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Sporophyte production and population structure of two species of Pottiaceae in an Atlantic Forest remnant in Pernambuco, Brazil

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Résumé – Les populations de *Hyophila involuta* (Hook.) Jaeg. et *Barbula agraria* Hedw. ont été observées avec des sporophytes dans un reliquat de fôret Atlantique, à Recife, État de Pernambuco, Brésil. Le but de cette étude a été d'évaluer chez ces espèces les relations entre la formation de sporophytes et les paramètres populationnels que sont le taux de production de sporophytes, la répartition des sexes, la densité de gamétophytes, la proportion et la répartition des individus mâles, femelles, femelles avec sporophyte et stérile. La prédominance d'individus femelles par rapport aux mâles est remarquable chez les deux espèces. Par contre, les proportions d'individus stériles et sexués sont presque identiques. La densité moyenne des gamétophytes est de 19 cm^{-2} chez *H. involuta* et de 27 cm^{-2} chez *B. agraria*. Finalement, le taux de formation de sporophyte est de 48 % chez *H. involuta* et de 55% chez *B. agraria*, et varie indépendamment des paramètres populationnels mesurés. D'après les résultats on peut conclure que la formation de sporophytes chez *H. involuta* et *B. agraria* subît les variations dans les paramètres populationnels, sans être influencée par ceux-là, dû au fait que la répartition non groupée des individus femelles et mâles permet davantage la reproduction sexuée.

Répartition de sexes / reproduction sexuée / taux de fécondation / Pottiaceae / cycle reproductif / succès de la reproduction

Abstract – Populations of *Hyophila involuta* (Hook.) Jaeg. and *Barbula agraria* Hedw. are found fruiting in an Atlantic Forest remnant in Recife, Pernambuco, Brazil. In order to verify the relationship between sporophyte production and population parameters, ten populations of each species were studied. The sporophyte production, sex ratios, shoot densities, and the proportion and spatial distribution of fertile females, fruiting females, males and sterile shoots were measured. The predominance of females over males was significant for both species. The proportion of sterile and sexual shoots, however, was almost 1:1. Average shoot density was 19 per cm^2 for *H. involuta* and 27 per cm^2 for *B. agraria*. Finally, the sporophyte production of 48% for *H. involuta* and of 55% for *B. agraria*; this variation was not related to any of the other population parameters measured. Therefore, sporophyte production in *H. involuta* and *B. agraria* must withstand the variations in population parameters without being influenced. The non-clumped spatial distribution of female and male shoots favors sporophyte production.

Sexual reproduction / sexual rate / Pottiaceae / reproductive cycle / population ecology

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INTRODUCTION

Sexual reproduction in mosses is more frequent in monoecious than in dioecious taxa: in the former, there is a higher chance of both sexes occurring in the same population and the proximity among male and female gametangia favors fertilization (Gemmel, 1950; Rohrer, 1982; Longton, 1992; Oliveira & Pôrto, 1998). Thus, the main factors related to the absence or low rates of sporophyte production in dioecious species are the availability of gametes of both sexes and the distance between male and female gametangia. The identification of population parameters that represent these conditions is essential for understanding sexual reproduction in these species.

During the last four decades, several relationships between sexual reproduction and population parameters have been studied, such as sexual ratios (Longton & Greene, 1969), spatial distribution of male and female gametophores (Wyatt, 1977), sterile gametophore proportions (Stoneburner, 1979), and gametophore density (Kimmerer, 1991a).

One of the characteristics of the family Pottiaceae is its ability to establish populations in restrictive habitats that include environmental pressures such as desiccation, freezing, or frequent anthropic perturbations (Zander, 1996). The two species studied, *Hyophila involuta* (Hook.) Jaeg. and *Barbula agraria* Hedw., are usually found in forest borders, in open areas, or in urban centers.

In a recent study at the Reserva Ecológica de Dois Irmãos (Dois Irmãos Ecological Reserve), Pôrto & Oliveira (1998) described various characteristics of the bryophyte flora, such as substrate preference and the phenology of some species. The authors cited the occurrence of *Hyophila involuta* and *Barbula agraria*, which formed with *Bryum argenteum* Hedw. communities on substrates of anthropic origin. Both pottiaceous species reproduced sexually although not consistently so: some patches bore large numbers of sporophytes whereas other were apparently completely sterile. Based upon this previous knowledge about sexual reproduction in Pottiaceae at this reserve, this study was conducted with the aim of answering the following question: Is the frequency of sporophyte production in *Hyophila involuta* and *Barbula agraria* influenced by some kind of population parameter, such as the proportion of female, male and sterile gametophores, sex ratio, and gametophore density and/or by the spatial distribution of female and male shoots?

STUDY AREA

The Reserva Ecológica de Dois Irmãos is located in the city of Recife (Lat. 8°04'00"S and Long. 34°52'00"W), state of Pernambuco, Brazil where it covers an area of 387.4 ha. Annual temperature and precipitation means are of 25.5°C and 2450.2 mm, respectively. The forest is a remnant of the tropical lowland rain forest, locally known as Atlantic Forest. There is diversity of available substrates and microhabitats for different species of mosses due to the presence of three arboreal strata, as well as shrubs, and a herbaceous layer. The patches of *Hyophila involuta* and *Barbula agraria* studied typically colonize parts of the forest border with herbaceous vegetation and were found on slopes and cement plaques.

MATERIAL AND METHODS

Field sampling

Ten populations of each species were selected; all had sporophytes and were found under the same micro-environmental conditions. Every continuous clump of shoots of the same species separated from another from at least 5 cm was considered a population (Kimmerer, 1991a). All samples – minimum dimension of 6 × 6 cm – were removed with the aid of a spatula and packed in plastic containers without altering the shoots' spatial distribution. The sampling was undertaken during five consecutive months (from March to August 2000). During this period the reproductive structures were not undergoing maturation and represented the result of the population's last reproductive season.

The samples were taken to the laboratory and analyzed in the following manner: a grid of 5.5 × 5.5 cm with horizontal and vertical lines at 0.5 cm intervals was placed over the sample for observation under a dissecting microscope (Wyatt, 1977). All shoots positioned exactly under each one of the grid's one-hundred intersection points was selected for analysis. The selected gametophores were each classified as female, female bearing sporophyte, male or sterile. Shoots without gametangia or sporophytes (i.e., any sex-indicating structure) were considered sterile (Longton & Greene, 1969).

Statistical analyses

Using the procedure described above it was possible to obtain the proportion of gametophores in each classification (female, male, and sterile), to calculate the sex ratio and the sporophyte production, and to verify the shoots' spatial distribution. For the calculation of shoot and sporophyte density in each sample, ten areas of 0.25 cm^2 were selected randomly inside the grid, and the total number of shoots and the number of shoots with sporophytes were counted. The sex ratio was calculated considering all female shoots (including those bearing sporophytes) in relation to male shoots. Similarly, the proportion of sterile shoots was calculated as the number of sterile shoots divided by the total number of shoots in the population. The sporophyte production was calculated as the number of female shoots bearing sporophytes divided by the total number of female shoots in the population.

Shoots and sporophyte densities were recorded as the total number of gametophytes per cm^2 and the total number of sporophytes per cm^2, respectively.

The following tests (Zar, 1998) were performed on the data: a) the Wilcoxon t paired test, to verify differences between the number of male and female shoots, as well as between sexual and sterile shoots; and b) the Spearman rank correlation for the relationship between sporophyte production and sporophyte density, to verify whether the sporophyte production is a good indicator of sporophyte density, and to verify the relationship between the sporophyte production and the other population parameters analyzed.

Finally, the following hypothesis was tested: females bearing sporophytes (*i.e.*, those that had been fertilized) should be nearer to male shoots than females without sporophytes. Therefore, the distances from each of the population's male shoots to each female bearing a sporophyte was measured, as well as the distances between each male to each female without a sporophyte. The average distances were then compared.

RESULTS

A total of 839 shoots of *Hyophila involuta* and 776 shoots of *Barbula agraria* from ten populations of each species were analyzed. There were not 1000 individuals for each species studied because some of the spots analyzed presented bare soil at the intersections. All populations of both species studied were bisexual and had female, female bearing sporophyte, male, and sterile shoots (Tabs 1, 2). For *H. involuta* the average of shoots for each of these categories was 20%, 15%, 23%, and 42%, respectively. For *B. agraria*, the results were similar: the average of shoots for each category was 12%, 14%, 12%, and 62%, respectively. Gemmae were also observed in sterile and sexual shoots of both species.

The sex ratio was female biased in seven among ten populations of *H. involuta*, and also female biased in eight among ten populations of *B. agraria*

Tab. 1. Number of shoots in each reproductive category of ten populations of *Hyophila involuta* in the Reserva Ecológica de Dois Irmãos, Pernambuco, Brazil.

Population	*Female without sporophyte*	*Female with sporophyte*	*Male*	*Sterile*	*Total*
1	5	16	19	23	63
2	9	8	20	41	78
3	5	15	50	15	85
4	24	5	8	40	77
5	11	9	7	46	73
6	2	9	56	30	97
7	20	14	6	57	97
8	38	10	17	30	95
9	17	8	3	54	82
10	38	35	7	12	92
Total	169	129	193	348	839

Tab. 2. Number of shoots in each reproductive category of ten populations of *Barbula agraria* in the Reserva Ecológica de Dois Irmãos, Pernambuco, Brazil.

Population	*Female without sporophyte*	*Female with sporophyte*	*Male*	*Sterile*	*Total*
1	2	9	1	46	58
2	6	12	4	48	70
3	5	37	13	19	74
4	3	3	5	53	64
5	2	9	20	50	81
6	10	22	23	36	91
7	2	3	13	77	95
8	12	3	8	52	75
9	20	7	7	37	71
10	31	4	2	60	97
Total	93	109	96	478	776

(Tabs 3, 4). In both species the number of female shoots was higher than that of male shoots.

Gametophore density was, on average, 19.08 per cm^2 (s = 3.88) in populations of *H. involuta* and 27.36 (s = 7.4) in populations of *B. agraria.* Density variation in both species was not related to any other population parameter, not even the sporophyte production (Figs 1a, b).

The sporophyte production in these populations was extremely variable, and the values recorded were x = 48.42% and s = 22.8 for *H. involuta* and x = 55.43% and s = 27.6 for *B. agraria*. The variation was not related to the other population parameters.

Distances between female and male shoots were not significantly different from distances between females bearing sporophytes to males.

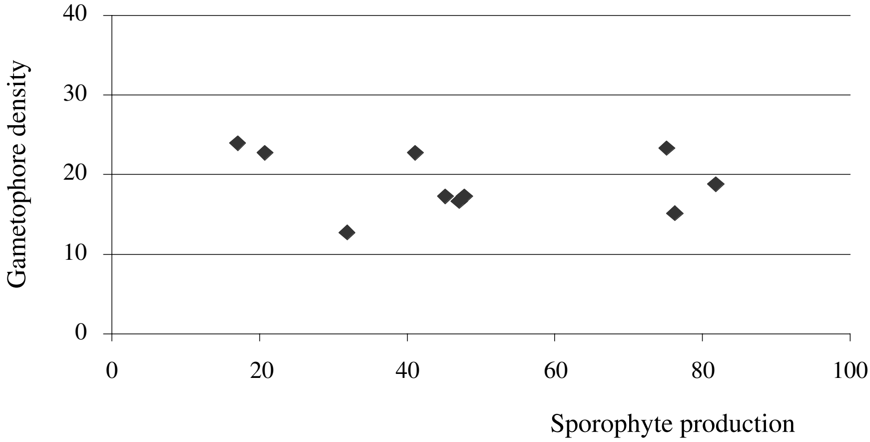
Tab. 3. Population parameters of ten populations of *Hyophila involuta* in the Reserva Ecológica de Dois Irmãos, Pernambuco, Brazil.

Population	*Sporophyte production*	*Density (gametophytes cm^{-2})*	*Sex ratio (♀: ♂)*
1	76.2	15.2	1.1 : 1
2	47.1	16.8	0.8 : 1
3	75.0	23.2	0.4 : 1
4	17.2	24.0	3.6 : 1
5	45.0	17.2	2.9 : 1
6	81.8	18.8	0.2 : 1
7	41.2	22.8	5.6 : 1
8	20.8	22.8	2.8 : 1
9	32.0	12.8	8.3 : 1
10	47.9	17.2	10.4 : 1
X	48.42	19.08	

Tab. 4. Population parameters of ten populations of *Barbula agraria* in the Reserva Ecológica de Dois Irmãos, Pernambuco, Brazil.

Population	*Sporophyte production*	*Density (gametophytes cm^{-2})*	*Sex ratio (♀: ♂)*
1	81.8	26.8	11.0 : 1
2	66.6	32.4	4.5 : 1
3	88.1	26.4	3.2 : 1
4	50.0	36.0	1.2 : 1
5	81.8	14.8	0.5 : 1
6	68.7	20.8	1.4 : 1
7	60.0	34.4	0.4 : 1
8	20.0	26.8	1.9 : 1
9	25.9	36.0	3.9 : 1
10	11.4	19.2	17.5 : 1
X	55.43	27.36	

a)



b)

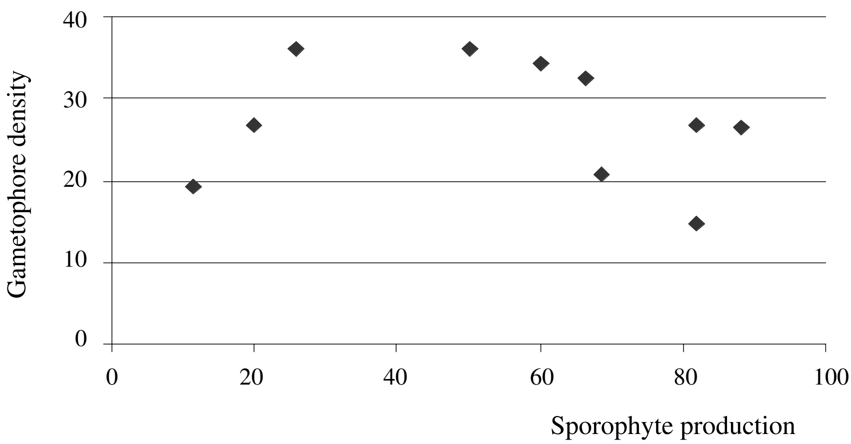


Fig. 1. Relation between gametophore density and sporophyte production in ten populations of *Hyophila involuta* (**a**) and *Barbula agraria* (**b**) in the Reserva Ecológica de Dois Irmãos, Pernambuco, Brazil.

DISCUSSION

The populations of *Hyophila involuta* (Hook.) Jaeg. and *Barbula agraria* Hedw. showed high variability in population parameter values, such as sporophyte production, sex ratio and shoot density. Nevertheless, patterns recurrently cited in the literature, as well as others specific to the species studied, could also be observed, as discussed below.

The predominance of females is commonly reported in papers dealing with sex ratios (Riemman, 1972; Blackstock, 1987; Shaw *et al.*, 1991) and was confirmed in this study for two more acrocarpous species.

Sexual bias in a population can have several different causes. There are records on the influence of microhabitats in female biased populations of *Syntrichia caninervis* Mitt. (Bowker *et al.*, 2000) and of a density-dependent relationship for *Tetraphis pellucida* Hedw. (Kimmerer, 1991a). However, when comparing those examples to the species studied, density and microhabitat conditions do not seem to be related to the predominance of female shoots. In *B. agraria*, female bias was not related to any other population parameter and the microhabitat conditions were the same among populations with predominance of females or males. Thus, sexual bias in these species may be due to a more efficient asexual reproduction in female shoots than in male shoots, through gemmae production. As a result, sexual reproduction plays an important role in the recruitment of new male shoots, avoiding a progressive increase in the proportion of female shoots, which would hinder sexual reproduction (Solli *et al.*, 2000).

The number of sterile gametophores was close to the number of sexual gametophores – female plus male shoots. This agrees with the 1:1 ratio already recorded in some mosses (Stoneburner, 1979; McQueen, 1985; Shaw & Gaughan, 1993), but differs from what is known about two other species of Pottiaceae: Bowker *et al.* (2000) found that only 15% of the shoots in the populations of *Syntrichia caninervis* at Mojave Desert, USA were sexual**,** and in populations of *Scopelophila cataractae* (Mitt.) Broth. from different localities sterile shoots were predominant (Shaw, 1993). However, it must be taken into account that the species cited above were found in regions drier than where *H. involuta* and *B. agraria* were studied.

Regarding gametophore density in the populations, lower densities did not mean lower sporophyte production. This suggests that sexual reproduction can occur even in recently established populations, and it brings the advantage of maintaining both sexes in the same population. This is not a usual pattern - in *Tetraphis pellucida*, lower densities are associated with an investment in asexual propagula at the expense of gametangia production (Kimmerer, 1991b). According to Kimmerer, this strategy generates fast population growth and habitat occupancy. Increasing population age was also related to sporophyte production in *Hylocomium splendens*, as pointed out by Cronberg (2002).

Although gemmae production was not calculated, their presence was recorded for all populations of *H. involuta* and *B. agraria* studied, which probably means that resources for sexual and asexual reproduction are not mutually exclusive for these species. Thus, the occurrence of sexual reproduction and production of asexual propagula may match, as it is currently considered, long and short term advantages, respectively.

Variations in population parameters are usually closely related to sporophyte production. Stoneburner (1979) found that the sex ratio and the proportion of sterile shoots were related to sporophyte production in different populations of *Pleurozium schreberi* (Brid.) Mitt. In addition, Kimmerer (1994), in a study of *Dicranum flagellare* Hedw., observed that density may also influence sporophyte production; it was verified that there is an optimum density for sexual reproduction and density values higher or lower than this optimum result in reduced sporophyte production. Regarding the population's spatial distribution of shoots, Wyatt (1977) suggested that clusters of female and male shoots and their spatial segregation mean less chances of sexual reproduction in dioecious mosses. After studying *Atrichum angustatum* (Brid.) Bruch, Schimp. & Gümbel, Clayton-Greene *et al.*

(1977) presented similar results for *Dawsonia superba* Grev. It was also experimentally proven that the distance between male and female shoots affects sporophyte production in *Rhytidiadelphus triquetrus* (Hedw.) Warnst. (Bisang *et al.,* 2004).

Nevertheless, the frequency of sporophyte production in *H. involuta* and *B. agraria* is not determined by the population parameters. It is suggested that these populations are spatially structured to withstand variations in sex ratio, in the proportion of sterile shoots, and even in gametophore density, without hindering sexual reproduction. The non-clumped spatial distribution of female and male shoots favors sporophyte production by avoiding distances between them that could make syngamy impossible. This pattern was also recorded for *Sphagnum subtile* (Russow) Warnst. (McQueen, 1985), but it is not commonly referred to in literature.

Another important advantage of the spatial distribution observed is linked to the reaction to anthropic pressures. Habitat fragmentation is probably less dangerous for these species since the non-clumped spatial distribution of female and male shoots allows small populations to have both sexes even after patching and to maintain sexual reproduction.

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