Bryophytes of arable fields: current state of knowledge and conservation

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Summary

Bryophytes are a characteristic component of cultivated land in Britain, but knowledge of their status, distribution and ecology lags well behind that of arable vascular plants. There are at least 17 liverworts and hornworts and 73 mosses that have been recorded on arable, representing about 9% of the total British and Irish bryoflora. Many of the species also occur in other habitats. Bryophytes of arable land are well adapted to regular disturbance by virtue of ephemeral lifestyles and compressed life-histories. They produce a variety of sexual and asexual propagules and can form a persistent diaspore bank in the soil. The typical arable bryophyte community includes the liverworts Riccia glauca and R. sorocarpa, and the mosses Barbula convoluta, B. unguiculata, Bryum argenteum, B. bicolor, B. klingraeffii, B. rubens, B. subapiculatum, Dicranella schreberiana, D. staphylina, Ditrichum cylindricum, Entosthodon fasicularis, Ephemerum serratum var. minutissimum, Microbryum rectum, Tortula acaulon and T. truncata. An additional number of species are very rare, such as the Biodiversity Action Plan species Didymodon tomaculosus, Ephemerum stellatum and Weissia multicapsularis. These, and others such as Anthoceros and Sphaerocarpos, are more or less restricted to arable, and thus are particularly vulnerable to changes in agricultural management. There is ample anecdotal evidence that arable bryophytes are in decline in Britain and mainland Europe. It is suggested that changes in sowing and harvesting times and the use of agrochemicals are factors contributing to the decline, but the demise of stubble fields has probably had the greatest negative impact on the arable bryoflora. More survey work is needed in both Britain and Ireland to understand the distribution, status and occurrence of bryophytes in different crop types and under various management regimes, particularly in relation to organic farming. The presence and efficacy of the diaspore bank under different agricultural regimes is an area ripe for research.

Introduction

This paper reviews the rather small body of knowledge concerning arable bryophytes in Britain and Ireland. Those involved in wildlife conservation on the farm frequently express mild surprise at the suggestion that cultivated land may harbour mosses, liverworts and hornworts. This is, no doubt, partly due to their small size and their ephemeral nature; as a consequence they are relatively inconspicuous unless in abundance. Cultivated land does however support a characteristic suite of arable bryophyte species. In Britain, one of the earliest references to bryophytes of arable land is by Richards (1928) who even then suggested arable bryophytes in Middlesex might not be as common as they once were. He observed that ‘unfortunately in Middlesex bare soil is not often left undisturbed and therefore very few examples of ephemeral communities have been found’.

A problem at this time was that taxonomic knowledge of some bryophyte groups was rather rudimentary, and many of the most characteristic arable species were simply not known. In another early study, Schelpe (1959) investigated the ecology of bryophytes on arable land in Oxfordshire, but again it is clear that many species were overlooked. It was not until the 1960's and later that groups such as the *Bryum erythrocarpum* aggregate (Crundwell 1962, Crundwell & Nyholm 1964) was elucidated, and *Dicranella staphylina* (Whitehouse 1969) and *Ditrichum pusillum* (Whitehouse 1976) were described as new to science relatively recently. In 1974 to 1975 Side (1977) carried out some pioneering work on bryophytes in arable fields in Kent. She noted that the lack of any baseline knowledge of bryophytes on cultivated land in Kent precluded any conclusions as to how the bryoflora might be changing under the intensive agricultural regimes that were on the ascendancy.

There is often debate over the status of vascular arable plants in Britain, and whether they are native or introductions. Less controversy surrounds arable bryophytes. Although many of the small bryophytes that grow on soil, such as *Ephemerum, Tortula, Microbryum* and *Weissia*, are unknown as subfossils in Britain (Dickson, 1973) there is no question of their native status, although it is likely that they increased as a result of agriculture which maintains bare soil. It has however been suggested that the liverwort *Sphaerocarpos* is a long-established introduction (Hill et al., 1991) and that man has played a role in the global dispersal of this species (Paton, 1999) through agriculture. Only two plants of arable are regarded as certain introductions, the liverwort *Riccia crystallina* (Paton, 1999) and the moss *Chenia leptophylla* (Hill et al., 1992), but both are rare and restricted plants. *Anthoceros*, a hornwort, is exceptional amongst the bryophytes in that spore records extend back to the Cromerian stage of the Pleistocene (300,000 years ago), including the two later interglacials and the Flandrian. In The Netherlands Anthoceros and Riccia spores were found together in the same post-Atlantic agricultural horizons (c. 5000 years ago), and occurred with pollen of such angiosperms as *Centaurea cyanus, Plantago* and cereals. In this context such spores are considered as indicators of agriculture (Koelblod & Kroeze, 1965), as they may do in the British Isles (Dickson, 1973).

Although arable covers a large proportion of the land surface in Britain and Ireland, knowledge of the bryoflora is still very patchy, and only a few bryologists consistently record in this habitat. Much work in recent years has been done by the late Harold Whitehouse, who has perhaps done more than anyone else in Britain to raise the profile of arable bryophytes. Nomenclature of bryophytes follows Blockeel & Long (1998).

The bryophyte flora of arable fields

Based upon a review of the relevant literature and fieldwork by the author some 17 liverworts and hornworts and 73 mosses have been recorded in arable (Appendix A), which represents about 9% of the total British bryoflora. Some of the species are of casual occurrence, and undoubtedly further species will be found. However, most of the species in Table 1 are frequently encountered on cultivated land and some are only rarely found off arable.

Several species can be considered members of a typical arable bryophyte community. These are the liverworts *Riccia glauca* and *R. sorocarpa,* and the mosses *Barbula convoluta, B. unguiculata, Bryum argenteum, B. bicolor, B. klingraeffii, B. rubens, B. subapiculatum, Dicranella schreberiana, D. staphylina, Ditrichum cylindricum, Entosthodon fasicularis, Ephemerum serratum* var*. minutissimum, Microbryum rectum, Tortula acaulon* and *T. truncata*. Where conditions are favourable for bryophyte growth, these species can usually be found at least on arable margins, although many sites will not necessarily support all species. Some of the species are relatively new additions to the British bryoflora, such as *Dicranella staphylina*, but once recognised in the 1960's, records increased steadily and it is now known from 128 vice-counties in Britain and Ireland (Blockeel & Long, 1998). *Dicranella schreberiana* was for many years considered to be a very rare northern plant in Britain, but once bryologists learnt how to recognise it, it began to be recorded in numerous southern counties (Jones, 1991). Similarly, *Ditrichum cylindricum*, once bryologists became familiar with it in a sterile condition, was being found in arable fields across the country, and today is known from all but two vice-counties in Britain (Blockeel & Long, 1998).

Even amongst these more or less constant members of the arable community, there are some subtle geographical differences in distribution, for example *Entosthodon fasicularis* appears to be more common in southern Britain, and *Bryum klingraeffii* tends to be more frequent in eastern England. By contrast *B. sauteri* shows a western distribution in Britain, and with many records from the Weald. In Cornwall it tends to be associated with paths, woodland margins and Cornish hedges in close proximity to arable, as well as in the field itself. A few species are characteristic of arable under specific conditions, such as *Bryum riparium*, which is found in fields subject to flooding by streams (Hill et al., 1994). However, caution should be exercised since recording of bryophytes in arable is distinctly patchy, and Ireland in particular is poorly recorded. The distribution of arable in Britain and Ireland has undoubtedly a significant affect on the distribution of bryophytes of cultivated ground, although many of the species can and do commonly occur in woodland rides, in quarries, along tracks and on disturbed ground in many other habitats. It is also interesting to note that there are similarities between the British arable bryoflora and those of other countries as far apart as Slovakia and Québec (Whitehouse, in press).

Several species are however highly characteristic of arable and only rarely found in other habitats. A good example is *Sphaerocarpos.* This distinctive liverwort is, with the exception of the Isles of Scilly, more-or-less restricted to south-east England from the Wash west to Dorset, and south Wales. *S. texanus* is the rarer species, and is listed as Vulnerable in Britain (Church et al., in press). There are more records for *S. michelii,* and although it can be very persistent (Bates, 1995), it too may be declining. Both species are highly characteristic of cabbage and flower-fields in the Isles of Scilly (Hill et al., 1991) but are not mentioned in the National Vegetation Classification section on arable communities (Rodwell, 2000), presumably because they had died back before field recording began in the new season. The hornworts *Anthoceros agrestis* and *A. punctatus* are also typically found in arable, particularly on damp clays, but tend to be very local and sporadic in appearance. In Central Europe Bisang (1998) presents evidence that agricultural management is the most important predictor of hornwort occurrences, and that weather conditions and soil characteristics are less relevant.

Three of the species in Appendix A are listed as priority species within the UK Biodiversity Action Plan (Anon., 1999; 1995), and these are also strongly associated with cultivated land. The British and Irish endemic *Didymodon tomaculosus* is known from 3 vice-counties in England (Derbyshire, South-west Yorkshire & Mid-west Yorkshire) and 2 vice-counties in Ireland (Offaly & Kildare), and all are from arable fields. It was described as new to science very recently (Blockeel, 1981), and since publication has been found in a further four vice-counties, including those in Ireland. All collections to date are female, and sporophytes are unknown. It does possess however distinctive rhizoidal gemmae (tubers) which have been present in all gatherings, and thus *D. tomaculosus* should not be confused with other similar looking species. *Ephemerum stellatum* has been recorded from 5 vice-counties in England (South & North Hampshire, West & East Sussex, West Kent) and 1 vice-county in Ireland (South Kerry). It has only been seen recently in South Hampshire and West Sussex, although a an attempt to find it in 2000 in the latter county was unsuccessful. In England it is known from a single locality in each county, the two most recent records from arable fields. This plant is considered to be rare at a world level, known perhaps from less than ten localities (Hill et al., 1994). The third species, *Weissia multicapsularis*, has been recorded from nine scattered vice-counties in England and Wales (single record). Endemic to western Europe, it has declined markedly in Britain and has been seen recently in only two vice-counties (West & East Cornwall) where populations are precariously small (Holyoak, 1999). All three species are in need of further survey to establish their precise status in Britain and Ireland.

Some features of the ecology and reproductive biology of arable bryophytes

Farmland is a transient habitat subjected to regular disturbance, and arable bryophytes are well adapted to such a regime. A feature of many of the bryophytes typical of cultivated land is the production of asexual propagules, either as tubers (rhizoidal gemmae), bulbils or gemmae

(Whitehouse, 1966). Such structures are particularly prevalent within the genera *Bryum, Dicranella, Ditrichum* and *Pohlia* (Appendix A). These structures are important in enabling the plants to persist through unfavourable periods and rapidly colonise new ground when conditions become suitable. With the notable exception of the work by Bisang in Switzerland (see below), the bryophyte component of the diaspore bank in arable fields has received relatively little attention (During, 1997). There is however ample evidence that bryophyte diaspore banks exist in a variety of other habitats. During & ter Horst (1983) showed that there is a bryophyte diaspore bank in chalk grassland soils, and is presumed to consist chiefly of vegetative propagules. Jonsson (1993) also presented evidence of a diaspore bank in a boreal forest, a relatively stable ecosystem with low frequency of disturbance.

Bisang (1995, 1996) investigated bryophyte diaspore banks in arable fields by removing soil samples and in vitro culture. Although she made no attempt to identify the type of diaspore the cultured plants derived from, she presumed that species frequently producing sporophytes on the study sites, such as *Anthoceros agrestis, Riccia spp., Ephemerum serratum* var. *minutissimum, Tortula truncata* and *Tortula acaulon*, developed from spores present in the soil. However, species rarely or never producing sporophytes on the surface of the study sites, including *Bryum* spp. and *Dicranella* spp. were presumed to have regenerated from asexual propagules or gametophyte fragments. Furthermore, several bryophytes were found to be present in the diaspore bank but were not recorded from the surface vegetation, including *Bryum klingraeffii.* She concluded that the presence of a bryophyte diaspore bank is essential for the local survival of a number of species, particularly hornwort populations (*Phaeoceros carolinianus*) which are more or less confined to arable fields.

Very little work has been done on arable soils but it is likely that there is a persistent diaspore bank. Some of the earliest work on persistent bryophyte diaspore banks in soil was by Furness & Hall (1981) studying *Physcomitrium sphaericum*, the spores of which remain buried in submerged mud of reservoirs for long periods of time and germinate only in years of drought when mud is exposed. Similarly, spores of *Micromitrium tenerum* may survive for decades in the soil (Schmidt & Kohn, 1993). It seems that species differ considerably with respect to longevity of their spores in soil, and that larger spores of at least some annual shuttle species may survive longer than species with smaller spores such as in the fugitive *Funaria hygrometrica*, the spores of which apparently die within a few years (During, 1986). There is also evidence that tubers have the ability to remain viable for long periods of time. Whitehouse (1966) cites an example of a tuber of *Bryum bornholmense* germinating after 12 years in a herbarium. More extraordinary is the conclusion reached by Whitehouse (1984) that a tuber of *Dicranella staphylina*, present in stored soil samples (Bristol, 1919) germinated after a period of nearly 50 years. There is also some evidence that tubers and spores are able to survive the passage through an earthworms digestive tract (During et al., 1987), and thus propagules can be brought to the surface and taken down into the soil by such activities. Bisang (1996) found most bryophyte diaspores to be within 0-25 cm below the surface in arable fields. At greater depths the diaspore bank is considerably depleted and germinated propagules from deeper zones show less vigour. Arable land is regularly disturbed by ploughing to about 25 cm, which will have the effect of distributing diaspores within the soil profile. She also found the actual farming regime had a major influence on species composition at various depths within the soil profile, and that species may be represented in the diaspore bank but not on the surface of the field. During & ter Horst (1983) and During et al. (1987) reported the same phenomenon in other habitats, where tuber-bearing species may be very abundant in the diaspore bank, while their above ground populations are extremely sparse. In regularly disturbed habitats however, such as arable fields, above ground shoot densities may be considerably higher (During, 1995).

Out of the 73 mosses recorded in arable (Appendix A), 58 are known to produce sporophytes. Species that produce sporophytes freely, such as *Entosthodon fasicularis, Funaria hygrometrica, Tortula acaulon, T. truncata. Microbryum curvicolle* and *Ephemerum serratum* var. *minutissimum* are probably represented in the diaspore bank as spores. These are also all monoicous, and lack specialised asexual propagules. Indeed there is a correlation between sexuality and tuber or gemmae production; of the arable mosses in Appendix A, only two monoicous species, *Fissidens taxifolius* and *Leptobryum pryriforme*, are known to produce asexual propagules. In arable most of the tuber bearing mosses are dioicous, and in many of these sporophytes are rare or unknown. In such cases it seems safe to assume that the diaspores bank of these species (*Bryum* sp., *Dicranella* sp.) consists largely if not exclusively of tubers.

Most of the arable liverworts are monoicous but those that are dioicous (*Blasia pusilla, Lunularia cruciata* and *Phaeoceros carolinianus*) possess asexual propagules in the form of gemmae or perennating tubers. *Blasia* (although only occasionally in arable fields) possesses two types of gemmae, a stellate form that is packed with starch and are short lived, and ellipsoidal gemmae that contain abundant lipid droplets and protein reserves and retain viability for several months (Duckett & Renzaglia, 1993). *Sphaerocarpos* is rather a specialised case. Although this liverwort is dioicous, and produces no specialised asexual propagules, it has evolved permanently coherent spore tetrads consisting of two males and two females. *Sphaerocarpos* is sexually dimorphic, with male plants being much smaller than female. Upon germination of the spore tetrads there is a greater chance that male and female plants will remain together in mixed clumps, thus optimising fertilisation opportunity. It has been shown however that in *S. texanus* that there is a deviation from the expected 1:1 sex ratio in favour of females (McLetchie, 1992); this may be due to higher susceptibility of males to environmental conditions, to their competitive inferiority to females, or to differential resource allocation to the sexes in the spore tetrad.

The various reproductive strategies shown in the arable bryophytes as a group are linked to their adaptation to regular disturbance which is a feature of cultivated land. Many demonstrate ephemeral lifestyles and compressed life-histories that enable them to germinate, mature rapidly, produce spores, followed by adult mortality, in very short periods. Water availability is an important limiting factor for bryophytes; the reliance on water for fertilisation is one the most fundamental aspects in which bryophytes differ from phanerogams. Arable, particularly in parts of Britain, is an arid habitat, and thus sporophyte production occurs during the autumn through to early spring. The above-ground gametophyte is also very sensitive to desiccation, particularly in liverworts, and most die back completely by March or April. The winter ephemeral *Sphaerocarpos* is typical of this strategy, germinating in the autumn and senescing in the early spring, completing its life cycle in a matter of months. During (1979, 1992) has developed a theoretical classification of life histories in bryophytes based on parameters such as reproductive effort (asexual and sexual), size and numbers of spores and annual production of biomass. Much more work is needed in determining these parameters for bryophytes, but a number of life strategies can be distinguished. A large number of arable bryophytes are represented by the annual shuttle strategy. This is characterised by a short life-span, a high investment in sexual reproductive effort and sporophyte production, asexual reproduction absent, production of a few, large-sized spores at an early reproductive age, normally less than a year. Species showing this type of strategy include *Tortula acaulon, T. truncata, Microbryum curvicolle, Ephemerum serratum* var. *minutissimum, Physcomitrium pyriforme, Entosthodon fasicularis* and the liverworts *Ricca sorocarpa* and *Sphaerocarpos texanus.* The other life-history strategy well represented in arable bryophytes are the ephemeral colonists, where the species are very short-lived above ground but maintain themselves by subterranean tubers, often forming a considerable diaspore bank in the soil. Fruiting is rare but if it occurs large numbers of small spores are produced. The tuberous *Bryum* species exemplify this type of life-strategy, such as *Bryum rubens, B. subapiculatum, B. klingraeffii* and *B. violaceum*. They are characterised by a moderately short life span, high reproductive effort in asexual and sexual production, asexual reproduction mostly in early stages of life cycle, spores small and very persistent and asexual propagules large. Other typical arable species include *Bryum bicolor, Barbula convoluta* and *Dicranella staphylina.*

Dispersal of arable bryophytes is clearly of great importance in the colonisation of new sites, but little is known of their ability to spread to neighbouring fields by spore liberation. Clearly the more isolated sites become, the less chance a spore has of finding an appropriate substrate for establishment and development. A useful discussion of spore dispersal in bryophytes is given in Longton & Schuster (1983). Miles & Longton (1992) counted spores trapped on sticky slides released from colonies of *Atrichum undulatum* and *Bryum argenteum* and confirmed a leptokurtic distribution of spores, where spore catch is high in the immediate vicinity of the colony, but declines rapidly with increasing distance. They estimated however that between 85 to 95% of the spores were dispersed to unknown distances beyond the trapping areas. Stoneburner et al. (1992) estimated that 94% of spores from *Atrichum angustatum* fell within 2 m of the colony centres, and 1% from 15 m, the perimeter of their sampling zone. They also argued that, under suitable conditions it is likely that dispersal distances may be much greater than the distances indicated in their study. Many arable mosses possess immersed and/or cleistocarpous capsules with relatively large spores; it is reasonable to speculate that dispersal distances may be less than in than those mosses with seta that lift the capsule above the boundary laminar layer. Furthermore, some of the ephemerals that have been investigated, including *Tortula acaulon, T. truncata* and *Physcomitrium pryriforme* produce spore counts in the lower range of 5000 - 10000 (Longton & Schuster, 1983). Spore production is normally seasonal, although this is apparently not detectable in the soil spore bank (During et al., 1987; During 1997). Dispersal distances of rhizoidal tubers are likely to be extremely short, although the extent to which earthworms and other animals play in dispersal of diaspores is very difficult to assess (During, 1995).

Impact of modern agriculture on arable bryophytes

Although definitive evidence of a decline in arable bryophytes in Britain is lacking, many bryologists concur that they are much scarcer in the arable habitat than they were in the past. Regional bryophyte floras (eg: Bates, 1995) also allude to a decline in certain arable species, particularly the hornworts, but without a baseline it is difficult to quantify the scale of loss. It is not unreasonable to suggest that the factors implemented in the decline of the vascular arable flora, such as changes in traditional crop sowing times, loss of fallow land and stubbles, decline in crop rotation practises, and the increasing reliance on chemicals to control weeds and to boost yields of modern crop varieties (Wilson, 1992; 1993), are also operating on bryophytes.

Timing of cultivation The most important factor impacting on bryophyte richness is the crop-growing cycle. A perusal through county bryophyte floras and the Atlases (Hill et al., 1991, 1992, 1994) consistently cite stubble as the main habitat for many of the arable species in Appendix A. Jones (1991) noted that stubble fields once remained unploughed as late as November, enabling ephemeral species to develop, but that the practice now is to plough and re-seed within weeks of harvest. Thus in early winter there are large areas of arable where a single bryophyte cannot be found. Many mosses that propagate from spores are autumn germinating, and will mature and produce sporophytes over the winter period, from November to February, therefore, depending on weather conditions, spores can be dispersed in late autumn through to early spring. Species such as *Ephemerum* will germinate and develop very rapidly so that ripe sporophytes are typically abundant in autumn (Hill et al., 1994), although capsules can be found at other times of the year (*Ephemerum* has persistent protonema). If conditions are suitable fruiting material of some annual shuttle species, such as *Microbryum rectum*, can sometimes be found in early summer, although this is not typical. A cultivation that interrupts this life cycle will thus prevent incorporation into the diaspore bank. For some species, cultivation in late autumn (October) is beneficial, since this will bring to the surface buried spores. This is particularly the case with hornworts and *Sphaerocarpos*, plants that in particular appear to be declining. Bisang (1995) recommended ploughing in late autumn to allow sporophyte production, especially for *Phaeoceros carolinianus*, in arable fields in Central Europe. *Sphaerocarpos* is a winter ephemeral, germinating in the autumn and senescing in early spring. Spring crops are often sown up to a month earlier than was traditionally practised, before the spores have had time to fully mature.

It has already been noted that the hornworts (*Anthoceros, Phaeoceros*) in particular appear to be declining in arable (eg: Brewis et al., 1996; Killick et al., 1998; Wigginton, 1995). In Britain they generally behave as summer annuals, germinating in early summer and producing sporophytes in early winter. The agricultural treatment that a crop receives therefore has considerable impact on hornworts. Cultivation and harvesting times are probably limiting factors, and it has also been suggested that herbicide application may be damaging (Bisang, 1992; Bates, 1995).

Herbicides The response of bryophytes to herbicide application is complex, and a review is given by Brown (1992). Although bryophytes generally absorb water and nutrients over the entire gametophyte surface, chemicals may be bound to cell walls or inactivated by some other physiological process. Preliminary work suggests that some bryophytes are susceptible to some herbicides applied at the manufacturer's recommended dose, and therefore as a precautionary approach chemicals should be considered as potentially harmful. Since many bryophytes generally undergo their main period of growth during autumn through to early spring, which is generally outside the window of herbicide application to control vascular weeds, they may avoid contact (with the notable exception of hornworts). What effect, if any, herbicides have on the diaspore bank is unknown, although one may infer a gradual depletion.

Fertilizers Bryophytes are capable of utilizing a range of inorganic and organic nitrogen compounds (Brown, 1992), although there is at present only a limited understanding of the assimilation of nutrients under field conditions (Brown & Bates, 1990). It is difficult to disentangle the indirect and direct effects of additions of fertilizer on bryophytes and more work is required. It is a reasonable assumption however that vascular plant competition, including that of the crop, will be considerably enhanced. Small acrocarpous bryophytes typical of arable land are poor competitors (Grime et al., 1990) and thus would be expected to decline; studies on other habitats have indicated that increased nutrients do lead to a loss of certain bryophytes (During & Willems, 1986; and see Brown, 1992). In conventional cereal crops bryophytes are more or less confined to crop margins and corners that have escaped, or suffer less from, fertilizers and herbicides, and in this respect have much in common with vascular arable plants. The bryoflora of margins bordering and overhung by trees is typically less diverse than unshaded open margins, often being visually mossy, but dominated by a few ubiquitous species. Such differences may be due leachate from the canopy of leaves and input of nutrients from leaf fall, in addition to shading and amelioration of the microclimate.

Next steps

It is generally acknowledged that the distribution and status of many vascular arable plants in Britain and Ireland is poorly known. Knowledge of arable bryophytes lags far behind.

Arable mosses and liverworts are physically so much smaller than most vascular plants so they can potentially exploit open, disturbed ground over a much wider area of countryside, including gardens, flower beds, tracks, rides, quarries, banks, lake and reservoir margins and open patches in grassland. A diaspore bank means colonists and shuttle species are able to quickly exploit suitable, often impermanent conditions. Apart from a few notable exceptions, such as *Didymodon tomaculosus, Ephemerum stellatum, Weissia multicapsularis, Sphaerocarpos* and hornworts, it is unlikely that the more widespread, characteristic arable bryophytes would decline to the point where, individually, they would be classified as threatened (IUCN, 1994). However, as part of a typical arable community of vascular and non-vascular plants, and within the context of soil type, crop and management regime, it is conceivable that they could become threatened at the community level. The generally accepted view amongst bryologists is that the typical arable field bryophyte assemblage is much less frequently encountered than in the past. Bryophytes have been neglected in comparison to vascular arable plants in terms of biological survey of arable fields; this imbalance should be addressed as a priority before the situation becomes acute.

Survey Nationally, coverage of arable habitats for bryophytes is very patchy, and farmland tends not to attract the botanical recorder unless they have a particular interest. In this context there is currently underway extensive survey of arable fields in North-East Yorkshire (Blackburn, pers. comm.) and Suffolk (Fisk, pers. comm.). Targeted survey is however required across the country to provide a better understanding of the occurrence, population size, distribution and status of arable bryophytes. It is hoped to engage members of the British Bryological Society in a nationwide survey in the near future. The three species that have published Action Plans (Anon., 1999; 1995) require targeted work immediately, and it is also desirable to focus on *Sphaerocarpos* and the hornworts. The work by Side (1977) has provided a unique arable bryophyte flora baseline for Kent, and it would be particularly informative if it were to be repeated. It is unknown whether an arable field noted for the vascular plant interest supports a notable bryophyte flora. A site for *Lythrum hyssopifolia* in Cambridgeshire supports a number of typical arable bryophytes, including *Riccia subbifurca* (Preston & Whitehouse, 1986). However, a brief inspection of an arable field Site of Scientific Interest in Somerset, notified for the vascular plant interest, showed the bryophyte component to be virtually absent (pers. obs.) although this may be more to do with timing of the visit. A useful exercise therefore would be to evaluate arable fields of known vascular plant interest for the bryophyte interest. It is important to note however that a bryological survey needs to be conducted from autumn through to spring, which is often outside the period deemed desirable for vascular plant survey.

Crop type The particular crop type and management is a major determinant of the bryophyte assemblage. Most arable bryophytes are recorded from stubble fields, largely because cereals (barley, oats and wheat) constitute a large proportion of arable land-use. Other crops can be locally important, such as flower fields in the Isles of Scilly (Paton, 1969), cabbages, cauliflower, and sugar-beet fields. A perusal of new vice-county records given in the Bulletin of the British Bryological Society from the years 1979 - 1999 also lists potato, bean, turnip, leek and rape fields. Recent examination of an asparagus field in Suffolk revealed a community of bryophytes including *Sphaerocarpos michelii* growing on cultivated ridges. Sphaerocarpos appears to be often associated with non-cereal crops, including leek, rape and a Brussels sprout allotment. However, Bisang (1998) suggested a paucity of Swiss hornwort populations in crops such as potato, beet-roots and maize may be due to compaction of the soil during the growing season by heavy machinery. The value of set-aside for bryophytes needs evaluation, although it is likely that any land left uncultivated for more than two seasons will be dominated by vascular plants with the less competitive bryophytes on the decline. In Scotland Anthoceros agrestis has been recorded in set-aside, but the period for which the fields were uncultivated is unknown. Undersown crops also need to be evaluated, since these appear to provide favourable conditions for bryophytes (pers. obs.). Survey effort therefore needs to cover a representative sample of crop types and management regimes on a regional basis.

Soils More information is also needed on soil types, structure and pH. Bisang (1998) reviews some data on soil characteristics particularly in relation to hornwort occurrence in the Swiss Plateau. Most British floras suggest arable bryophytes are characteristic of neutral to slightly acid loams, and on clays and sands. Typical arable bryophyte assemblages can also be found over chalk and limestone (pers. obs.) although this may indicate surface leaching. Fitter (1985) remarks that the stubble field bryophyte flora is poor on the Cotswolds, but much richer on the chalk with such species as *Dicranella schreberiana, Tortula floerkeanum* and *Pterygoneurum ovatum.*

Organic farmland Work in Bavaria (Albrect & Mattheis, 1998) suggests that organic farming does hold promise for rare vascular plants, and preliminary work in Britain also supports this (Kay &

Gregory, 1999). There is however little if any data available on the bryophyte interest of organic fields. Given that the area of land in the UK under organic regimes is likely to increase in response to a demand for organic produce, there is a need to establish the importance of organic land for arable bryophytes. One organic farm in Oxfordshire revealed very few bryophytes, although surprisingly there was an abundance of the common pleurocarps *Euryhnchium praelongum* and *Brachythecium rutabulum*. These species are thought not to be represented in the diaspore bank, or at least in low quantities (During et al., 1987). Their presence above ground may be explained by fragments of shoots in the diaspore bank, incorporated as a result of mechanical weeding of the crop. A much greater sample of organic farms needs to be assessed before any conclusions can be drawn.

Diaspore banks In regularly disturbed habitats, such as arable fields, it is assumed regeneration of bryophytes occurs largely from the diaspore bank. Although ephemeral colonists are likely to regenerate from tubers, and annual shuttle species from spores, gametophyte fragments with resting buds, protonemal gemmae and persistent protonema may also play a role. Little is known of the nature of the diaspore bank under different cultivation regimes, and whether certain management practises lead to a depletion of spores and asexual propagules over time.

Taxonomy In such an under-worked habitat as arable land, it is possible that new species will turn up that were previously overlooked (Whitehouse, 1976) or even new to science (Blockeel, 1981; Whitehouse, 1969), or species thought to be geographically restricted, such as *Didymodon tomaculosus*, may prove to be more widespread. Crundwell (in Whitehouse, in press) reports the possible occurrence of the non-British *Bryum demaretianum* (Arts, 1992) in an arable field in Somerset; unfortunately a herbarium specimen cannot be traced. *Anthoceros caucasicus*, recently reported new to The Netherlands and representing a considerable range extension (During et al., 1996), is also likely to be found in the British Isles (Paton, 1999).

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References

Albrecht H, Mattheis A. (1998). The effects of organic and integrated farming on rare arable weeds on the Forschungsverbund Agrarökosysteme München (FAM) research station in southern Bavaria. Biological Conservation 86: 347-356.

Anon. (1999). Biodiversity: The UK Steering Group Report Volume 2. Action Plans. HMSO, London.

Anon. (1999). UK Biodiversity Group Tranche 2 Action Plans. Volume III Plants and fungi. English Nature, Peterborough.

Arts T. (1992). *Bryum demaretianum sp. nov*., a new species of the B. erythrocarpum complex from Belgium. Journal of Bryology 17: 263-267.

Bates JW. (1995). A bryophyte flora of Berkshire. Journal of Bryology 18: 503-620.

Bisang I. (1992). Hornworts in Switzerland - endangered? Biological Conservation 59: 145-149.

Bisang I. (1995). The diaspore bank of hornworts (Anthocerotae, Bryophyta) and its role in the maintenance of populations in cultivated fields. Cryptogama Helvetica 18: 107-161.

Bisang I. (1996). Quantitative analysis of the diaspore bank of bryophytes and ferns in cultivated fields in Switzerland. Lindbergia 21: 9-20.

Bisang I. (1998). The occurrence of hornwort populations (Anthocerotae, Anthocerotopsida) in the Swiss Plateau: the role of management, weather conditions and soil characteristics. Lindbergia 23: 94-104.

Blockeel TL. (1981). *Barbula tomaculosa*, a new species from arable fields in Yorkshire. Journal of Bryology 11: 583-589.

Blockeel TL, Long DG. (1998). A check list and census catalogue of British and Irish bryophytes. British Bryological Society, Cardiff.

Brewis A, Bowman P Rose F. (1996). The flora of Hampshire. Harley Books, Colchester.

Bristol BM. (1919). On the retention of vitality by algae from old stored soils. New Phytologist 18: 92-107.

Brown DH. (1992) Impact of agriculture on bryophytes and lichens. In Bryophytes and lichens in a changing environment, 259-283. Eds JW Bates and AM Farmer. Clarendon Press, Oxford.

Brown DH, Bates JW. (1990). Bryophytes and mineral cycling. Botanical Journal of the Linnean Society 104: 129-147.

Church JM, Hodgetts NG, Preston CD, Stewart NF. (In press). British Red Data Books 2. Mosses and liverworts. Joint Nature Conservation Committee, Peterborough.

Crundwell AC. (1962). *Bryum sauteri* and *B. klingraeffii* in Britain. Transactions of the British Bryological Society 3: 563-564.

Crundwell AC. (1964). The European species of the *Bryum erythrocarpum* complex. Transactions of the British Bryological Society 4: 597-637.

Dickson JH. (1973). Bryophytes of the Pleistocene. Cambridge University Press, Cambridge.Duckett JG, Renzaglia KS. (1993). Reproductive biology of *Blasia pusilla*. Journal of Bryology 17: 541-552.

During HJ. (1979). Life strategies of bryophytes: a preliminary review. Lindbergia 5: 2-18.

During HJ. (1986). Longevity of spores of *Funaria hygrometrica* in chalk grassland soil. Lindbergia 12: 132-134.

During HJ. (1992). Ecological classifications of bryophytes and lichens. In Bryophytes and lichens in a changing environment, 1-31. Eds JW Bates and AM Farmer. Clarendon Press, Oxford.

During HJ. (1995). Population regulation in tuber-bearing mosses: a simulation model. Lindbergia 20: 26-34.

During HJ. (1997). Bryophyte diaspore banks. Advances in Bryology 6: 103-134.

During HJ, Bruqués M, Cros RM, Lloret F. (1987). The diaspore banks of bryophytes and ferns in the soil in some contrasting habitat around Barcelona, Spain. Lindbergia 13: 137-149.

During HJ, Eysink ATW, Sérgio C. *Anthoceros caucasicus* Steph. found in the Netherlands. Lindbergia 21: 97-100.

During HJ, ter Horst B. (1983). The diaspore bank of bryophytes and ferns in chalk grassland. Lindbergia 9: 57-64.

Fitter R. (1985). The wildlife of the Thames Counties. Robert Dugdale, Oxford.

Furness SB, Hall RH. (1981). An explanation of the intermittent occurrence of *Physcomitrium sphaericum* (Hedw.)Brid. Journal of Bryology 11: 733-742.

Grime JP, Rincorn ER, Wickerson BE. (1990). Bryophytes and plant strategy theory. Botanical Journal of the Linnean Society. 104: 175-186.

Hill MO, Preston CD, Smith AJE. (1991). Atlas of the bryophytes of Britain and Ireland. Volume 1. Liverworts (Hepaticae and Anthocerotae). Harley Books, Colchester.

Hill MO, Preston CD, Smith AJE. (1992). Atlas of the bryophytes of Britain and Ireland. Volume 2. Mosses (except Diplolepidae). Harley Books, Colchester.

Hill MO, Preston CD, Smith AJE. (1994). Atlas of the bryophytes of Britain and Ireland. Volume 3. Mosses (Diplolepidae). Harley Books, Colchester.

Holyoak DT. (1999). Distribution, status and conservation of the moss *Weissia multicapsularis*. Final report to English Nature Species Recovery Programme. English Nature, Truro.

IUCN. (1994). IUCN Red List categories. Prepared by the IUCN Species Survival Commission. As approved by the 40th Meeting of the IUCN Council, Gland, Switzerland, The World Conservation Union.

Jones EW. (1991). The changing bryophyte flora of Oxfordshire. Journal of Bryology 16: 513-549.

Jonsson BG. (1993). The bryophyte diaspore bank and its role after small-scale disturbance in a boreal forest. Journal of Vegetation Science 4: 819-826.

Kay S, Gregory S. (1999). Rare arable flora survey 1999. Northmoor Trust, Abingdon.

Killick J, Perry R, Woodell S. (1998). The flora of Oxfordshire. Pisces Publications, Newbury.

Koelbloed KK, Kroeze JM. (1965). *Anthoceros* species as indicators of cultivation. Boor spade 14: 104-109.

McLetchie DN. (1992). Sex ratio from germination through maturity and its reproductive consequences in the liverwort Sphaerocarpos texanus. Oecologia 92: 273-278.

Miles CJ, Longton RE. (1992). Deposition of moss spores in relation to distance from parent gametophytes. Journal of Bryology 17: 355-368.

Paton JA. (1969). A bryophyte flora of Cornwall. Transactions of the British Bryological Society 5: 669-756.

Paton JA. (1999). The liverwort flora of the British Isles. Harley Books, Colchester.

Preston CD, Whitehouse HLK. (1986). The habitat of *Lythrum hyssopifolia* L. in Cambridgeshire, its only surviving English locality. Biological Conservation 35: 41-62.

Richards PWM. (1928). Ecological notes on the ecology of the bryophytes of Middlesex. Journal of Ecology 16: 269-300.

Rodwell JS. (2000). British Plant Communities Volume 5. Maritime communities and vegetation of open habitats. Cambridge University Press, Cambridge.

Schelpe EACLE. (1959). Ecology of bryophytes on arable land in the Oxford District. PhD Thesis, University of Oxford.

Schmidt C, Kohn J. (1993). Zum Vorkommen von *Micromitrium tenerum* (B.& S.) Crosby in Nordwest-deutschland. Drosera 1993: 1-5.

Side AG. (1977). Bryophytes in arable fields in Kent. Transactions of the British Bryological Society 6: 63-70.

Stoneburner A, Lane DM, Anderson LE. (1992). Spore dispersal distance in *Atrichum angustatum* (Polytrichaceae). The Bryologist 95: 324-328.

Whitehouse HLK. (1966). The occurrence of tubers in European mosses. Transactions of the British Bryological Society 5: 103-116.

Whitehouse HLK. (1969). *Dicranella staphylina*, a new European species. Transactions of the British Bryological Society 5: 757-765.

Whitehouse HLK. (1976). *Ditrichum pusillum* (Hedw.) Britt. in arable fields. Journal of Bryology 9: 7-11.

Whitehouse HLK. (1984). Survival of a moss, probably *Dicranella staphylina*, in soil stored for nearly 50 years. Journal of Bryology 13: 131-133.

Whitehouse HLK. (In press). Bryophytes of arable fields in Québec and Slovakia, including new records of *Bryum demaretianum* Arts. Lindbergia.

Wigginton MJ. (1995). Mosses and liverworts of North Lancashire. University of Lancashire.

Wilson PJ. (1992). Britain's arable weeds. British Wildlife 3: 149-161.

Wilson PJ. (1993). Wiltshire's arable weed flora. In The Wiltshire Flora. Ed B Gillam. Pisces Publications, Newbury.

Appendix A

Bryophytes associated with arable land

(from Fields of Vision Conference, Cambridge 2000, Ron Porley)

Species	Status	Asexual	Sporophytes	Sexuality	Frequency of occurrence in arable
Liverworts and hornworts	.	.	.	.	.
Anthoceros agrestis	.	.	common	mono	often in arable but uncommon
Anthoceros punctatus	.	.	common	mono	often in arable but very local
Blasia pusilla	.	gemmae (two types)	occasional	dioi	occassionally recorded from arable
Fossombronia caespitiformis	NS	.	frequent	mono	most records from arable but rare
Fossombronia pusilla	.	.	frequent	mono	occassionally recorded from arable
Fossombronia wondraczeckii	.	.	common	mono	occassionally recorded from arable
Lophocolea bidentata	.	.	common	auto	opportunistic and not typically an arable species
Lunularia cruciata	.	gemmae	very rare	dioi	opportunistic and not typically an arable species
Phaeoceros carolinianus	EN	.	common	mono	occurs in arable but very rare
Phaeoceros laevis	.	perennating tubers	frequent	dioi	occasionally found in arable but uncommon
Riccia cavernosa	NS	.	common	mono	typical of damp arable but uncommon
Riccia crystallina	Intro	.	common	mono	characteristic of bulb & potato fields on Scilly
Riccia glauca	.	.	common	mono	a characteristic arable

					species
Riccia sorocarpa	.	.	common	mono	a characteristic arable species
Riccia subbifurca	NS	.	common	mono	uncommon in arable
Sphaerocarpos michelii	NS	.	frequent	dioi	characteristic plant of arable but uncommon
Sphaerocarpos texanus	VU	.	frequent	dioi	characteristic plant of arable but rare
Mosses	.	.	.	.	.
Acaulon muticum	.	.	abundant	auto or dioi	scarce and only occassional in arable
Aphanorhegma patens	.	.	abundant	paro or syno	rare in arable
Atrichum undulatum	.	.	common	mono	opportunistic and not typically an arable species
Barbula convoluta	.	tubers, Pcul	occasional	dioi	frequent in arable on calcareous soils
Barbula unguiculata	.	Pcul	occasional	dioi	frequent in arable on calcareous soils
Brachythecium rutabulum	.	.	common	auto	opportunistic and occurrence variable
Brachythecium velutinum	.	.	common	auto	opportunistic and occurrence variable
Bryum argenteum	.	bulbils, Pcul	occasional	dioi	common in arable
Bryum bicolor	.	bulbils, Pwild, tubers	frequent	dioi	a characteristic arable species
Bryum gemmiferum	.	bulbils, tubers (cul)	occasional	dioi	scarce in arable
Bryum gemmilucens	.	bulbils, Pcul	unknown	dioi	typically found in arable but very rare
Bryum klinggraeffii	.	tubers, Pwild+cul	unknown	dioi	a characteristic arable species
Bryum riparium	.	tubers	unknown	?	in arable within flood zone of streams but rare

Bryum rubens	.	tubers, Pwild+cul	occasional	dioi	a characteristic arable species, often abundant
Bryum ruderale	.	tubers, Pwild+cul	unknown	dioi	not typically found in regularly disturbed arable
Bryum sauteri	.	tubers, Pcul	unknown	dioi	occasionally found in arable but uncommon
Bryum subapiculatum	.	tubers, Pcul	frequent	dioi	a characteristic arable species
Bryum violaceum	.	tubers	unknown	dioi	occasionally found in arable but uncommon
Ceratodon purpureus	.	Pwild+cul	frequent	dioi	common in arable
Chenia leptophylla	Intro	tubers	unknown	dioi	3 British records, 1 in arable
Dicranella schreberiana	.	tubers	occasional	dioi	a characteristic arable species
Dicranella staphylina	.	tubers, Pcul	unknown	dioi	a characteristic arable species
Dicranella rufescens	.	tubers	occasional	dioi	uncommon in arable
Dicranella varia	.	tubers	frequent	dioi	common in arable
Didymodon fallax	.	Pcul	occasional	dioi	uncommon in arable
Didymodon tomaculosus	NT/BAP	tubers	unknown	dioi	most records from arable but very rare
Didymodon vinealis	.	Pcul	rare	dioi	rare in arable, perhaps overlooked
Ditrichum cylindricum	.	tubers	very rare	dioi	a characteristic arable species
Ditrichum pusillum	NS	tubers, Pcul	unknown*	dioi	rare in arable
Entosthodon fasicularis	.	.	frequent	auto	a characteristic arable species but uncommon
Ephemerum recurvifolium	NS	.	frequent	pseudodioi	uncommon in arable
Ephemerum serratum var. minutissimum	.	.	frequent	pseudodioi	occurrence sporadic but typically in arable
Ephemerum stellatum	EN/BAP	.	frequent	pseudodioi	5 British records, 2 recently in arable

Eurhynchium hians	.	Pcul	rare	dioi	opportunistic and occurrence variable
Eurhynchium praelongum	.	.	frequent	dioi	opportunistic and occurrence variable
Fissidens bryoides	.	.	abundant	auto (rarely syno)	occasional in arable
Fissidens incurvus	.	.	abundant	dioi or auto	occasional in arable
Fissidens taxifolius	.	tubers	frequent	auto	occasional in arable
Fissidens viridulus	.	.	frequent	dioi, auto or syno	rare in arable
Funaria hygrometrica	.	Pwild+cul	frequent	auto	common in arable
Hennediella stanfordensis	NS	tubers	very rare	dioi	rare in arable
Leptobryum pyriforme	.	tubers	abundant	syno	occasional in arable
Microbryum curvicolle	.	.	abundant	auto	occasional in arable
Microbryum floerkeanum	NS	.	abundant	auto	often in arable but local
Microbryum davallianum	.	.	abundant	auto	occasional in arable
Microbryum starckeanum	.	.	abundant	auto	occasional in arable
Microbryum rectum	.	.	abundant	auto	occasional to frequent in arable
Physcomitrium pyriforme	.	.	abundant	auto	occasional in arable
Plagiomnium rostratum	.	.	frequent	syno	opportunistic and occurrence variable
Pleuridium acuminatum	.	.	abundant	paro	occasional in arable
Pleuridium subulatum	.	.	abundant	auto	occasional in arable
Pohlia camptotrachela	.	bulbils	unknown	dioi	rare in arable
Pohlia melanodon	.	tubers	occasional	dioi	uncommon in arable
Pohlia lescuriana	.	tubers	rare	dioi	uncommon in arable
Pohlia lutescens	.	tubers	unknown	dioi	uncommon in arable
Pterygoneurum ovatum	NS	.	frequent	auto	rare in arable

Pseudephemerum nitidum	.	.	abundant	syno	uncommon in arable
Pseudocrossidium hornschuchianum	.	Pcul	rare	dioi	rare in arable
Rhytidiadelphus squarrosus	.	.	rare	dioi	opportunistic and occurrence variable
Tortula acaulon	.	Pcul	abundant	auto	a characteristic arable species
Tortula acaulon var. papillosa	.	.	abundant	auto	a characteristic arable species but rare
Tortula acaulon var. schreberiana	.	.	abundant	auto	a characteristic arable species but rare
Tortula modica	.	.	abundant	auto	uncommon in arable
Tortula truncata	.	.	frequent	auto	a characteristic arable species
Weissia brachycarpa	.	.	abundant	auto	occasional in arable
Weissia longifolia var.angustifolia	.	.	abundant	auto	rare in arable
Weissia longifolia var. longifolia	.	.	abundant	auto	uncommon in arable
Weissia mittenii	EX	.	common	auto	5 British localities, not all in arable
Weissia multicapsularis	VU/BAP	.	abundant	auto	very rare, recent records on Cornish hedges within arable
Weissia rostellata	NT	.	abundant	auto	rare in arable
Weissia rutilans	.	.	abundant	auto	rare in arable
Weissia squarrosa	EN	.	abundant	auto	rare in arable