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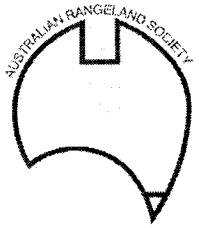

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SEXUAL LABILITY IN BLADDER SALTBUSH (*ATRIPLEX VESICARIA*)

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ABSTRACT

The sexual expression of over 600 shrubs in two South Australian bladder saltbush populations was recorded at intervals during a two-year period. Almost half the individuals were found to change their sexual phenotype. Shrubs that were bisexual at the inception of the study were more labile than those which were male or female. Even though the genus has been described as 'relatively labile' elsewhere, this is apparently the first reported case of sex change in an Australian Atriplex *species.*

INTRODUCTION

According to the definitions of Westergaard (1958), *Atriplex vesicaria* is subdioecious. Male and female flowers are mostly carried on separate plants, but some plants do carry flowers of both sexes (i.e. they are bisexual). In any given reproductive event there are some adult shrubs which do not flower or fruit. In this paper I term these shrubs 'vegetative'.

Freeman *et al.* (1980) list 66 species (in 25 Families) which are known to be dioecious (or subdioecious) and sexually labile. Of the Families listed in that paper, the Chenopodiaceae, Orchidaceae and Salicaceae have the most representatives (although this may be an artifact of the concentration of research). Freeman and McArthur (1984) noted that sex change is a feature of at least six North American *Atriplex* species, and Renner and Ricklefs (1995) regard *Atriplex* as 'a relatively labile genus'.

Sexual expression is reported to vary in response to external manipulations and environmental growth conditions such as disease, age, injury, light intensity, weather, temperature, soil fertility, soil moisture and chemical treatments (Freeman *et al.* 1980, Charnov 1982, McArthur and Freeman 1982). 'Stress' (as defined by Charnov 1982) tends to promote a switch to maleness, except in the case of leaf removal or pruning, which causes a switch to femaleness in many species (Charnov 1982). Many researchers believe that environmental influences cause sex change by altering the balance of internal hormones in plants (Chailakhyan 1979, Freeman *et al.* 1980).

Freeman *et al.* (1980) suggest that lability is selectively advantageous for species living in areas of spatial and temporal variability (like rangelands) because it allows plants to adapt to changing site conditions (Freeman *et al.* 1976, McArthur 1977, McArthur and Freeman 1982, Bierzychudek and Eckhart 1988). Many researchers believe that males are more likely to successfully reproduce on xeric sites because, unlike females, they do not require a persistent moisture supply to bring fruits to maturation (McArthur 1977, Freeman *et al.* 1993, El-Keblawy *et al.* 1995). Individuals can thus maximise their chance of passing genes on to the next generation by exhibiting the sexual phenotype best suited to particular microsite conditions. Lability may allow plants to reproduce during conditions that would normally preclude them from doing so.

METHODS

These results are derived from two permanently tagged subpopulations of *Atriplex vesicaria* on Middleback Station, which is in the southern semi-arid chenopod rangelands of South Australia. The abiotic and biotic features of the area have been described by Lange (1971), Wright (1985) and Lange *et al.* (1992).

The Barbers Dam site is continuously and moderately grazed by sheep and is within one kilometre of Barbers Dam. In August 1994, 220 shrubs were randomly selected from both the grazed and ungrazed pool of sexually mature shrubs in a larger population, to produce a total of 440 tagged shrubs in a 0.5 hectare area.

The Little One Mile population has only received infrequent grazing during small-scale grazing trial research conducted as part of the Middleback Field Centre Program. In September 1994, the population at Little One Mile was approximately half female and half bisexual, and twelve shrubs of each sex were randomly tagged in each of nine contiguous 10 m^2 patches. This produced a total of 216 tagged shrubs in an area of 0.09 hectares.

At both sites, each shrub had a small numbered aluminium tag attached to its base and was mapped for relocation. During each survey shrubs were recorded as male, female, bisexual or vegetative, after careful inspection for flowers and fruits. All shrubs in a population were surveyed in a single day. Throughout the study some shrubs died, so the results reported below are for those shrubs which were sexed in all surveys.

The shrubs at the Barbers Dam site were surveyed four times (August 1994, November 1994, March 1995 and June 1995). The shrubs at the Little One Mile site were surveyed three times (September 1994, February 1995 and September 1995).

RESULTS

For the purposes of this paper, the vegetative state is not considered a sexual phenotype. Shrubs which exhibited vegetativeness on one or more occasions are not included in the lability calculations that follow.

Table 1. The sex dynamics of two *Atriplex vesicaria* populations at Middleback Station.

	Barbers Dam	Little One Mile
Number of shrubs monitored in all surveys	424	203
Population sex ratio (average) F:M:B:V*	8:5:1:3	8:5:4:1
% population stability (average ± s.e.)#	81 ± 2	60 ± 7
% population lability (average ± s.e.)#†	8 ± 1	33 ± 10
% shrubs which did not change sex in any survey†	57	45
% of shrubs which displayed all three phenotypes†	0.5	4
Sex Transition Percentages†		
Male to bisexual	3.6	7.2
Bisexual to male	5.2	23.4
Female to bisexual	0.8	0.0
Bisexual to female	0.6	2.1
Female to male	0.4	0.3
Male to female	0.2	2.4
Male stayed male	31.7	10.9
Bisexual stayed bisexual	2.0	6.9
Female stayed female	55.5	46.8

* F=female, M=male, B=bisexual and V=vegetative.
# The number of shrubs which were stable [or labile] divided by the total number of shrubs in the population × 100 (percentage then averaged across surveys).
† Does not include vegetatives.

At the Barbers Dam site, 116 shrubs (27%) were vegetative in at least one survey. Of the remaining 308 shrubs, 65 (15% of the entire population) changed their sexual expression at least once. Shrubs which were initially female in August 1994 were less likely to change than any other phenotype (94% were consistently female across all four surveys). Shrubs which were initially bisexual in August 1994 were the most likely to change (only 4% were consistently bisexual across all four surveys). Most of the sex phenotype changes were explained by oscillations between the male and bisexual states.

At the Little One Mile site, 22 shrubs (11%) were vegetative in at least one survey. Of the remaining 181 shrubs, 90 (44% of the entire population) changed their sexual expression at least once throughout the study. Shrubs which were initially female in September 1994 were less likely to change than any other phenotype (84% were consistently female across all three surveys). Shrubs which were initially bisexual in September 1994 were the most likely to change (only 8% were consistently bisexual across all three surveys). Like the Barbers Dam population, oscillations between the male and bisexual states accounted for most of the sexual phenotype changes.

DISCUSSION

Given the amount of research that has been conducted on the species, it is interesting that sex lability has not been previously reported for *Atriplex vesicaria*. McArthur *et al.* (1992) found that the number of individuals changing sex in some North American *Atriplex* populations was high, but the magnitude of the change was masked because the sex ratio remained relatively static. Sex lability can only be reliably detected if a relatively large number of individual shrubs are tagged and subsequently surveyed over time (McArthur *et al.* 1992).

The average lability at the Little One Mile site (33% ± 10%) is comparable to that recorded for some North American *Atriplex* populations. McArthur and Freeman (1982) found that 41% of *Atriplex canescens* individuals changed phenotype in a seven-year study of 20 populations, whilst Freeman and McArthur (1984) found that 21% of shrubs in a plantation population of *A. canescens* changed phenotype from year to year in the same time frame. Like at least four North American *Atriplex* species (Freeman and McArthur 1984), the bisexual phenotype was found to be the most labile in both populations of *A. vesicaria* at Middleback. The higher proportion of bisexuals in the Little One Mile population may explain why that site was relatively more labile than the Barbers Dam site. Both populations would have to be surveyed together over time to verify this.

The results reported in this paper have been derived from two grazed populations with different histories from the southern semi-arid rangelands of the Middleback region. Initial results from recently tagged populations further afield (Leigh Creek and Gawler Ranges districts, SA) indicate that lability is also a feature of ungrazed and geographically separated populations. Widely separated populations of different grazing status and history will be monitored in order to further characterise the phenomenon of lability in bladder saltbush.

The discovery of sexual lability in *Atriplex vesicaria* has created an excellent opportunity for further research into the sexual biology of this and other dioecious and subdioecious plants in Australia's rangelands.

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