Sex ratios in dioecious Australian grasses: a preliminary assessment

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Abstract

Connor, H.E.[1] *& Jacobs, S.W.L.*[2] *([1] Centre for Resource Management, University of Canterbury, Christchurch, New Zealand; [2] National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, NSW, Australia 2000) 1991. Sex ratios in dioecious Australian grasses: a preliminary assessment.* Cunninghamia *2(3): 385–390.* Four grass genera in Australia are dioecious: *Spinifex, Zygochloa, Pseudochaetochloa* and *Distichlis*. In three genera the sex ratio equals or approximates the primary sex ratio of 1M:1F but in *Distichlis* the populations at most sites consist exclusively of female plants. Australia offers the best opportunity in the Old World to collect in nature basic information to advance knowledge of dioecism in the Poaceae. This preliminary assessment is intended to generate interest in that topic.

Introduction

The primary sex ratio males:females = 1 was established by Fisher (1930) and the theory was extended by Shaw & Mohler (1953). A recent re-examination of the topic is that of Bull & Charnov (1988). For dioecious plants data on sex-form frequencies are derived from counts in natural populations or from genetic experiments. Because of the scarcity of sex-form frequency data in the grasses, Connor (1987) advocated their collection to help substantiate current theories or substitute for them. In Australia four genera of grasses are dioecious: *Spinifex*, three species, and *Zygochloa*, monotypic (Spinificinae, Paniceae); *Pseudochaetochloa*, monotypic (Cenchrinae, Paniceae), and *Distichlis*, one species (Monanthochloinae, Eragrostideae). This is the highest concentration of dioecious grass genera in the Old World; in the New World about 20 genera are dioecious with at least 16 of them present in Mexico.

In Australia sex-form frequencies are known for *Spinifex hirsutus* and *S. sericeus* (Kirby 1988; McDonald 1983; Maze & Whalley 1990a). Here we report those for *S. longifolius*, and for *Distichlis, Pseudochaetochloa*, and *Zygochloa*. Three conform to 1M:1F; the exception is *Distichlis distichophylla* where females alone are found at many sites in Victoria. None of these results assists in the formulation of better models describing sex ratios in wind-pollinated dioecious plants.

Methods

Populations of four of the six Australian dioecious grass species were examined in New South Wales, Victoria, and Western Australia (Tables 1 & 2).

As all species were at anthesis, or nearly so, sex-forms and their frequencies were determined by inspection of single plants (genets) along transects whose lengths were determined by the size of the population. *Pseudochaetochloa* frequency was determined in a rectangular quadrat.

In *Distichlis* two other counts were made at most sites: (i) the number of spikelets in 10 inflorescences of the sex-form, and (ii) the number of florets per spikelet in the penultimate spikelets of five inflorescences. These allow an estimate to be made of differences in resource investment at an early stage of the reproductive cycle.

Results

Distichlis distichophylla (Labill.) Fassett

This short, rhizomatous grass tends to form long narrow strips. In Victoria and New South Wales it was at anthesis at all sites in early December 1987. Stigmas in females are purple, up to 5 mm long, and emerge from the apex of a very slightly opened floret; the sterile anthers, c. 0.1 mm long on filaments up to 2 mm long, are not exserted. In male flowers, tailed anthers c. 3 mm long are borne on filaments c. 4 mm long, but the stigma-styles, c. 2 mm long, are not evidently exserted.

Sex-form frequencies were collected from nine sites, all but one in Victoria (Table 1). At two localities, both male and female plants were found together; everywhere else all populations consisted of female plants only. On the flat, salt-marsh margin of the Betka River, Malacoota, Victoria, one population was exclusively female, but a second, some 50 m upstream, contained 20M and 2F. Ecological differences could not be detected that would account for such a major change.

At Lake Tyer's Boat Ramp No. 2, Victoria, there were six colonies, three of each sex, and judging from their lengths (M = 50 m, 15 m, 5 m; F = 50 m, 5 m, 5 m) they probably represented an initial migration of both sex-forms followed by fragmentation into the present subpopulations. Mixed through one female patch were occasional small male plants. This is the only site at which both sex-forms are present in something approaching 1M:1F.

Exclusively female populations were found at four localities; the sole population exclusively of male plants was found at Lakes Entrance, Victoria.

The mean numbers of spikelets per inflorescence and florets per spikelet are not significantly different between sex-forms in *D. distichophylla* (Table 1).

Spinifex longifolius R. Br.

This Western Australian stoloniferous plant of coastal sand dunes was at pre-anthesis in early June 1988 at Cable Beach. Female inflorescences are globular heads, about 20 cm in diameter, of sessile racemes reduced to a single spikelet on a stout bristle 5–10 cm long. Male inflorescences are terminal clusters of racemes of two-flowered spikelets. There were no problems with sex-form recognition. In the single sample examined the sex ratio was 1M:1F (Table 2).

Zygochloa paradoxa (R. Br.) S. T. Blake

Shrub-like, wiry, and rhizomatous, this is a tall species of inland sand hills. In western New South Wales in December 1987 it was still at anthesis even though seeds were present in some female florets. The male floret opens widely, and versatile, 3 mm long, maculate orange, polliniferous anthers are exserted on filaments about 5 mm long. In female florets stigmas are about 5 mm long and are exserted apically from the floret; the small (0.5 mm) sterile, white anthers emerge at the floret apex. In these characters of anthesis *Zygochloa* behaves like *Spinifex* as described by Connor (1984). In *Z. paradoxa* there is a slight excess of females reflected in their overall frequency of 0.57. In total there is a fit to 1:1 (Table 2), and the significant heterogeneity (X^2_4 = 10.36) is substantially contributed by the sample listed as Lake Menindee (b). No ecological differentiation for sex-form within sites was evident.

Table 1. Sex-form frequencies and allied data for *Distichlis distichophylla*.

	No. plants		Transect length m	Mean spikelets/ inflorescence		Mean florets/ spikelet		Herbarium collections
	M	F		M	F	M	F	
VICTORIA								
1. Betka River, Malacoota (a)	0	21	30	-	5.0	-	7.4	S.J. 5505, 5506
37°36'S 149°45'E (b)	20	2	30	3.9	-	7.8	-	
2. French Narrows (a)	0	19	10	-	3.9	-	5.8	S.J. 5507, 5508
37°48'S 148°35'E (b)	0	19	12	-	3.6	-	8.4	
3. Lake Tyers Boat Ramp No.2 37°50'S 148°06'E	3*	3*	Colonies of each sex up to 50 m	3.7	4.6	9.2	6.6	S.J. 5509, 5510
4. Lake Tyers Fishermans Landing 37°50'S 148°05'E	0	1*	Colony c. 75 m	-	3.8	-	7.8	S.J. 5511, 5512
5. Lakes Entrance 37°52'S 148°00'E	1*	0	Small colony < 10 m	3.3	-	7.6	-	S.J. 5513
6. Metung Shaving Point Reserve 37°55'S 147°50'E	0	2*	Colonies c. 10 m	-	-			S.J. 5514, 5515
N.S.W								
7. Lake Cargelligo 33°18'S 146°20'E	0	2*	Small colonies < 10 m	-	4.6	-	5.4	S.J. 5524
Mean				3.63±0.18	4.25±0.23	8.2±0.50	6.86±0.48	
				t = 1.747 NS		t = 1.732 NS		

Note: *Colonies not individual plants. Specimens from all populations are in National Herbariium of NSW and duplicates at CHR; numbers preceded by S.J. are S.W.L. Jacobs' collecting numbers.

Pseudochaetochloa australiensis A. Hitchc.

In this shortly rhizomatous, inland, endemic perennial, the two sex-forms are so different that they were originally described in separate genera (T. D. Macfarlane, pers. comm.). At Wyndham, Western Australia, some male plants were at anthesis in early May 1988 with the yellow anthers partly extruded apically; in the female plants some spikelets had white stigmas long-exserted apically through the dense white indumentum surrounding the involucre, while other spikelets in the same inflorescence bore mature caryopses. In the one population sampled the sex ratio did not depart from 1M:1F (Table 2).

Discussion

Sex ratios are now known for all dioecious Australian grasses even though some estimates are preliminary. In general they fit a 1M:1F ratio, but the data should not be extended beyond their limits; those for *D. distichophylla* are extensive enough to be reliable, and those for *Z. paradoxa* will reflect the composition of populations in inland New South Wales, but the sex ratio based on a single sample of *Pseudochaetochloa* must remain only a preliminary indication.

The sex ratio for *Spinifex longifolius* in Western Australia was 1M:1F, which is concordant with ratios found elsewhere on Australian coasts for *Spinifex* spp. Kirby (1988) reported an overall fit to 1M:1F for *S. sericeus* in South Australia, and for *S. hirsutus* in Western Australia, but there were some '*S. longifolius*-like' colonies mixed with *S. hirsutus* at three of his sites. In Queensland, McDonald (1983) found 1:1 in *S. sericeus*, and Maze & Whalley (1990a) reported 1M:1F for one beach in New South Wales, but an excess of males on others.

There is general agreement, too, between the sex ratios found in Australia and those in the New World grasses *Buchloe dactyloides* (Schaffner 1920, Quinn & Engel 1986, Wu et al. 1984), *Hesperochloa (Festuca) kingii* (Fox and Harrison 1981), and *Distichlis spicata* (Freeman et al. 1976). *Distichlis distichophylla* is the exception.

There was no evidence of ecological differentiation between sex-forms as reported in *Distichlis spicata* by Freeman et al. (1976), or of a shift in sex ratio with a change in ecological conditions as detected in *Hesperochloa kingii* (Fox & Harrison 1981); ecological conditions were probably too uniform at the sites examined.

The predominance of females in *D. distichophylla* must result from some factor other than the rhizomatous habit. It seems logical to assume that the local distribution reflects vegetative reproduction by fragmentation and water dispersal. This species may have been distributed vegetatively on a much larger scale than our localised samples show, because specimens held in NSW, representing its whole geographic range, are mostly female. There may be, in fact, a series of very large clones. This distribution seems unrelated to female preponderance as discussed by Lloyd (1974).

We have no data of the kind Charnov (1982) would find essential to test sex ratio theory, for example, form of sex ratio control, investment of resources, differential mortality by sex. We do, as Charnov said '...refer to adult sex ratios and question the extent of deviation from equality'; we can do little else. But for *Spinifex sericeus* some results of McDonald (1983) in Queensland and in New South Wales of Maze & Whalley (1990b) are relevant to Charnov's points. In New South Wales among plants raised from seeds (some transplanted into a dune) there were 15M and 15F; in the plants that grew from seeds sown into dunes on South Stradbroke Island, Queensland, the frequency of female inflorescences was 0.41, a little less than the frequency in natural populations.

Reproductive effort in *S. sericeus* (Maze & Whalley 1990b) is also consistent with what Lloyd & Webb (1977) consider to be generally characteristic of dioecious species in: (i) male colonies producing significantly more inflorescences than female colonies; (ii) a preponderance of male inflorescences at the beginning of the flowering season; and

Table 2. Sex-form frequencies in three grasses.

	No. plants		Frequency of females	1:1 X^2	Transect length m	Herbarium collection
	M	F				
Zygochloa paradoxa						
New South Wales Lake Menindee						
(a)	12	12	0.50	0	100	S.J. 5517, 5518, 5519 5520, 5521
(b)	11	28	0.72	7.410	100	
(c)	6	12	0.67	2.0	100	
(d)	10	18	0.64	2.286	100	
Kinchega	27	18	0.40	1.8	250	S.J. 5522, 5523
32°20′S 142°25′E Total	66	88	0.57	3.143		
Spinifex longifolius						
Western Australia Cable Beach	19	20	0.51	0.025	120	S.J. 5833, 5834, 5835
17°56′S 122°12′E						
Pseudochaetochloa australiensis						
Western Australia Wyndham; Five Rivers Lookout	31	35	0.53	0.242	50 m x 10 m	S.J. 5547, 5548
15°22′S 128°12′E						

Note: Specimens from all populations are in NSW and duplicates at CHR; numbers preceded by S.J. are S.W.L. Jacobs' collecting numbers.

(iii) male inflorescences producing more florets than female inflorescences. Resource investment in maleness ensures a relatively high proportion of male:female gametes early in the season, but this alone does not allow of any estimate of the opportunities for fitness gain.

In *Distichlis* there was no significant difference in the number of florets per spikelet and number of spikelets per inflorescence, and thus no suggestion of initial resource investment at different levels. Because the two sex-forms rarely co-occur and because of their habit, it may be difficult to assess quantities such as the relative number of inflorescences per plant, or relative differences in colony sizes.

Kaplan (1972) and Gregorius (1983) proposed that wind-pollinated, dioecious species maximise the average number of pollinated ovules per plant — optimal pollination efficiency — when females are in excess of males. So far, female frequency is not known to exceed 0.5 in natural populations of dioecious grasses. Either, optimal pollination efficiency is not attained, or their models are inappropriate.

These initial results are insufficient to generate new insight into sex ratio interpretation or of the significance of wind-pollination on fitness, but support the 1M:1F sex ratio, *Distichlis distichophylla* excepted. Sex-form frequency and data on differential reproductive effort measured in Australian dioecious grasses, as begun by Maze & Whalley (op.cit.), will be information of the kind which could advance knowledge of the sex ratio in the grasses, and advance its theoretical base.

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