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Gynodioecism in *Sarcocornia quinqueflora* (Salicornieae) in New Zealand

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"The flowers of the Salicornieae are remarkable in their obscurity and in their unusual structure".

(E. Yale Dawson, 1945)

Abstract *Sarcocornia quinqueflora* in New Zealand consists of populations of hermaphrodite plants except in Golden and Tasman Bays, at Foxton, and on the Otago Peninsula where the species is gynodioecious. Among Nelson populations the frequency of female plants (F) ranged from 0.12 to 0.53; at Aramoana, Otago Harbour, females were not as frequent lying within the values $0.05 < F < 0.10$. *S. quinqueflora* is protogynous and in the gynodioecious populations stigma exsertion from female flowers coincides with anther exsertion from hermaphrodite flowers. Gynodioecism is found in other Southern Hemisphere species of *Sarcocornia*; the possible evolutionary pathway to gynodioecism is outlined. Other reproductive systems found in the Salicornieae are discussed and related to the frequency of gynodioecism.

Keywords *Sarcocornia quinqueflora* ssp. *quinqueflora*; Salicornieae; reproductive systems; hermaphroditism; gynodioecism; male-sterility; wind pollination; sex-form frequency; dichogamy

INTRODUCTION

The succulent palustrine plant with articulated and apparently leafless stems, *Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) A. J. Scott ssp. *quinqueflora*, was known in New Zealand in the past as *Salicornia australis*. It is a diploid perennial glasswort ($2n = 18$), abundant on salt marshes,

sandy beaches, and rock platforms on both coasts of North Island, the eastern coast of South Island, and on Chatham and Stewart Islands. It is also known at two inland localities in Central Otago.

Flowers of *S. quinqueflora* in New Zealand are for the most part perfect and protogynous. At three localities at least, the populations are gynodioecious. In these populations stigma exsertion in female plants coincides with anther exsertion in hermaphrodites.

This paper describes the frequency of hermaphrodite and female plants in several populations, reports self-compatibility in hermaphrodites, discusses the evolution of the gynodioecious breeding system, and relates it to other reproductive systems in the genus and in the Salicornieae.

METHODS

Over the summer months and during a period of several years, populations of *Sarcocornia quinqueflora* were repetitively sampled to determine the sex-form of the flowers. Where monomorphic populations occur no further data were gathered; where dimorphic populations were found sex-forms were verified, and in the Nelson Province the frequencies of each sex-form were estimated from population counts at 12 localities.

In North Island populations were checked between the Kaipara Harbour in the north, Wellington to the south, Foxton in the west, and Whakatane in the east (Fig. 1). South Island populations were examined from Whanganui Inlet, north-west Nelson, to the Otago Peninsula in the east (Fig. 1). These data were complemented by information from specimens in CHR which extend the geographic range to include Northland, Southland, and Stewart Island.

RESULTS

Flowers and flowering

The flowers of *S. quinqueflora* are very clearly illustrated by Wilson (1980, fig. 6); they are surrounded by succulent bracts and occur in axillary cymes of 5-12 flowers, concentrated in terminal spike-like thyrses. Each flower consists of a perianth of two

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long lateral lobes and a small semicircular outer adaxial lobe, two stamens one adaxial and the other abaxial to the gynoecium, and a uniovulate ovary surmounted by a bifid stigma.

In addition to plants with hermaphrodite flowers, plants bearing exclusively pistillate flowers are found at some localities. These are not the polygamous flowers that Cooke (1912) discussed but could not resolve. Female flowers consist of the same 3-partite perianth found in hermaphrodite flowers; the gynoecium alone is present, female flowers lacking even staminodes. This is consistent with the Salicornieae as a whole, and for *S. quinqueflora* at Port Victoria, Australia, as described by Black (1919). Anther filaments in post-anthesis hermaphrodite flowers might be misinterpreted as staminodes.

Throughout New Zealand *S. quinqueflora* is protogynous as Cooke (1912) had reported. The stigma are exerted 1–2 days before the anthers and remain visible for 4–6 days. Anthers are exerted one at a time, and wind pollination prevails (Cooke 1912). Anthers are dehiscent by 8 a.m., or 9 a.m. on a bright morning. Pollen is liberated into the air if an inflorescence is sharply knocked. No insects were seen to be working the flowers, and no nectar is associated with these inconspicuous flowers.

This dichogamy is imprecise. Individual inflorescences at Shoal Bay, Auckland, on 7 January showed some emergent anthers on a spike where stigmas were still present; on a single conical spike at Whanganui Inlet, north-west Nelson, some anthers were emerging while stigmas were present on 15 January. On 17 January, at Lake Grassmere, Marlborough, and in early February in Canterbury and Otago there was some overlap between stigmas and anthers on the same inflorescence.

Thus on a single hermaphrodite plant on the salt marsh near, for example Glorit, Auckland, differences in timing between inflorescences are such that in one the stigmas may be protogynously fully exerted, in another anthers are being exerted and dehiscent, and in a third seed may be maturing from an earlier flowering.

In females of gynodioecious populations stigma exertion coincides with anther exertion of hermaphrodite plants, and not with stigma exertion of hermaphrodites. Thus on a salt marsh in Golden Bay, Nelson, plants may, during a period of a week or so, flower in the following way (i) stigma exertion in hermaphrodites (ii) anther exertion in hermaphrodites and coincident stigma exertion in females. The system has some of the qualities of reciprocation described by Stout (1928); it offers maximum opportunity for cross-fertilisation in females.

In a confusing report McCann (1952) indicated that there are five anthers in the flowers of New

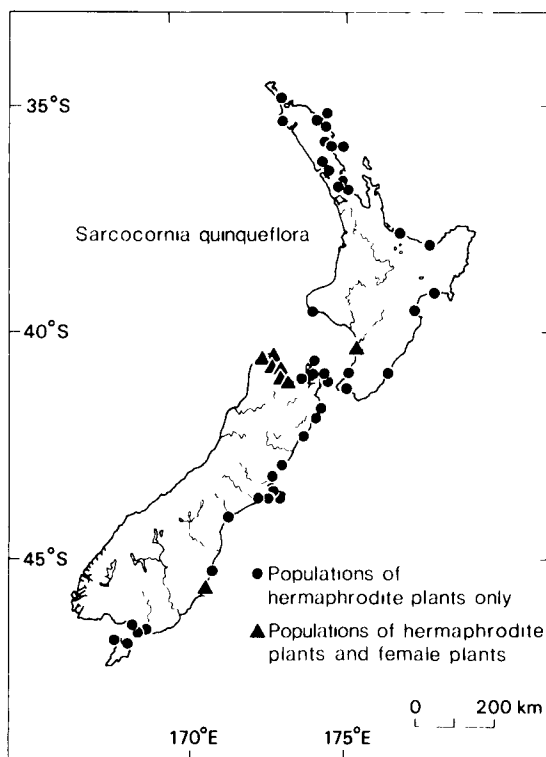


Fig. 1 Distribution of sex-forms in *Sarcocornia quinqueflora* in New Zealand (compiled from field studies and herbarium specimens).

Zealand plants, and that firstly one anther emerges and then the stigmas, followed by the remaining anthers. I am unable to confirm any of his observations.

Sex-form frequencies

The breeding populations consist of hermaphrodite and female plants in Golden and Tasman Bays, Nelson coast; on the coast near Foxton; and on the Otago Peninsula. Elsewhere all plants bear hermaphrodite flowers as seen in extensive searching in the field, and in herbarium specimens (Fig. 1).

Sarcocornia quinqueflora is found in moving sand or deep sand where it forms hummocks, on shell beaches, stony banks and stream margins, rocky places, and mudflats. The ecology of the gynodioecious populations cannot be distinguished in general from the sites where hermaphrodite populations occur except perhaps for the sand habitat.

Table 1 Sex-form frequencies in *S. quinqueflora* in Nelson Province. (Sites outside Nelson Province are discussed below).

| Locality and habitat | Hermaphrodite | Female | Female frequency (F) |
|-------------------------|---------------|--------|----------------------|
| Golden Bay | | | |
| Taupata Stream | | | |
| — sand and stones | 58 | 8 | 0.12 |
| Pakawau Inlet | | | |
| — rock platform | 28 | 15 | 0.35 |
| Totara Terrace | | | |
| — sand and shells | 40 | 29 | 0.42 |
| Onekaka — stone beach | 25 | 4 | 0.14 |
| Motupipi — sand | 16 | 9 | 0.36 |
| Tata Beach — sand dune | 46 | 26 | 0.36 |
| Wainui Inlet — sand | 19 | 21 | 0.53 |
| Tasman Bay | | | |
| Kaiteriteri — sand | 86 | 56 | 0.39 |
| Richmond — mud flat | 33 | 8 | 0.19 |
| Tahuna — sand | 19 | 13 | 0.41 |
| Whakapuaka — mud flat | 16 | 11 | 0.41 |
| Nelson Haven — mud flat | 29 | 15 | 0.34 |
| Total | 415 | 215 | 0.34 |

It is relatively simple in mid-summer, January and February, to determine the sex-form of individual flowers, inflorescences, and plants; protogyny assists in the recognition of hermaphrodite flowers because unemerged anthers are easily seen, and the absence of anthers helps identify female plants.

Sex-form counts were made at 12 sites on salt marshes, sandy beaches, or rocky places in Golden Bay and Tasman Bay (Table 1). The frequency of females (F) was, on average, 0.34 ranging from 0.12 to 0.53; there is significant heterogeneity among the samples.

In Otago at Hoopers Inlet and at Aramoana female plants are present in the population; at Aramoana $0.05 < F < 0.10$ and at Hoopers Inlet even less.

At Waikawa Bay, east of Picton, I was unable in January 1983 to relocate a population that had once consisted of two female plants and 25 hermaphrodites ($F = 0.07$).

No count of sex-form frequency was made at Foxton.

Self-compatibility

One hermaphrodite plant of *S. quinqueflora* from Lake Ellesmere, Canterbury, was isolated from other pollen sources. Seed-set in 10 spikes varied from 37.1% to 86.0%, mean 56.2%. In 10 spikes from one hermaphrodite plant open-pollinated in the presence of others the seed-set was on average

94.5%, ranging from 83.3% to 98.6%. *S. quinqueflora* is self-compatible, and sexual reproduction is assumed. Undoubtedly intra-plant pollination will occur in nature; the extent to which it does is not measurable from this experiment, but the average of 56% seed-set is an estimate of the efficiency of dichogamy and of the inbreeding potentiality.

DISCUSSION

The taxonomy of the tribe Salicornieae, subfamily Salicornioideae, has been long confused but is now well founded as seen from the recent treatments of Scott (1978) and Wilson (1972, 1980). The reproductive biology of the group had remained obscured by an inappropriate taxonomy, and an inadequate appreciation of the flowers themselves (Dawson 1945). These recent taxonomic revisions for the first time correctly align sex-forms among the several genera.

Gynodioecism

The genus *Sarcocornia*, which comprises species formerly included in *Salicornia* and *Arthrocnemum* (Scott 1978), is characterised by regularly perfect flowers but has at least four gynodioecious species: (i) *S. fruticosa* in Argentina (Soriano 1947, as *Salicornia ambigua*); (ii) *S. pillansiae* var. *pillansiae* and var. *dunensis* in South Africa (Tölken 1967, as *Arthrocnemum*) where stigmas longer than

those in hermaphrodites are reported in female plants; (iii) *S. mossiana*, the only protandrous species in the genus (Tölken 1967, as *Arthrocnemum*); and (iv) *Sarcocornia quinqueflora* in New Zealand; Black (1919) described the two sex-forms in plants from Port Victoria, Australia (as *Salicornia australis*). For California, *S. pacifica* was illustrated as gynodioecious (Jepson 1923, as *Salicornia ambigua*), but no one has since commented on the flowers of this taxon. In addition, *S. pulvinata* is gynomonocious in Argentina (Soriano 1947, as *Salicornia pulvinata*).

The evolution of gynodioecism has attracted considerable attention since the initial reports of Darwin (1877) and the important paper of Lewis (1941); recent papers include Charlesworth & Charlesworth (1978a, 1978b), Ross (1978, 1982), Charlesworth & Ganders (1979), Webb (1979), Lloyd (1980, 1982), Charlesworth (1981), Gregorius et al. (1982, 1983) among others.

Gynodioecism necessitates the presence of a gene(s) causing male sterility in part of the population; such a gene is frequently recessive in action and associated with male heterogamety. The most favourable conditions under which male sterility gene(s) allow the evolution of gynodioecism are likely to be those where a high level of self-fertilisation occurs and there is marked inbreeding depression, and female plants have an increased ovule production (Charlesworth & Charlesworth 1978a). Gregorius et al. (1982) emphasise the selfing in hermaphrodites but not the inbreeding depression described by the Charlesworths.

In *S. quinqueflora* hermaphrodites are self-compatible and seed-set is high. Tölken (1967) showed that female plants of *S. pillansiae* did not set seed when isolated from pollen. There are no data on the genetics of male sterility. The simple route to gynodioecism in *Sarcocornia* by way of a male sterility gene(s) should not obscure gynomonocism in *S. pulvinata* where two lateral female flowers surround a hermaphrodite flower. Charlesworth & Charlesworth (1978b) consider that gynomonocism is unlikely to be the beginning of any significant evolutionary pathway to gynodioecism because the spread of yet another male sterility mutation is harder on the second occasion than it was on the first.

The frequencies of females in gynodioecious species are not expected to exceed 0.50 (Lewis 1941), and only at Wainui Inlet was such a female frequency approached. In general, the frequency of females matches those reported in other gynodioecious New Zealand plants in genera such as *Fuchsia*, *Cortaderia*, *Pimelea*, and some apioid umbellifers (see Godley 1979 for summary).

Without additional data I cannot offer an explanation for the well established gynodioecism on the

Golden Bay – Tasman Bay coasts. Selection pressure to which outcrossings to females is an appropriate response is the more easily suggested than substantiated. The isolated population of females and hermaphrodites at Foxton could be interpreted as migrants from the Nelson populations to the west. The low frequency of female plants in Otago might represent an early stage in the establishment of the male sterility gene(s), or selection against gene(s) that control gynodioecism.

Integrated dichogamy

Dichogamy, either as protandry or protogyny, is a most consistent feature of the Salicornieae, so much so that Moss (1954) emphasised the difference between protogynous *Arthrocnemum* and protandrous *Salicornia*. Although *Sarcocornia* now comprises species from both these genera, protogyny typifies it (Cooke 1912; Moss 1954; Dalby 1962; Ferguson 1964; Tölken 1967), but *S. mossiana* is protandrous and an exception (Tölken 1967).

Gleeson (1982) and Lloyd & Yates (1982) emphasise that protogyny and protandry of themselves do not act as outcrossing systems, but that the time differences they generate are sufficient to increase opportunities for outcrossing; dichogamy may allow an increase in fitness in other ways than the avoidance of selfing.

Protogyny has only a moderate effect on the prevention of selfing in hermaphrodite plants of *Sarcocornia quinqueflora* allowing an average 56% seed-set in isolation; selfing was high, too, in the protogynous species of *Salicornia* that Dalby (1962) tested. The within-individual overlap between stigmas and pollen is large as Dalby (1962), and Ferguson (1964) illustrated, and as Tölken mentioned; it may be, as Gleeson (1982) suspects, a characteristic of dichogamy.

Dichogamy in protogynous *Sarcocornia quinqueflora* is integrated in gynodioecious populations by the coincidence of anther exertion in hermaphrodite plants and stigma exertion in female plants. It is assumed that a similarly integrated dichogamy operates in South African *S. pillansiae* and in *S. fruticosa* in Argentina. Such a system could have arisen in this way — (i) a mutation causing the evolution of the very common protogyny possibly as a single dominant gene as Gleeson (1982) found in *Juglans*, and (ii) much later, a male sterility mutant must have arisen. Once this second mutant had become fixed, a stable gynodioecious system would obtain. A delay in maturation of flowers on female plants so that they reach anthesis later than hermaphrodites would bring about coincident exertion of anthers in hermaphrodites and stigmas in females. A shift to later anthesis of female flowers must be a response to sexual selection.

Protandrous *S. mossiana* probably behaves like most gynodioecious species with hermaphrodites flowering first and the overlap between the two sexes being sufficient to ensure adequate pollination of the females (see Lloyd & Webb 1977).

Reproductive systems in the Salicornieae

The relative position of four gynodioecious species of *Sarcocornia* among the tribe Salicornieae can be assessed from an analysis of the reproductive system found in the tribe. The detailed illustrations in Wilson (1980) ensure that the flowers of the Salicornieae are no longer obscure, and that the structure and disposition on and between plants is better comprehended. Although hermaphroditism is the reproduction mainstay of the tribe, the floral array is quite diverse particularly in the subtribe Salicorninae. Phylogenetic constraint, however, is severe because the flowers are uniovulate, anther number is either one or two, anemophily is a very unspecialised pollination system, flowers are disposed in inflorescences in a limited number of ways, and seed dispersal is passively unspecialised.

Two features are consistent — dichogamy and anemophily; the former is expressed either as protogyny or protandry, and wind pollination may be reduced to dispersal of pollen from anthers to adjacent receptive stigmas.

Two trends are evident — the production of 3-flowered cymes and of unistaminate flowers. Although a single stamen is a high frequency phenomenon, two stamens are characteristic of *Sarcocornia*, *Heterostachys*, and *Salicornia* Section *Dolichostachya*. In *Sarcocornia* and *Halosarcia* a cyme may have 3–12 flowers, and solitary flowers are found in *Salicornia pusilla*, *S. uniflora*, *Tegicornia uniflora*, and *Heterostachys*; otherwise, 3-flowered cymes predominate.

Self-compatibility has been recognised in three species of *Salicornia* (Dalby 1962), and *Sarcocornia quinqueflora* is self-fertile. Cleistogamy, a specialised and adaptive form of the self-pollination state, has evolved in *Salicornia* (Ball & Tutin 1959; Dalby 1962; Ferguson 1964; Tölken 1967; Jeffries, et al. 1981; Jeffries & Gottlieb 1982).

Gender diversification involves some redistribution of ovules and stamens either within the inflorescence or between plants (Lloyd 1980; Bawa & Beach 1981). Among taxa displaying dimorphic gender diversification, gynodioecism has been discussed above. Dioecism occurs solely in the monotypic genus *Tegicornia* restricted in distribution to a small part of southern Western Australia. Flowers are solitary, and the single stamen is abaxial (Wilson 1980). *Halosarcia pruinosa* may be dioecious but there are some plants with perfect flowers (Wilson 1980).

Wilson (1980) indicated that *Halosarcia pluriflora*, a species of inland central and southern Australia, is androdioecious but the background data seem sparse and in need of clearer documentation.

Monomorphic gender diversification is seen in two states, andro- and gynomonoeicism. Gynomonoeicism occurs in *Sarcocornia pulvinata* where in a cymule two female flowers are lateral to the single hermaphrodite flower (Soriano 1947). In monotypic *Microcnemum coralloides* the floral arrangement is identical (Scott 1978). Charlesworth & Charlesworth (1978b) showed that fixation of the partial male sterility mutation that is essential to gynomonoeicism will always be differentially favoured because where there is self-fertilisation the conditions determining its spread in the population become easier to satisfy. Yet gynomonoeicism is less frequent than andromonoeicism (Lloyd 1979).

Andromonoeicism in 3-flowered cymules of which two are lateral unistaminate male flowers and the central flower is hermaphrodite, is entrenched in *Pachycornia* (one species), and also in *Sclerostegia* (five species) (Wilson 1980). These protandrous genera are Australian endemics, and the andromonoeicism there should be interpreted as a response to the forces of sexual selection on that very old continent. These selection forces have produced an alternative method of increasing the duration of pollen presentation in unistaminate flowers (see Lloyd & Yates 1982).

The gender diversified sexual systems account for fewer than 15 species among about 60 in the Salicornieae. A departure from sexual reproduction was also indentified by Wilson (1980). Apomixis is known or inferred, in *Halosarcia* only and then solely in female populations in (i) *Halosarcia pergranulata* subspecies *pergranulata* and *queenslandica*; (ii) *H. leptoclada* in both the typical subspecies and in *ssp. inclusa*; and (iii) *H. indica ssp. indica* which had been interpreted by some authors as dioecious because anthers are lacking.

Stigmas are not exerted from the perianth except in *H. indica ssp. indica*. This avoidance of anthesis and the presence of autonomous agamospermy represents an ultimate developmental stage in asexual reproduction. It could lead us to assume that pseudogamy may never have been part of the apomictic syndrome in *Halosarcia* although it is almost universal in apomictic angiosperms.

In *Halosarcia* Wilson (1980) described apparent dioecism and gynodioecism, indicating that pathways to the sustained production of female plants was sufficiently established in the genus to allow the evolution of apomixis in female plants. It is improbable that femaleness evolved after the adoption of agamospermy.

CONCLUSION

Much of the described diversity in reproduction systems can be found in the six salicornioid genera that occur in Australia. Gynodioecism, known so far in four species of *Sarcocornia* that are found in South America, New Zealand, Australia, and South Africa, must qualify as one of the more successful reproductive systems in the Salicornieae. Its actual areal extent is unmeasured. Its presence in the Northern Hemisphere needs to be confirmed although Jepson (1923) illustrated it for California. Species of *Halosarcia* in Australia appear to be gynodioecious, too. At the other end of the distribution spectrum, dioecism is restricted to a small area in southern Western Australia in *Tegicornia uniflora*.

Andromonoecism, occurring in two closely related endemic Australian genera totalling about six species (*Pachycornia* and *Sclerostegia*), is the most frequent gender diversification in the Salicornieae; it is interpreted as a response to sexual selection on that old continent. Gynomonoecism, in keeping with its overall frequency in flowering plants, is found in two species only, in Argentinian *Sarcocornia pulvinata* and in *Microcnemum coralloides* of southern Spain, Turkey, and the Caucasus.

Autonomous apospory occurs in *Halosarcia* in plants that bear female flowers only; in these flowers the stigmas are never exerted outside the perianth except in *H. indica* ssp. *indica*. This latter taxon is widespread —tropical coast of the Indian Ocean and northern Australia. The other apomicts are restricted to Australia.

The coastal salt marshes and the inland salt deserts of the world contain species of 15 salicornioid genera. In most members of the Salicornieae, and the two genera of the allied tribe Haloepeliidae (*Haloepelis* and *Kalidium*), flowers are hermaphrodite. From perfect flowers the other reproductive system must have evolved in different places and at different times and in response to different ecogenetic demands. Gynodioecism in *Sarcocornia* is one successful adaptation among coastal plants.

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