

Gender modification and resource allocation in subdioecious *Wurmbea dioica* (Colchicaceae)

SPENCER C. H. BARRETT* ANDREA L. CASE* and GREGORY B. PETERS†

*Department of Botany, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2; and

†Department of Botany, Australian National University, Canberra, ACT 2600, Australia

Summary

1 Populations of subdioecious species contain female, male and cosexual plants. Here we investigate factors influencing gender expression and patterns of resource allocation among the sex phenotypes in subdioecious populations of the diminutive geophyte *Wurmbea dioica* (Colchicaceae) from the Australian Capital Territory, south-east Australia.

2 Demographic studies and population comparisons of the sex phenotypes were conducted to determine their distinguishing features, and whether sex expression was labile. Comparisons of biomass allocation were made to assess whether plants with hermaphrodite flowers were larger than unisexual plants. The seed fertilities of sex phenotypes were measured and related to the sex ratio of populations.

3 Female plants exhibited canalized gender producing only ovuliferous flowers, which were smaller and less showy compared to flowers of other plants. Some male plants displayed labile gender expression, producing varying numbers of male and hermaphrodite flowers (fruiting males). Maternal investment among male plants was size-dependent.

4 Fruiting males were significantly larger and produced more flowers than unisexual plants. At flowering, we found no evidence for changes in proportional allocation with increases in size after controlling for total biomass. At fruiting, allocation patterns differed between females and fruiting males independently of size.

5 Total seed output by fruiting males was 70% of that produced by females. The number of seeds per fruit declined acropetally in both sexes, and males produced, on average, more seeds per fruit than females. Data on the relation between female frequency and the relative seed fertilities of males and females gave a poor fit to Lloyd's (1976) genetic model predicting equilibrium female frequency. The lack of congruence probably occurs because size-dependent gender modification in males complicates the assumptions of the model.

Keywords: allocation strategies, sex ratios, sexual dimorphism, size-dependent gender modification

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Introduction

Gender strategies in flowering plants concern the femaleness and maleness of reproductive individuals and should reflect the relative contribution to fitness that occurs from maternal and paternal investment (Lloyd 1979). Patterns of gender expression vary considerably among angiosperms, ranging from species

with highly canalized gender, as in dioecious species where individuals are either exclusively male or female regardless of environmental conditions (Bawa 1980; Barrett & Helenurm 1981; Lloyd & Bawa 1984; but see Freeman *et al.* 1980), to hermaphroditic (cosexual) species, where gender varies continuously among individuals as a result of both genetic and environmental factors (Primack & Lloyd 1980; Freeman *et al.* 1981; Thomson & Barrett 1981; Emms 1993; Diggle 1995; Klinkhamer *et al.* 1997). The modular construction and plasticity in reproductive allocations that charac-

terize many flowering plants provide opportunities for gender to be modified under varying environmental circumstances and with changes in plant condition.

Where environmental conditions or plant status play a role in gender modification in cosexual organisms, a common finding in animal-pollinated species has been that relative allocation to female vs. male function increases with size (reviewed in Policansky 1982; Klinkhamer *et al.* 1997). For example, in plant species with sequential hermaphroditism (diphasy) small plants are generally male and large plants are either female (Policansky 1981; Lovett Doust & Cavers 1982; Bierzychudek 1984) or hermaphrodite (Schlessman 1988, 1991). This behaviour is consistent with several theoretical models concerned with size-dependent sex allocation that incorporate both the reproductive costs of male and female function, and the fitness consequences of particular allocation strategies among different-sized individuals (Ghiselin 1969; Charnov 1982; Policansky 1982; Lloyd & Bawa 1984; Day & Aarssen 1997). Both factors are important in determining which gender strategies are favoured.

Sexually dimorphic species that possess gynodioecious and subdioecious sexual systems are of particular interest for studies of gender modification. Subdioecious populations are often composed of plants with three distinct sexual phenotypes: female, male and cosexual (Darwin 1877; Lloyd 1975, 1976). Female plants are often constant in their gender expression, producing only ovules, while polleniferous plants (i.e. male and cosexual phenotypes) commonly exhibit gender inconstancy, producing both pollen and ovules to varying degrees (Darwin 1877; Burrows 1960; Young 1972; Arroyo & Raven 1975; Webb 1979; Delph 1990a, b; Wolfe & Shmida 1997). Here, we follow the convention of referring to polleniferous plants that also produce ovules as fruiting males rather than cosexuals because they derive the majority of their fitness through male function (see arguments in Lloyd 1976; Webb 1979; Delph 1990a; Wolfe & Shmida 1997). Gender inconstancy is not predicted to occur in females because even a relatively small amount of pollen is sufficient to self-fertilize ovules, thus compromising the fitness achieved through female function (Charlesworth & Charlesworth 1978). Although this pattern of gender variation has been documented previously and predicted theoretically, few studies have explicitly examined to what extent individual plants are capable of modifying their gender (McArthur *et al.* 1992; Koelewijn & Van Damme 1996). In species exhibiting male inconstancy, opportunities are available to examine whether gender modification occurs, whether it is size-dependent, and what level of maternal investment is favoured in plants that obtain the majority of their fitness through male function.

Patterns of resource investment to male and female function are of significance in sexually dimorphic populations because of their influence on the fitness of

sex phenotypes and hence the sex ratio of populations. Theoretical models of sex-ratio variation under nuclear inheritance of male sterility indicate that the equilibrium female frequency varies depending on the relative seed fitnesses of female and male plants (Lewis 1941; Lloyd 1976; Charlesworth 1981). Sex-ratio variation in species with nuclear-cytoplasmic control of male sterility is considerably more complex, and in this situation females can be predicted to occur at frequencies above 0.5 (Frank 1989; Gouyon *et al.* 1991; Schultz 1994). Under nuclear control of gender and where males exhibit little sex inconstancy, female frequencies should approach 0.5, whereas in those in which males set abundant seed, owing to a high level of inconstancy, female frequencies should be considerably lower. Surveys of sex-ratio variation in natural populations of diverse gynodioecious and subdioecious species provide empirical support for these theoretical predictions (Lloyd 1976; Webb 1981; Delph 1990b; Barrett 1992; Wolfe & Shmida 1997). Comparisons of the seed fertility of morphs and an understanding of the proximate ecological factors governing patterns of resource allocation are necessary for understanding sex-ratio variation in sexually dimorphic populations.

Wurmbea dioica (R. Br.) F. Muell (Colchicaceae) is a diminutive geophyte of widespread distribution throughout much of temperate Australia (Macfarlane 1980). The species exhibits striking intraspecific variation in sexual systems ranging from cosexual populations through gynodioecious and subdioecious populations to fully dioecious populations (Barrett 1992). Populations in Western Australia, referred to as *W. dioica* ssp. *alba* Macfarlane, display this full spectrum of variation, whereas those in eastern Australia (*W. dioica* ssp. *dioica* Macfarlane) are uniformly sexually dimorphic. In subdioecious populations, plants of three contrasting sex phenotypes occur: female, male and cosexual. Based on the patterns of gender variation in *W. dioica* populations, Barrett (1992) reported that in subdioecious populations plants with hermaphrodite flowers were male plants displaying sex inconstancy. A major goal of the present study was to provide direct evidence for this assertion by examining the extent of gender modification in the sex phenotypes and by investigating their distinguishing features.

Our study focused on comparisons of the sex phenotypes in subdioecious populations of *W. dioica* ssp. *dioica* occurring in the Australian Capital Territory (ACT) and involved three specific objectives. (i) To determine the relationships among the sex phenotypes by comparing their floral biology and potential for lability in sex expression between flowering episodes. We predicted that phenotypes producing hermaphrodite flowers were male plants exhibiting sex inconstancy. (ii) To compare patterns of biomass allocation to vegetative and reproductive functions at flowering and fruiting in the three sex

phenotypes. We predicted that plants with hermaphrodite flowers would be larger in size than unisexual plants because of the increased reproductive costs associated with producing both pollen and ovules. (iii) To compare the fertility of female plants in comparison with male plants exhibiting female function (i.e. fruiting males). This was important because the models discussed above indicate that the relative female fertilities of the two morphs play an important role in governing the sex ratios of populations. We predicted that the frequency of females and the seed fertility of fruiting males would vary negatively among populations.

Materials and methods

STUDY ORGANISM

Wurmbea dioica has a simple architecture typical of many geophytes and is composed of an underground corm, three linear leaves and an erect cymose inflorescence (Macfarlane 1980; Pate & Dixon 1982). Leaves emerge in winter and, in ACT, populations flower in early spring (September–October) depending on winter rainfall. Plants usually produce a single inflorescence with an average of 3–6 flowers (range 1–14) which can be female, male or hermaphrodite. Plants produce either all female (F), all male (M) or varying proportions of male and hermaphrodite flowers (fruiting males, FM). All flowers are small, actinomorphic and white in colour. The major pollinators in ACT are flies, primarily Syrphidae, especially *Melangyna* cf. *collatus* (Walk.), and Calliphoridae, especially *Calliphora augur* (Fabr.) and *Chrysomya rufifacies* (Macq.). Plants are self-compatible and protogynous, with the sequence of anthesis from basal flowers upwards. Flowers last for up to 12 days and exhibit protracted anther dehiscence. Fruits mature in October and November with seeds shaken from the dry dehiscent capsules by wind. Populations occur mostly in open pastures and roadsides, although they can inhabit shaded woodland sites. In this study six populations (ACT 2, 3, 6, 9, 12, 18) were investigated. Of these, four have been the subject of previous work and information on their sex ratios and aspects of their floral biology are given in Barrett (1992) along with localities. Data from ACT 12 and 18 have not been reported previously; both populations occurred in *Eucalyptus* woodlands, at Tidbinbilla Nature Reserve and near the summit of Black Mountain, Canberra, respectively.

RELATIONS AMONG SEX PHENOTYPES

To determine whether *W. dioica* plants exhibit labile sex expression and to investigate the relations between the three sex phenotypes, we permanently marked a total of 90 flowering plants in ACT 18 in 1981 using quadrat coordinates and metal plant tags. The num-

ber of male, female and hermaphrodite flowers on each plant was recorded, and plant height was taken as a non-destructive estimate of plant size. Height is correlated with both total biomass and flower production in *W. dioica* (see the Results), and was therefore an acceptable surrogate for resource status and overall size. The sex ratio of the population was determined from an additional random sample of 434 plants. The following year (1982), a thorough search was made for plants. However, due to extreme drought throughout the region no plants emerged above the soil surface that year. In 1983 winter rains occurred and the population re-appeared. We relocated marked individuals, and recorded the height and sex expression (number of male, female and hermaphrodite flowers) of each plant. We obtained an additional random sample of 470 plants in 1983 to determine the population sex ratio.

Sex expression from one season to the next may be influenced by resource availability (i.e. size) as well as by reproductive investment (i.e. flower number, floral sex ratio). For example, plants investing heavily into reproduction in one season may not be able to maintain the same level of investment in later years unless they are relatively large. To assess whether these phenotypic traits were associated with sex expression, we grouped plants based on their sex phenotype in both 1981 and 1983 and compared the height, total flower number and the number of ovuliferous flowers among the groups.

COMPONENTS OF FLORAL DISPLAY

To determine further the relations between the three sex phenotypes, three floral traits were compared among them. We sampled 10 plants from each phenotype in each of three populations (ACT 2, 3, 9) at peak flowering in September 1983. Flower diameter of the two most basal flowers, the average distance between flowers and the total number of flowers per plant were recorded; the size, number and arrangement of flowers contribute to the overall showiness of floral display. We predicted that floral traits in the two groups of plants bearing polleniferous flowers would be more similar to one another than to plants bearing only female flowers, reflecting the fact that plants with hermaphrodite flowers are actually males.

We tested for differences in flower diameter and intrafloral distance among sex phenotypes and populations using two-way analyses of covariance (ANCOVA) in JMP (version 3.0.2; SAS Institute 1994). Flower number was included as a covariate in both analyses to assess differences in floral display independent of flower number. For this and all subsequent ANCOVAs, sex was treated as a fixed effect, and population a random effect. All response variables and covariates were natural log transformed to meet assumptions of normality. We tested for possible interactions between covariates and main effects, and

removed these interactions when they were not statistically significant at $\alpha = 0.05$.

BIOMASS ALLOCATION

To investigate patterns of biomass allocation among the three sex phenotypes at peak flowering, we carefully excavated 30 plants of each sex phenotype, randomly chosen from each of two populations (ACT 2 and 3) in September 1983. Plants were dried for 1 week in an oven and divided into their component parts prior to weighing: corms and roots, leaves and stems, and flowers and accompanying inflorescence parts, representing underground, vegetative and reproductive biomass, respectively. To determine biomass allocation to these components at fruiting we obtained a second sample ($n = 21$ plants per sex phenotype) from ACT 3 for females and plants with hermaphrodite flowers just prior to capsule dehiscence.

We tested for differences in biomass allocation patterns among sex phenotypes (at flowering and fruiting) and populations (at flowering) using ANCOVA. Total biomass was included as the covariate in each analysis to assess differences in allocation patterns independent of plant size.

PATTERNS OF SEED FERTILITY

To compare the seed fertility of females and plants with hermaphrodite flowers, we obtained random samples of 15–31 plants of each sex phenotype from each of four populations (ACT 3, 6, 9 and 12) just prior to capsule dehiscence in November 1983 (pooled $n = 95$ per sex). The number of seeds per capsule was counted and the position of each fruit on the inflorescence axis recorded. We weighed all seeds produced by a capsule as a group to determine average seed weight per fruit.

We compared total seeds per plant, seed set per capsule, seed weight and the relation between flower position and seed number between sexes and among populations using ANCOVA. Total number of flowers (#fls) and total number of fruit (#frt) were each used as covariates in separate analyses for all response variables except number of seeds per fruit, for which fruit position was used instead of #frt. The inclusion of #fls and #frt as covariates enabled us to assess patterns of seed production independently of flower and fruit production. We included fruit position to test whether seed production per fruit varied independently of proximity to the resource source (i.e. from the bottom to the top of the infructescence).

Results

DYNAMICS OF GENDER EXPRESSION

Our census of sex ratios at the Black Mountain population (ACT 18) in two consecutive flowering seasons

revealed differences in the relative frequencies of the sex phenotypes. While the frequency of female plants remained stable over the two flowering seasons (48.6% in 1981, $n = 211$; 48.9% in 1983, $n = 230$), the frequency of plants bearing only male flowers declined by 13.5% from 1981 (43.1%, $n = 187$) to 1983 (29.6%, $n = 139$), while the frequency of plants with hermaphrodite flowers increased by a similar amount, from 8.3% in 1981 ($n = 36$) to 21.5% in 1983 ($n = 101$).

Data collected on the sex expression of marked plants at the same site showed similar patterns and provided an explanation for the observed changes in sex ratio of the population (Table 1). Female plants that flowered in both years exhibited the same sex phenotype. Among the plants that were male in 1981, half of those flowering in 1983 remained male and half produced hermaphrodite flowers. Among the plants that produced hermaphrodite flowers in 1981, about a third of them produced only male flowers in 1983 and the others produced hermaphrodite flowers. Hence, among plants that produced polleniferous flowers in 1981, none were female in 1983. These data provide convincing evidence that labile gender modification occurs in the male morph of *W. dioica* through the production of varying numbers of hermaphrodite flowers on male plants. In contrast, we found no evidence of gender modification in the female morph.

A quarter of the plants that flowered in 1981 did not flower in 1983 (Table 1). The probability of flowering in 1983 occurred independently of sex phenotype in 1981 ($G = 4.56$, d.f. = 2, $0.15 > P > 0.10$), although fruiting males in 1981 were more likely to flower again in 1983 than were the other phenotypes.

Fruiting males were significantly taller than both male (M) and female (F) plants in 1981 (FM and FM-M; Fig. 1a) and significantly taller than M plants in 1983 (FM and M-FM; Fig. 1b). Plants that changed sex from 1981 to 1983 (M- and FM-M) tended to be smaller when they were males than when they were fruiting males, and larger than plants that were male in both years (M). The height of stems may vary among individuals solely because they produce different numbers of flowers, which may be more or less widely spaced along the inflorescence. In this sample, there was no significant difference in the total number of flowers per plant among gender classes (Fig. 1c,d), so patterns of height after adjusting for flower number were identical to those for unadjusted height. The sex phenotypes also differ in the spacing of flowers (Fig. 2b), and hence the length of inflorescences, which may contribute to overall differences in height. When adjusted for inflorescence length (i.e. flower number \times mean distance between flowers), patterns of vegetative height in 1981 were the same, but differences between means were greater and significance levels increased. There were no significant

Table 1 Sex expression of 90 marked plants in two flowering seasons in a subdioecious population of *Wurmbea dioica* in the Australian Capital Territory. Plants were classified as female (ovules only), male (pollen only) or fruiting males (both ovules and pollen) in 1981 (row 1). The sex of these plants was recorded in 1983; no flowering occurred in 1982 due to drought. Evidence for sex lability in the polleniferous morph and sex constancy in the female morph is outlined by the box

Year	Status	Female	Male	Fruiting male	Total
1981	–	27	37	26	90
	Not flowering	10	9	3	22
1983	Female	17	0	0	17
	Male	0	14	7	21
	Fruiting Male	0	14	16	30

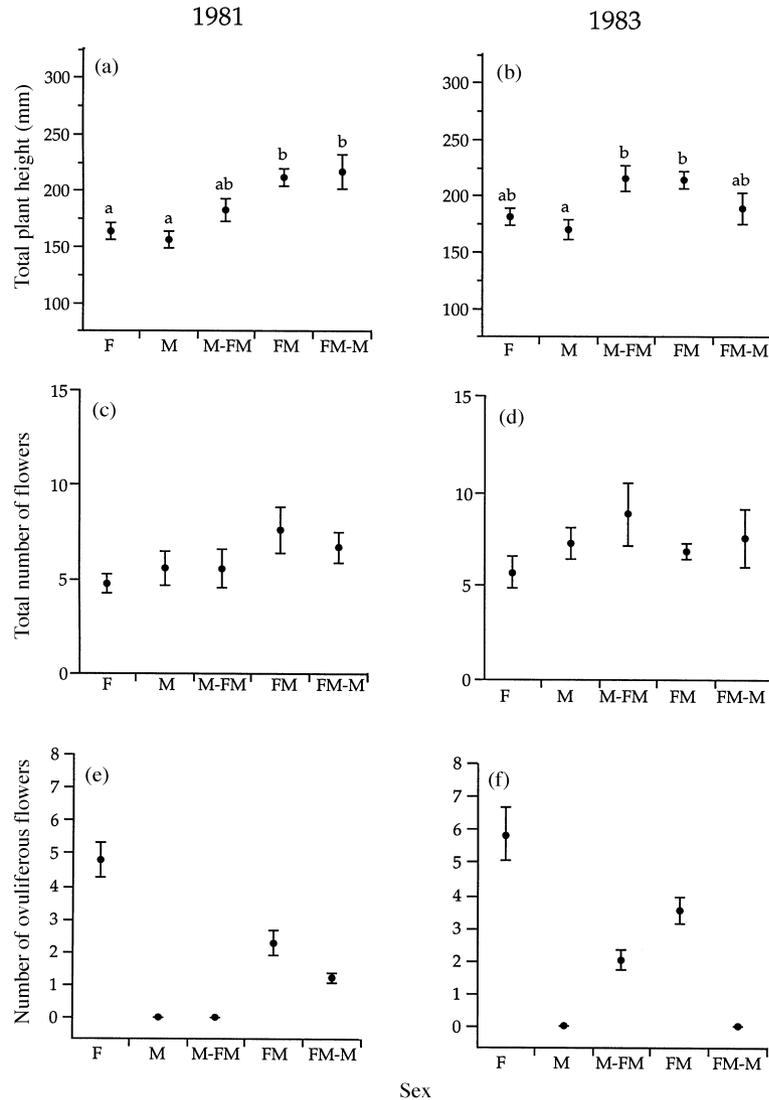


Fig. 1 Height and flower production of 90 marked plants in two flowering seasons in a subdioecious population of *Wurmbea dioica* in the Australian Capital Territory (ACT 18). Plants were assigned to one of five classes based on their sex expression in both 1981 and 1983: F = female both years; M = male in both years; M-FM = male in 1981, fruiting male in 1983; FM = fruiting male in both years; FM-M = fruiting male in 1981, male in 1983. Sample sizes for each class are given in Table 1. Means \pm SE are shown for height (a,b), total flower production (c,d), and number of ovuliferous flowers (e,f) for each class in both 1981 (a,c,e) and in 1983 (b,d,f). Letters indicate means significantly different from one another within a year at $P < 0.05$ (Tukey–Kramer comparisons).

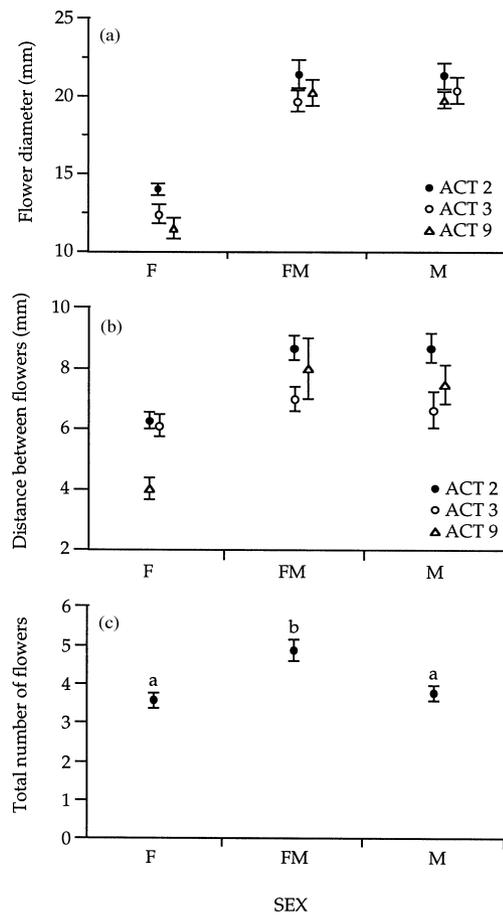


Fig. 2 Components of floral display among the three sex phenotypes in subdioecious populations of *Wurmbea dioica* in the Australian Capital Territory (ACT 2, 3, 9). Means \pm SE for (a) flower diameter, (b) distance between flowers and (c) flower number are shown for females (F), males (M) and fruiting males (FM), and from each population (a,b). Populations did not differ for flower number (c); letters indicate pooled means significantly different from one another at $P < 0.01$ (Tukey–Kramer comparisons).

(Tukey–Kramer comparison, $Q > 0.75$, $P < 0.05$ for all comparisons in both years; Fig. 1e,f). All of the males sampled (M, M-FM, FM, FM-M) produced similar numbers of polleniferous flowers in both years (Fig. 1c,d). However, fruiting males that did not change sex (FM) produced more ovuliferous flowers than fruiting males that were males in either season (M-FM and FM-M; Fig. 1e,f). When this comparison was analysed statistically, there was no significant difference in the number of ovuliferous flowers between these classes within each year (1981: $Q = -1.29$, $P > 0.05$; 1983: $Q = -0.59$, $P > 0.05$). However, in both 1981 and 1983 we found that the mean proportion of ovuliferous flowers produced by plants that were FM in both years was significantly greater than by plants that were FM in only 1 of the 2 years (1981: FM = 0.33 ± 0.06 , FM-M = 0.20 ± 0.03 , $Q = 0.002$, $P < 0.05$; 1983: FM = 0.50 ± 0.08 , M-FM = 0.26 ± 0.03 , $Q = -0.007$, $P < 0.05$).

SEXUAL DIMORPHISM IN FLORAL DISPLAY

Further evidence that plants with hermaphrodite flowers are males was obtained from the comparisons of floral traits among the three sex phenotypes (Fig. 2a,b). Flower size and the distance between flowers were not significantly different between male and fruiting male plants. In contrast, female plants had significantly smaller flowers that were positioned closer to one another on the inflorescence. Fruiting males produced significantly more flowers per plant than either female or male plants (Fig. 2c).

Significant differences among populations for the floral traits measured were also evident. Flowers of plants in ACT 2 were larger than those in both ACT 3 and ACT 9 (ANCOVA: $F_{2,80} = 8.56$, $P < 0.01$; Fig. 2a). There was also a significant population \times sex interaction for the distance between flowers (ANCOVA: $F_{4,80} = 2.59$, $P < 0.05$). Flowers were more closely spaced on female than on male or fruiting male inflorescences in all populations; however, these differences were not statistically significant in ACT 3 (Fig. 2b).

BIOMASS ALLOCATION STRATEGIES

During flowering

For all components of size, fruiting males tended to be larger than the other two sex phenotypes. These differences were statistically significant within ACT 3 (Fig. 3) but only marginally significant in ACT 2 (population \times sex interactions in Table 2; data not shown). Total biomass was positively related to underground, vegetative and reproductive biomass in all three sex phenotypes, but did not affect relative allocation above- vs. below-ground or between reproductive and vegetative biomass (Table 2). In three cases, the relations between total biomass and the response variables differed between populations and among the sexes. As total size increased, plants in ACT 2 allocated more to vegetative biomass than plants in ACT 3. Size-dependent allocation to reproductive biomass, both directly and relative to vegetative biomass, was similar among the sexes in ACT 2, but differed among them in ACT 3. In the latter population, the slope (m) of the relation between total and reproductive biomass was greater among fruiting males ($m = 0.119 \pm 0.019$) and females ($m = 0.097 \pm 0.011$) than among males ($m = 0.052 \pm 0.012$).

Flower production varied positively with total biomass in all three sex phenotypes, but the slope of the relations differed among them (Fig. 4). In M and FM plants, increases in total biomass resulted in virtually identical increases in the number of polleniferous flowers (ANCOVA biomass \times sex: $F_{1,114} = 0.007$, $P > 0.90$; Fig. 4a). In contrast, FM plants did not invest in as many ovuliferous flowers as F plants (ANCOVA biomass \times sex: $F_{1,114} = 19.36$,

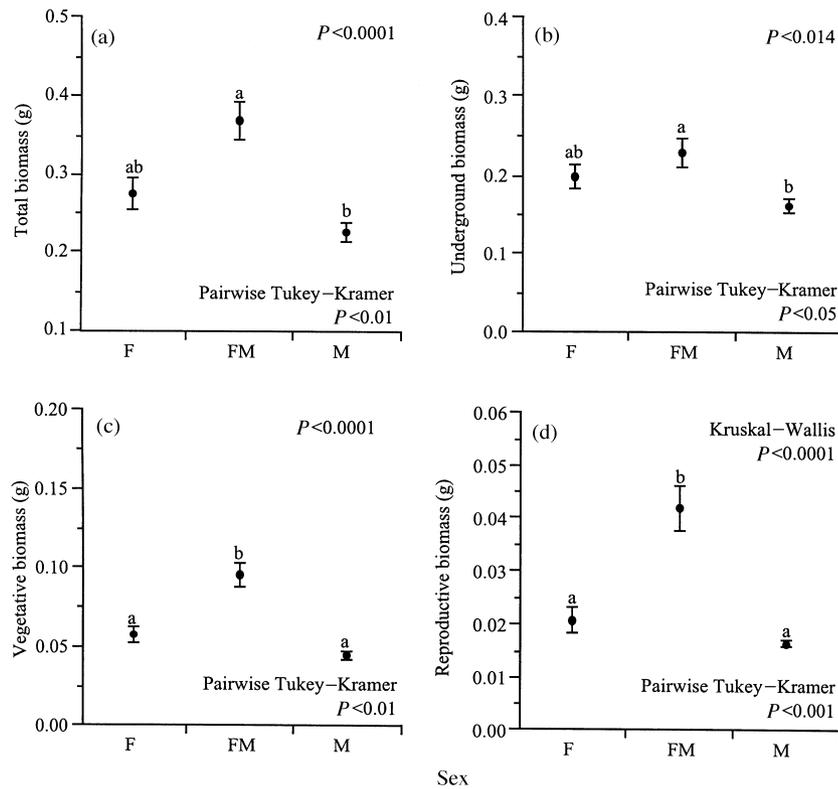


Fig. 3 Biomass allocation to (a) total, (b) below-ground, (c) vegetative and (d) reproductive biomass during flowering in a subdioecious population of *Wurmbea dioica* in the Australian Capital Territory (ACT 3). Means \pm SE are shown for females (F), males (M) and fruiting males (FM). Letters indicate means significantly different from one another (Tukey–Kramer comparisons). *P*-values indicate the effect of sex in one-way ANOVA (a) and ANCOVA (b–c) on ACT 3 data. Total biomass was used as the covariate in the ANCOVAs. Two-way ANOVA and ANCOVA results for both populations studied (ACT 2 and 3) are reported in Table 2.

Table 2 ANCOVA of biomass allocation during flowering among three sex phenotypes of *Wurmbea dioica* in two populations in the Australian Capital Territory (ACT 2 and 3). Total biomass (biom) was used as a covariate in each analysis. Interactions between covariates and main effects were tested and removed using backwards elimination ($\alpha = 0.05$). Sex was included as a fixed effect, and population (pop) was included as a random effect in the model. All response variables and covariates were natural log transformed for analysis. $n = 60$ plants per sex. *F*-values are shown for each response variable, *P*-values are indicated by superscripts

Source (d.f.)	Total biomass	Underground biomass	Vegetative biomass	Reproductive biomass	Above: below-ground biomass	Repro: veg biomass
pop (1)	0.62	4.97	3.54	1.32	4.20	0.14
sex (2)	9.46†	1.76	0.76	0.68	1.74	0.36
pop \times sex (2)	1.27	3.23*	6.28**	3.58*	3.82*	3.33*
biom (1)	–	1673.4****	455.5****	267.8****	0.53	2.27
biom \times sex (2)	–	–	–	0.51	–	0.35
biom \times pop (1)	–	–	6.42*	2.54	–	0.03
biom \times pop \times sex (2)	–	–	–	3.32*	–	6.61**

$P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

$P > 0.0001$; Fig. 4b). On average, half of the flowers produced by FM plants contained ovules (Fig. 5).

During fruiting

Fruiting males and females differed significantly in biomass allocation during fruiting, independently of strong positive relations with plant size (Table 3).

Both sexes doubled their total biomass since flowering (cf. Figures 3a and 6a), but did so in different ways. Fruiting males gained most of their mass below-ground (cf. Figures 3b and 6b), with relatively smaller increases in vegetative (cf. Figures 3c and 6c) and reproductive biomass (cf. Figures 3d and 6d). Females, on the other hand, did not gain in underground biomass but more than doubled their veg-

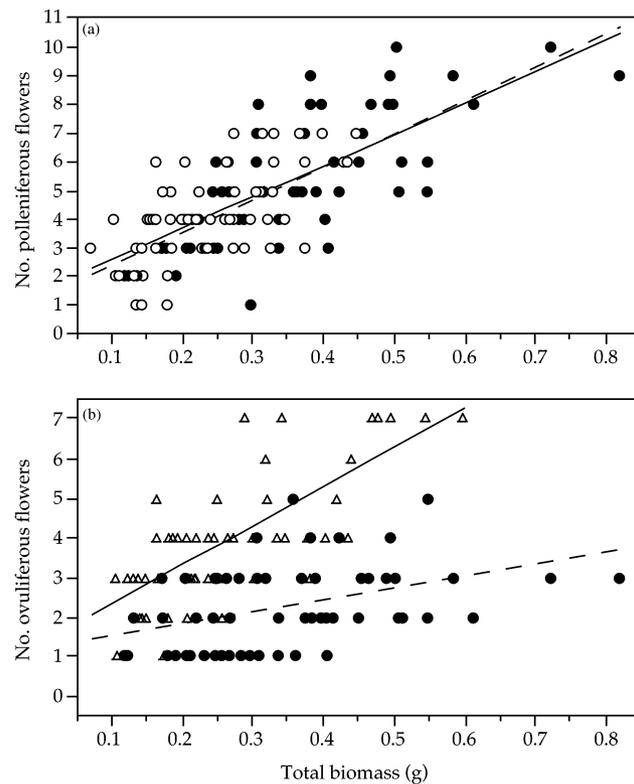


Fig. 4 Relations between total biomass (g) and (a) the number of polleniferous flowers produced by males (○) and fruiting males (●) and (b) the number of ovuliferous flowers produced by females (△) and fruiting males (●) of *Wurmbea dioica*. Lines represent least squares regressions for each sex. (a) FM: $y = 11.56x + 1.22$, $r^2 = 0.56$, $P < 0.0001$; M: $y = 10.9x + 1.51$, $r^2 = 0.41$, $P < 0.0001$; slopes are not significantly different (see the Results). (b) FM: $y = 3.07x + 1.22$, $r^2 = 0.16$, $P < 0.0011$; F: $y = 9.84x + 1.35$, $r^2 = 0.53$, $P < 0.0001$; slopes are significantly different (see the Results).

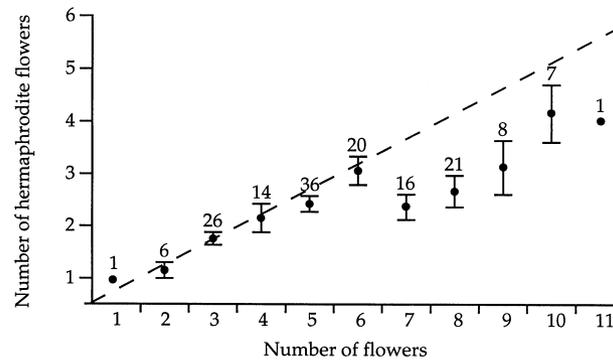


Fig. 5 Relation between total number of flowers and the number of hermaphrodite flowers in fruiting males of *Wurmbea dioica*. $n = 156$ plants from five subdioecious populations in the Australian Capital Territory (ACT 2, 3, 6, 9, 12). Sample size for each flower number class is indicated above each mean. The dashed line represents a 1:2 ratio of hermaphrodite to total flowers.

etative biomass and increased their reproductive mass 10-fold. This pattern resulted in several significant interactions between sex and biomass (Table 3), where the relations between total biomass and each component reflected the differences in relative allocation between the sexes.

SEX DIFFERENCES IN SEED FERTILITY

Although fruiting males produced more total flowers than females, females produced more fruit, and conse-

quently more seeds per plant (Fig. 7a,b). On average, the seed output of fruiting males was 70% of that produced by females (mean total seeds per plant $F = 100.2 \pm 5.8$, FM $= 70.8 \pm 5.1$). The contrast in fruit number and hence seed output between the two sex phenotypes reflects differences in the number of ovuliferous flowers produced by males and females, not fruit abortion or pollen limitation.

Fruits of male plants contained, on average, more seeds than fruits of females (Fig. 7c). This can be explained by a strong effect of fruit position on num-

Table 3 ANCOVA of biomass allocation during fruiting between males and females of *Wurmbea dioica* in the Australian Capital Territory (ACT 3). Total biomass (biom) was used as a covariate in each analysis. Interaction between the covariate and main effect were tested and removed using backwards elimination ($\alpha = 0.05$). Sex was included as a fixed effect in the model. The response variables and covariate were natural log transformed for analysis. $n = 60$ plants per sex. F -values are shown for each response variable, P -values are indicated by superscripts

Source (d.f.)	Total biomass	Underground biomass	Vegetative biomass	Reproductive biomass	Above: below-ground biomass	Repro: veg biomass
sex (1)	5.41*	34.7****	15.4***	34.7****	36.5****	23.6****
biom (1)	–	49.6****	160.6****	38.3****	9.85**	0.32
biom \times sex (1)	–	4.6*	10.3**	–	5.58*	–

$P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

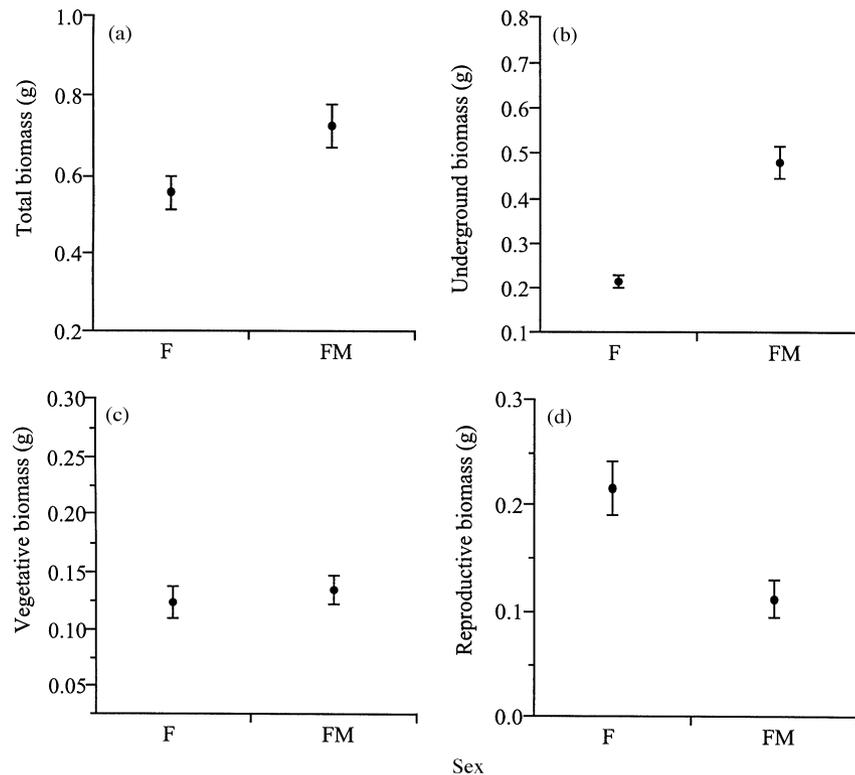


Fig. 6 Biomass allocation during fruiting in a subdioecious population of *Wurmbea dioica* in the Australian Capital Territory (ACT 3). Means \pm SE for (a) total biomass, (b) below-ground, (c) vegetative and (d) reproductive biomass are shown for females (F) and fruiting males (FM). ANOVA and ANCOVA results are reported in Table 3.

ber of seeds per fruit (Table 4 and Fig. 8). FM plants produced fewer total fruits per plant, but these fruits occurred at the most basal positions on the infructescence (closest to the resource source). This pattern was largely responsible for the greater mean number of seeds per fruit in FM than F plants, because the number of seeds per fruit did not differ significantly between the two sex phenotypes at any position along the infructescence (Fig. 8).

As expected, both the number of flowers and the number of fruit were positively related to the total number of seeds per plant produced by both sexes (Table 4). Total seed production increased more rapidly with the addition of each fruit in FM than in F plants ($\#frt \times$ sex interaction in Table 4). This can be

partially explained by the difference in the number of seeds per fruit between F and FM plants. However, as the number of fruits increased among FM plants, the number of seeds per fruit also increased at each position along the infructescence, i.e. there was a positive relation between the number of fruit and the number of seeds per fruit produced by FM plants. In contrast, we found a negative relation between fruit production and seeds per fruit in F plants, perhaps reflecting a resource trade-off between the number of units (fruits) and investment per unit (seeds per fruit). The similar relations we found between flower production and total number of seeds between the two sexes (Table 4) reflected the relation between the number of flowers and number of fruits in FM plants

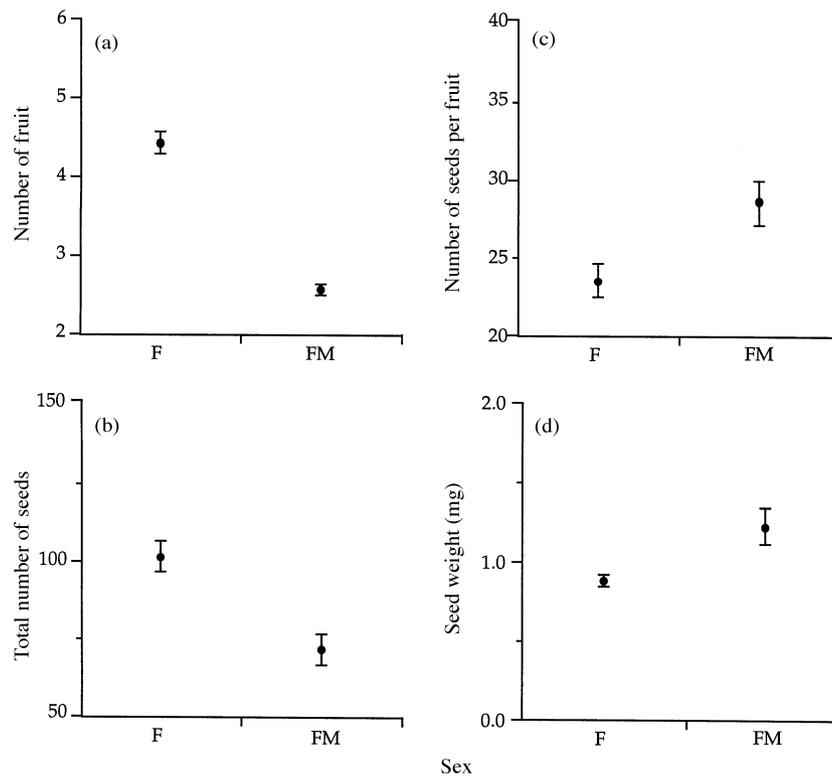


Fig. 7 Fruit and seed production of fruiting males (FM) and females (F) averaged across four subdioecious populations of *Wurmbea dioica* in the Australian Capital Territory (ACT 3, 6, 9, 12). Means \pm SE for (a) total number of fruit, (b) total number of seeds, (c) number of seeds per fruit and (d) seed weight are shown.

Table 4 ANCOVA of seed production between fruiting males and females of *Wurmbea dioica* in four subdioecious populations in the Australian Capital Territory (ACT 3, 6, 9, 12). Total number of flowers (#fls) and total number of fruits (#frt) were each used as covariates in separate analyses for all response variables except number of seeds per fruit (seed/frt) for which fruit position (frt pos) was used as a covariate instead of #frt. Interactions between covariates and main effects were tested and removed using backwards elimination ($\alpha = 0.05$). All variables and covariates were natural log transformed for analysis. $n = 95$ for each sex, F -values are shown, P -values are indicated by superscripts

Source (d.f.)	#Flowers	#Fruits	Total seed	Total seed	Seed/frt	Seed/frt	Seed wgt	Seed wgt
pop (3)	1.68	1.00	1.30	0.95	0.55	1.45	1.46	2.36
sex (1)	8.20†	2.06	31.1**	3.56†	0.32	0.53	1.64	1.65
pop \times sex (3)	4.10**	1.86	1.49	1.42	1.52	3.74**	2.29	2.29
#fls (1)	–	286.9****	42.0****	–	<0.001	–	0.67	–
#fls \times sex (1)	–	65.0****	–	–	–	–	–	–
#frt (1)	–	–	–	111.0****	–	–	–	0.48
#frt \times sex (1)	–	–	–	6.53*	–	–	–	–
frt pos (1)	–	–	–	–	–	7.9****	–	–

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

(Fig. 5). The addition of each fruit corresponded to the addition of two flowers in FM plants, on average, whereas in F plants two additional flowers resulted in two additional fruits. The contribution to total seed production by one fruit on FM plants was similar to the contribution by two fruits on F plants.

Mean seed weight did not differ between the sexes (Table 4) although seed weights were more variable among fruit produced by fruiting males than females (Fig. 7d).

Discussion

Gender in subdioecious populations of *W. dioica* from south-eastern Australia is governed by the interplay of both genetic and environmental factors. The major finding of this study is that canalized sex function is typical of female plants because these individuals are only capable of producing ovuliferous flowers. In contrast, size-dependent gender modification occurs in male plants with increased size associated with the

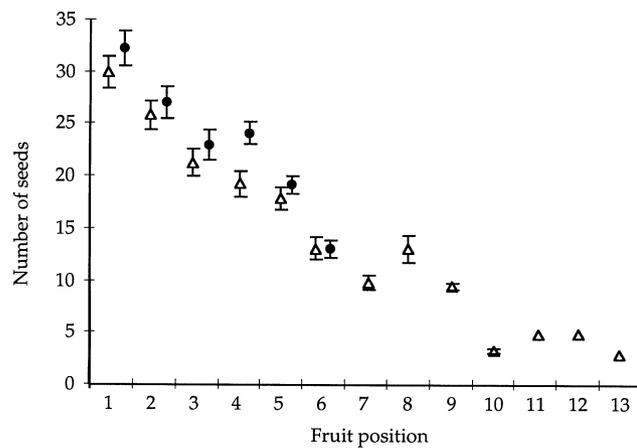


Fig. 8 Number of seeds per fruit by position in females (Δ) and fruiting males (\bullet) of *Wurmbea dioica*, pooled over four subdioecious populations in the Australian Capital Territory (ACT 3, 6, 9, 12). Fruits numbered from the bottom to top of the infructescence. $n = 96$ plants per sex.

production of hermaphrodite flowers. This represents the best example to date of polymorphism for size-dependent gender modification in a flowering plant. Below we review the nature of sexual dimorphism in *W. dioica*, evidence of size-dependent gender modification, and conclude by discussing their implications for the ecology and evolution of gender strategies in the species.

THE NATURE OF SEXUAL DIMORPHISM

Although subdioecious populations of *W. dioica* consist of three distinct sex phenotypes, there are only two functional gender classes: females and males (Fig. 9). Females function solely as maternal parents, and cannot modify their gender beyond changes in the num-

ber of flowers or seeds produced. Males vary continuously in their gender expression, from those producing only pollen to those producing both pollen and seed. This variation does not simply reflect variation in sex allocation, but the ability of individual plants to modify their gender between reproductive episodes.

Comparisons of floral display among the three sex phenotypes also suggest that polleniferous plants belong to a single sex class. Floral displays of male and fruiting male plants were characterized by larger flowers and inflorescences compared with the smaller flowers and more compact displays of female plants. Flower-size dimorphism commonly occurs in sexually dimorphic species, especially those with gynodioecious and subdioecious sexual systems, and this pattern has been interpreted as resulting from sexual selection involving male–male competition (Darwin 1877; Baker 1948; Bell 1985; although see Delph 1996 for additional interpretations). The fact that male and fruiting male plants have similar floral displays supports the assumption that fruiting male plants obtain most of their fitness through pollen, regardless of the fact that they also produce seed.

Allocation strategies are expected to differ between male and female plants of sexually dimorphic species, reflecting differences in the cost of reproduction and in their ecological roles. Empirical studies of biomass allocation generally indicate that males invest more into vegetative functions, whereas reproductive allocation is greater in females than in males as a result of the costs of fruiting (Lloyd & Webb 1977; Gross & Soule 1981). In our study, comparisons of allocation patterns were made more complicated by the presence of three sex phenotypes within populations, two of which gain the majority of their fitness through the same (male) function. Fruiting male plants were larger than both females and males by all measures of absolute size. However, we found no evidence for changes in proportional allocation with increases in total plant

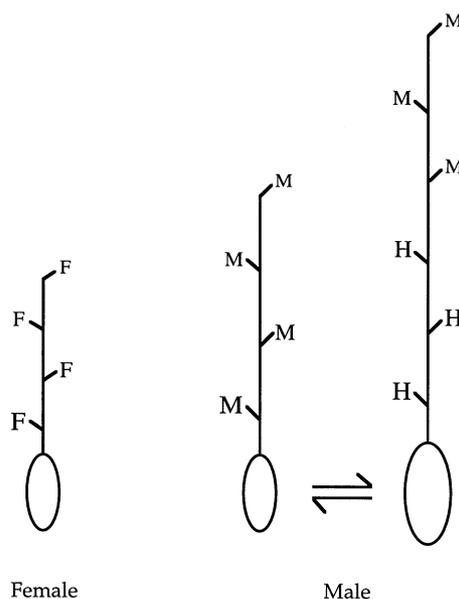


Fig. 9 Polymorphism for size-dependent gender modification in *Wurmbea dioica*. Females exhibit canalized gender whereas males can modify their gender according to size.

size during flowering. In contrast at fruiting, allocation patterns differed between females and fruiting males independent of their size, reflecting differences in the total cost of fruiting. Both sex phenotypes increased in average size from flowering to fruiting, but female plants invested nearly all of their additional biomass above-ground (vegetative and especially reproductive structures), whereas males allocated most to storage in the corm.

While proportional allocation at flowering in the three sex phenotypes was relatively insensitive to size, the number of flowers produced by plants was strongly correlated with their total biomass. Males and fruiting male plants had identical relations between plant size and the number of polleniferous flowers, despite the fact that fruiting males are encumbered by the additional cost of femaleness. However, fruiting males produced significantly fewer ovuliferous flowers than females of equivalent size. This difference is presumably explained by the fact that fruiting males obtain most of their fitness via male function, hence investment in ovules may divert resources away from pollen and may also interfere with fitness gain because of increased opportunities for selfing and pollen discounting (Harder & Barrett 1995). This may also explain the larger size of fruiting male plants, as these individuals are able to produce ovules without compromising reproduction via pollen.

To what extent gender variation in males of *W. dioica* is under genetic control and whether any individuals are incapable of producing hermaphrodite flowers is not known. This problem highlights the difficulty in using the terms gynodioecious and subdioecious to refer to the sexual systems of *W. dioica*. If all male plants in populations in the ACT are capable of producing hermaphrodite flowers then the species would be described as gynodioecious. However, survey data of the relative frequencies of the three sex phenotypes in 19 populations from ACT indicate average frequencies of $F = 0.40$, $M = 0.49$ and $FM = 0.11$, with FM plants ranging in frequency from 0.02 to 0.33 (Barrett 1992 and unpublished data), suggesting that males with fixed sex expression probably occur in some populations. In functional terms most of these populations are closer to the dioecious end of the range of sexual systems that link cosexuality via gynodioecy and subdioecy to dioecy, hence they are best described as subdioecious.

SIZE-DEPENDENT GENDER MODIFICATION

Gender modification in males of *W. dioica* represents variation in maternal investment among individuals and between reproductive episodes. Potential mechanisms for male inconstancy must account for both the increased reproductive costs of producing both pollen and ovules, and the constraints imposed by maximizing fitness gain through male function.

Our population-level comparisons of plant size and

flower number in the three sex phenotypes indicated that fruiting males were significantly larger in size and produced more flowers than both female plants and male plants without hermaphrodite flowers (Figs 2c and 3), although we did observe several large male plants and some relatively small fruiting male plants (Fig. 4a). These results suggest that the gender of some male plants can be modified by environmental conditions and resource status, with larger plants capable of bearing the reproductive costs of simultaneous hermaphroditism. This hypothesis was confirmed by observations of marked plants during the period 1981–83. Of particular significance was the finding that plants that changed sex from 1981 to 1983 (M-FM and FM-M) tended to be smaller when they were males than when they were fruiting males, and larger than plants that were male in both years (M). They also produced fewer hermaphrodite flowers than plants that were fruiting males in both years (FM). These results demonstrate that allocation to female function in male plants is partially size-dependent, and that only plants of relatively large size can maintain allocation to both male and female function.

Within fruiting males, evidence in favour of size-dependent gender modification was not as clear. As plant size increased among fruiting males, the proportion of hermaphrodite flowers did not increase and, if anything, slightly decreased (Fig. 5). However, the number of seeds per fruit increased with plant size in FM (see the Results), which may represent an overall increase in proportional allocation to female function. This allocation pattern could be associated with selective constraints. For example, a high proportion of hermaphrodite flowers on large plants may compromise fitness gain through male function by increasing opportunities for geitonogamy and pollen discounting (Harder & Barrett 1995). Our finding that flower number but not the number of seeds per flower increased with size in females supports this argument. An alternative explanation may be spatial or temporal variability in the probability of fruiting (Lloyd 1980; Lloyd *et al.* 1980; Emms 1993; Klinkhamer & de Jong 1993). For example, flowers at the base of the inflorescence are positioned nearest to the resource source and flower earliest in the season, which may contribute to the successful maturation of fruit and seed such that allocation to female function is not favoured at more distal positions in males. Indeed, we found that fruits at basal positions of the infructescence contained significantly more seeds than those at more distal positions in both sexes (Fig. 8 and see below).

Evidence for gender modification exists for other sexually dimorphic species, where fruit production by males was associated with increased vigour (*Hebe subalpina*; Delph & Lloyd 1991), greater number of ramets (*Schiedea globosa*; Weller & Sakai 1990) and decreasing aridity (*Ochradenus baccatus*; Wolfe & Shmida 1997). Gender variation in *W. dioica* appears to be manifested differently from these taxa. For

example, in *H. subalpina*, male plants produce only hermaphrodite flowers, and gender variation results from different levels of fruit set among plants. In contrast, in *W. dioica* all ovuliferous flowers produce fruit, and gender expression is determined at floral initiation through the production of male vs. hermaphrodite flowers in varying proportions. Delph & Lloyd (1991) suggested that a mechanism for size-dependent gender modification in sexually dimorphic species may involve a resource threshold and seed reduction modifiers that determine patterns of fruit set among males. If a similar mechanism exists in *W. dioica*, these factors must operate at an earlier stage, during floral development.

Differences in the timing of gender regulation among taxa may reflect their contrasting life histories. Sequential adjustment of maternal investment can potentially occur at three developmental stages: flower initiation, pre-anthesis ovary development, and post-anthesis fruit maturation (Lloyd 1980). Variation in the maturation of fruit appears to be a more widespread mechanism of gender adjustment than variation in ovary development (Lloyd *et al.* 1980). Several life-history characteristics are predicted to be associated with each of these mechanisms. For example, in *W. dioica* the simple structure of the inflorescence permits flowers at specific locations a greater likelihood of setting fruit (e.g. at the base of the inflorescence nearer to the resource source) than at other locations (at the apex). In this case, gender adjustment is less wasteful of resources when it occurs at the stage of ovary development. This contrasts with species lacking highly organized inflorescences, where such positional effects on the probability of fruit set are less likely to occur, and gender adjustment at fruiting is most effective (Lloyd 1980). Shrubs with many flowers, such as *H. subalpina*, may fall into this category.

Many of our results support the existence of a resource threshold for gender modification in *W. dioica*, similar to that proposed by Delph & Lloyd (1991). In males of *W. dioica*, stored resources available in the corm at the time of floral initiation may determine the sexual identity of individual flowers, such that plants with resources surpassing a given threshold would allocate resources to both male and female function. Resource availability can vary significantly from year to year, as plants age or local environmental conditions change, such that an individual may pass the threshold in one season but not in another.

IMPLICATIONS FOR SEX-RATIO VARIATION

Distinctions between various polymorphic sexual systems are typically based on the frequencies of sex phenotypes. The sex ratios of gynodioecious and subdioecious populations are governed by several factors, including the relative seed fertilities of males and

females, the inheritance of sex and the fitnesses of the sex phenotypes (Lewis 1941; Lloyd 1976; Webb 1981; Delph 1990b). When nuclear genes govern the inheritance of the sexual system, the expected equilibrium frequency of females (p) following Lloyd (1976) is given by:

$$C = \frac{1-2p}{2(1-p)}$$

where C , the relative seed fertility of males, is the average seed fertility of males divided by the average seed fertility of females. According to this relation, as the frequency of females increases to a maximum of 0.5 the seed fertility of males (C) will decrease to 0. While the fitness of seeds produced by females and fruiting males is not known in *W. dioica* and information on the genetics of the sexual system are not available, it is nonetheless worth exploring to what extent the above model fits the observed data available for ACT populations.

From 19 populations for which sex ratio and flower number data were available, we used the frequency of females in each population (p) to predict the relative seed fertility of males (C^*), and compared this estimate to the observed C , estimated as the average proportion of ovuliferous flowers on males times the average number of flowers on males relative to females (Lloyd 1976; Webb 1981). Our data on the relative seed fertilities of males (C) gave a poor fit to C^* predicted from female frequency by Lloyd's (1976) model ($r^2 = 0.0009$, $P = 0.90$), with no consistent bias in either direction. The lack of congruence may reflect violation of several assumptions of the model, such as equivalent survivorship and seed qualities of males and females, or nuclear control of sex determination. Size-dependent gender modification in males could also complicate predictions of the model. Results of the demographic study showed that the frequency of fruiting on males varied dramatically from 1981 to 1983, while female frequencies were unchanged. Clearly, allocation to female function in *W. dioica* males can respond rapidly to environmental conditions independently of constraints imposed by the sex ratio. As female frequency increases, selection should favour greater allocation to pollen at the expense of ovule production in males. However, if environmental conditions or the resource status of plants permit the production of seed without compromising male fitness, then the proportional allocation to female function in males should reflect their size.

Lloyd's (1976) model concerns variation in the sexual systems of populations in relation to the sex ratio and the relative fitnesses of each sex. He proposed that such variation constitutes a continuum of gender expression from gynodioecy to dioecy, rather than a series of discrete steps. Once gynodioecy is established, dioecy should evolve by the gradual reduction

of maternal investment among polleniferous plants as they gain more fitness through male function in the presence of females. It may be argued that dioecy cannot evolve unless such changes in sex allocation among males reflect genetic variation, rather than plasticity in gender expression (Delph 1990b). The presence of male inconstancy in this and other sexually dimorphic species may hinder the evolution of dioecy, except perhaps under extreme resource limitation where gender modification may be restricted.

In conclusion, while our studies have not identified the specific ecological conditions that regulate gender expression among populations in the ACT, one might expect that factors favouring large plant size would lead to higher levels of male inconstancy. On the other hand, under more resource-limited conditions, unisexuality would be favoured and populations would appear closer to a dioecious state. Studies on the geographical variation in sexual systems in *W. dioica* from different regions of Australia support this hypothesis. In South Australia, where plants experience the most desert-like conditions, populations are fully dioecious with no evidence of sex inconstancy. The above pattern is also reflected at a local scale in Western Australia, where entirely cosexual populations occur on rich moist soils and sexually dimorphic populations occur in drier areas (Barrett 1992; A.L. Case & S.C.H. Barrett, unpublished data). Collectively, these findings support the view that ecological conditions play a critical role in the evolution and maintenance of combined vs. separate sexes in seed plants.

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