Notes on the seasonal reproductive cycle and sporophyte frequency in the leafy liverwort *Nardia scalaris*

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Introduction

There are rather few published reports of detailed field studies on reproductive seasonality in leafy liverworts. By comparison, mosses have been somewhat more intensively studied, and a larger body of information has accumulated on the seasonal periodicity (phenology) of antheridia, archegonia and sporophyte development (Longton, 1990; Stark, 2002); such data have relevance to understanding ecological behaviour, and contribute to various other aspects of bryology.

Some of the major patterns of reproductive phenology among leafy hepatics were outlined by Schuster (1966), but few time-series data sets are available, although the importance of photoperiod and other factors has long been established under laboratory conditions (e.g. Benson-Evans, 1961). One group of liverworts that is being intensively studied in the natural environment by Sanna Laaka-Lindberg and colleagues includes several specialist hepatics associated with decaying timber in boreal forest habitats in southern Finland. Among the study species is *Lophozia silvicola* Buch, for which quantified information on reproductive phenology has recently been recorded over a three-year period (Laaka-Lindberg, 2005).

In the late 1980s, I recorded analogous (but less quantified) descriptive observations on *Nardia scalaris* in north-west Wales. This study was undertaken primarily out of personal curiosity but, as the findings from this oceanic-temperate region show some interesting contrasts with those of the boreal epixylic *L. silvicola*, it seemed worthwhile to prepare a summarised account of the results.

Methods

N. scalaris is common in north-west Wales and was chosen as a study species as it is dioicous and lacks specialised non-sexual propagules, so that sexual reproduction and establishment from spores presumably play an important role in its dispersal and colonisation. It most commonly occurs on acidic mineral soil banks, often by paths, tracks and roads in the lowlands, and by paths and on unstable slopes in the uplands; it is also found on streamside banks. Such habitats may be rather short-lived or subject to disturbance, and *N. scalaris* is frequently accompanied by other hepatics, notably *Cephalozia bicuspidata*, *Diplophyllum albicans* and *Jungermannia gracillima*, that are able to adopt a ruderal life-style with a high reproductive output. Mild winters and cool summers characterise the climate of the region, but there are marked gradients in temperature and rainfall from the coast to the uplands of Snowdonia (Hill, 1988).

Monthly observations were made, between September 1986 and September 1989, on the occurrence and development of gametangia and sporophytes at the main study site, near Tregarth, where a large but confined population of *N. scalaris* was present on a rocky soil bank, under partial shade from adjoining woodland, at an altitude of 150 m. At each monthly visit, three small samples (2-4 cm in diameter) were collected from isolated patches and field observations on reproductive structures were made across the population. The samples were later examined under a dissecting microscope. Simple data were recorded on the stages of development of male and female gametangia and sporophytes; in each case they were allocated to immature (including gametangial initials), mature and post-mature phases, and any variability was noted. Gynoecia were sectioned to score immature sporophytes, and gynoecial shoot innovations were also recorded. This approach does not allow a quantified assessment of the majority state of each reproductive component, such as the 'maturity index' applied by Laaka-Lindberg (2005) to characterise the main stages in seasonal development. Non sex-expressing shoots were also present in all samples.

Information on seasonal reproductive development was also obtained from samples collected (mostly between 1986 and 1989) from a further 40 populations of *N. scalaris* at widely dispersed localities across north-west Wales; 24 of these were in the lowlands (below 300 m altitude) and 16 were in the uplands (above 300 m altitude). One or more samples (84 in total) were collected from isolated patches in each population; gametangia and sporophyte stages were assessed for comparison with their development at the main study site. The data were also used to gain an indication of the regional frequency of males, females and sporophytes in *N. scalaris*.

Additionally, two samples (approximately 5 cm in diameter) were collected in September 1986 from the Tregarth site and maintained in cultivation at room temperature, with more or less constant moisture and east-facing light, to observe more closely the final phase of sporophyte maturation.

Seasons were treated as follows: spring (March-May), summer (June-August), autumn (September-November) and winter (December-February).

Results

Sporophyte frequency in north-west Wales

Sporophytes were found in 35 (88%) of the 40 populations sampled across north-west Wales (Table 1), as well as at the main study site. Of the 84 separate patches sampled from the secondary sites, 63 (75%) had sporophytes, but did not necessarily have male shoots. There was no indication of a major sexual imbalance in the regional populations of *N. scalaris*.

Table 1. Numbers of *Nardia scalaris* populations and patches sampled in north-west Wales with records of males, females and sporophytes.

	Populations (n=40)	**Patches (n=84)**
+ Sporophytes	35	63
+ Males + Females	35	54
+ Males – Females	2	8
– Males + Females	2	19
– Males – Females	2	2

Seasonal development of gametangia and sporophytes

Since phenological progress between years and among populations was broadly compatible, records are combined below to describe the major seasonal phases. Nevertheless, there was often considerable variability within a single sample that would be difficult to interpret in isolation.

Antheridia

New androecia with immature antheridia developing at shoot apices, often above intercalary bracts of a previous male generation, appeared in the winter to early spring period. Antheridia started to reach maturity in mid spring to early summer when dehiscence commenced. Further antheridia formation took place through the summer and autumn periods when males at different phases often occurred in the same patch; in some cases, maturing antheridia were observed in autumn androecia on shoots with intercalary post-mature spring androecia. Male inflorescences were variable in extent, with 3-9 (or occasionally more) pairs of bracts and with 1-3 antheridia per bract.

Archegonia

Gynoecia with immature and maturing archegonia began to appear in late spring (late April-May), and often developed on innovations from barren females of the previous year. Archegonia production continued into the autumn, and in some cases these later gynoecia were on innovations from females that had borne sporophytes in the spring or, rarely, from barren spring females. Mature archegonia were thus present through much of the spring to autumn, developing in part on shoots with differing previous reproductive experience.

Archegonia production ceased in females following successful fertilisation. Post-mature barren gynoecia usually had 20-30 pink or brown archegonia.

Sporophytes

Immature sporophytes were divided into early (largely premeiotic) and late phases. Early immature sporophytes were recorded from June onwards through to autumn and occasionally in early winter when many had entered the late immature phase. There was thus a major phase of fertilisation in late spring and early summer, with an indication that this continued into the autumn period to some extent. The final short phase of sporophyte maturation, when capsules darken and seta elongation takes place, followed by capsule dehiscence and exposure of the spore-elater mass, was observed occasionally in February, most commonly in March-April, and was mainly complete by early May when most spores had been liberated. But there was variation in the timing of sporophyte maturation within populations, and this is examined in the following section. The latest post-mature sporophyte remnants were observed in June at upland localities at 500-750 m altitude.

Very little immature sporophyte mortality was noted. Occasionally, and in a wide range of samples, early immature twin sporophytes were present within a single gynoecium, but by later stages only single sporophytes had successfully developed.

Sporophyte maturation in cultivation

The two samples (A and B) that were brought into cultivation in September 1986 both had immature sporophytes. Sample A had males as well as females, but males were absent in sample B.

In sample A 14 mature sporophytes developed between 1 March and 21 April 1987, and in sample B 49 sporophytes matured between 26 February and 15 April 1987 (Figure 1). The period of initial seta elongation to capsule dehiscence in individual sporophytes generally took place over 1-3(-4) days.

Maturing archegonia were present in both cultures from May onwards through to September 1987 and February 1988, and antheridia production was more or less continuous in sample A over the same period. By autumn 1987, inflorescences at varying phases were present, and innovations were developing from barren females. Immature sporophytes were detected in sample A in the summer of 1987, and the final phase of maturation took place between 13 March and 12 April 1988 when 22 capsules ripened and shed spores (Figure 1).

Discussion

Although only a small sample was assessed, it is apparent that *N. scalaris* was highly sexually active in north-west Wales during the late 1980s. The great majority of populations had both females and males, usually within fertilisation range and often closely intermingled. Copious spore production in this species, that lacks gemmae and other asexual propagules, may be required for successful population spread and colonisation of freshly exposed substrate.

Fertilisation took place in late spring and early summer, and probably to some extent onwards into the early autumn. The final phase of sporophyte maturation was mostly compressed into the following (February-)March-April period (Figure 2). The annual reproductive cycle of *N. scalaris* thus conforms to a common pattern recognised by Schuster (1966).

Antheridia development in *N. scalaris* occurred in late winter and early spring, somewhat before a major phase of archegonial production, and males at differing phases were present in the autumn indicating differential phenology among, and possibly within, male shoot complexes. Archegonial maturation took place in late spring and at later times of the year; the first arose in part on shoots from barren females of the previous year, while later archegonia ripened on shoots from spring sporophyte-bearing females. Different cohorts of archegonia were thus partly due to variation in the earlier reproductive burden of individual female shoots. The role of shoots that lacked sex expression in relation to reproductive activity is something of an enigma.

Laaka-Lindberg (2005) related variation in the phenology of *Lophozia silvicola* to climatic conditions (temperature, rainfall and humidity) in a boreal locality that is snowbound in the winter. She also concluded that the reproductive cycle took two growing seasons.

Other British liverworts are known to undergo sporophyte maturation and spore release in the spring, as indicated in Table 2 in which information on the frequency and maturation of sporophytes has been summarised from data presented in Paton (1999) for the ten most common dioicous (excluding *N. scalaris*) and the ten most common monoicous liverworts in Britain (Hill, Preston & Smith, 1991). Common British liverwort species are more likely than rare species to produce sporophytes (Laaka-Lindberg, Hedderson & Longton, 2000), and in most of the taxa in Table 2 sporophytes are produced at least occasionally and often at quite high frequency, at least over parts of their range. As well as those with spring-maturing sporophytes, some species have different patterns. Although there may be seasonal peaks, in the unisexual epiphytes *Frullania dilatata*, *F. tamarisci* and *Metzgeria furcata*, for instance, mature sporophytes have been recorded throughout the year; there are other species, such as *Lophocolea bidentata*, *Lophozia ventricosa* and *Porella porelloides*, which liberate spores from spring to autumn.

New information in this comparatively neglected aspect of hepaticology can be gleaned from quite simple seasonal observations on populations in the field and from herbarium material (e.g. Zehr, 1979). They contribute to elucidation of general patterns of reproductive behaviour and output.

Acknowledgement

I am grateful to Jeff Bates for advice.

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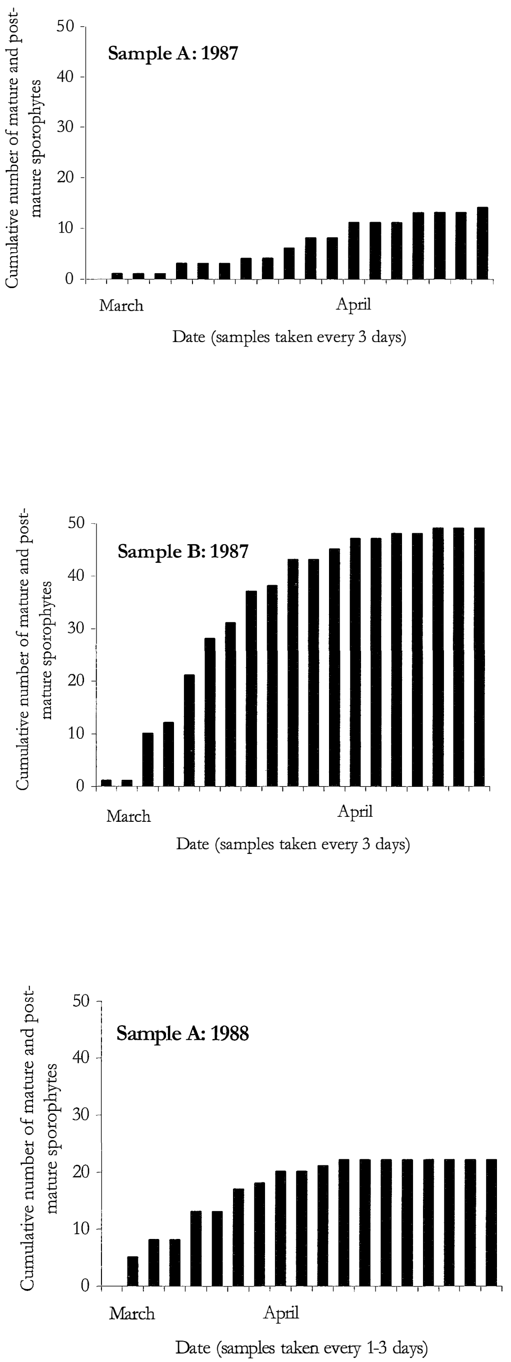

Figure 1. Final phase of sporophyte maturation in two cultures of *Nardia scalaris*.

Table 2. Sporophyte frequency and phenology (from Paton, 1999) of the ten most common dioicous and monoicous liverworts in Britain (from Hill *et al.*, 1991).

	Frequency	**Period of maturity**
Dioicous species		
Aneura pinguis	Frequent	February - October
Conocephalum conicum	Occasional-rare	February - May
Diplophyllum albicans	Frequent	February - June
Frullania dilatata	Fairly common	January - December
Frullania tamarisci	Fairly frequent	January - December
Lophozia ventricosa	Occasional	February - September
Metzgeria furcata	Fairly frequent	January - December
Pellia endiviifolia	Fairly frequent	February - May
Plagiochila porelloides	Rather rare	April - October
Scapania undulata	Frequent	February - July
Monoicous species		
Calypogeia fissa	Frequent	March - June
Calypogeia muelleriana	Fairly frequent	March - June
Cephalozia bicuspidata	Common	January - December
Chiloscyphus polyanthos	Frequent	March - May
Lepidozia reptans	Fairly common	February - November
Lophocolea bidentata	Common	January - August
Lophocolea heterophylla	Very common	January - December
Pellia epiphylla	Common	February - May
Radula complanata	Very common	February - November
Riccardia chamedryfolia	Fairly frequent	February - June

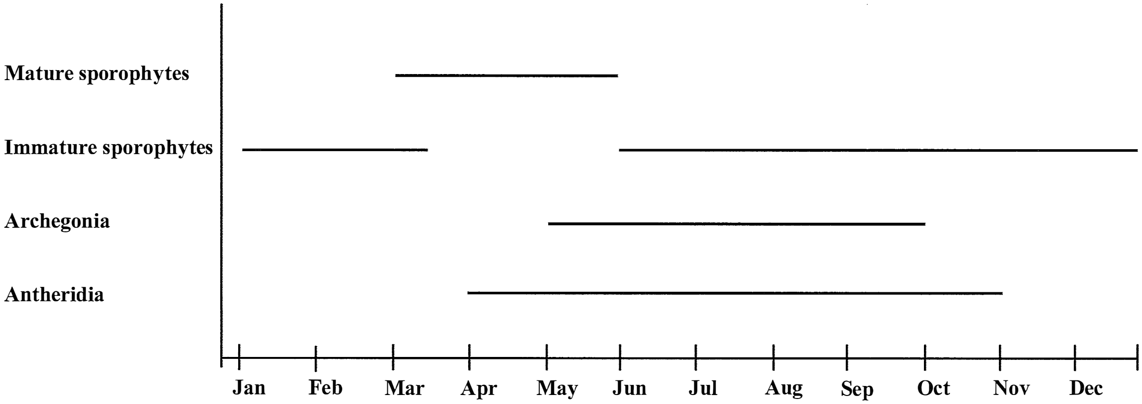

Figure 2. Main phases of gametangia maturation and sporophyte development in *Nardia scalaris*.

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The changing bryophyte flora of Chawley Brick Pit, Oxford

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Many bryologists have recorded the bryoflora at Chawley Brick Pit, a small quarry cut into the side of a heathy hill just outside Oxford. It is the continuity of recording that provides such an intriguing insight to the clay pit and the changes that have occurred during the 20th century. A remarkable bryoflora developed at the pit, relating to a spontaneous geo-chemical combustion event shortly after the pit closed in 1940. This very acidic episode is thought to be associated with the presence of iron pyrites in the Kimmeridge Clay associated with the fossilisation of Jurassic fauna (dinosaurs) found at the site.