

Thursley Common NNR: bryophyte recolonization one year after the great fire of July 2006

The fire that raged across Thursley Common in 2006 could not be described as anything other than a major disaster, but this devastating event has provided an opportunity to study the effects of a major heathland fire on bryophyte communities as **Jeff Duckett**, **Howard Matcham** and **Silvia Pressel** describe.

Ecological literature abounds with statements about the fires in bog and heathlands with the principal focus being vascular plants. Despite an extensive fossick through the literature we found very few articles that set out in detail the overall effects of fires on bryophytes in these ecosystems. Clement & Touffet (1990) provide data showing that fires lead to mono-

specific dominance of species like *Polytrichum commune*, whereas the focus of Southern's (1976, 1977) studies was on factors affecting recolonization of bonfire sites by *Funaria*. Bradbury's (2006) list of post-fire specialists in boreal mixed forest in Canada includes several species also noted by Southern (1976), for example *Ceratodon purpureus*, *Leptobryum pyriforme*, *Marchantia polymorpha*, *Pohlia nutans* and *Polytrichum juniperinum*. Floras and atlases refer to a wider range of individual species associated with recolonization after fires but scarcely

△ Fig. 1. Extensive bare ground in July 2007 in an area of dry heath dominated by *Calluna* before the fire. Jeff Duckett

mention the bryophyte communities of burnt areas. None of the foregoing explore the likely provenance of the pyrophilic species.

On 14–15 July 2006, following a hot dry summer, a fire raged across Thursley Common, one of the best nature reserves in Britain, destroying almost all the vegetation over an area covering some 3 km². Vast areas of dry heath, dominated by *Calluna vulgaris*, together with wetter areas with *Erica tetralix* and *Sphagnum compactum* were severely damaged. Press releases at the time (www.naturalengland.org.uk) described the damage as devastating, particularly for ground-nesting birds, lizards and butterflies with up to 60 % of the heathland destroyed. In fact, the Reserve had scarcely recovered fully from the last major fire some 20 years previously.

However, sometimes a major disaster can provide unique opportunities and, in the case of Thursley Common, the chance to document in detail for the first time the effects and after-effects of a major heathland fire on bryophyte communities. Thus the aims of this account are: (1) to set out the details of the principal bryophyte casualties of the fire; (2) to describe recolonization one year after the event; and (3) to assess the probable origins of each species with their reproductive states providing new insights into their reproductive biology. We also detail results of a competition experiment between *Campylopus introflexus* and *Campylopus brevipilus*, with Thursley being one of the few places in Britain where the two taxa have extensive populations growing side-by-side, and we describe the gemiferous protonemata of *Ceratodon purpureus* and *Campylopus pyriformis*. We hope that the data in this account will provide a framework for studies on bryophyte recolonization at Thursley in the years to come and for developing the most appropriate bryophyte conservation strategies.

Fire damage

The main bryophyte casualties of the fire, in terms of the overall surface of the Common affected, were those growing on the dry heath dominated by *Calluna* and with areas of *Pinus* and *Betula* colonization (Fig. 1). The bryophyte species here were as follows: *Campylopus introflexus*, *Cephaloziella* spp., *Dicranum scoparium*, *Hypnum jutlandicum*, *Pleurozium schreberi*, *Polytrichum formosum* and *P. juniperinum*. The wetter areas experienced extensive mortality of *Sphagnum compactum* with *Cephalozia connivens* and *Cephalozia bicuspidata* growing through it and, more locally, *Campylopus brevipilus*. The fire was, however, brought to a halt where the water table was at or near the surface and damage to other sphagna, including *S. capillifolium*, *S. magellanicum*, *S. palustre*, *S. papillosum*, *S. subnitens* and *S. tenellum* was very patchy, except where these species formed hummocks that dried out during the summer. The main liverworts wiped out in these habitats were *Cephalozia* spp., *Cladopodiella fluitans*, *Gymnocolea inflata* and *Odontoschisma sphagni*. *Polytrichum commune*, growing from old *Molinia* tussocks, was also affected as were the liverworts *Cephalozia bicuspidata* and *Calypogeia* species around their bases. Fortunately, the fire missed, by a few metres, a group of *Sphagnum* hummocks with *Polytrichum strictum* recently rediscovered at this, its only extant site in Surrey. The depletion of *Campylopus brevipilus* at one of its national strongholds at Thursley must be ranked on a par with the major reductions in the animal populations as the most serious effects of the 2006 fire.

Heathland lichens were completely wiped out by the fire, but by the summer of 2007 charcoal specialists were beginning to colonize some of the fire damaged boardwalks and burned fragments of gorse (*Ulex europaeus*), Scots pine (*Pinus sylvestris*) and heather (*Calluna vulgaris*). Exposed,

desiccated bones of small animals were being colonized by *Funaria hygrometrica* protonemata and, although a colony of *Tetraplodon mnioides* had recently been seen at this site, the lack of nutrients in the long dead animal remains precluded colonization by this species.

The escapees

Unsurprisingly, bryophytes growing in the wetter areas of the central bog were unaffected. Most important is the rich assemblage of liverworts, including *Calypogeia sphagnicola*, *Cephalozia macrostachya*, *Cladopodiella fluitans*, *Kurzia pauciflora* and *Mylia anomala*. However, in future years these should be monitored carefully to assess possible effects of the nutrients released from the dead plant remains and washed into their vicinity. It may well be that such an influx of nutrients may also affect the distribution of the sphagna and of the two *Drosera* spp., at Thursley.

Bryophyte recolonization

Table 1 summarizes bryophyte recolonization of the burnt areas of Thursley in July 2007, and Table 2 lists vascular plants. In terms of surface areas covered the most abundant bryophytes in the burnt areas were *Campylopus pyriformis* (Fig. 2), *Ceratodon purpureus* and *Pohlia nutans*. Whereas the *Campylopus* and the *Pohlia* almost certainly survived the fire by dint of their rhizoid systems in the peaty substratum, the *Ceratodon* colonies were more likely to be established from spores. The occurrence of *Funaria hygrometrica* in small, 2–4 cm diameter, scattered patches throughout the burnt areas indicates the same origin. Similarly patchy, but forming extensive lawns locally were *Polytrichum juniperinum* and *Marchantia polymorpha* (Fig. 3). Most of the *Polytrichum* was purely vegetative, but occasional lawns contained patches with inflorescences. Sporophytes were conspicuously absent. From this situation we



△ Fig. 2. Lawn of *Campylopus pyriformis* and dead pine trees. Jeff Duckett



△ Fig. 3. Silvia and Howard admiring/worshipping (?) a sea of *Marchantia*. Jeff Duckett

infer that the vegetative stems originated either from spores or rhizomes whereas the fertile shoots were those that survived the fire.

In contrast, virtually every patch of *Marchantia* was abundantly fertile with numerous archegoniophores or antheridiophores being produced by each colony, save for very young ones, which were solely gemmiferous. In the absence of signifi-

cant colonies of *Marchantia* at Thursley prior to the fire, it would seem almost certain that the new plants derived from spores blown in from elsewhere. In the context of such long distance dispersal it is perhaps significant that *Marchantia* spores (10–16 µm) are much smaller than those of other British Marchantiales (Paton, 1999; Longton & Schuster, 1983). Also indicative of

colony origins from spores was the very unequal distribution of the sexes; some patches were mixed whilst others were almost entirely male or female. There was, however, no evidence of a preponderance of male plants as predicted from population models of sex ratios in *Marchantia* (McLetchie *et al.*, 2002; Crowley *et al.*, 2005; Garcia-Ramos *et al.*, 2007).

With a much denser spore rain produced *in situ* in 2007 we predict that *Marchantia* growing at Thursley in 2008 will comprise a uniform mosaic of plants of both sexes. A further interesting feature of the *Marchantia* at Thursley in 2007 was that it comprised subsp. *ruderalis* and subsp. *polymorpha* growing side by side, and yet always very clearly distinct. The progeny of this year's spores should be examined in detail for the possible occurrence of hybrids.

In line with the enhanced nutrient status of the soil following the fire, neither of these two subspecies contains a fungal endophyte which is also the case for subsp. *ruderalis* growing in urban areas and subsp. *polymorpha* in base-rich fens and marshes. An absence of ectomycorrhizal roots on *Betula* seedlings growing in the burnt areas was similarly indicative of an abundance of nutrients. In contrast to these two 'weedy' and often ephemeral *Marchantia* subspecies, the thalli of perennial subspecies *montivagans* growing in more stable habitats invariably contain a glomeromycotean endophyte (Ligrone *et al.*, 2007).

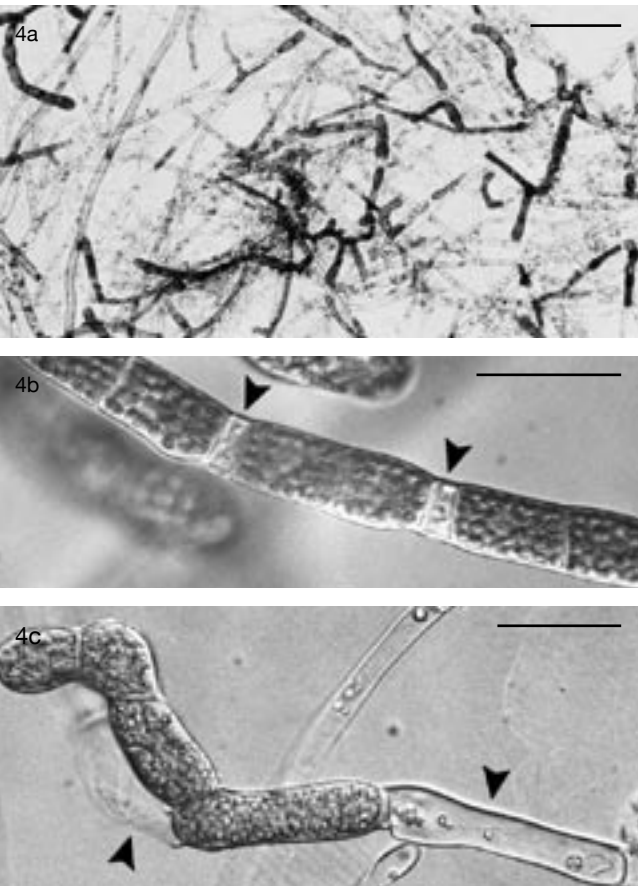
Also in the context of high soil nutrient levels after fires, it is noteworthy that no fewer than six of the recolonizing mosses (Table 1) were producing protonemal gemmae, mirroring their production in culture on nutrient-rich media (Duckett *et al.*, 2004, 2001). Whereas in *Bryum* (Pressel *et al.*, 2007) and *Funaria* (Bopp *et al.*, 1991) these have been described previously, those of *Ceratodon* (Fig. 4) and *Campylopus pyriformis* (Fig. 5) are illustrated here for the first time from British specimens. In the *Campylopus*, gemmiferous protonema was most abundant on sides of depressions and pits dug for invertebrates. The only previous account of this protonema of which we are aware is from thermal vents in Antarctica (Skotnicki *et al.*, 2001). Interestingly, it also occurs around fumaroles in the north island of New Zealand (J.G. Duckett, unpublished data).

Table 1. Bryophyte recolonization of burned areas

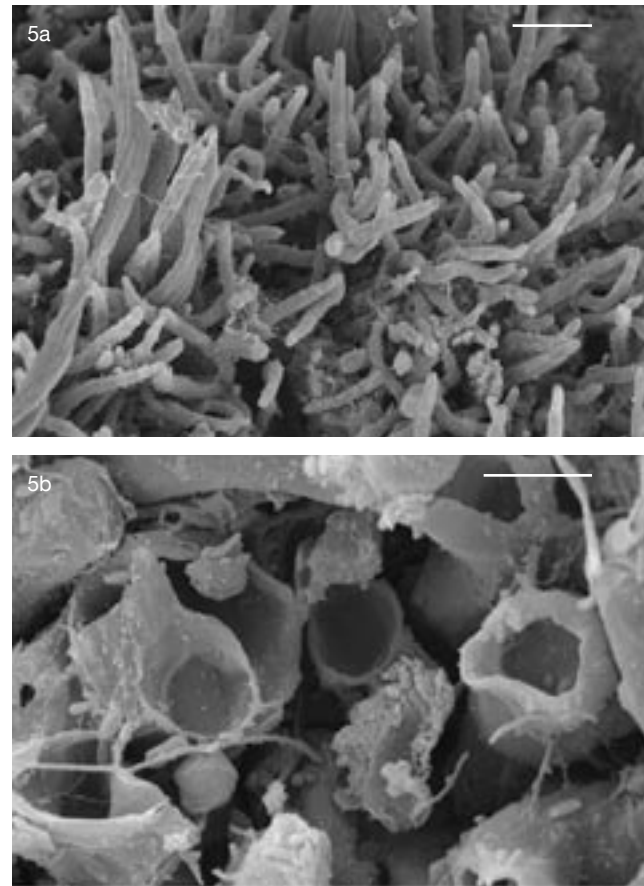
Species	Frequency	Probable origin	Principle mode of spread since origin	Reproductive state
<i>Campylopus introflexus</i>	Scattered small clumps	Rhizoids, spores	Rhizoids, spores	Male and female inflorescences
<i>Campylopus pyriformis</i>	Extensive lawns, especially in small depressions	Rhizoids, caducous leaves	Caducous leaves and protonemal gemmae	Vegetative
<i>Ceratodon purpureus</i>	Extensive patches	Spores	Rhizoids, protonemal gemmae	Male and female inflorescences
<i>Bryum bicolor</i>	Occasional small patches	Spores, bulbils	Bulbils, protonemal gemmae	Male and female inflorescences
<i>Bryum bornholmense</i>	Occasional small patches	Tubers	Caducous stems, rhizoids, protonemal gemmae	Vegetative
<i>Funaria hygrometrica</i>	Frequent small patches	Spores	Rhizoids, protonemal gemmae	Sporophytes
<i>Polytrichum commune</i>	Small patches amongst <i>Molinia</i> tussocks	Rhizomes	Rhizomes	Vegetative
<i>Polytrichum juniperinum</i>	Extensive lawns	Rhizomes, spores	Rhizomes	Occasional inflorescences
<i>Pohlia nutans</i>	Extensive lawns	Rhizoids, spores	Rhizoids, caducous stems	Male and female inflorescences
<i>Sphagnum</i> spp.	Scattered; from single stems to small patches	Old stems	Stems	Vegetative
<i>Calypogeia fissa</i>	Base of <i>Molinia</i> tussocks; sides of pits	Existing stems	Gemmae, existing stems	Vegetative
<i>Cephalozia bicuspidata</i>	Base of <i>Molinia</i> tussocks	Existing stems	Existing stems	Vegetative
<i>Marchantia polymorpha</i>	Extensive patches	Spores	Gemmae	Sporophytes and gemmae

Table 2. Vascular plants in burned areas

Species	Probable origin
<i>Betula</i> spp.	Seeds
<i>Calluna vulgaris</i>	Seeds
<i>Drosera intermedia</i>	Seeds
<i>Drosera rotundifolia</i>	Seeds
<i>Erica tetralix</i>	Seeds
<i>Epilobium angustifolium</i>	Seeds (and old rootstocks)
<i>Epilobium ciliatum</i>	Seeds
<i>Eriophorum angustifolium</i>	Rhizomes
<i>Hypericum pulchrum</i>	Seeds
<i>Juncus bufonius</i>	Seeds
<i>Juncus squarrosus</i>	Old rootstocks
<i>Molinia caerulea</i>	Old rootstocks
<i>Narthecium ossifragum</i>	Rhizomes
<i>Ornithopus perpusillus</i>	Seeds
<i>Pteridium aquilinum</i>	Rhizomes
<i>Rhynchospora alba</i>	Seeds
<i>Rumex acetosella</i>	Seeds
<i>Salix repens</i>	Old rootstocks
<i>Senecio sylvaticus</i>	Seeds
<i>Triglochin palustre</i>	Old rootstocks
<i>Ulex europaeus</i>	Seedlings (and old rootstocks)
<i>Ulex minor</i>	Seedlings (and old rootstocks)



△ Fig. 4. Light micrographs of living gemmiferous protonemata of *Ceratodon purpureus*. (a) General aspect showing numerous gemmae with pigmented walls. Bar, 200 µm. (b) Gemmiferous filament with two young abscission cells (arrowed). Bar, 50 µm. (c) Mature gemmae with two elongate abscission cells (arrowed). The one on the right is at the base of the gemma, the other remaining after detachment of another gemma. Bar, 50 µm. *Silvia Pressel*



△ Fig. 5. Scanning electron micrographs of gemmiferous protonemata of *Campylopus pyriformis*. (a) General aspect showing numerous bluntly pointed gemmiferous chloronemal filaments typical of the Dicranales. Bar, 100 µm. (b) Scars of ruptured abscission cells remaining after gemma detachment. Bar, 20 µm. *Jeff Duckett*

The other bryophytes growing in the burnt areas (Table 1) were most probably survivors of the fire via subterranean organs rather than colonists. The presence of abundant sex organs on *Ceratodon* and *Pohlia nutans*, indicates that both these species will produce sporophytes in the coming winter. The most conspicuous absentees from the recolonists, previously

abundant prior to the fire, were all the pleurocarpous mosses and *Dicranum scoparium*. This is almost certainly because the living parts of these mosses are exclusively above ground in contrast to the living subterranean rhizomes and rhizoids of the survivors. In contrast the absence of the pyrophiles *Leptobryum pyriforme* and *Brachythecium rutabulum* (Southern, 1976;

Bradbury, 2006) more likely reflects a paucity of spore-producing plants in the vicinity.

The regeneration behaviour of *Sphagnum* was particularly striking with most of the burnt colonies of *S. compactum* showing at least some regrowth (Fig. 6). In contrast, burnt hummocks of other species were bleached and dead (Fig. 7). Considering the extent of the bare ground following the fire, the abundant production of sporophytes in several species at Thursley and the well-documented longevity of *Sphagnum* spores (Clymo & Duckett, 1986) our failure to find a single thalloid protonema of *Sphagnum*, despite rigorous searches on several visits to Thursley in the summer of 2007, was at first sight most surprising. Phenological considerations, however, provide a possible explanation – namely an absence of viable spores. When the fire struck in mid-July, spore discharge in all but a few sporophytes in *S. papillosum* and *S. palustre* was almost over and long past in *S. tenellum* where it occurs at the end of May. Thus, any spores that had landed in the burnt areas almost certainly perished in the fire. We therefore suggest that an optimum time to search for the establishment of *Sphagnum* from spores will be in the autumn and winter months following fires the previous year.

Competition experiments between *Campylopus brevipilus* and *C. introflexus*

In the late summer of 2002, Silvia Pressel, Jeff Duckett and Ron Porley set up a series of experimental plots at Thursley to investigate the hypothesis that the dramatic decline in *Campylopus brevipilus* might be due to competition from the supposedly more aggressive and invasive introduced species *C. introflexus*. The site chosen had the two *Campylopus* species growing side-by-side in damp heath with *Sphagnum compactum*, *Drosera rotundifolia*, *Rhynchospora alba* and *Erica tetralix*. Twelve interfaces were marked by



△ Fig. 6. Regenerating *Sphagnum compactum*. *Jeff Duckett*

△ Fig. 7. Hummock of *Sphagnum* killed by the fire. *Jeff Duckett*

coloured pins and, at a further 12 locations, tufts of *C. brevipilus*, approximately 3 cm in diameter, were transplanted into clumps of *C. introflexus* and vice versa. It proved to be relatively easy to relocate the individual sites, and the experiments were monitored at 3- to 6-monthly intervals. After 3 years there was absolutely no evidence that *C. brevipilus* was being overgrown by *C. introflexus* (Duckett *et al.*, 2006). In the early summer of 2007 the transplanted tufts of both species were still alive and thriving in their new locations

(Fig. 8). Of the species interfaces (only 9 of the original 12 were still visible; the pins at the other three having disappeared beneath new growth of the mosses), 4 remained unchanged, 3 were dominated by *C. brevipilus* and 2 by *C. introflexus*. We therefore conclude that over the 6 years of the experiment there was no evidence that *C. introflexus* out-competes *C. brevipilus*. Similarly, in culture the protonemata of both species have similar growth rates and when grown together there is no evidence that *C. introflexus* out-competes *C. brevipilus* (S. Pressel, unpublished data).

However, these experiments only involved mature populations of the two species. The situation may be very different when initial establishment

is involved. Paradoxically, the fire has provided a unique opportunity to investigate this question, since some of the transplant sites were destroyed. We will now be carefully monitoring *Campylopus* regrowth from these burnt areas. Unlike *C. introflexus*, there was no evidence of regeneration in *C. brevipilus* in the summer of 2007, suggesting that the former species, with its more robust habit may be more fire resistant. If *C. brevipilus* has been destroyed by the fire, as these observations appear to indicate, recolonization by *C. introflexus* would seem the most likely scenario with the new plants deriving from both surviving colonies and from spores. The production of abundant sporophytes by *C. introflexus* and their absence in *C. brevipilus* will certainly give the introduced species a clear advantage in colonization. We therefore suggest that an inability to recover quickly from fires in the presence of *C. introflexus* may be one of the key factors responsible for the decline in *C. brevipilus*.

The future

The foregoing account about *Campylopus* naturally leads to considerations as to the probable bryophyte species dynamics on the burned areas of Thursley in future years. Nutrient leaching will almost certainly lead to a decline in *Marchantia* and *Funaria*, and in the prevalence of gemmiferous protonemata. In 2008 we should witness abundant sporophyte production by *Ceratodon*, *Pohlia nutans* and *Polytrichum juniperinum* and a gradual recolonization by *Dicranum scoparium* from spores, followed more slowly by *Hypnum jutlandicum* and *Pleurozium schreberi*

◀ Fig. 8. The *Campylopus brevipilus*–*introflexus* competition experiments. (a) An interface between the two species, marked by coloured pins in the summer of 2002, remained almost unchanged in 2007. (b) A tuft of *C. introflexus* transplanted into *C. brevipilus* in 2002 showed no sign of outgrowing the latter species 6 years later. Jeff Duckett

from stem fragments. Subsequent years may also see the appearance of *Leptobryum pyriforme*, *Brachythecium rutabulum*, *Barbula convoluta* and *Barbula unguiculata*. Within 2–3 years *Sphagnum compactum* is likely to have made a very substantial, if not full recovery, but reformation of the hummocks of other sphagna and re-establishment of the associated liverworts in their former abundance may take rather longer.

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