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Comparative sexuality of conspecific stream-side and stream-rock mosses

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The sexuality of conspecific stream-rock and stream-side bryophytes at Cement Creek in the Yarra Ranges National Park, Victoria, Australia was examined in terms of sex ratios and sporophyte production. Generally, stream-side colonies had higher numbers of stems, inflorescences and gametangia than their stream-rock counterparts. A higher number of stream-side than stream-rock species produced sporophytes although *Cyathophorum bulbosum* (Hedw.) Müll.Hal. produced more sporophytes on stream-rocks than in the stream-side habitat. Sex ratios generally showed a female bias with regard to stem numbers and number of inflorescences.

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Introduction

Bryophytes can be either monoicous, where male and female inflorescences are on the same plant, or dioicous, where male and female inflorescences occur on separate plants (Gemmell 1949). Dioicous species show lower levels of sexual reproduction, compared to monoicous species, possibly due to the fact that the sexes are spatially separated from each other (Gemmell 1949; van der Velde & Bijlsma 2000). It is not surprising, therefore, that sexual reproduction in dioicous species is more common when population densities are high (Kimmerer 1991; van der Velde & Bijlsma 2000). A pattern of female biased sex ratios seems common in bryophytes (Longton 1990; Bowker *et al.* 2000; Wyatt 1994) although male biases do occur (Mc Lechtie & Puterbaugh 2000), and many stems do not show sexual expression (Bowker *et al.* 2000). It is hardly surprising, therefore, that sporophyte production frequently does not occur (Cronberg 2002).

This study examined sex ratios and sporophyte production of conspecific stream-rock and stream-side sporophytes at Cement Creek in the Yarra Ranges National Park in Victoria, Australia.

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Method

The study site was located at the Cement Creek Turntable, on the southern slope of Mt. Donna Buang, in the Yarra Ranges National Park in Victoria, Australia. The site occurs within a Cool Temperate Rainforest pocket dominated by *Nothofagus cunninghamii* (Hook.) Oerst. (Myrtle Beech) and overtopped by *Eucalyptus regnans* F. Muell. (Mountain Ash). It is surrounded by Wet Sclerophyll Forest. The National Park is dissected by Cement Creek, which has fluctuating water levels and is relatively fast flowing. Small populations of bryophytes are common along the edge of the creek and on boulders within the creek with most species occurring in both habitats.

Twenty-five stems from each of eight moss species were collected on the 29th August, 2002, from both the stream edge and from nearby stream rocks. Only rocks of homogenous granitic composition were sampled. All rocks were approximately the same size, with a diameter of 50 cm, as this reflected the most common rock size at the site. All rocks were completely surrounded

by water and could not be considered an extension of the stream bank but, rather, they may be considered as islands. During winter they were frequently inundated. Stems were collected randomly, placed in labelled envelopes and transported to the laboratory where they were stored at 4℃ and examined within a week of collection. Each stem was examined for the presence of perigonia and perichaetia, which were counted, excised from the plant and dissected using an Olympus SZ–PT dissecting microscope. The number of antheridia and archegonia were determined using an Olympus BH–2 compound microscope at 100 × magnification. Any sporophytes present also were counted.

Results

Of the eight species examined, six were dioicous and two monoicous (Table 1). Generally, stream-side colonies were more fertile than their stream-rock counterparts. *Cyathophorum bulbosum* (Hedw.) Müll.Hal. and *Rosulabryum billardieri* (Schwägr.) J.R.Spence were most fertile with, respectively, 24 and 17 of the possible 50 stems fertile. Both species had approximately twice the number of stems fertile on the stream side than on stream rocks. *Hypnodendron vitiense* Mitt., *Ptychomnion aciculare* (Brid.) Mitt., and *Achrophyllum dentatum* (Hook. f. & Wilson) Dix. were not fertile on the stream rocks at this time and *Thuidiopsis furfurosa* (Hook. f. & Wilson) M. Fleisch. was not fertile on the stream side. *Sematophyllum homomallum* (Hampe) Broth. and *Wijkia extenuata* (Brid.) Crum had about equal numbers of fertile stems in both habitats.

Perigonia occurred on four species on the stream side but in only three species on stream rocks (Table 1). Conversely, perichaetia occurred on seven stream-side species and five stream-rock species (Table 1). Perigonia were found on five species and perichaetia on all species. All *R. billardieri, H. vitiense, P. aciculare* and *A. dentatum* stems had perichaetia only, although *H. vitiense* is dioicous. Of species with perigonia, more inflorescences occurred in stream-side colonies than in stream-rock colonies with the exceptions of *Thuidiopsis furfurosa* and *Wijkia extenuata* (Table 1). Five of the eight species had more perichaetia when growing on the stream side while only three species had more perichaetia when growing on stream rocks (Table 1). The mean numbers of perigonia and perichaetia per fertile stem were more variable (Table 2) although quite low in both habitats.

Achrophyllum dentatum produced the highest mean number of antheridia per perigonium (Table 2), which was for stream-side specimens. *Cyathophorum bulbosum* and *S. homomallum* also had higher numbers of antheridia per perigonium for stream-side specimens compared to stream rock specimens. *Wijkia extenuata*, however, had more antheridia per perigonium on stream-rock specimens. The highest mean number of archegonia per perichaetium was 9.7 and occurred on stream-side specimens of *R. billardieri*. The range of antheridia per perigonium and archegonia per perichaetium generally was greater in stream-side colonies than stream-rock colonies (Table 2).

With the exception of *R. billardieri*, sporophytes occurred in all species (Table 3). *Thuidiopsis furfurosa* produced a large number of sporophytes in stream rock specimens (143), while *C. bulbosum* produced 332 and 92 sporophytes respectively in stream-rock and stream-side specimens. Most sporophytes were at the swollen venter stage, at which there is normally a high abortion rate. The high numbers of sporophytes, therefore, do not necessarily reflect the number that survives to maturity. They do, however, indicate the high number of archegonia produced in these species.

Discussion

Many species show little difference in sexual reproductive capacity between habitats (Milne 2001), however, it does occur. Differences in sex ratios or population density are usually nominated as the cause (Longton & Miles 1982). Large differences, however, occur when comparing sexual reproductive capacity of a species growing in both a terrestrial and aquatic environment (Slack & Glime 1985) with sexual reproduction occurring more commonly in terrestrial habitats. In this study, a greater number of species producing sporophytes occurred in the stream-side habitat *i.e.* six species compared to four on stream rocks.

Table 1. Sexuality of conspecific stream-side and stream-rock species.

Species	No. of Fertile Stems (n=25)		No. of Fertile Stems with Perigonia		No. of Fertile Stems with Perichaetia		Mean No. of Inflorescences per Fertile Stem	
	SS	SR	SS	SR	SS	SR	SS	SR
Rosulabryum billardieri (D)	11	6	0	0	11	6	1	1
Hypnodendron vitiense (D)	4	0	0	0	4	0	3.7	0
Ptychomnion aciculare (M)	1	0	0	0	1	0	1	0
Achrophyllum dentatum (D)	7	0	3	0	4	0	3.9	0
Cyathophorum bulbosum (D)	16	8	12	3	4	5	7	6.9
Thuidiopsis furfurosa (D)	0	8	0	3	0	5	0	3
Sematophyllum homomallum (M)	6	7	1	0	5	7	1.2	1.3
Wijkia extenuata (D)	5	5	2	4	3	1	1.4	4.8

(D = dioicous, M = monoicous, SS = Stream-side, SR = stream-rocks)

Table 2. Mean numbers of perigonia, perichaetia, antheridia and archegonia of fertile stems of congeneric stream-side (SS) and stream-rock (SR) mosses.

Species	Mean No. of Perigonia per Fertile Stem		Mean No. of Perichaetia per Fertile Stem		Mean No. of Antheridia per Perigonium		Mean No. of Archegonia per Perichaetium		Range of Antheridia per Perigonium		Range of Archegonia per Perichaetium	
	SS	SR	SS	SR	SS	SR	SS	SR	SS	SR	SS	SR
Rosulabryum billardieri	0	0	1	1	0	0	9.7	4.8	0	0	3-29	2-8
Hypnodendron vitiense	0	0	3.7	0	0	0	0	0	0	0	0	0
Ptychomnion aciculare	0	0	1	0	0	0	0	0	0	0	0	0
Achrophyllum dentatum	3.3	0	0.6	0	18	0	0	0	1-32	0	0	0
Cyathophorum bulbosum	4.7	2.1	1.2	3	9.2	7.5	0	1.3	1-20	3-14	0	3-11
Thuidiopsis furfurosa	0	1.1	0	1.9	0	7	0	1.3	0	4-14	0	1-9
Sematophyllum homomallum	0.2	0	1.2	1.3	9	0	0	0	0-9	0	0	0
Wijkia extenuata	0.8	4.6	0.6	0.2	4.8	7.6	0	1	3-8	1-13	0	0

Table 3. Sporophytic numbers of congeneric stream-side (SS) and stream-rock (SR) mosses.

Species	Total No. of Sporophytes		Mean No. of Sporophytes per Fertile Stem		Mean No. of Sporophytes per Perichaetium		Range of Sporophytes per Perichaetium	
	SS	SR	SS	SR	SS	SR	SS	SR
Rosulabryum billardieri	0	0	0	0	0	0	0	0
Hypnodendron vitiense	11	0	3.7	0	1	0	1	0
Ptychomnion aciculare	9	0	9	0	9	0	0-9	0
Achrophyllum dentatum	4	0	0.8	0	1	0	0-1	0
Cyathophorum bulbosum	92	332	6.5	41.5	1	16.6	0-1	1-39
Thuidiopsis furfurosa	0	143	0	17.9	0	15.9	0	6-20
Sematophyllum homomallum	6	9	1.2	1.3	1	1	0-1	0-1
Wijkia extenuata	3	1	0.6	0.2	1	1	0-1	0-1

In flowing waters, released sperm may be dispersed before fertilization occurs. However, in *C. bulbosum*, by far the greater number of sporophytes occurred on stream-rock specimens and in *T. furfurosa*, no fertile stems occurred on the stream side but eight occurred on stream rocks with five of these being female and having a total of 143 sporophytes. Growing on stream rocks does not make a species truly aquatic. Indeed, most species of this study grew on the upper por-

tion of the rocks and occurred above the water line except after rainfall during winter.

As with sporophyte numbers, sex ratios varied between the two habitats, with stream-side specimens showing higher rates of expression in terms of numbers of stems, of inflorescences and of gametangia. This was in accordance with other published findings (*e.g.* Slack & Glime 1985), similarly, sex ratios generally showed a female bias in terms of stem numbers and inflorescences. This was not unexpected and has often been reported (Longton 1990; Bowker *et al.* 2000; Wyatt 1994).

All stream rock bryophytes that produced sporophytes in this study, were monosetous, even though, in some instances, numerous archegonia were fertilised and reached the swollen venter stage. This phenomenon occurs in many species (Stark 1985; Stark & Stephenson 1983), with many of these immature sporophytes subsequently aborting.

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