. 5. Plants belonging to the two sub-population were ecologically differentiated and exhibited different flowering times. The dimorphic sub-population (WA4) was composed of scattered plants at low density on rocky well-drained soils. In 1984 the flowering period for this sub-population was from late June–July. In contrast, plants in the monomorphic sub-populations (WA3) flowered in late July and August (1984), and occurred in patches of high density on rich waterlogged soils associated with drainage seeps. There were no significant differences in mean flower number among the sexual morphs in the two sub-populations (WA3, hermaphrodite, 2.5; WA4, female, 2.3; male, 2.5; $F_{2,315} = 2.24$; $P = 0.1083$).

Variation in reproductive traits

The total number of flowers produced per plant during a single season in dimorphic populations differed significantly among regions, populations within

Table 2. Mixed model analysis of variance of the effect of region (fixed), populations within regions (random), and sexual morph (fixed) on the logarithm of flower number per plant in 35 dimorphic populations of *Wurmbea dioica*. The appropriate expected mean square error was calculated using the random test option in the GLM procedure of SAS (SAS Institute, 1988). The Satterwaite (1946) approximation was used to calculate the degrees of freedom where the mean square error is a composite of more than one source (*). Since the Region \times Morph interaction was not significant tests of main effects were legitimate.

Source	df	MS	F	P
Region*	3	17.07	38.97	0.0001
Morph*	1	3.23	42.62	0.0001
Region \times Morph*	3	0.06	0.77	0.5199
Populations (Region)	31	0.51	5.815	0.0001
Morph \times Population (Region)	31	0.09	2.98	0.0001
Error	4614	0.03		

regions, and between female and male plants (Table 2). Data for individual populations are given in the Appendix. Most of the variation in flower number was accounted for by the effect of region and sexual morph. Mean flower number was highest in the ACT and lowest in populations from Vic and WA (Fig. 6). In WA mean flower number was significantly higher in dimorphic populations in comparison with monomorphic populations ($F_{1,1456} = 30.91$; $P < 0.0001$).

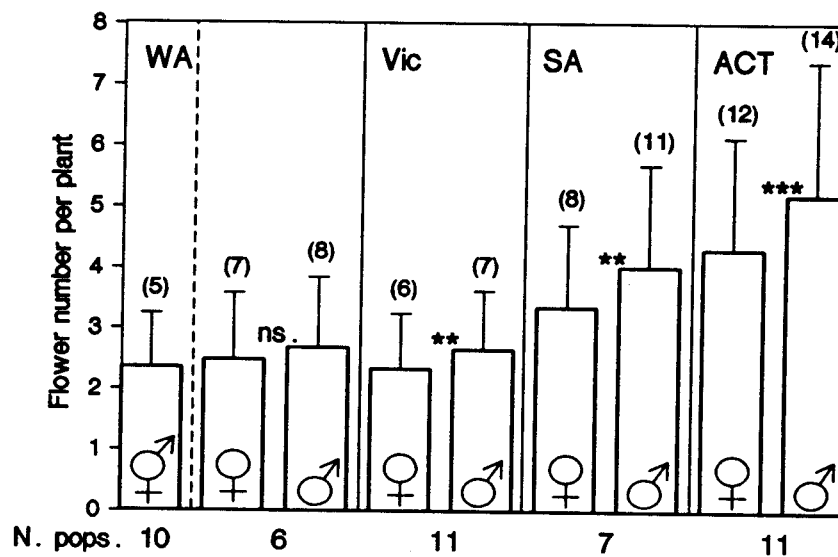


Fig. 6. The number of flowers per plant in the sexual morphs of *Wurmbea dioica* from different regions of Australia. The histograms represent the grand mean with standard deviation and maximum (in parentheses) flower number of morphs within each region. The total number of populations sampled is also given. ANOVA results for differences within each region in flower number (\log_{10} transformed) in males and females: WA - $F_{1,5.40} = 5.80$; $P = 0.573$; Vic - $F_{1,11.60} = 6.76$; $P = .0238$; SA - $F_{1,6.35} = 9.239$; $P = .0213$; ACT - $F_{1,10.25} = 30.64$; $P = 0.0002$.

In 32 of the 35 dimorphic populations sampled, male flower number was greater than female flower number. Within each region ANOVA results indicated that male plants produced significantly more flowers than female plants in SA, Vic and ACT but not in WA (Fig. 6). Sequential Bonferroni tests (Holm, 1979), with a table-wide significance level of 5%, indicated that male flower number was significantly higher than female flower number in 2 of the 6 populations sampled in WA. In each region mean maximum flower number was always greater in male plants than in female plants (Fig. 6).

Flower size also differed among regions, populations and between sexual morphs. Flower sizes were most variable among monomorphic populations in WA (Table 3). In each of the seven dimorphic populations sampled, mean flower diameter was greater in male plants than female plants, but in only five (WA8, Vic5, ACT2,3,9) was this difference significant. The largest differences in flower size between female and male plants were in populations from ACT (Table 3). Only one dimorphic population was sampled in WA, therefore quantitative comparisons among gender morphs in this region were not possible. Field observations in WA, however,

Table 3. Flower diameter (in mm) in 12 populations of *Wurmbea dioica* with contrasting patterns of gender from different regions of Australia. (M-monomorphic, D-dimorphic).

Region & Population	Gender	Mean	Standard deviation	Range	N
Western Australia					
WA 1	M ♂	18.8	3.26	13–25	20
WA 2	M ♂	15.7	3.08	9–22	20
WA 5	M ♂	19.3	2.91	14–24	20
WA 6	M ♂	21.9	1.90	19–26	20
WA 7	M ♂	11.2	2.12	8–16	20
WA 8	D ♀	6.9	1.13	5–8	8
	♂	10.4***	1.76	7–14	27
Victoria					
Vic 2	D ♀	14.1	2.18	12–20	20
	♂	15.8	2.08	12–20	20
Vic 5	D ♀	14.7	1.55	11–17	20
	♂	17.3***	1.98	13–20	20
Vic 11	D ♀	14.1	2.20	10–18	20
	♂	15.2	1.44	12–17	20
ACT					
ACT 2	D ♀	14.1	1.74	11–18	20
	♂	21.3***	2.74	16–26	20
ACT 3	D ♀	12.5	2.33	8–16	20
	♂	20.4***	3.03	16–25	20
ACT 9	D ♀	11.6	2.52	8–17	20
	♂	19.9***	2.15	15–24	20

*** $P < 0.001$

Table 4. Mean and standard deviation of pollen production, ovule number, and open-pollinated seed set per flower in three populations of *Wurmbea dioica* with contrasting patterns of gender.

Trait	Monomorphic WA 3	Dimorphic ACT 2	Dimorphic ACT 3
sex phenotype	♂	♀	♂
sample size (flowers)	16	15	12
pollen number per flower	136,361 ^a 58,961	–	88,062 ^b 30,782
ovule number per flower	53.4 ^a 13.9	83.7 ^b 14.3	–
seed set per fruit (n = 20)	22.7 ^a 10.1	27.6 ^a 13.0	–

ANOVA results: pollen number – $F = 33.6$, $P < 0.001$, analysis conducted on raw haemocytometer counts, ovule number – $F = 27.2$, $P < 0.001$; seed set – $F = 1.31$ ns. Shared letters indicate means that are not significantly different following Bonferroni (Dunn) T test for variable.

indicated that cosexual plants in monomorphic populations possessed larger flowers than female plants in dimorphic populations.

Data on pollen production, ovule number and open-pollinated seed set per flower in a monomorphic and two dimorphic populations are presented in Table 4. Ovule number was significantly lower in the monomorphic population in comparison with the two dimorphic populations. However, the proportion of ovules maturing into seed was considerably lower in the two dimorphic populations, since seed set per flower did not differ significantly among the three populations. Significant differences in mean pollen production per flower were evident among the three populations. Pollen production was highest in WA3 (monomorphic) and lowest in ACT2 (dimorphic). More extensive sampling of populations is required to determine whether the observed differences in reproductive traits are generally associated with the two gender conditions.

Discussion

The major finding of this study is that *Wurmbea dioica* possesses two distinct classes of sexual system. Natural populations are either monomorphic or dimorphic for gender. Within each of these two classes there is considerable variation in the sexual condition of flowers and plants resulting in a range of sex phenotypes within populations. In monomorphic populations loss of female function in hermaphrodite flowers produces continuous variation in the number of hermaphrodite and male flowers borne by cosexual plants. At one extreme are individuals with only hermaphrodite flowers; at the other are small numbers of plants bearing only male

flowers. These end points are linked by individuals with different numbers of hermaphrodite and male flowers. The relative importance of ecological and genetic controls on this variation is unknown. However, the occurrence of male flowers at distal positions within inflorescences, and the association between small plant size and the production of male-only flowers, suggest that the suppression of gynoeceial development may be, in part, associated with resource limitation owing to stress conditions or immature plant status (see Lloyd & Bawa, 1984; Whalen and Costich, 1986; Diggle, 1988).

Similar patterns of gender variation occur in the male morph of dimorphic populations. Males display considerable sex inconstancy, giving rise to continuous variation in gender values from plants bearing only male flowers, the commonest phenotype, to those with only hermaphrodite flowers. As in the case of cosexual individuals in monomorphic populations these extremes are joined by plants with different numbers of hermaphrodite and male flowers. However, the presence of purely female plants in dimorphic populations distinguishes them from monomorphic populations. In addition, while in dimorphic populations plants bearing only male flowers are common and plants bearing only hermaphrodite flowers are rare, in monomorphic populations this pattern is reversed.

While the morphological nature of variation in cosexual and male plants is quite similar, their respective functional roles in monomorphic and dimorphic populations are quite different. On average, cosexual plants must transmit genes equally through both female and male function. In contrast, the presence of female plants in dimorphic populations ensures that, on average, male plants will be more effective as pollen parents, notwithstanding the ability of some individuals to produce varying amounts of seed. Studies of variation in the functional gender of individuals, using genetic markers, would be required to determine their relative genetic contributions to the next generation through male and female function (Meagher, 1986).

The complex nature of gender variation in *W. dioica* limits the usefulness of typological descriptions of sexual conditions based on botanical terminology. In addition, the marked regional patterns of gender differentiation point to the need for quantitative approaches involving population samples over a wide geographical area. A recent study by Ornduff (1985) of a single population of *W. dioica* from WA concluded that it contained a sexual polymorphism involving "monoclinous and andromonoecious morphs". As the present study demonstrates, however, when this pattern is considered within a broader quantitative framework it can be seen that this description is misleading and results from an attempt to force continuous variation into discrete categories. My own sampling of this population (WA5 in Appendix) indicated that it was monomorphic for gender (Mean G_p 0.50, range 0.36–0.53), with continuous variation in the number of hermaphrodite and male flowers borne by cosexual plants.

A related problem concerning botanical terminology involves the range of sexual variation that occurs within dimorphic populations of *W. dioica*. Populations can be classified as either gynodioecious, sub-dioecious, or dioecious depending on the

magnitude of sex inconstancy in males and the frequency of females. These sexual systems frequently form a continuum and opinions differ as to where the boundaries between them should be drawn (Lloyd, 1976). Gynodioecy, in particular, has not been treated as a uniform system but as a wide range of conditions involving gender dimorphism with inconstancy restricted to the male sex. At one extreme, near the cosexual end of the continuum, female frequencies are low and male plants exhibit high levels of seed production. At the other end, where populations approach dioecy, female frequencies are close to 50% and inconstancy in the male morph is uncommon.

Evolutionary considerations

The genus *Wurmbea* is likely of African origin with 14 species reported from the continent, particularly southern Africa (Nordenstam, 1964, 1978). Since African species are uniformly hermaphroditic (Macfarlane, 1980) it seems likely that dioecy may have originated during establishment and spread of the genus in Australia. Species diversity in *Wurmbea* is highest in WA, with 16 of the 20 Australian species reported from the region and most restricted to it (Macfarlane, 1980, 1986). This suggests that the genus may have initially established in WA, after dispersal from Africa, followed by eastward migration to other parts of the continent. The occurrence of several dioecious *Wurmbea* species in WA (Macfarlane, 1980), as well as monomorphic and dimorphic populations of *W. dioica*, suggests that dioecy may have originated in this region, followed by migration of dimorphic populations to other parts of temperate Australia. When, and how often, dioecy has evolved in *Wurmbea* is not known but the patterns of gender variation suggest the possibility of multiple origins for the polymorphism in the genus. Since the degree of gender dimorphism varies both intraspecifically (this study) and interspecifically (see Macfarlane, 1980) it is possible that dioecy is of relatively recent origin in some taxa.

Dioecy has arisen independently from hermaphroditism on many occasions in the flowering plants by several different evolutionary pathways (Charlesworth and Charlesworth, 1978; Lloyd, 1979b, 1980b; Bawa, 1980; Ross, 1982). There is evidence that dioecy has evolved from hermaphroditism via gynodioecy, monoecy, and heterostyly. The range of gender variation found in *W. dioica* provides important clues concerning the likely evolutionary pathway by which dioecy originated in the species. The series of sexual systems connecting hermaphroditism and dioecy strongly suggest an evolutionary sequence involving the gynodioecious pathway. This sequence, involving a gradual reduction in the seed set of males, following the spread of female plants in cosexual populations, is perhaps the commonest pathway by which dioecy has evolved and has been documented in several unrelated families (e.g. Burrows, 1960; Connor, 1973; Arroyo and Raven, 1975; Webb, 1979; Delph, 1990a).

Microevolutionary studies of *W. dioica* in WA would be of particular value for understanding the evolution of gender dimorphism in the genus. Field observations indicated that although monomorphic and dimorphic populations were not strongly

segregated on a geographical level within WA, some degree of ecological differentiation occurs. While monomorphic populations were more commonly encountered on rich, wet soils, dimorphic populations were often found on shallow soils under more arid conditions. This pattern was evident at both wider geographical and local scales. Along the Darling Range, near Perth, ecological differentiation was associated with differences in plant density and flowering time. Clearly, more detailed ecological data are required to determine whether these differences are generally associated with the two sexual systems. It is interesting to note that in one of the few other species with gender monomorphism and dimorphism (*Ecbalium elaterium*), monoecious and dioecious populations are ecologically segregated, with the latter occurring in more arid parts of Spain (Costich and Galán, 1988; Costich, 1989). Similarly, Arroyo and Squeo (1990) have documented a higher incidence of sexual dimorphism in Patagonian plant communities that experience harsh growing conditions. In these cases, field studies are required to address whether the observed ecological correlates are a cause or a consequence of differences in sexual system.

Selective forces

Attempts to determine the selective forces responsible for the evolution of dioecy are fraught with difficulty (Thomson and Brunet, 1990). Several of the life history correlates associated with dioecy (e.g. fleshy fruits, woodiness and large plant size) do not, however, occur in *Wurmbea*. This eliminates several of the possible ecological mechanisms invoked by some authors to account for the evolution of dioecy (e.g. Willson, 1979; Bawa, 1980; Givnish, 1980). Details of the floral biology of *W. dioica*, in conjunction with ecological observations made in this study, suggest a working hypothesis that may explain the evolution of gender dimorphism in the species.

While flowers of *W. dioica* are similar to many animal-pollinated dioecious plants in being white, relatively small, and pollinated by unspecialized insects (e.g. flies – Macfarlane, 1980; S. C. H. Barrett, unpubl. data), they differ in being produced in very small numbers during each flowering season, even in fully mature plants. Work on the floral biology of *W. dioica* indicates that plants are self-compatible, individual flowers are long-lived, strongly protogynous with protracted anther dehiscence, and populations flower in early spring (S. C. H. Barrett, unpubl. data). In monomorphic populations, particularly those at high density, opportunities for geitonogamy may be limited because of the extremely low flower number per plant and reliable pollinator service. The later flowering time of monomorphic populations compared with dimorphic populations may be associated with increased pollinator activity, owing to more favourable climatic conditions. Under these conditions high rates of outcrossing seem likely, particularly if pollinator service is reliable. Under these ecological circumstances, it is difficult to imagine what advantages a female mutant might benefit from particularly since the available data (Fig. 6, Table 4) provides no evidence to suggest that male sterility in WA is

associated with significant reproductive compensation (e.g. elevated flower number or seed set).

Where monomorphic populations of *W. dioica* encounter more stressful conditions (e.g. migration inland away from coastal areas of Western Australia with higher rainfall) a different situation may arise. In more arid sites plant density is generally lower and flowering occurs earlier in the season. These factors may result in less reliable pollinator service and increased levels of self-pollination. Under these conditions, sufficient inbreeding depression may occur to provide an outbreeding advantage to females, thus favouring the establishment of gynodioecy. The long-lived flowers of *W. dioica* may be particularly susceptible to increased self-pollination when pollinator visits become unreliable. Prolonged anther dehiscence makes it likely that considerable overlap in male and female function will occur. Despite protogyny stigmas may not receive outcross pollen before anthers open in the same or different flowers on an inflorescence. Since flies forage in an unsystematic fashion on inflorescences (S. C. H. Barrett, pers. observ.) considerable opportunities for self- and geitonogamous pollination are likely to exist. The evolution of unisexual flowers in *Wurmbea* may therefore be a solution to resolving conflicts between the optimal timing of stigma receptivity and anther dehiscence in monomorphic populations confronted with an altered pollinator regime.

Similar models involving altered pollinator regimes, increased selfing, and inbreeding depression have been proposed by Ganders (1978), Delph (1990b) and Weller and Sakai (1990) to account for the evolution of gender dimorphisms, in *Nemophila*, *Hebe* and *Schiedea*, respectively. These models all require a demonstration of 1) increased selfing rates associated with altered or reduced pollinator service and 2) sufficient inbreeding depression to favour the spread of females. Comparative data from monomorphic and dimorphic populations of *W. dioica* on the duration of female and male function at the flower and plant level, pollinator visitation rates, and delivery of outcross pollen would be valuable for assessing whether the floral biology of monomorphic populations makes them susceptible to invasion by females, particularly when growing in stressful conditions at low density.

Genetic data on the inheritance of male sterility in *W. dioica* is required to assess the validity of the inbreeding depression hypothesis outlined above. Genetic models of the evolution of dioecy (e.g. Charlesworth and Charlesworth, 1978) suggest that nuclear control of sex expression is likely to lead to the evolution of dioecy, with gynodioecy representing an unstable intermediate step. In contrast, cytoplasmic or nuclear-cytoplasmic mechanisms of sex determination can result in stable gynodioecous breeding systems involving a wide range of female frequencies (Frank, 1989). If these latter forms of sex determination occur in *W. dioica* then the evolutionary scenario proposed above is likely to be a good deal more complex.

Once females become established in *W. dioica* populations the next question concerns the conditions that favour the subsequent evolution of dioecy from gynodioecy. As discussed above, this evolutionary pathway is well documented and results from the gradual sterilization of ovules in male plants. Charlesworth and Charlesworth (1978) have modelled the spread of genetic modifiers influencing

female fertility. Their results indicate that the presence of females in a population makes it considerably easier for modifiers reducing female fertility to spread, but that some increase in pollen fitness in male plants is always required (and see Charlesworth, 1989). The situation in *Wurmbea* is particularly interesting in this regard because of the wide variation in gender already present in monomorphic populations. If at least some of this variation has a genetic basis the evolution of maleness would be greatly facilitated.

Comparative work on reproductive allocation is required to determine whether reductions in ovule fertility in male plants are associated with increased pollen production. Detailed studies of reproductive compensation in monomorphic and dimorphic populations from WA would be particularly important since populations appear to represent early stages in the evolution of gender dimorphism. If this is true it would enable a more realistic assessment of whether male sterility and female sterility mutations have direct effects on patterns of reproductive allocation, once they arise in populations. Variation in the magnitude of gender dimorphism among regions (e.g. flower size and flower number differences between female and males) may reflect differences in the intensity of sexual selection and/or different amounts of genetic divergence from the ancestral hermaphrodite condition. Whatever the cause(s), the existence of this variation in *W. dioica* provides an unusual opportunity to examine the changes in life history and allocation patterns that accompany the evolution of gender dimorphism in plants.

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References

- Arroyo, M. T. K. de. and F. Squeo. 1990. Relationship between plant breeding systems and pollination, pp. 205–227. In S. Kawano (ed.), *Biological Approaches and Evolutionary Trends in Plants*. Academic Press, London.
- Arroyo, M. T. K. de. and P. H. Raven. 1975. The evolution of sub-dioecy in morphologically gynodioecious species of *Fuchsia* Sect. *Encliandra* (Onagraceae). *Evolution* 29: 500–511.
- Baker, H. G. 1961. Rapid speciation in relation to changes in the breeding system of plants, pp. 881–885. In *Recent Advances in Botany*. University of Toronto Press, Toronto.
- Barrett, S. C. H. 1989. Mating system evolution and speciation in heterostylous plants, pp. 257–283. In D. Otte and J. A. Endler (eds.), *Speciation and its Consequences*. Sinauer Associates Inc., Mass.
- Barrett, S. C. H. and K. Helenurm. 1987. The reproductive biology of boreal forest herbs. I. Breeding systems and pollination. *Can. J. Bot.* 65: 2036–2046.
- Bawa, K. S. 1980. Evolution of dioecy in flowering plants. *A. Rev. Ecol. Syst.* 11: 15–39.

- Burrows, C. J. 1960. Studies in *Pimelea*. I. The breeding system. *Trans. Soc. New. Zeal.* 88: 29–45.
- Charlesworth, D. 1989. Allocation to male and female function in hermaphrodites in sexually polymorphic populations. *J. Theor. Biol.* 139: 327–342.
- Charlesworth, B. and D. Charlesworth. 1978. A model for the evolution of dioecy. *Am. Nat.* 112: 975–997.
- Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton University Press, Princeton.
- Connor, H. E. 1973. Breeding systems in *Cortaderia* (Gramineae). *Evolution* 27: 663–678.
- Costich, D. E. 1989. The ecology of breeding-system variation in *Ecballium elaterium* (L.) A. Rich. Ph.D. Thesis, University of Iowa, Iowa City.
- Costich, D. E. and F. Galán. 1988. The ecology of monoecious and dioecious subspecies of *Ecballium elaterium* (L.) Richard (Cucurbitaceae). I. Geographic distribution and its relationship to climatic conditions in Spain. *Lagascalia* 15: 697–710.
- Delph, L. F. 1990a. Sex ratio variation in the gynodioecious shrub *Hebe strictissima* (Scrophulariaceae). *Evolution* 44: 134–142.
- Delph, L. F. 1990b. The evolution of gender dimorphism in New Zealand *Hebe* (Scrophulariaceae) species. *Evolutionary Trends in Plants* 4: 85–97.
- Darwin, C. 1877. *Different Forms of Flowers on Plants of the Same Species*. J. Murray, London.
- Diggle, P. K. 1988. Labile sex expression in the andromonoecious *Solanum hirtum*. Ph.D. Thesis, University of California, Berkeley.
- Donoghue, M.J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43: 1137–1156.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125: 1–15.
- Frank, S. A. 1989. The evolutionary dynamics of male sterility. *Am. Nat.* 133: 345–376.
- Frankel, R. and E. Galun. 1977. *Pollination Mechanisms, Reproduction and Plant Breeding*. Springer-Verlag, New York.
- Galán, F. 1946. Sur la génétique de la monoécie et la dioécie zygotique chez *Ecballium elaterium* Rich. *C.R. Acad. Sci. Paris* 222: 1130–1131.
- Ganders, F. R. 1978. The genetics and evolution of gynodioecy in *Nemophila menziesii* (Hydrophyllaceae). *Can. J. Bot.* 56: 1400–1408.
- Givnish, T. J. 1980. Outcrossing versus ecological constraints in the evolution of dioecy. *Am. Nat.* 119: 849–865.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* 6: 65–70.
- Linnaeus, C. 1737. *Genera Plantarum*. 1st ed. Microfiche, International Documentation Centre, Tumba, Sweden.
- Lloyd, D. G. 1972. Breeding systems in *Cotula* L. (Compositae, Anthemideae). I. The array of monoclinal and diclinous systems. *New Phytol.* 71: 1181–1194.
- Lloyd, D. G. 1976. The transmission of genes via pollen and ovules in gynodioecious angiosperms. *Theor. Pop. Biol.* 9: 299–216.
- Lloyd, D. G. 1979a. Parental strategies of angiosperms. *New Zeal. J. Bot.* 17: 596–606.
- Lloyd, D. G. 1979b. Evolution towards dioecy in heterostylous populations. *Pl. Syst. Evol.* 131: 71–80.
- Lloyd, D. G. 1980a. Sexual strategies in plants. III. A quantitative method for describing the gender of plants. *New Zeal. J. Bot.* 18: 103–108.
- Lloyd, D. G. 1980b. The distributions of gender in four angiosperm species illustrating two evolutionary pathways to dioecy. *Evolution* 34: 103–108.
- Lloyd, D. G. 1982. Selection of combined versus separate sexes in seed plants. *Am. Nat.* 120: 571–585.
- Lloyd, D. G. and K. S. Bawa. 1984. Modification of the gender of seed plants in varying conditions. *Evol. Biol.* 17: 255–388.
- Macfarlane, T. D. 1980. A revision of *Wurmbea* (Liliaceae) in Australia. *Brunonia* 3: 145–208.
- Macfarlane, T. D. 1986. Two new species of *Wurmbea* (Colchicaceae or Liliaceae s. Lat) from south Western Australia. *Nuytsia* 5: 407–413.
- McComb, J. A. 1968. The occurrence of unisexuality and polyploidy in *Isotoma fluviatilis*. *Aust. J. Bot.* 16: 525–537.

- Meagher, T. R. 1986. Analysis of paternity within a natural population of *Chamaelirium luteum*. I. Identification of most-likely male parents. *Am. Nat.* 127: 199–215.
- Muenchow, G. E. 1987. Is dioecy associated with fleshy fruits? *Amer. J. Bot.* 74: 287–293.
- Nordenstam, B. 1964. Studies in South African Liliaceae. I. New species of *Wurmbea*. *Bot. Not.* 117: 173–182.
- Nordenstam, B. 1978. The genus *Wurmbea* in Africa except the Cape region. *Notes Roy. Bot. Gard. Edinburgh* 36: 211–233.
- Ornduff, R. 1985. Comparative fecundity of morphs in a mixed monoclinal-andromonoecious population of *Wurmbea dioica* subsp. *alba* (Liliaceae) in Western Australia. *Pl. Syst. Evol.* 149: 299–302.
- Pagel, M. D. and P. H. Harvey. 1988. Recent developments in the analysis of comparative data. *Quart. Rev. Biol.* 63: 413–440.
- Richards, A. J. 1986. *Plant Breeding Systems*. George Allen and Unwin, London.
- Ross, M. D. 1982. Five evolutionary pathways to sub-dioecy. *Am. Nat.* 119: 297–318.
- SAS Institute. 1988. *SAS/STAT user's guide: statistics*. SAS Institute, Cary NC., U.S.A.
- Satterwaite, F. E. 1946. An approximate distribution of estimates of variance components. *Biometric Bulletin* 2: 110–114.
- Thomson, J. D. and S. C. H. Barrett. 1981. Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. *Am. Nat.* 118: 443–449.
- Thomson, J. D. and J. Brunet. 1990. Hypotheses for the evolution of dioecy in seed plants. *Trends in Ecol. and Evol.* 5: 11–15.
- Webb, C. J. 1979. Breeding systems and the evolution of dioecy in New Zealand Apiod Umbelliferae. *Evolution* 33: 662–672.
- Westergaard, M. 1958. The mechanism of sex determination in dioecious flowering plants. *Adv. Genet.* 9: 217–281.
- Weller, S. G. and A. K. Sakai. 1990. The evolution of dicliny in *Schiedea* (Caryophyllaceae), an endemic Hawaiian genus. *Plant Species. Biology* 5: 83–96.
- Whalen, M. D. and D. E. Costich. Andromonoecy in *Solanum*, pp. 284–302. *In* D'Arcy, W. G. (ed.). *Solanaceae Biology and Systematics*. Columbia Univ. Press, N. Y.
- Willson, M. F. 1979. Sexual selection in plants. *Am. Nat.* 113: 777–790.
- Wooten, J. W. 1971. The monoecious and dioecious conditions in *Sagittaria latifolia* L. (Alismataceae). *Evolution* 25: 549–553.

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Appendix

The frequencies of sex condition in plants and flowers sampled in 45 populations of *Wurmbea dioica* from different regions of Australia with localities and sample sizes. Also given is the average number of flowers per plant for sex phenotypes within each population.

Pop. Locality	Plants		Flowers		\bar{x} flowers/plant			
	N	♀	♂	♀	♂	♀	♂	
Western Australia - monomorphic populations								
1 Beckenham, Perth	50	-	.02	.98	.11	.89	-	2.8
2 Gosnells, Mills Rd.	50	-	.06	.94	.24	.76	-	1.9
3 Gosnells, Mills Rd.	50	-	0	1.0	.13	.87	-	2.5
5 Medina, Johnson Rd	50	-	0	1.0	.11	.89	-	2.5
6 The Lakes, Dooning Rd.	50	-	0	1.0	.03	.97	-	3.2
7 Meckering, Reynolds Rd.	23	-	0.9	.91	.11	.89	-	1.6
12 Badgingarra, Brand Hwy.	10	-	0	1.0	.25	.75	-	2.8
14 Geraldton, E. Chapman Rd.	52	-	0	1.0	.19	.81	-	2.4
15 Northampton, Chilimony Rd.	40	-	0	1.0	.01	.99	-	2.0
16 Serp. Nat. Park, Scribner Rd.	72	-	.17	.83	.33	.67	-	1.9
Western Australia - dimorphic populations								
4 Gosnells, Mills Rd.	268	.47	.42	.11	.48	.06	2.3	2.5
8 Bindoon, Calingiri Rd.	299	.2	.60	.14	.68	.08	1.8	2.0
9 Barbeton, Moora Rd.	123	.4	.46	.08	.55	.05	2.3	2.9
10 Cataby, Dandaragon Rd.	148	.3	.55	.09	.68	.03	3.1	4.3
11 Cataby, Brand Hwy.	58	.5	.36	.14	.49	.07	2.2	2.8
13 Eneabba Creek, Brand Hwy.	129	.46	.47	.07	.49	.03	2.9	2.7
South Australia - dimorphic populations								
1 Burra, Burra Ck. Gorge	56	.41	.59	0	.93	0	2.9	2.8
2 Orroro, Wilmington Rd.	80	.50	.50	0	.54	0	3.1	3.7
3 Mambay Ck., Mt. Remarkable N.P.	125	.49	.50	.01	.61	<0.01	3.2	4.8
4 Quorn, Gladstone Rd.	96	.51	.49	0	.54	0	3.4	4.2
5 Hawker, Flinders Rg.	77	.44	.56	0	.58	0	3.3	3.6
6 Wilpena, Flinders Rg.	72	.49	.51	0	.53	0	3.7	3.9
7 Wilpena, Flinders Rg.	127	.48	.52	0	.56	0	3.6	4.3

Victoria - dimorphic populations											
1	Anakie Gorge, Brisbane Range	46	.39	.59	.02	117	.37	.61	.02	2.4	2.6
2	Anakie Gorge, Brisbane Range	159	.49	.48	.03	436	.48	.51	.01	2.7	2.8
3	Plenty, Yan Yean Rd.	30	.50	.47	.03	81	.49	.49	.02	2.7	2.7
4	Cottles Bridge	83	.48	.49	.03	224	.40	.58	.02	2.3	3.1
5	Cottles Bridge	91	.58	.33	.09	233	.55	.39	.06	2.4	2.8
6	St. Andrews	82	.54	.45	.01	206	.53	.46	.01	2.5	2.5
7	Kinglake Nat. Park	62	.40	.57	.03	140	.39	.59	.02	2.2	2.3
8	Kangaroo Ground	61	.61	.33	.06	182	.64	.33	.03	3.1	2.8
9	Yarrambat	69	.48	.48	.04	169	.42	.56	.02	2.2	2.7
10	Hurstbridge	68	.32	.66	.02	164	.30	.69	.01	2.2	2.5
11	Arthurs Creek	79	.49	.47	.04	176	.45	.53	.02	2.0	2.4
Australian Capital Territory - dimorphic populations											
1	Cotter Dam Rd.	163	.50	.47	.02	704	.49	.50	.01	4.2	4.4
2	Cotter Dam Rd.	264	.33	.44	.23	1188	.30	.54	.16	4.1	4.7
3	Cotter Dam Rd.	253	.22	.53	.25	1401	.21	.65	.14	5.1	5.7
4	Tidbinbilla	187	.27	.59	.14	829	.23	.67	.10	3.7	4.1
5	Tidbinbilla	168	.30	.66	.04	675	.28	.70	.02	3.8	4.1
6	Molongolo Gorge	195	.47	.44	.09	1059	.40	.56	.04	4.6	6.1
7	Weston Creek	193	.38	.60	.02	1141	.36	.63	.01	5.5	6.1
8	Woden Valley	270	.41	.55	.04	1301	.38	.60	.02	4.4	5.1
9	Thawa, Booroomba Rd.	190	.38	.56	.06	718	.33	.63	.04	3.3	4.1
10	Canberra, Black Mountain Reserve	133	.35	.56	.09	696	.30	.63	.07	4.6	5.6
11	Canberra, Garran	180	.33	.33	.33	1009	.24	.61	.15	4.1	6.4