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Breeding systems in New Zealand grasses IX: Sex ratios in dioecious *Spinifex sericeus** †

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Abstract Male and female colonies are of equal frequency and of equal size in *S. sericeus* in New Zealand. This sex ratio is consistent with counts in other dioecious grasses including *S. sericeus* in Australia. Dioecism, its evolution and the associated selection pressures, is discussed. Androdioecism which is described for several species is considered relative to the strict dioecism of *S. sericeus* in New Zealand.

Keywords *Spinifex sericeus* R. Br.; Gramineae; dioecism; sex ratios; seed dispersal

INTRODUCTION

Dioecism is relatively rare among the grasses. It occurs in about 20 genera, and is most common in two tribes (i) Aeluropodeae with five genera and (ii) Chlorideae with six genera (Pilger 1904, Reeder 1969; Connor 1979, 1981). *Spinifex* is one of two dioecious Old World genera in the tribe Paniceae; the other, *Zygochloa*, is an Australian endemic; both are psammophilous, the former coastal and the latter inland.

Data on sex-form frequencies are essential to the formation of an adequate genetic theory for dioecism, but the grasses have largely remained unexamined for this quality, the frequency of male

(staminate) and female (pistillate) plants in dioecious grasses being known from a single count in the stoloniferous perennial *Buchloe dactyloides* of North America (Schaffner 1920). For the rhizomatous salt grass *Distichlis spicata* there is an estimate of sex-form frequency in North America (Freeman et al. 1976), and for *Spinifex* an estimate based on inflorescence counts in quadrats on South Stradbroke Island, Queensland (McDonald 1983). In all three the ratios fit .50M:.50F. Here I report a similar sex-form ratio in North Island populations of the prominent coastal perennial and stoloniferous grass *Spinifex sericeus*. Flowers and flowering are described.

The preferred binomial for this eastern Australian and New Zealand taxon is *Spinifex sericeus* R. Br.; it is usually referred to as *S. hirsutus* in most New Zealand literature, and Hair and Beuzenberg (1966) reported $2n = 18$ for it.

Spinifex sericeus is the only important indigenous sand binding grass in New Zealand, and is almost the sole component of the foredune grassland at many sites. The female infructescence is large, spiny, and at maturity disarticulates at its base and may be seen wheeling along the beach; the inflorescence of the male is never as conspicuous. The probable evolution of inflorescences is discussed.

Species of *Spinifex* contain a harmony of wind pollination and wind dispersal related to dioecism on the one hand, and to wind-driven sand on the other.

METHODS

At 15 sites in North Island the frequency of the two sex-forms was determined from counts of the colonies on the dunes. Esler (1969, 1970, 1974) described the dunes and sandplains in the Manawatu, and at Whatipu, Auckland, sites for samples 5, 12, 13 of Table 1. In some populations all the plants present were sexed, but on some very extensive dune systems such as at Kawhia Harbour, Whatipu, or northern Muriwai Beach near Parakai, c. 0.5 km of dune was sampled. The assumptions made are that a colony can be recognised, and that every colony is a single plant or at least a series of

*Dedicated to Dr E. J. Godley, Director, Botany Division, DSIR 1958-1980 and founder of the New Zealand Journal of Botany, on the occasion of his 65th birthday.

†For part VIII see Connor, H. E. and Matthews, B. A. *New Zealand journal of botany* 15: 531-534; 1977, on *Microlaena*; that part was incorrectly numbered VII. Part VII is Periodic flowering of snow tussock, *Chionochloa rigida*. *New Zealand journal of botany* 4: 392-397; 1966, by H. E. Connor.

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Table 1 Sex-form frequencies in *Spinifex sericeus* in North Island (see Fig. 1 for general location).

Locality	Male	Female	Female frequency
1. Matai Bay	26	25	.49
2. Ahipara Bay	4	1	.25
3. Parakai	31	21	.40
4. Muriwai Beach‡	10	3	.23
5. Whatipu	20	15	.43
6. East Cape	12	12	.50
7. Raglan Harbour‡	6	6	.50
8. Waipiro Bay	1	1	.50
9. Kawhai Harbour	14	21	.60
10. Mokau River	1	2	.67
11. Wanganui River	18	18	.50
12. Himatangi Beach	16	4	.20*
13. Foxton Beach	6	13	.68
14. Otaki Beach	10	8	.44
15. Waikanae Beach‡	4	12	.75*

* Significantly different from .50:50 at 5% level.

‡ Populations conspicuously damaged by man or his animals.

autonomous clones derived from a single plant; some clearly are single plants as it is unlikely that patches of plants 50–60 m long with exclusively male flowers represent several male plants non-randomly distributed.

RESULTS AND DISCUSSION

Flowers

Flowers are present in dimorphic inflorescences. In the male inflorescence up to 15 spikelets are borne on an individual raceme which terminates in a short (1 cm) bristle; in the female inflorescence spikelets are solitary and hidden at the base of a strict bract c. 15 cm long. In male plants in New Zealand the spikelet comprises a pair of florets each with two lodicules and three large (6 mm long) pollen-filled anthers. In female plants the spikelet consists of (i) a small lower floret with two lodicules, and three pollenless, white, small (0.7–1.0 mm long), rudimentary anthers atop stout filaments: there is no gynoecium; (ii) a larger upper floret with two lodicules, three stamens with stout filaments bearing white pollenless anthers (up to 1.5 mm long), and a fully developed bistylar gynoecium. Lodicules of upper female flowers are c. 1 mm × 1 mm, and emarginate; in male flowers they are of the same shape but 0.6 mm long and 0.3 mm wide. This lodicule dimorphism was noted by Pilger (1904) and Vickery (1975). The illustrations in Labillardière

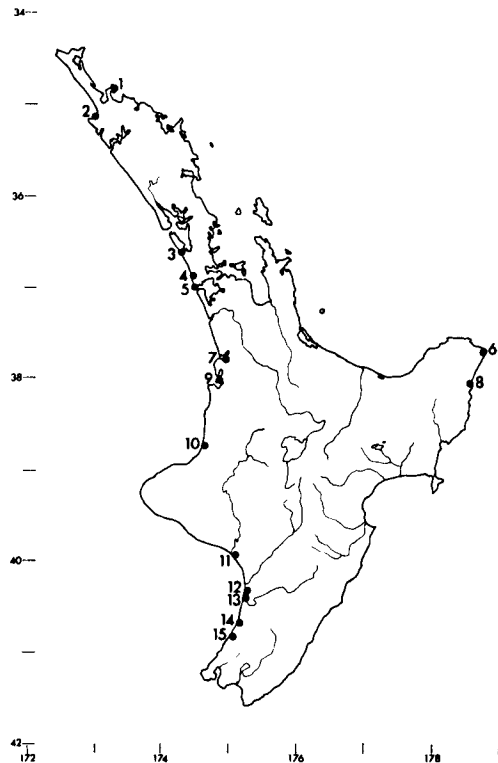


Fig. 1 Locality map for sampling sites.

(1804), Buchanan (1880), and Pilger (1904) correctly portray the structure of the flowers.

At anthesis — mid to late October onwards — in male plants anthers are flexible on long filaments from open florets; in flowers on female plants stigmas are exerted through the apex of the upper anthoecium as in other genera in the tribe, and the sterile anthers are very frequently borne on elongated ligulate filaments up to the tip of the floret and are then clearly visible. Anthers in female flowers of New Zealand plants produce no pollen.

Sex-form frequencies

The frequency of male and female colonies of *S. sericeus* is about equal ($\chi^2 = 0.848$, Table 1) over the sites examined (Fig. 1). There is no significant heterogeneity among the samples ($\chi^2_{14} = 22.28$); the populations at Waikanae and Himatangi beaches depart statistically from .50M:.50F, and in opposite directions.

This frequency of males and females agrees with those found in *Buchloe dactyloides* (Schaffner 1920),

Table 2 Frequency distribution of colony sizes, and mean colony size at 10 sites.

Colony size m	Matai Bay		Parakai		Muriwai		Whatipu		Raglan		Kawhia		Wanganui		Himatangi		Foxton		Otaki		Totals	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Up to 10	15	16	16	7	5	1	5	2	4	4	5	10	6	14	5	3	5	7	3	4	69	68
11-20	6	2	8	3	3	1	6	5	2	2	5	6	7	2	6	1	6	4	4	2	47	30
21-40	1	4	2	6	2	1	6	5			2	3	3	2	4						20	21
41-80	2	1	3	3			3	3			2	2	1		1		1		2	1	15	10
81-160	1	2	2	1							2	2	1						1	1	5	4
> 161	1			1																	1	1
Mean Male	24.4 ± 8.6		20.1 ± 4.9		14.1 ± 2.9		22.9 ± 3.7		9.2 ± 3.7		17.9 ± 4.5		22.2 ± 5.1		18.0 ± 3.5		11.8 ± 6.7		28.9 ± 9.6		157	
Mean Female	19.3 ± 5.7		35.1 ± 9.6		20.0 ± 4.7		30.3 ± 3.9		8.5 ± 2.6		14.9 ± 3.4		9.4 ± 2.3*		9.5 ± 1.6		10.6 ± 2.4		26.3 ± 13.8			

*Significantly different at 5% level.
M = male; F = female.

in *Distichlis spicata* (Freeman et al. 1976), and *Spinifex sericeus* (McDonald 1983). In *D. spicata* the sexes were not distributed at random, males favouring, or being favoured by, higher salinity levels than females. In *S. sericeus* there is no evidence of any ecological differentiation.

Sex-form frequencies where males are in excess in natural populations are more common in New Zealand than equality of sex-forms (Godley 1964, 1979; Lloyd 1973; Webb 1979; Webb & Lloyd 1980), but those plants are individual trees, shrubs or herbs, and not great colony-forming species like the three grasses listed above. Lloyd (1975a) reported an equal sex ratio in four rhizomatous species of *Cotula* in New Zealand.

The sex-form frequencies in grasses were reported from plants in the wild; sex-form frequencies in plants raised from seed collected in the wild have been determined in three species. Schaffner (1920) and Quinn & Engel (1980) recorded .50M:.50F in families of *Buchloe dactyloides*; Reeder & Reeder (1966) recorded .31M:.69F in three families from seed of *Bouteloua chondrosioides*, but there is a chance that this species may actually be gynodioecious. In trial areas on South Stradbroke Island, McDonald (1983) found a lower frequency of female inflorescences (.41F) among plants from experimentally sown seed of *Spinifex sericeus* relative to natural populations (.49F).

These few results indicate that departures from unity may occur in young populations; in *B. dactyloides*, at least, results are consistent between germination and field observations. The departure from .50M:.50F in *S. sericeus* may not disappear when the plants become mature and the colonies better developed, because in *S. sericeus* plants peregrinate from old rhizomes and could thus preserve the sex ratio.

Colony size

Lloyd and Webb (1977) discussed the secondary (non-sexual) differences and similarities between sex-forms in dioecious species. In many long-lived perennials, because a lower investment in reproductive effort may increase the opportunity for vegetative growth or for a higher survival rate, male plants may become larger or more numerous than females.

Colony size in *S. sericeus* was examined at 10 sites; each value in Table 2 represents the average length of a colony, the width being more or less constant because it is the front of the foredune. No differences between colony size of male and female plants could be detected except at Wanganui where males formed significantly larger colonies than did females. Nor is there any difference in the ranges of sizes of the colonies on the dunes; large female

and large male colonies occur, on the average, equally frequently. In the only other dioecious grass for which colony size data are available, *Distichlis spicata*, male plants appear to form larger colonies than female plants (Freeman et al. 1976, fig. 1). Both *Spinifex* and *Distichlis* share the capacity for extensive vegetative growth.

Dispersal

The female infructescence in *S. sericeus* is chamaechorous — it blows along the sand and as the wind drops it rests where it lies until another strong wind sends it wheeling along the strand. Many inflorescences finally lodge among *S. sericeus* colonies and in other vegetation, but many others become covered by moving sand which allows the generation of new plants from seed. The numerous long, stiff bristles assist in dispersal and in anchoring the inflorescence in sand.

Conditions for germination were described by Harty and McDonald (1973); germination is better in the dark than in the light, and when buried in sand (at field capacity) 2.5 – 3.75 cm deep; there is no after-ripening requirement but germination is enhanced if caryopses are freed from spikelets.

Chamaechory in *Spinifex* is probably a response to inflorescence size and to the need to anchor it for sand burial; whether or not its passage along a beach assists in liberating caryopses from the floret so that germination is bettered, I do not know. Wind dispersal itself seems related to the need to transport inflorescences long distances from extant large colonies to vacant habitats in wind-driven mobile sand.

The characteristic inflorescences could have begun to evolve during or after the formation of a monoecious phase. Spikelets would be redistributed in the inflorescence so that male spikelets were at the top and female ones at the base, as is common enough (see table 3 in Connor 1979). Later, and with more emphasis on seed dispersal than formerly, racemes of solitary female spikelets would become aggregated through branch contraction into compact, coherent easily dispersed units. Dioecism would only reinforce these characters.

Dioecism

Dioecism is known only in *Spinifex* and *Zygochloa* in the tribe Paniceae. A common sequence in that tribe is the shift from an ancestral hermaphroditism to andromonoecism and back to a modified hermaphroditism where the lower floret of a pair is neuter and the upper hermaphrodite. However, the lower floret is male and the upper female in monoecious *Chamaeraphis* and *Pseudoraphis* (see

Connor 1979). Monoecious *Hygrochloa*, an endemic Australian, aquatic, inland grass, is exceptional in the Paniceae in that male and female spikelets are distributed separately on the inflorescence (Larzarides 1979).

Spinifex has adopted dioecism rather than monomorphic gender diversification syndromes typical of the Paniceae. This evolution, which Charlesworth & Charlesworth (1978b) envisage as a protracted development, has taken place without any change in the level of ploidy in *S. sericeus* at least — that taxon being diploid.

The selection pressures that favoured the evolution of dioecism in *Spinifex* will undoubtedly include the outbreeding advantage that accrues to dioecism (Thomson & Barrett 1981; Lloyd 1982; but see also the opinions of Givnish 1982, and Bawa 1982). Another character that Lloyd (1982) sees as selective for dioecism, large size and long life, is particularly well developed in *Spinifex*; dioecism would reduce the risks of high levels of geitonogamous wind pollination in very large hermaphrodite colonies of long-lived plants. The route to dioecism may well have been from hermaphroditism to andromonoecism, followed by monoecism and later by dioecism (see Connor 1981, but also the view of van der Pijl 1978). This involves "...the incorporation of an alternating sequence of mutations affecting male and female fertility..." (Charlesworth & Charlesworth 1978b) and the possibility that males and females with traces of the activity of the opposite sex, not just traces of the morphology of the opposite sex, could be expected in cases where linkage among those genes was not extremely strong.

Dioecism in *Spinifex* may not be as absolute as I have described for *S. sericeus* in New Zealand. Vickery (1975) indicated that in *S. sericeus* in New South Wales the pair of florets of a female spikelet may occasionally bear pollen-filled anthers, thus generating a minor androdioecious system since the male plants remain in the breeding populations. Gardner (1952) describes *S. longifolius* in much the same terms for Western Australia. Androdioecism is also described for *S. hirsutus* s.s. in Western Australia, female plants bearing florets that are "...usually bisexual" (Gardner 1952). Backer & Bakhuizen van den Brink (1968) are positive that *S. littoreus* of Java is androdioecious, noting that the upper floret of both forms is always stamiferous, and van der Pijl (1978) reported that in *Spinifex squarrosus* "... andromonoecy had progressed to androdioecy, where it is also associated with seed dispersal, all important in grasses".

I have seen no pollen in the anthers in female plants of *S. sericeus* in New Zealand, nor in herbarium material of eastern Australian provenance.

Female plants of *S. hirsutus* from Western Australia bear single flowers in a spikelet; that flower consists of two many-nerved, c. 3 mm long lodicules, three ligulately filamented, pollenless anthers 1.0–1.7 mm long, and a gynoecium with a stigma bifid in the upper two-thirds of its c. 25 mm length. In the limited array of material that I have examined no anthers were exerted alongside the emerged stigmas. Pollen-filled anthers in male plants are up to 7 mm long. In *S. longifolius*, again of Western Australian origin, anthers in male plants are up to 6 mm long and polliniferous. In the single female flower of a spikelet with nerved lodicules c. 1.5 mm long, three sterile, flared anthers 0.6–1.6 mm long, borne on long filaments, are exerted from the apex of the floret. Stigma-styles are 12–18 mm long, and bifid to the apex of the ovary.

These two Australian species conform to the description of the flowers of *S. sericeus* which I presented above; the flowers of female plants cannot be described as bisexual. The Javan species should be checked to determine whether or not pollen is present in the anthers of stamiferous florets.

The sporadic male-fertility reported by Vickery (1975) is quite likely. Restoration of fertility in species of *Spinifex* would involve a step from filamented, rudimentary, bilobed, small, pollenless anthers to polliniferous ones; this Harlan (1982) calls "genetic recall" of the presumed ancestral condition. This step is not very great and would probably require no more than a dominant gene.

Androdioecism, no case of which has been adequately documented, is regarded as an unlikely candidate for a successful breeding system according to Charlesworth & Charlesworth (1978a) and to Lloyd (1975b, 1982), because the seed bearing (female) sex-form alone can produce heterotic progeny. Further, it is considered unlikely that pollen fitness will be able to be increased by at least twice, the factor needed for the establishment of female sterility in an otherwise hermaphrodite population.

The androdioecism attributed to Malesian *Spinifex* spp. by Backer & Bakhuizen van den Brink (1968) and by van der Pijl (1978) needs to be carefully examined; judged from the present evidence it appears improbable.

Wind dominates *Spinifex*; it is obligately wind pollinated; its seed-bearing inflorescences are conspicuously wind dispersed; and actian winds generate the habitats for its growth and the development of the grassland communities it forms.

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APPENDIX I

Sex-form frequencies in Australian *Spinifex*.

At Queenscliff, Port Philip, Victoria, on 22 September 1983, 21 male plants and 6 female plants of *S. sericeus* were at early emergence. This significant excess of males may reflect the earlier emergence of male inflorescences relative to those on female plants. A month later in New Zealand there were no detectable time differences between panicle emergence of the two sex-forms.

At Bullock Creek, near Darwin, Northern Territory, on 3 September 1982, a population of *S. longifolius* along about 1 km of beach consisted of 17 male and 2 female plants all with fully emergent inflorescences. This departs significantly from .5M:.5F.

NOTE ADDED IN PROOF

Craig (1984) lectotypified *Spinifex hirsutus* by a Western Australian specimen, and reinstated *S. sericeus* R. Br. for New Zealand and eastern Australian plants.

Craig, G. F. 1984: Reinstatement of *Spinifex sericeus* R. Br. and hybrid status of *S. alterniflorus* Nees (Poaceae). *Nuytsia* 5: 67-74.