



Fires, drought, extinction and regeneration

Jeff Duckett, Jill Kowal, Liz Andrew and **Silvia Pressel** provide new insights into bryophyte succession on two lowland heathlands in southern England

Following a major fire on 30 May 2020 at Thursley Common National Nature Reserve (NNR), we documented in detail, for the first time for any post-fire succession, the early months of bryophyte recolonisation (Pressel *et al.*, 2021). *Funaria hygrometrica* and *Campylopus pyriformis* were the first new arrivals (mid-July, 56 days), from spores and caducous leaves or tubers respectively, with both taxa producing abundant protonemal gemmae initially. By mid-December (202 days) *C. pyriformis* had formed extensive vegetative colonies, while *Funaria* had numerous sporophytes of different ages. *Ceratodon purpureus*, from spores and abundant protonemal gemmae initially, *Polytrichum juniperinum* and *P. formosum* from rhizomes, and *Marchantia polymorpha* subsp. *ruderalis* from spores, did not appear until early September (104 days). By

△ Figure 1. A sea of *Ceratodon purpureus* (brown) and *Funaria hygrometrica* (green) at Chobham, 4 March 2022. All photos Jeff Duckett

mid-December (202 days) *Ceratodon* had young spear stage sporophytes, the *Polytrichum* species remained vegetative, while *Marchantia* was highly gemmiferous with young carpocephala.

The present account advances the initial observations with two further years of post-fire bryophyte recolonisation data (December 2020 until December 2022). Here we also compare Thursley NNR and Chobham Common, the site of another major lowland heathland wildfire which occurred in late August 2020. Chobham Common is 35 km north of Thursley and has comparable weather.

Fortuitously, our recordings also included the driest summer ever in southern England.

Rainfall figures for the last 20 years at Thursley and Chobham range from 11–16 mm in June, 15–18 mm in July and 17–22 mm in August. Most of the 18 mm of rain in July 2022 fell at the beginning of the month and in August there was no significant precipitation until the end of the month. In addition, the temperatures exceeded 40°C for several days. Whereas throughout 2021 and until the beginning of July 2022 the bryophytes remained hydrated on all our visits, by mid-July 2022 all the dry and damp heath bryophytes had dried out completely and remained in this state until the onset of rainstorms at the end of August. It was thus of major interest to find out how different species might have been affected by this period of extreme weather. One unforeseen benefit of the drought was that it provided ideal conditions for the replacement of the boardwalks destroyed by the 2020 fire at Thursley (Fig. 2).

Field bryologists do not like droughts, or even dry weather, except for ephemeral enthusiasts enthralled by exposed mud surfaces. British Bryological Society field meetings, both national and local, are geared to the seasons when bryophytes are at their best, thus facilitating identification, recording and photography. What we seldom if ever do is to observe bryophytes at the extremes of desiccation and, in the normal course of events, would not go anywhere near lowland heathlands at the height of a drought. Thus, the possible effects of extreme droughts on heathlands are rarely recorded.

Since the 2020 fires there have been less than 20 light frosts at both sites, so bryophyte growth has hardly been halted by freezing. A week of sub-zero temperatures in early December 2022 had no perceptible effects on the bryophytes.

In addition to comparing bryophyte community succession at two fire sites and the effects of the 2022 summer drought, our new

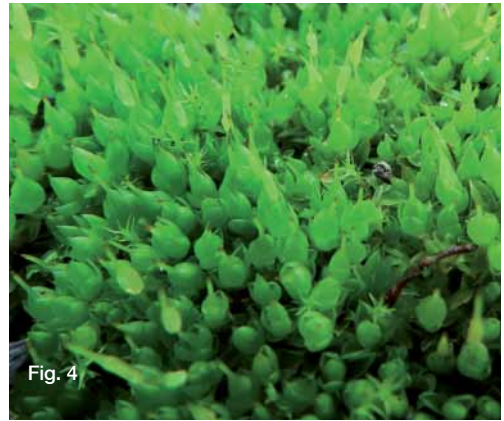
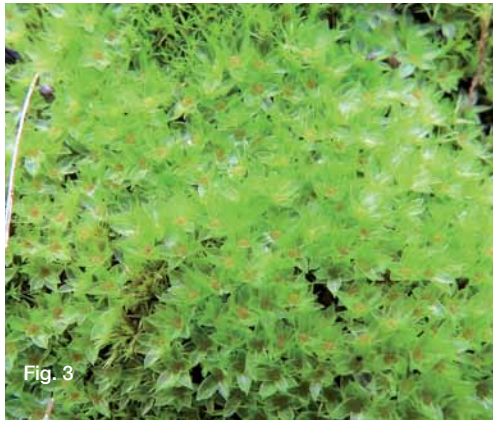
data provide novel insights into the interactions between *Funaria* and *Ceratodon*; an explanation for how the latter replaces *Funaria* in post-fire successions; and sexual and asexual reproduction in *Marchantia*. The sex ratios in *Marchantia* and *Ceratodon* also turn out to be much more variable than hitherto assumed. Our images highlight the varied appearance of post-fire bryophytes through the seasons.

The life cycles of *Funaria* and *Ceratodon*

From casual observations, *Funaria* and *Ceratodon* might appear to have very similar life cycles, each regularly producing abundant sporophytes. More detailed scrutiny, however, particularly from recent studies since the adoption of *Ceratodon* as a model organism, reveals fundamental differences (Shaw & Gaughan, 1993). *Funaria* is mainly a short-lived annual with more than one cycle of sporophyte production each year (Duckett & Pressel, 2017, 2022). The majority grow and mature from late winter to early spring in the wild but also sporadically throughout the year, as can

▽ Figure 2. Boardwalk replacement at Thursley, summer 2022.





△ Figures 3–6. *Funaria* phenology. 3, Mature male inflorescences, Thursley, Oct. 2022. 4, Spears just emerging from swollen perichaetia, Thursley, Nov. 2022. 5, Young spears, Thursley, Jan. 2022. 6, Long persistent dead sporophytes, Thursley, Nov. 2022.

be seen at garden centres and in greenhouses. The life cycle is much longer in nature (c. 200 days) than in culture and in greenhouses (65–70 days), with most of the difference due to a much longer period for capsule maturation in the wild. The old, dehisced capsules persist well into the winter months. The sexual gametophores produced from the protonema and rhizoids are male followed by female lateral branches (Bold 1967, figs 14–16, p. 274; Parihar 1963, fig. 78, p. 197). Vegetative gametophores are uncommon. By the time sporophytes are changing colour almost the entire shoot system is usually dead while the

rhizoids remain alive. The gametophore system of *Funaria* effectively behaves like a monocarpic vascular plant.

Ceratodon is a short- to long-lived perennial with strictly one cycle of sporophyte production per year. Following gametangia production in the autumn, the sporophytes mature in the spring and the spores are liberated in the summer. Many gametophores on female colonies are vegetative and produce numerous new shoots throughout the year when fully hydrated. They often reach lengths of 10–20 mm whereas those bearing sporophytes die before these mature. After



△ Figures 7–12. *Ceratodon* phenology. 7, *Ceratodon* (arrowed) and *Funaria* male gametophores, Chobham, Aug. 2021. 8, *Ceratodon* male gametophores, Thursley, Oct. 2022. 9, *Ceratodon* spear stage sporophytes, Thursley, Nov. 2021. 10, Elongated setae with expanding capsules in *Funaria* alongside *Ceratodon* sporophytes at the spear stage, Chobham, Jan. 2022. 11, *Ceratodon* in long-established unburned areas (note the associated lichens) has a vivid red coloration, Thursley, Mar. 2021. 12, Mature undehisced capsules, Thursley, Apr. 2022.

Table 1. Post-fire bryophyte succession at Thursley Common 2021. Dates of recording are followed by the number of days after the 2020 fire. For 2020 data, see Pressel *et al.* (2021).

Species	25 Feb (277 days)	25 Mar (302 days)	14 Apr (324 days)	25 May (363 days)	23 July (422 days)	30 Aug (460 days)	28 Sept (489 days)	2 Nov (524 days)
<i>Campylopus introflexus</i>	Occasional small colonies, vegetative	As previous	As previous	As previous	As previous	As previous	Many small patches, vegetative	As previous
<i>C. flexuosus</i>	-	Occasional small patches encroaching on <i>C. pyriformis</i>	As previous	As previous	As previous	As previous	As previous	Larger colonies
<i>C. pyriformis</i>	Extensive colonies in damp depressions with abundant caducous leaves	As previous	As previous	As previous	As previous	As previous	As previous	Fewer colonies
<i>Ceratodon purpureus</i>	Spear stage	Capsules expanding to fully expanded	Fully expanded green capsules	Capsules changing colour	Brown capsules	Brown dehisced capsules	Mature males, shoots up to 20 mm long	Spear stage 5 mm
<i>Funaria hygrometrica</i>	Spear stage to young expanding to fully expanded sporophytes	From young expanding to fully expanded capsules, green setae	From young to expanded capsules, brown setae, gametophytes dead	From young expanding to dehisced capsules	Nearly all capsules mature and dehisced	As previous	Long dead capsules	Mature males
<i>Polytrichum commune</i>	Vegetative	As previous	As previous	As previous	As previous	As previous	As previous	As previous
<i>P. formosum</i>	Vegetative	Vegetative	Young male inflorescences	Mature male inflorescences	Percurrent growth through male inflorescences	As previous	As previous	Just emerging spears
<i>P. juniperinum</i>	Young male inflorescences, young female terete shoots	Mature male inflorescences, young female terete shoots	Mature male inflorescences	Percurrent growth through male inflorescences	As previous	Percurrent growth through male inflorescences, spears just emerging	As previous	Just emerging spears
<i>Marchantia polymorpha</i>	Old thalli no gemmae, young thalli highly gemmiferous, carpocephala primordia	Old thalli no gemmae, young thalli highly gemmiferous, young carpocephala	As previous	Mature males, younger females	As previous	Post-dehiscence male and female, some young female	Post-dehiscence male and female, some young males	Dead carpocephala, some young males

antheridial dehiscence, the male plants produce far fewer lateral branches. Previous experimental studies on *Ceratodon*, based almost exclusively

on cultured materials, do not mention the above attributes, but focus on genetic differences between populations and sexual dimorphism,

with female-biased sex ratios being attributed to the more robust females (Eppley *et al.*, 2018; Kollar *et al.*, 2021; McDaniel, 2005; Nieto-Lugilde *et al.*, 2018; Norrell *et al.*, 2014; Shaw & Beer, 1999; Shaw & Gaughan, 1993; Slate *et al.*, 2017).

Chronology

2021

The later winter months of 2021 (25 February, 25 March) at Thursley saw the slow development of the sporophytes of *Funaria* (Figs 3–6) and *Ceratodon* (Figs 7–12), young male inflorescences in *Polytrichum formosum* and the first appearance of small colonies of *Campylopus introflexus* (not seen in 2020; Table 1 and Fig. 30). This species appears to be particularly prone to superficial fire damage. *Marchantia* was either vegetative or had young carpocephala with abundant gemmae on new thalli (Table 1). The *Ceratodon* and *Funaria* capsules matured in the spring (14 April, 25 May) with the earlier stages of sporophyte development in *Funaria* (Duckett & Pressel, 2022) slightly ahead of *Ceratodon* (Fig. 10). Maturation and spore dispersal times are the same in both, apart from the scattered colonies of *Funaria* that mature throughout the year. After spore dispersal, the dead sporophytes of *Funaria* persist long into the autumn (Fig. 6), while those of *Ceratodon* had largely decayed. In the dense swards of *Ceratodon*, with shoots up to 20 mm long, male colonies became clearly visible in the early autumn (Figs 7, 8), while *Funaria* comprised just male gametophores (Fig. 3), with other lateral shoots, destined to become female, largely vegetative. The *Ceratodon* colonies in long-established unburned areas, as evidenced by the lichen associates, had a vivid red coloration (Fig. 11).

Percurrent growth through male inflorescences of *Polytrichum juniperinum* from

25 May onwards signalled dehiscence of all the antheridia (Figs 13, 14). Only after this did the capsules begin to expand (Figs 15, 16) and spore liberation did not begin until the middle of the summer.

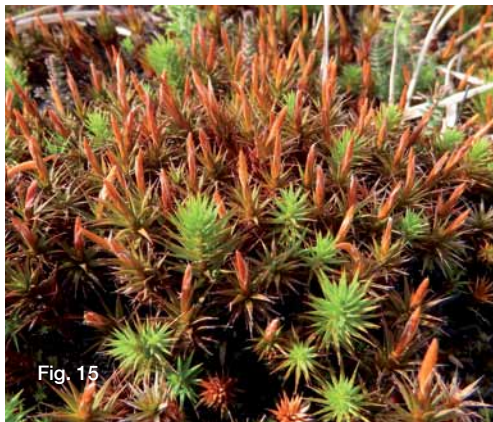
By late summer (30 August), with no significant dry period, there was an increase in the size of the *Campylopus introflexus* colonies which continued through the autumn, and the new appearance of *C. flexuosus* (25 March) (Fig. 29).

During 2021 a disparity in the maturation times of the antheridiophores and archegoniophores of *Marchantia* became increasingly apparent (Figs 17–24), with the males emerging clearly ahead of the females (Fig. 19). For example, in winter 2021 the *Marchantia* comprised a mixture of antheridiophores with mostly dehisced antheridia and mature and still developing archegoniophores (Fig. 20). By November 2022, all the *Marchantia* carpocephala that had grown over the earlier months were dead, but young antheridiophores were beginning to appear.

The chronology at Chobham (Table 2) matched that at Thursley except that no *Campylopus* species recolonised the bare areas. By the end of November, *Ceratodon* displayed a sea of spear stage sporophytes and *Funaria* had young sporophytes within the swollen perichaetial leaves.

2022

Capsule maturation in *Ceratodon* and *Funaria* mirrored that of the previous year as did the earlier production of antheridiophores in *Marchantia* (Tables 3 & 4). As in 2021, the dehisced capsules of *Ceratodon* had largely disappeared by the early autumn, while those of *Funaria* were much more persistent. *Ceratodon* was unchanged at the end of December (elongated spears), but *Funaria* had



△ Figures 13–16. *Polytrichum juniperinum*. 13, Mature male inflorescences, Thursley, Mar. 2021. 14, Percurrent growth from May onwards signals dehiscence of all the antheridia, Chobham, Oct. 2021. 15, Spear stage sporophytes, Thursley, Feb. 2022. 16, Mature undehisced capsules, Thursley, May 2022.

elongated setae and expanding capsules (Fig. 10).

The previous year's sporophytes of *Polytrichum formosum* matured over the late spring months. In the autumn of 2022, the *P. juniperinum* sporophytes were more advanced than in 2021, presumably the result of the very mild weather, with temperatures until late November rarely dipping below 10°C. Young male inflorescences of *P. juniperinum* were abundant in December 2022 compared to their later appearance in February 2021 (Fig. 13).

In striking contrast to the almost continuously moist conditions in 2021, the

▷ Figures 17–24. *Marchantia* phenology. 17, Young thallus with gemma cups and mature antheridiophores, Chobham, May 2021. 18, Older vegetative thalli lacking gemma cups, Thursley, Feb. 2021. 19, Thalli with mature antheridiophores and very young archegoniophores, Thursley, Apr. 2021. 20, Thalli with post-dehiscence antheridiophores and mature archegoniophores, Thursley, Apr. 2022. 21, Old thalli without gemmae producing new archegoniophores, Chobham, Aug. 2021. 22, Prolific sporophyte production well outside the peak early summer reproductive period, Chobham, Oct. 2021. 23, Thalli with old and developing archegoniophores, Chobham, Aug. 2021. 24, Thalli overrun with female *Ceratodon*, Chobham, Sept. 2021.



Fig. 17



Fig. 18

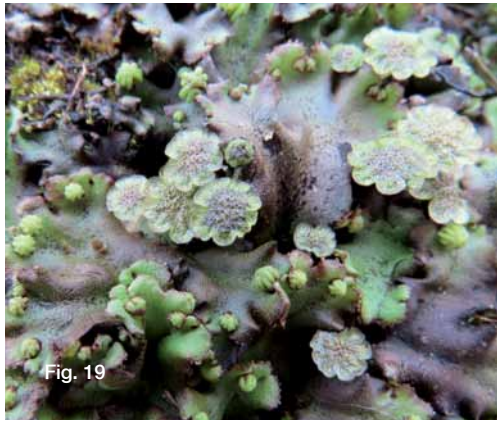


Fig. 19



Fig. 20



Fig. 21



Fig. 22



Fig. 23



Fig. 24

Table 2. Post-fire bryophyte succession at Chobham Common 2021. Dates of recording are followed by the number of days after the 2020 fire.

Species	30 Mar (245 days)	1 May (277 days)	31 May (307 days)	7 July (344 days)	15 Aug (383 days)	21 Sept (420 days)	22 Oct (451 days)	30 Nov (490 days)	31 Dec (521 days)
<i>Campylopus introflexus</i>	–	–	–	–	–	–	–	–	–
<i>C. flexuosus</i>	–	–	–	–	–	–	–	–	–
<i>C. pyriformis</i>	Colonies in damp hollows	Extensive patches in damp hollows	As previous	Some colonies succeeded by <i>Ceratodon</i>	Mainly succeeded by <i>Ceratodon</i>	As previous	As previous	As previous	As previous
<i>Ceratodon purpureus</i>	Spears	Mainly vegetative, a few expanding capsules	Mainly vegetative, a few mature capsules	As previous	Mainly vegetative, a few dehisced capsules	As previous	Male and female with short spears, 5 mm	Females with 10mm spears	As previous
<i>Funaria hygrometrica</i>	Young sporophytes, protonemal lawns	Green to browning capsules	As previous	90% dehisced capsules, scattered colonies with green capsules	As previous	As previous	Sheets of male	Young sporophytes inside perichaetial leaves	Emerging spears
<i>Polytrichum commune</i>	Vegetative	As previous	As previous	Spreading colonies	As previous	As previous	As previous	As previous	As previous
<i>P. formosum</i>	Vegetative	As previous	As previous	Succeeding <i>Ceratodon</i> and <i>Funaria</i>	As previous	As previous	As previous	As previous	As previous
<i>P. juniperinum</i>	Vegetative	As previous	As previous	Succeeding <i>Ceratodon</i> and <i>Funaria</i>	As previous	As previous	As previous	As previous	As previous
<i>Marchantia polymorpha</i>	Highly gemmiferous, a few young carpocephala	As previous	Numerous young carpocephala	Mature carpocephala	As previous	As previous	Mainly post-dehiscence carpocephala	Old carpocephala and a few young males	Dead carpocephala and a few young males

dry summer of 2022 accelerated the complete desiccation of all the bryophytes, even those in previously damp hollows (Figs 25–28). All the *Marchantia* appeared to be dead at the end of July and remained as such in October, even after the autumn rains (Figs 27, 28). Nearly all the *Polytrichum juniperinum* and *P. formosum* recovered, but most of the *P. commune* did not (Fig. 25).

The 2022 chronology at Chobham closely

followed that at Thursley except that *Campylopus pyriformis* was overrun by *Ceratodon* rather than *C. introflexus*. Here also *C. flexuosus* was a late arrival after the drought. By the end of October all the antheridia on *Ceratodon* and *Funaria* were dehisced and both species had swollen venters. At both sites not a single thallus of *Marchantia* survived the drought.

Regrowth of *Ceratodon* after the 2022 drought was rather different from 2021 when



△ Figures 25–28. Effects of drought on Thursley and Chobham bryophytes. 25, Completely dried out *Polytrichum commune*, Thursley, Aug. 2022. 26, Patches of *Polytrichum formosum* damaged by the drought, Thursley, Nov. 2022. 27, Dead *Marchantia*, Thursley, July 2022. 28, Dead *Marchantia*, Chobham, Sept. 2022.

all the shoots survived the summer and were up to 20 mm long when they produced sex organs. Almost all the pre-existing shoots were killed by the 2022 drought and the new shoots, derived from the rhizoid system, were much shorter (2–4 mm). In autumn 2022 *Ceratodon* comprised swards of very short male and female shoots unlike the much taller ones in 2021. *Funaria* was generally absent from the taller *Ceratodon* swards in 2021 but was more frequent amidst the shorter 2022 plants at Thursley. At Chobham in November 2022 it was restricted to small,

scattered clumps.

Campylopus introflexus and *C. flexuosus* gradually increased in extent at Thursley during 2022, but the former did not produce sporophytes until the autumn (Tables 3, 4). The period when the sporophytes emerge, before further growth of the recurved setae immerse these in the perichaetial leaves, lasts but a few days (Figs 31, 32). The new vegetative shoots are highly terete with leaves lacking hair points (Fig. 33). These two species gradually encroached on the areas with *C. pyriformis* (Fig. 29). The late

Table 3. Post-fire bryophyte succession at Thursley Common 2022. Dates of recording are followed by the number of days after the 2020 fire.

Species	4 Jan (587 days)	11 Feb (625 days)	25 Apr (689 days)	28 May (721 days)	28 July (782 days)	7 Oct (863 days)	10 Nov (896 days)
<i>Campylopus introflexus</i>	Many small colonies, vegetative	As previous	As previous	Expanding colonies	As previous, desiccated	Carpets, male inflorescences	Very young emerging sporophytes
<i>C. flexuosus</i>	Frequent small colonies, caducous stems and leaves	As previous	As previous	As previous	As previous, desiccated	Carpets	As previous
<i>C. pyriformis</i>	Scattered colonies	As previous	As previous	As previous	Smaller colonies, desiccated	Scattered small colonies	As previous
<i>Ceratodon purpureus</i>	Young spears	Fully elongated spears	Brown undehisced capsules	Dehisced and undehisced capsules, shoots up 20 mm long	Dehisced capsules	Mature males, shoots only 2–3 mm long, very few old capsules	Old males, capsules just emerging
<i>Funaria hygrometrica</i>	Young spears	Fully elongated spears	Green to brown undehisced capsules	Dehisced and undehisced capsules, gametophytes dead	Dehisced capsules	Mature males, shoots only 2–4 mm long, long dehisced capsules	Old males, straight spears
<i>Polytrichum commune</i>	Vegetative	As previous	As previous	As previous	All desiccated	Mostly dead	As previous
<i>P. formosum</i>	Emerging spears	As previous	Mature male, elongating spears	Expanding capsules	All desiccated, mature capsules	Some dead patches	Young spears, some dead patches
<i>P. juniperinum</i>	Elongating spears	Young male, elongating spears	Percurrent growth through male inflorescences, mature male, expanding capsules	Percurrent growth through male inflorescences, fully expanded green capsules	All desiccated, mature dehisced capsules	Occasional dead patches	Young spears
<i>Marchantia polymorpha</i>	Old thalli no gemmae, young thalli highly gemmiferous, dead carpocephala, a few young males	As previous	Mature male, younger females	Old carpocephala, a few young females	Dead	Dead	Dead

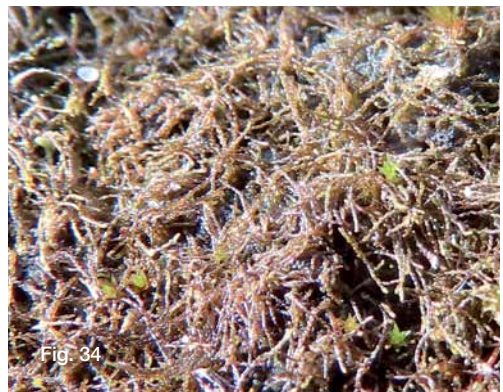
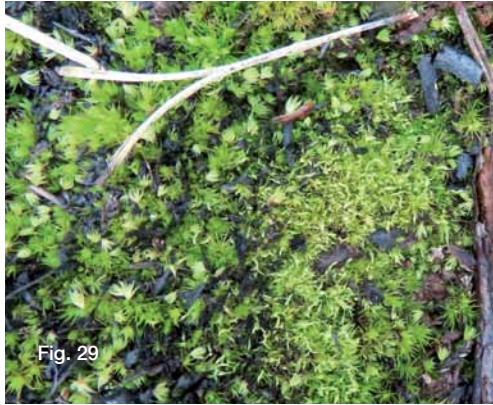
arrival of *C. flexuosus* may be attributed to its much larger asexual propagules than those of *C. pyriformis* (Hurtado *et al.*, 2022). The same was true for *C. flexuosus* at Chobham, where *C. introflexus* was not seen until November 2022, and then in just one area less than 2 m in diameter.

The presence of young capsules indicates that its arrival predated the 2022 drought.

Poblia nutans was a frequent recolonist after the 2006 fire and produced abundant sporophytes in 2008. However, it was not seen following the 2020 fire. In its place grew

Table 4. Post-fire bryophyte succession Chobham Common 2022 and January 2023. Dates of recording are followed by the number of days after the 2020 fire.

Species	31 Jan (551 days)	5 Mar (584 days)	25 Apr (635 days)	4 June (696 days)	6 Aug (728 days)	10 Sept (764 days)	31 Oct (815 days)	29 Nov (844 days)	3 Jan 2023 (880 days)
<i>Campylopus introflexus</i>	–	–	–	–	–	–	–	Several clumps in one localised area, very young sporophytes	Small clumps in several areas
<i>C. flexuosus</i>	–	–	–	–	–	–	Scattered clumps	Numerous large patches	As previous
<i>C. pyriformis</i>	A few scattered colonies	As previous	As previous	As previous	Dried out	As previous	Mostly overgrown by <i>Ceratodon</i>	Very little remaining in hollows	As previous
<i>Ceratodon purpureus</i>	Elongated spears, purple setae	Females with fully expanded green capsules	As previous	Brown undehisced capsules	Dried out, dehisced capsules	Young males and females	95% dehisced antheridia, spears level with top of perichaetial leaves	Dehisced antheridia, spears level with top of perichaetial leaves; sporophytes less frequent in large female patches	Fully elongated spears
<i>Funaria hygrometrica</i>	Elongating setae and expanding capsules	As previous	As previous	Brown undehisced capsules	Dried out, dehisced capsules	A few young males	Old antheridia, swollen venters	Scattered vegetative colonies	Old capsules overgrown by <i>Polytrichum</i>
<i>Polytrichum commune</i>	Vegetative	As previous	As previous	As previous	Dried out	Some dead, vegetative	As previous	As previous	As previous
<i>P. formosum</i>	Vegetative	As previous	As previous	As previous	Dried out	Vegetative	Colonies increasing in size	As previous	As previous
<i>P. juniperinum</i>	Vegetative	Young male inflorescences	Mature male inflorescences	Percurrent growth through male inflorescences	Dried out	Percurrent growth through male inflorescences	Colonies increasing in size	As previous	Young spears
<i>Marchantia polymorpha</i>	Dead archegoniophores, young males, no new gemmae	As previous	As previous	Mature carpocephala	Dried out	Dead	Dead	Long dead carpocephala	A cluster of ten young thalli, vegetative



△ Figures 29–34. *Campylopus* spp. (29–33) and *Cephaloziella* (34). 29, *C. flexuosus* encroaching on *C. pyriformis* (right), both with caducous shoots. 30–33, *C. introflexus*. 30, Young vegetative colony (note the hair points), Thursley, Feb. 2022. 31, Young capsules before immersion in the perichaetial leaves, Thursley, Oct. 2022. 32, The arcuate setae have immersed the young capsules in the perichaetial leaves, Thursley, Nov. 2022. 33, Terete secondary young shoots on fertile colony with leaves lacking hair points, Thursley, Nov. 2022. 34, Mat of *Cephaloziella divaricata* on a lightly burnt area, Thursley, Jan. 2022.

extensive patches of *Bryum bornholmense*, another post-fire species (Blockeel *et al.*, 2014). At both Thursley and Chobham this produced sex organs in the autumn of 2021, with capsules maturing the following spring. *Bryum argenteum* and *B. dichotomum* made a fleeting appearance at Thursley in autumn 2020, but then disappeared early in 2021 and did not produce sporophytes as they did after 2006. We did not observe *Pohlia* at Chobham.

Turf removal for golf courses

The occasional removal of strips of dry *Calluna* heath from Thursley to supply coarse turf for golf courses provides a comparison with post-fire recolonisation, particularly since this was done extensively after the fire in autumn 2020 (Figs 35, 36). The only bryophytes in the original turf were *Campylopus introflexus* and *Cephaloziella divaricata*. The stripped areas were devoid of bryophytes until the spring of 2022 when small vegetative colonies of *Campylopus introflexus* were first found followed by widespread stems of *Cephaloziella divaricata* (Fig. 36).

Lightly burned areas had the same recolonisation pattern with extensive areas

covered by *Cephaloziella* (Fig. 34). This liverwort was undoubtedly already present as subterranean axes rather than a new arrival via gemmae or spores (Duckett & Clymo, 1988). Perianths with sporophytes were seen only in the spring and early summer months. *Ceratodon* and *Funaria* were notably absent from the *Cephaloziella* sites. *C. divaricata* has been previously recorded as a rapid post-fire recolonist of dry upland moorland sites in Yorkshire (Blockeel *et al.*, 2014; Burch, 2008). Burch (2008) does not consider that these derive from subterranean axes.

It took nearly three years for sex organs and sporophytes to appear on the new *Campylopus introflexus* colonies. *C. flexuosus*, together with foliose lichens, also appeared on the stripped areas in autumn 2022, but the latter were conspicuously absent from the burnt areas. They were almost certainly blown in from the uncut areas as lichen recolonisation is a notably slow process (Miller *et al.*, 2021).

Phenological fluctuations in *Marchantia*

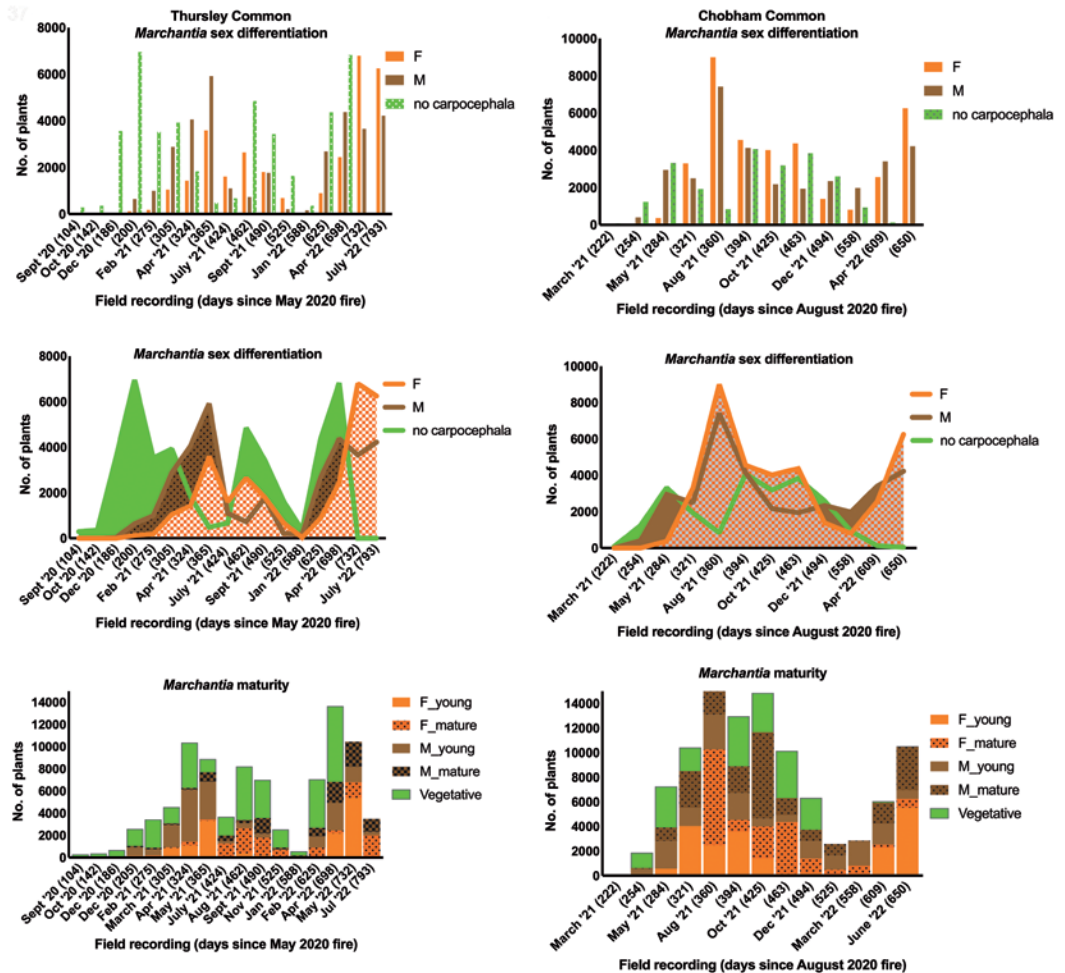
Previous accounts of *Marchantia* at Thursley after the 2006 wildfire (Duckett *et al.*, 2008) detail prolific sporophyte production in the early

▽ Figure 35. Turf removal at Thursley in progress, Nov. 2019.



▽ Figure 36. Recolonisation with *Campylopus* after removal of turf, Nov. 2022.



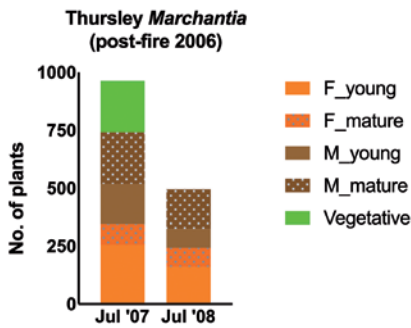


△ Figures 37 (left), 38 (right). Seasonal changes in the reproduction of *Marchantia*. 37, Thursley from the fire in May 2020 to the drought in 2022. 38, Chobham from the fire in August 2020 to the drought in 2022.

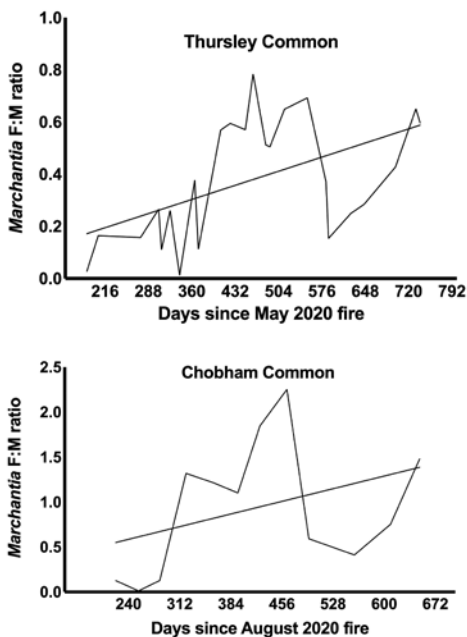
summers of 2008 and 2009 (Duckett & Pressel, 2009), an approximately 1:1 sex ratio, and its overrunning by *Polytrichum* in the autumn of 2009. The new data presented here reveal that this was a major oversimplification of the reproductive biology of this liverwort (Duckett *et al.*, 2022). Unfortunately, the much more closely clumped *Marchantia* populations after the 2020 fires at both sites did not permit new measurements of fertilisation distances (Pressel

& Duckett, 2019).

On a par with gemmiferous protonema production in the earliest colonisation stages in *Funaria* and *Ceratodon* (Pressel *et al.*, 2021) and not thereafter, only young thalli of *Marchantia* were highly gemmiferous (Fig. 17). By March 2021 very few thalli had gemma cups and this continued into 2022 (Fig. 18). Together these observations mirror the favouring of gemma production on media rich in nutrients (Duckett



△ Figure 39. Seasonal changes in the reproduction of *Marchantia*, cont. Comparable data to Fig. 38 after the 2006 fire.



△ Figure 40. Seasonal changes in the reproduction of *Marchantia*, cont. Changes in F:M sex ratios following the 2020 fires. Note the similarity between Chobham and Thursley.

& Ligrone, 1992). The later production of carpocephala by about two months at Chobham reflects the later fire date there. From late spring 2021 the *Marchantia* from both sites behaved similarly.

Following the initial establishment of *Marchantia* from spores, the distribution of males and females indicates a second wave of gemma-derived colonisation. Rather than a mosaic of the two sexes, we found marked unisex patches of over 300 thalli (measuring >50 cm in diameter), in one case over 900, which could only have come from gemmae.

Our temporal data also reveal a surprising major disparity between the maturation times of the antheridia and archegonia. *Marchantia* is clearly protandrous (Figs 19, 37–40). If young and maturing inflorescences are separated from those with post-mature sex organs, this shows that the 1:1 sex ratio is only strictly true for the early summer months. For brief periods during the summer females may exceed males, but at other times of the year, from winter to late spring, males predominate. These findings clearly suggest that future studies on bryophyte sex ratios should take on board the states of sex organ development in nature and investigate whether other *Marchantia* species behave like *M. polymorpha*. *Marchantia berteriana* on post-fire sites in New Zealand also appears to be markedly protandrous (John Bowman pers. comm.). Though sporophyte maturation peaks in early summer, archegoniophores are present throughout the year (Figs 37–40). These mature slowly over the winter, presumably as a consequence of low temperatures and occasional freezing. Each thallus of *Marchantia* may produce up to three successive waves of sex organs three or more months apart (Figs 19–23).

Unlike the death of *Marchantia* (Figs 27, 28), equally desiccated nearby populations of *Lunularia cruciata* made a full recovery from the drought within weeks. With a Submediterranean-Subatlantic distribution (Blockeel *et al.*, 2014), *Lunularia* regularly experiences summer droughts.

Female dominance in wild *Ceratodon*

Data on the visibility of male plants of *Ceratodon* and their highly seasonal appearance are summarised in Table 5. These data re-enforce the previous findings on cultured materials (Eppley *et al.*, 2018; Kollar *et al.*, 2021; McDaniel, 2005; Nieto-Lugilde *et al.*, 2018; Norrell *et al.*, 2014; Shaw & Beer, 1999; Shaw & Gaughan, 1993; Slate *et al.*, 2017), that females are also more robust and vigorous in nature.

We also noted extensive patches of *Ceratodon* over 3 m in diameter with no males at both Thursley and Chobham. Dissection of these swards confirmed this field observation. Males are certainly less frequent than our surface area estimates indicate. The diminished abundance of sporophytes in the female-only patches suggests that both the minority of the males and fertilisation distances of over 1 m may limit sexual reproduction in *Ceratodon* unlike in *Marchantia* (Pressel & Duckett, 2019) and *Polytrichum* (present paper).

Life-cycle lengths in model bryophytes

The life-cycle lengths of the post-fire and other ephemeral bryophytes are summarised in Table 6. The longest spore to spore cycles occur in the long-lived perennials *Campylopus introflexus* and the two *Polytrichum* species. The life cycle of *Polytrichum* observed at Thursley and Chobham almost exactly matches those described previously (Longton & Schuster, 1983). Although the two *Polytrichum* species survived the 2020 summer fires, the main consequence was that they missed out on sporophyte production in 2021 because the fires destroyed the young sporophytes produced before the fire in 2020. It is also noteworthy that many colonies of *P. formosum* still showed drought damage late in 2022. Sporophyte production was hardly depressed in *Ceratodon* as the sex organs were produced after

Table 5. The seasonal visibility of male *Ceratodon*, as determined from % surface areas occupied by males and females on digital field images. Female dominance over males in wild *Ceratodon* is clearly evident. These data also reveal that male plants are only readily visible for a short period in the autumn. *Some areas dry so impossible to distinguish all the males.

Site	Date	No. of images analysed	% male	% female	
Thursley	23 July 2021	0	0	100	
	30 Aug 2021 *	7	37	63	
	28 Sept 2021	31	41	59	
	2 Nov 2021	1	<20	>80	
	30 Nov 2021	0	0	100	
	30 Dec 2021	0	0	100	
	28 July 2022	Drought	0	100	
	7 Oct 2022	12	37	63	
	10 Nov 2022	17	32	68	
30 Dec 2022	18	0	100		
Chobham	7 July 2021	0	0	100	
	18 Aug 2021	11	31	69	
	22 Oct 2021	21	34	64	
	30 Nov 2021	0	0	100	
	6 Aug 2022	Drought	0	100	
	10 Sept 2022	7	37	63	
	31 Oct 2022	15	21	79	
	29 Nov 2022	3	10	90	
	3 Jan 2023	10	0	100	

the fire and not at all in *Funaria* as sex organs may appear throughout the year.

Attesting to the regrowth of *Polytrichum* from rhizomes rather than spores was the occurrence of large unisexual colonies, many over 50 cm in diameter, rather than a small-scale mosaic of males and females. These observations are in line with the finding from a microsatellite study that *P. formosum* mainly spreads by clonal growth and not *de novo* establishment via spores (Van der Velde *et al.*, 2001). The presence of sporophyte-bearing colonies 5 m or more from the nearest

Table 6. Approximate life-cycle lengths in days or years of post-fire bryophytes with comparative data for *Physcomitrium* spp., *Ephemerum stoloniferum* and *Anthoceros agrestis*. The times given for the other taxa are based on our own observations and on information from H. During, B. Goffinet & B. Zander (pers. comm.).

Post-fire bryophytes	Spore to spore	Sex organ to spores (days)	Time from fertilisation to spore liberation (days)	Period of sex organ formation	Spore liberation	Axenic culture, spore to spore (days)
<i>Campylopus introflexus</i>	3 yrs	250	250	Autumn	Spring, summer	?
<i>Ceratodon purpureus</i>	>400 days	250	250	Autumn	Spring, summer	?
<i>Funaria hygrometrica</i>	140 days or longer	80	100–200	Mostly autumn plus all the year round	Mainly spring, summer	65–70
<i>Polytrichum formosum</i>	At least 3 yrs	400–420	>400	Spring	Spring, summer	?
<i>P. juniperinum</i>	At least 3 yrs	400–420	>400	Spring	Spring, summer	?
<i>Marchantia polymorpha</i>	>185 days	50–60	50–185	Almost continuous, peak in spring & early summer	Mainly spring, summer	90
Other taxa						
<i>Physcomitrium patens</i>	60–180 days	<60	60–180	Late summer and autumn	Autumn & winter	240–360
<i>P. serratum</i> , <i>P. immersum</i>	60–90 days	<60	60–90	Late summer and autumn	Winter	?
<i>P. pyriforme</i>	60–180 days	<60	60–180	Autumn	Spring	?
<i>P. sphaericum</i>	60–180 days	<60	60–180	Summer	Autumn	?
<i>P. eurystomum</i>	60–180 days	<60	60–180	Summer	Autumn	?
<i>Ephemerum stoloniferum</i>	60–180 days	<60	60–180	Late summer and autumn	Autumn to spring	?
<i>Anthoceros agrestis</i>	90 days	<60	<180	July to December	Autumn to spring	?

males underlines that spermatozoid dispersal distances far exceed the 1–2 m assumed via the splash cup mechanism. As in *Marchantia* (Pressel & Duckett, 2019), the main fertilisation route in *Polytrichum* is most likely via surface water films between male and female plants (Muggoch & Walton, 1942). Facilitating this route is water retention by the antheridial cups, often for several hours after rain. Thus, there are extended periods during which spermatozoids are released.

The shortest life cycles both in nature and in

culture are in *Funaria* and *Marchantia*. Lengths of the annual cycles depend on the weather, especially dry periods and temperature. *Funaria* and the other ephemeral species have the shortest spore to spore cycle, but *Marchantia* is faster from sex organ to spores under favourable conditions. *Funaria* is delayed by dry periods in the spring and summer, *Marchantia* is slower through the cooler winter months.

Remarkably, *Funaria* may reproduce even faster than *Physcomitrium patens*. Our estimates,

from incidental observations on *P. pyriforme*, other *Physcomitrium* species and *Ephemerum* (one of the most ephemeral members of the Pottiaceae), suggest that these are also longer than *Funaria*. *Funaria* may, in terms of reproduction, turn out to be a complete outlier, although the position of *F. hygrometrica* in the latest chronogram of the Funariaceae (Medina *et al.*, 2018) gives no indication of this. The above ground gametophores of all these species are short-lived but the rhizoids are perennial; only *Ephemerum* produces tubers (Pressel & Duckett, 2005).

Anthoceros agrestis appears to have similar life-cycle parameters to *P. patens* and *Funaria* (Proskauer, 1967; Szövényi *et al.*, 2015; Frangedakis *et al.*, 2021). A drop in temperature from 22°C to 16°C and an eight-hour day length are the most significant factors promoting sex organ formation in both *A. agrestis* and *P. patens*, whereas the more likely triggers are shorter autumn days in *Ceratodon* and *Campylopus*, and short winter days in *Polytrichum*. *Marchantia* appears to lack any of these intrinsic environmental mechanisms.

Competition effects

Ultimately, the areas burnt in 2020 will almost certainly become dominated by *Polytrichum* spp. and *Campylopus introflexus* in the driest areas, just as they were after the 2006 fire (Pressel *et al.*, 2021). The present data now enable the first dissection of the interspecific interactions along the way. Since the primary colonists were growing initially on completely bare ground, competition did not come into play until the end of 2021. At this time *Ceratodon* was clearly overrunning many of the *Marchantia* thalli (Fig. 24). Nonetheless these survived and went on to reproduce vigorously in 2022.

After sporophyte maturation, the vegetative

shoots of *Ceratodon* overran the dead gametophytes of *Funaria*. However, as the post-drought observations show, the *Funaria* clearly survived. This must have been via the rhizoid system as there was insufficient time after the drought (<60 days) for sexually mature gametophytes to have developed (Pressel & Duckett, 2021); under hydrated conditions, *Ceratodon* clearly outcompetes *Funaria* via its more vigorous and season-long vegetative growth.

Other effects of the drought on this interspecific interaction were more subtle. With the above ground shoots of *Ceratodon* killed by the 2022 drought, regrowth of leafy shoots from the rhizoids in the autumn of 2022 was much more limited (<4 mm) than had this killing event not occurred. Thus, the drought gave *Funaria* a new lease of life and in 2023 there will likely be much more *Funaria* than otherwise expected at Thursley. Desiccation tolerant rhizoids are an overlooked dimension important in the longer-term perennation of *Funaria*. It would now be of interest to compare the long-term survival of rhizoids versus tubers in taxa that produce the latter.

Conspectus

This is the first account that documents post-fire phenology and competition effects amongst pioneering bryophytes on dry heathland. The fact that the chronology of life-cycle maturation and sex differentiation was much the same at two unrelated sites for two years indicates that we have documented typical post-fire regeneration on lowland heathland and that our observations could become a model for future studies. Our article includes the most complete sets of field images of the life cycles of post-fire bryophytes.

This is also the first account of the effects of a major drought on heathland bryophytes. Most

dramatic was the almost complete extinction of *Marchantia*. Its failure to regenerate may be attributed to a mixture of cover by other bryophytes and a fall in nutrient levels. Other firsts are the documentation of female-biased sex ratios in *Ceratodon* in nature, seasonal changes in these and in *Marchantia* and post-fire survival of *Cephaloziella divaricata* via its subterranean axes.

Since the adoption of *Marchantia* as a model organism (Shaw & Gaughan, 1993) there have been detailed studies of drought stress (Ghosh *et al.*, 2021; Marks *et al.*, 2021). Osmotic stress, induced by sucrose and mannitol, as a proxy for drought stress (direct drying out was not used), leads to severe growth inhibition and degradation of the photosynthetic apparatus in line with that in angiosperms. It is unsurprising therefore that drought killed the heathland *Marchantia*. Paradoxically, however, the *Marchantia* carpocephala remained hydrated through less severe dry periods when all the mosses had dried out. The pegged rhizoid water-conducting apparatus thus appears to be more effective at maintaining water balance than moss hydroids (Duckett *et al.*, 2014). Whether or not urban populations of *Marchantia* are similarly affected by extreme weather now awaits further investigation. More frequent fires notwithstanding, in the longer term *Marchantia* may well be more threatened by climate change than the heathland mosses.

Looking to the future, we predict 2023 as the last year with *Funaria*, but longer persistence of *Ceratodon*. Dry areas will become dominated by *Campylopus introflexus* and wetter ones by *Polytrichum juniperinum* and *P. formosum*, with small amounts of *C. introflexus*, *C. flexuosus* and *C. pyriformis*. Whether or not *C. brevipilus*, frequent in the areas burnt by the 2006 fire, also returns is an open question.

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