

Fen-meadow, rush pasture, mire and swamp communities:

A review of knowledge gaps,
restoration issues and their potential
to deliver Ecosystem Services

CTE1021

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Executive Summary

The aims of this review were to identify gaps in knowledge and areas requiring research on the abiotic and biotic conditions required for the restoration or re-creation of fens, 'purple moor-grass and rush pastures' (PMGRP) and swamp communities. Past and present land management practices on existing and restored habitats; restoration/re-creation methods including seed introduction, soil/hydrological management and vegetation management were reviewed. Information on the Ecosystem Services provided by these wetland communities was also reviewed.

The quantity, quality and distribution of wetland community types in the UK

Data on the extent and quality of existing wetland communities in the UK and across Europe needs to be collated. Within the UK, our database on wetland communities appears to be deficient for the upland fringe zone for which a comprehensive inventory is needed.

Abiotic constraints on wetland community restoration

Enhanced site fertility and soil drainage are the two key constraints to the restoration or creation of high nature value wetlands in the UK. Remediation techniques to reduce fertility, such as topsoil removal, although of proven value can produce disappointing results despite careful targeting based on soil chemical analysis. Further detailed studies of ecological and environmental constraints to targeted wetland restoration/creation via soil ameliorative strategies including topsoil removal, soil organic matter manipulation and rewetting are needed.

The extent to which acidification is a factor impeding the restoration/creation and maintenance of more basophilic PMGRP and other wetland communities in the UK is uncertain due to a paucity of systematic monitoring of soil and hydrochemistry of sites. High ammonium concentrations have been found to reduce germination and seedling survival of some characteristic PMGRP species. However, insufficient is known about the effects of elevated ammonium levels on the recruitment of PMGRP species in the UK.

The hydrological processes that underpin the existence of PMGRP in the UK are poorly understood. Lateral water movement in the root zone appears to be a typical characteristic of these vegetation types, but knowledge of the soil-water regime of different communities and their tolerance to hydrological variation is deficient. This information will provide a basis for successful restoration/creation of these communities.

Biotic drivers of unsustainable changes in wetland communities

There are severe gaps in knowledge on the scale of genetic erosion and the consequences for regeneration and resilience to environmental change in fragmented, isolated small populations of wetland species. There is a need for long-term manipulative experiments to examine interactions between habitat management, dispersal processes and population dynamics. There is an urgent need for evidence to support or otherwise, genetic reinforcement through the periodic introduction of seed of rare/declining species from a wide range of sites to prevent continued genetic erosion.

Gaps in knowledge on the autecology of several wetland species were identified, notably those that dominate swamp communities with the exceptions of *Phragmites australis* and *Typha* species. It is suggested that the research needs that exist for wetland species can be addressed to some extent through targeted effort in the *Biological Flora of the British Isles*. There is a paucity of information on mycorrhization of species in wetland communities. It is considered important that this knowledge gap be addressed, not least to identify the potential role of mycorrhiza in the restoration/creation of these communities.

There is a need for a comprehensive study/quantification of the risks posed by alien species to the different wetland community types in the UK.

Management and climate change effects on wetlands

Management information on fens, fen-meadows, mires were generally extensive and detailed, with the exception that for many swamp communities the information was anecdotal at best. However, the extent to which environmental changes such as atmospheric nutrient deposition, increased temperatures, shifts in rainfall and droughting patterns are likely to affect wetland community structure and interact with management practices, such as timing of mowing or grazing, is largely unknown. Research to examine long-term effects of manipulated changes in the above environmental drivers and their interaction with management practices is considered to be a priority.

A 50-year projection by the Wetland Vision project suggested that the viability of wetlands in the UK will be highly dependent on geographic location and water source with sites that are either rain-fed or groundwater-fed in SE England being particularly vulnerable to climate change. Wetland species with a more southern distribution are likely to disperse northwards providing that appropriate hydrological and edaphic conditions are available and that active conservation measures to aid dispersal, such as seed sowing and green “hay” /litter strewing are implemented. In order to ensure resilience to climate change close attention will need to be paid to understanding and maintaining good hydrological conditions in existing and restored/created wetland sites, which may mean removing pressures such as reducing or stopping water abstraction and blocking drainage ditches.

Ecosystem-service value knowledge gaps

It is suggested that restoration/creation of high ecological value wetlands should, where possible, be closely linked to future landscape scenarios in the UK to optimise their Ecosystem Service values. However, information on the regulatory services, such as water quality and storage, GHG emissions and carbon storage provided by many of the reviewed wetlands was found to be patchy. Gaps in information on methane emissions particularly where wetland communities are established on stagnogley and stagnogley humic soils, on the role played by the plants themselves in facilitating methane release and on carbon-storage potential of many wetland communities were identified as priority areas needing further research.

Introduction and the aims of Project CTE1021

The majority of fens, purple moor-grass and rush pastures (PMGRP) in lowland Europe have disappeared or been degraded particularly during the 20th Century by drainage and land use intensification (Bragg and Lindsay, 2003; Vasander *et al.*, 2003; Montanarella *et al.*, 2006). Designation as priority habitats within the UK Biodiversity Action Plan recognizes the parlous state of existence for these habitats in a geographic region that should be their stronghold. In addition to the loss of biodiversity and their cultural service, the degradation of fen and PMGRP systems also diminishes their regulatory and supporting ecosystem functions and services (Millennium Ecosystem Assessment 2005). Fens and PMGRP play a critically important role in regulating GHGs and water, for example drained peat soils can lose 700 g CO₂-C m⁻² per year, mostly as a direct contribution to the atmosphere (Kluge *et al.*, 2008). The maintenance of existing fen and PMGRP systems is therefore extremely important, but also important is to achieve successful restoration of degraded sites and re-creation of these habitats where possible and appropriate (English Nature *et al.*, 2006; Klimkowska *et al.*, 2007; Hume, 2007; Holliday, 2008).

Most ecological and floristic variation within north-west European mire vegetation is accounted for by three ecological gradients: the acid base-poor vs. neutral, base- and bicarbonate-rich gradient; the gradient in fertility related to availability of the limiting nutrient elements N and P; and the water level gradient (Wheeler and Proctor, 2000). An important characteristic of most lowland fen and PMGRP habitats is their complexity; many existing sites show continuous variation in floristic composition among the principal types of wetland vegetation (Van Diggelen *et al.*, 1996; Blackstock *et al.*, 1998). The complexity of existing fen and PMGRP systems therefore provides considerable challenges for their conservation and potential constraints on the scope of their restoration or re-creation within contemporary highly modified and multifunctional European landscapes (Van Diggelen *et al.*, 2006). Use of existing fen and PMGRP systems as 'reference' sites for restoration objectives may also mislead where the 'reference' site is itself in the process of degrading. It is therefore important to understand the criteria for quantifying the condition of these habitats.

Restoration goals may vary depending on whether the focus is on target species or system function, on the spatial and temporal scale from species to landscape, years to centuries and whether the overall objective is to restore the original system or simply improve the condition (Ehrenfeld, 2000; Hobbs and Harris, 2001). Restoration of fen and PMGRP systems will depend upon the ability to restore hydrological conditions, often at a landscape scale, for specific and functional wetland requirements (Wheeler *et al.*, 2004; Grootjans *et al.*, 2006). Achievement of the low fertility requirements of functioning wetlands can require quite drastic remediation practices particularly on former agricultural land (Tallowin and Smith, 2001; Klimkowska *et al.*, 2007; Klimkowska, 2008). Successful restoration of fen and PMGRP habitats also depends upon the provision of clear technical and targeting guidelines to land-owners, restoration practitioners and the policy community.

The aims of this review were to summarize information from the European literature and other primary and secondary data sources to identify the habitat conditions required for the existence, restoration or re-creation of fens, 'purple moor-grass and rush pastures' and swamp communities. Specifically the review examines the physio-chemical conditions, including topography, soils and hydrology under which existing fens, purple moor-grass and/or rush pasture and swamp habitats occur or may be restored. Past and present land management practices of existing and restored habitats; restoration/re-creation methods including details of initial targeting and subsequent management techniques (e.g. seed introduction, soil/hydrological management and vegetation management) have been examined. Knowledge, where available, of the Ecosystem Services provided by these wetland communities have been reviewed. Gaps in knowledge and areas requiring research have been identified.

Section 1.

Fen-meadows, rush pasture and associated mire communities

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Fen-meadows, rush pasture and associated mire communities

The following communities of the National Vegetation Classification (Rodwell, 1991) have been included in this section of the review: the *Juncus subnodulosus-Cirsium palustre* (M22) fen-meadow, *Juncus effusus/acutiflorus-Galium palustre* (M23) rush-pasture, *Molinia caerulea -Cirsium dissectum* (M24) fen-meadow, *Molinia caerulea-Potentilla erecta* (M25) mire, *Molinia caerulea -Crepis paludosa* (M26) mire, *Filipendula ulmaria-Angelica sylvestris* (M27) mire and the *Iris pseudacorus-Filipendula ulmaria* (M28) mire. The M22 – M26 communities comprise the purple moor-grass and rush pasture (PMGRP) BAP habitat, as defined by the UK Lowland Grassland HAP Steering Group (1998). The PMGRP have comparable Molinietales associations of the Molinion, Junco-Molinion, Calthion and Juncion acutiflori alliances in other parts of Europe (Rodwell *et al.*, 2007). The NVC account of the M22 fen-meadow in Rodwell (1991) was largely based on the work of Wheeler (1980) who was concerned primarily with the communities of lowland rich fens in England and Wales. The analyses and distribution maps of the M22 fen-meadow in Rodwell (1991), as a consequence, does not adequately cover more upland or northern examples of this community (Tratt *et al.*, 2011). For example, Tratt *et al.*, (2011) point out that M22 fen-meadow and M23a rush pasture may not be generally separated by the presence/dominance of either *Juncus subnodulosus* or *Juncus acutiflorus*, respectively, but by other floristic differences. Indeed in some examples of M22 fen-meadow *J. subnodulosus* may be absent. In a similar vein the NVC account of the M24 fen-meadow has limitations with respect to Welsh samples of the community. Supplementary details for the Welsh nodum of the M24 community are provided by Yeo *et al.* (1998) and Blackstock *et al.* (1998).

National databases of species' distributions can be used to produce lists of species which are typical of PMGRP habitats and used for targeting restoration of this habitat. NVC mire communities M22-M26 provide one source of typical species, but this is not precise because PMGRP habitats include vegetation types other than those of PMGRP communities. Project BD1318 produced a list of typical PMGRP species derived from survey data, which gave a potentially more accurate list. These lists can be used to map areas of Britain where the typical species co-occur and help target areas for restoration of PMGRP habitats.

Conservation status

The fen-meadows, rush pasture and associated mires, named above, are component communities of the the UK Biodiversity Action Plan (BAP) purple moor-grass and rush pasture (PMGRP) priority habitat (<http://www.ukbap.org.uk/UKPlans>; http://ukbars.defra.gov.uk/plans/national_plan - purple moor-grass and rush pastures).

The UK National Ecosystem Assessment (Bullock *et al.*, 2011) gives a figure of 79392 ha for the total PMGRP resource in the UK, which accords with the estimate of ca. 80000 ha by Rodwell *et al.* (2007) and 81903 ha provided by the JNCC (Joint Nature Conservation Committee, 2007) report on the conservation status of *Molinia* meadows in the UK. Rodwell *et al.* (2007) estimated that approximately 17000 ha of the remaining PMGRP resource were in designated (SSSI/ASSI) sites in the UK, of which 1100 ha were in Devon and Cornwall, 1802 ha in Wales, 317 ha in Scotland and 375 ha in N Ireland. Although not stated in the report by Rodwell *et al.* (2007) it is assumed that the remainder of the designated resource, 13406 ha, were in other parts of England. Inclusion of PMGRP habitats in agri-environment scheme agreements had resulted in significant enhancement of conservation condition compared with sites outside AE schemes (Hewins *et al.*, 2005). In Wales, for example, 19347 ha of PMGRP habitat were under maintenance agreements within the Tir Gofal agri-environment scheme (Bullock *et al.*, 2011). However, as Tratt *et al.* (2011) observed, different AE agreement objective priorities such as conservation of birds (curlew, lapwing, snipe) can result in sub-optimal management for the vegetation of upland fringe fen-meadows and mire communities. In the *Common Standards Monitoring of Designated Sites: First Six Year Report* (Williams, 2006), only 38.3 % of SSSI/ASSI designated lowland fens and marshes, which include PMGRP habitats, were

assessed as being in favourable condition. More recent statements by Defra/NE indicate that there has been a general improvement in condition of SSSIs, but details of the current status of designated PMGRP habitats are needed. In the random sample of English non-statutory sites, mostly M23 *Juncus-Galium* rush pasture and M25 *Molinia-Potentilla* mire, 35% of stands were found to be Favourable (Rodwell *et al.*, 2007). The latter review and that by Lawton *et al.* (2010) show clearly that a landscape-scale approach to the conservation of high nature value habitats such as PMGRP is urgently required, and this is indeed being initiated in some regions. The CCW's proposal for a South Wales Coalfield project, designed to include non-designated and unmanaged land, as well as SSSIs and holdings in agri-environment schemes encapsulated the need for a landscape-scale approach to the conservation of PMGRP habitats. The review by Rodwell *et al.* (2007) provided links to examples of landscape scale PMGRP conservation initiatives such as at Mynydd Mawr in Carmarthenshire (<http://www.carmarthenshire.gov.uk>) and on the Culm Grasslands in north Devon and north-east Cornwall (www.butterfly-conservation.org/ne.news/culm-grasslands.html). These landscape scale initiatives are designed to enable landowners to conserve PMGRP habitat by offering free support and advice on relevant farming and wildlife grants and fostering cooperative working among landowners aimed at encouraging extensive summer grazing by cattle.

Surveys particularly by Tratt *et al.* (2011) in NE Staffordshire and Shropshire and by O'Reilly in Upper Teesdale identified the importance of the upland fringe zone for fen-meadow and rush pasture conservation and restoration potential. Both of these surveys highlighted that there is no comprehensive inventory of wetland communities within this zone in the UK landscape. The new Upland Fens, Flushes and Swamps BAP priority habitat, (UK Biodiversity Action Plan; Priority Habitat Descriptions, see Biodiversity Reporting and Information Group (BRIG) (ed. Ant Maddock) 2008. <http://www.ukbap.org.uk/library/UKBAPPriorityHabitatDescriptionsfinalAllhabitats20081022.pdf>), identified that PMGRP communities are widespread but local in the uplands of Scotland, Wales, England and Northern Ireland. However, this report also states that the extent of the Upland Fens, Flushes and Swamps habitat is difficult to assess because it has not been comprehensively surveyed in many areas and tends to occur in small, sometimes numerous stands. This gap in knowledge of the extent of PMGRP communities in the uplands and upland fringe zone, therefore, needs to be remedied

Abiotic requirements for existence and restoration/creation

This section summarises the key abiotic requirements of the fen-meadows, rush pasture and associated mire communities and provides information, where available, on tolerance limits to variation in these variables and thus identifies edaphic and other environmental requirements for the restoration of this community.

Soil type

In the UK the fen-meadows, rush pasture and associated mires, the M22 – M28 NVC communities, are restricted to moist often seasonally waterlogged slowly permeable Stagnogley soils, Stagnohumic gley (humose) soils or Stagnohumic (peaty) soils, and Peat (Table 1); with Stagnohumic gley (humose) soils being the most common soil type found beneath these communities in lowland Wales (Blackstock *et al.*, 1998).

Soil chemistry

Limited information on the soil chemistry of the M22, M27 and M28 communities has meant that this review has been largely restricted to examining the soil chemistry of the M23 – M26 communities.

Differences in soil pH, exchangeable soil Ca amount, and overall base status provide some clear distinctions between the *Cirsio-Molinietum* fen-meadow (M24) and the rush pastures (M23) and mire (M25 and M26) communities, and between M24 sub communities (Table 2). Relatively small and subtle differences in base status appear to be important in influencing physiognomic differences in sub-community type (Rodwell, 1991). For example, distinction between the M23a and M23b and M25a and M25b sub communities was associated with a slightly lower soil pH, higher exchangeable acidity value and lower base saturation in the 'a' compared with the 'b' sub community types, respectively (Blackstock *et al.*, 1998) (Table 2). Difference in base status also separated the M24 sub-communities Blackstock *et al.* (1998). The M24 fen-meadows were found on soils with a pH range from 4.7 to 6.5 (Blackstock *et al.*, 1998; Tallowin & Smith, 2001; Critchley *et al.*, 2002; Smith *et al.*, unpublished data from BD1451) (Table 2). The M24c and Welsh Nodum of the M24 that have a more acidophilous character occupied the lower end of the pH range, from 4.7 to 5.2, in the 0 – 15 cm soil horizons. Examples of the typical sub-community, M24b, had pH values of 6.0 (Blackstock *et al.*, 1998). However, values as high as 6.5 have been recorded for M24 fen-meadows (Critchley *et al.*, 2002). The pH of soil below 15cm was, on average, 0.2 pH units higher than in the surface horizon of the soil in all of the communities that were examined by Blackstock *et al.* (1998) and Tallowin & Smith (2001) (Table 2).

Exchangeable soil calcium (Ca) was by far the largest soil base cation found in UK fen-meadow soils (Blackstock *et al.*, 1998; Tallowin & Smith, 2001; Critchley *et al.*, 2002; Smith *et al.*, unpublished data from BD1451) (Table 2). However, exchangeable soil Ca amount was also very variable even within the same community type. For example, exchangeable Ca amount at five separate M24c sites in Devon ranged from ca. 850 to 2700 mg kg⁻¹ dry soil in the top 7.5cm of soil (Smith *et al.*, unpublished data from BD1451). De Vere (2007) found the minimum value for exchangeable Ca amount at another M24c site in Devon of 248 mg kg⁻¹ dry soil within the top 15cm of soil. Blackstock *et al.* (1998) found exchangeable soil Ca amounts in what they termed the Welsh Nodum of the M24 community ranging from 1575 to 2697 mg kg⁻¹ of dry soil in the top 15cm of soil at 36 separate sites. In contrast, Blackstock *et al.* (1998) found values of 12675 mg kg⁻¹ in the top 15 cm of dry soil in an example of the M24b sub community. All of the above values relate to M24 communities under the most oceanic conditions of south-west and western UK. Exchangeable Ca amounts under *Juncus effusus/acuteiflorus-Galium palustre* (M23) rush pasture and *Holcus lanatus-Juncus effusus* (MG10) rush pasture tended to be similar to those of the M24 fen-meadow after correction for bulk density differences (Smith *et al.*, unpublished data from BD1451). Under agriculturally improved grassland such as the *Lolium perenne-Cynosurus cristatus* (MG6) and *Lolium perenne* (MG7a) (Rodwell, 1992) communities on stagnogley soils in south west England exchangeable Ca amount tended to be twice as high as under M24 communities, after correction for bulk density differences (Smith *et al.*, unpublished data from BD1451). However, an exchangeable soil Ca amount that was 2-3 times higher than under existing M24 fen-meadow did not impede restoration of a community with strong affinity to the fen-meadow (Tallowin & Smith, 2001). Enhanced Ca amount in the soil may be advantageous in the restoration process through soil phosphorus fixing by calcium hydroxides, as indicated by Tallowin & Smith (2001).

Measurement of the exchangeable acidity of soil and cation exchange capacity will provide guidance to the likely end point of a fen-meadow/mire restoration programme. Exchangeable soil acidity values in excess of 10 mmole kg⁻¹ dry soil are likely to result in the development of more acidophilous communities such as the M24c fen-meadow, M23 rush pasture or M25 mire communities (Table 2). Likewise where the cation exchange capacity is < 150 mmole kg⁻¹ dry soil, then again these more acidophilous communities are likely to develop. Certain fen-meadow species such as *Cirsium dissectum*, *Carex hostiana* and *C. pulicaris*, which are associated with more base-rich sites, may be difficult to establish in a restoration programme where exchangeable soil acidity is > 10 mmole kg⁻¹ dry soil and cation exchange capacity is < 150 mmole kg⁻¹ dry soil. In the case of *C.*

dissectum, the effect of acidity on the species appears to be due to its susceptibility to aluminium and ammonium toxicity (de Vere, 2007).

Acidification is a major factor impeding the restoration of more basophilic fen-meadow communities at some sites in the Netherlands (Grootjans *et al.*, 2002; Van der Hoek & Heijmans, 2007). The extent of this problem in the UK is, however, difficult to gauge, due to paucity of systematic monitoring of soil and hydro chemistry of fen-meadow restoration sites. In the Netherlands a 12 year study in which the organic rich eutrophicated surface horizon was removed at a degrading fen-meadow site indicated that gradual acidification was moving succession towards more acidophilous communities (Van der Hoek & Heijmans, 2007). The acidification was due to weakened upward flow of base-rich seepage/groundwater. Although the turf stripping treatment exposed a nutrient-poor soil layer with a greater acid-buffering capacity, Van der Hoek & Heijmans (2007) suggested that these positive effects might not be sufficient to combat the ongoing acidification in the long term. As Grootjans *et al.* (2002) contend, some of the processes consequent on acidification, such as loss of iron from the top-soil, makes the restoration of base-saturation very difficult to achieve, other than by drastic procedures such as top-soil removal to soil horizons that are not depleted in iron. The restoration/re-creation of more basiphilous fen-meadow, rush pasture and mire communities should, therefore, be targeted on to sites where the soil base status is within the range found in existing examples of these communities. Measurements of soil base status, at the very least pH, will provide edaphic criteria on which to assess the likely outcome of any restoration programme. If soil base status is sub or supra-optimal for target wetland species, then apart from direct toxicity effects of particular ions, negative competitive interactions between more competitive and more stress tolerant species may also affect establishment, as indicated by the studies of Rorison (1960).

Creation of acidic conditions to allow rush pasture restoration on wet grassland that have been semi-improved by agricultural practices including the addition of lime and NPK fertilizer were examined by Adams (2003) at Rhos Llawr-cwrt NNR. Aluminium sulphate was used by Adams (2003) because it could both increase the rate of soil acidification and decrease phosphorus availability by adsorption on precipitated $Al(OH)_3$. Soil acidification was indeed achieved, but this also occurred naturally due to base leaching from the soil surface. Restoration of a rush pasture with affinity to the target community that was present in the adjacent NNR was, however, disappointing in that the plant community that developed irrespective of the acidification treatment became rush (*Juncus effusus* and *J. acutiflorus*) dominated. The only significant effect on the vegetation of the restoration site by the acidification treatment was a change in abundance of two key bryophyte species. The addition of $Al_2(SO_4)_3$ also resulted in P adsorption, and increased concentration of inorganic P in the top 50mm of soil. However, as Adams (2003) concluded the effects on soil P of adding the amendment were complex and any long-term limitation of P availability for higher plant uptake was uncertain. This uncertainty over long-term effectiveness on P adsorption of using chemical soil amendments including ferrous and ferric oxides and calcium sulphate (gypsum) were also suggested by the findings of Tallowin *et al.* (1995).

Exchangeable soil potassium (K) values for fen-meadows, mires and rush pastures of high nature conservation interest were within the range found under agriculturally improved mesotrophic grassland on stagnogley soils (Tallowin *et al.*, 2004, final report on BD 1425) (Table 2). It is suggested, therefore, that soil K status is unlikely to be a critical factor that limits the restorability of these communities. However, where restoration practices such as top-soil removal or deep inversion of top-soil by ploughing severely reduce K availability, to < 0.5% in the herbage dry matter, then establishment of herb species characteristic of fen-meadows could be impeded (Pegtel, 1983; Grootjans *et al.*, 2002). Where such severe depletion of K availability has occurred then fertiliser addition of this nutrient would be appropriate to enable fen-meadow species to establish, providing that soil N and P availability remain limiting (Biewer, 1997).

Blackstock *et al.* (1998) provided evidence that other edaphic factors, which influence soil fertility, such as phosphorus (P) and nitrogen (N) availability could also be important in driving distinctive differences between fen-meadow, rush pasture and mire community types. What is universally clear is that the achievement of very low soil phosphorus availability is critical for the establishment and persistence of fen-meadows, mires and rush pastures of high nature-conservation value (Tallowin & Smith, 2001; Klimkowska *et al.*, 2007). Richness of rare and declining wetland plant species has been found to be generally higher in P (co)-limited sites than in N-limited sites in western Europe, indicating that increased P availabilities in wetlands may be particularly important in causing disappearance of threatened species (Venterink, *et al.*, 2003). Tables 3 and 4 summarize the soil P and N amounts found under the fen-meadows, rush pasture and associated mire communities. Expression of the total soil P and bicarbonate extractable (Olsen) P amounts in terms of mg/kg dry soil takes no account of variations in soil bulk density and thus amount of this macro-nutrient per unit volume of soil. Soil bulk density measurements were, however, only available for some of the studies that were examined (Table 5). When correction for bulk density differences was made the maximum and minimum for total soil P and Olsen extractable P for M24 fen-meadows were, 222 and 140 kg total P/ha and 8.0 and 0.8 kg extractable P/ha, respectively. For comparative purposes the maxima and minima for these variables under agriculturally improved grassland on the same soil type in SW England were 1026 and 438 kg total P/ha and 34.8 and 4.7 kg extractable P/ha, respectively. Assuming that the bulk densities were similar in the surface soil of the M23 to M26 communities, for which extractable soil P values were available, then all of these communities had similar amounts of extractable soil P. The studies by Chambers *et al.* (1998) and Critchley *et al.*, (2002) consistently found that extractable soil P at the high nature value fen-meadows and mires that they sampled was very low, index zero, by the agricultural standards required for productive grassland.

The use of top-soil removal as a first stage in the restoration of fen-meadow and other wetland communities has been demonstrated as a successful technique (Klimkowska *et al.*, 2007). Successful creation of a community with affinity to the relatively mesotrophic M24 fen-meadow was achieved only where the nutrient enriched topsoil was removed and in particular soil total and extractable P were reduced to within the ranges found under existing fen-meadows (Tallowin & Smith, 2001). Klimkowska *et al.* (2007) suggest that top-soil removal is likely to be more successful in reducing P and N availability on mineral soils compared with deep organic and peat soils. In the latter soil types eutrophication may enhance the N and P soil pool to a greater depth than in agriculturally improved mineral soils. Deep ploughing to bury the fertile top soil has been used as an alternative to topsoil removal in fen-meadow restoration (*pers comm*: P Burgess, Devon Wildlife Trust). Anecdotal evidence indicates that the effectiveness of deep ploughing in creating suitable edaphic conditions for fen-meadow restoration can be disappointing. Surface compaction of exposed clay and cal-loam soils by heavy rain following ploughing appeared to be a factor that severely reduced establishment of sown or green hay strewn species. Deep ploughing or topsoil removal should aim to create topographical variation at a site to impede water run-off and soil particulate loss. Contour ploughing to create shallow ridges at intervals down the slope of a site will allow localised shallow ponding of water on restoration sites, which may be of considerable biodiversity benefit by enhancing habitat diversity. A risk with deep ploughing is that over time buried soil nutrients, particularly soil P will be recycled back to the soil surface by deep rooted plants. Thus deep ploughing may not be a long-term solution to reducing the fertility of eutrophicated sites. However, further monitoring of sites where deep ploughing has been used is needed to quantify the risk of soil nutrient recycling back to the surface. As discussed earlier the use of chemical amendments to adsorb soil P do not appear to be long-term practical options for fen-meadow and rush pasture restoration/creation, as indicated by the studies of Adams (2003) and Tallowin *et al.* (1995). Site fertility impoverishment through

repeated cutting and removal of accumulated herbage can be a slow and uncertain restoration technique (Walker *et al.*, 2004).

High ammonium concentrations in the soil have been found to reduce germination and seedling survival of both *Cirsium dissectum* and *Succisa pratensis* (Dorland *et al.*, 2003). These authors found that increased ammonium concentrations were a problem where turf/sod removal was being used in wet heathland restoration sites. The amounts of KCl extractable NH_4 reached $570 \mu\text{mol kg}^{-1}$ dry soil ($10.3 \text{ mg NH}_4 \text{ kg}^{-1}$ dry soil) in the upper 10 cm of the turf-stripped plots, whereas in unstripped plots the NH_4 concentration did not exceed $150 \mu\text{mol kg}^{-1}$ dry soil ($2.71 \text{ mg NH}_4 \text{ kg}^{-1}$ dry soil). There was some evidence that turf stripping could have removed the nitrifying bacteria that exist in the topsoil layers. Recovery of the nitrifying bacterial population took several months. Whatever the mechanism behind the increase in NH_4 concentration with turf or topsoil removal the findings of Dorland *et al.*, (2003) have implications for fen-meadow restoration in the UK. At the very least NH_4 concentration in the soil should be monitored at fen-meadow restoration sites. Where values in excess of $150 \mu\text{mol kg}^{-1}$ dry soil are found, the re-introduction of target fen-meadow species should be delayed until the NH_4 concentration has declined and/or ameliorative procedures such as liming (Dorland *et al.*, 2004) are applied. It is noteworthy that soil $\text{NH}_3\text{-N}$ amount was above this lower threshold at the M23 sites and some M24 sites (Table 4) in the study by Smith *et al.* (2010). Catchment scale liming in the Netherlands created suitable conditions for the return of target plant species, and the positive effects lasted for at least 6 years (Dorland *et al.*, 2005).

Insufficient is known about the effects of elevated ammonium levels on the recruitment of fen-meadow and wetland species in the UK. Further research particularly in relation to using liming in the restoration of fen-meadow communities in the UK is merited.

Hydrology and Hydro-chemistry

Hydrology and hydro-chemistry are primary factors influencing the edaphic conditions of the M22 – M28 fen-meadows, rush pasture and mires (Rodwell, 1991). Successful restoration of these communities requires a comprehensive assessment of the hydrological functioning of these wetland systems (Middleton *et al.*, 2006). Research in the Netherlands highlighted that the maintenance of an upward capillary flow of base-rich groundwater to the root zone during the growing season was essential for the restoration/re-creation of *Cirsio-Molinietum* fen-meadows (Jansen *et al.*, 2000; Grootjans *et al.*, 2002). Stagnation of surface water and sulphate enrichment were identified as key factors impeding the restoration of fens at sites in Europe (Middleton *et al.*, 2006). However, the extent to which this is a problem in the UK is largely unknown.

Some data on the water-table regimes under these communities have been analysed (e.g Gowing *et al.*, 2002; Wheeler *et al.*, 2009) and some clear patterns are evident: e.g. the root zone is wet enough to impede gaseous oxygen diffusion throughout almost the entire year. Sum Exceedence Values (SEV) for waterlogging (*sensu* Silvertown *et al.*, 1999) have been calculated for stands of M22 and M24 and were found to be in excess of 7 metre.weeks, whilst the SEV for soil drying was less than one metre.week, suggesting these communities are rarely exposed to surface drying. No discernable pattern separates these two communities in terms of their water-table regime, in contrast to more mesotrophic associations which have all shown distinct hydrological niches (Gowing *et al.*, 2002.) This suggests that the ecological niches for these fen-meadow communities are described by dominant axes other than simple water-table depth; they probably relate to water movement (promoting delivery of dissolved oxygen and nutrients), water chemistry (Wheeler *et al.*, 2009; Grootjans *et al.*, 2002), and gradients in site fertility with for example M22 being associated with more fertile sites than M24 (see Table 3 in Wheeler and Shaw, 1992). M22 is found on sites fed by very base-rich water ($\text{pH}>6.5$) whilst M24 is usually fed by less basic water (Wheeler *et al.*,

2009.) More hydrological monitoring data has been collected for these communities by the Environment Agency, but much of it is yet to be analysed.

Table 1. Soil types associated with fen-meadows, rush pastures and selected mires.

NVC	Soil Types	Source
M22 <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow	Base rich Peat, Stagnogley, Pelostagnogley, Stagnohumic(gley, humose or peaty), calcareous pelosols	Rodwell (1991)
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	Stagnogley, Stagnohumic gley (humose), Stagnohumic (peaty),	Blackstock <i>et al.</i> , (1998)
M23b <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus effusus</i> sub-community	Stagnohumic gley (humose)	Blackstock <i>et al.</i> , (1998)
M24b <i>Molinia caerulea-Cirsium dissectum</i> , typical sub-community	Stagnohumic gley (humose), Stagnohumic (peaty) , Peat	Blackstock <i>et al.</i> , (1998)
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	Stagnohumic gley (humose), Stagnohumic (peaty), Peat	Blackstock <i>et al.</i> , (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum	Stagnogley, Stagnohumic gley (humose), Stagnohumic (peaty), peat	Blackstock <i>et al.</i> , (1998)
M25a <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Erica tetralix</i> sub-community	Stagnohumic gley (humose), Stagnohumic (peaty), peat	Blackstock <i>et al.</i> , (1998)
M25b <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Anthoxanthum odoratum</i> sub-community	Stagnogley, Stagnohumic gley (humose), Stagnohumic (peaty), peat	Blackstock <i>et al.</i> , (1998)
M25c <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	Stagnogley, Stagnohumic gley (humose), Stagnohumic (peaty), peat	Blackstock <i>et al.</i> , (1998)
M26 <i>Molinia caerulea-Crepis paludosa</i> mire	Base-rich and calcareous peats and peaty mineral soils	Rodwell (1991), Blackstock <i>et al.</i> , (1998)
M27 <i>Filipendula ulmaria- Angelica sylvestris</i> mire	Wide range of soil types including fen peats, stagnogleys, pelosols	Rodwell (1991)
M28 <i>Iris pseudacorus-Filipendula ulmaria</i> mire	Wide range of soil types including gravel, sand to gleys	Rodwell (1991)

Table 2. Values for soil pH, exchangeable amounts of soil potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na), exchangeable acidity, cation exchange capacity, and base saturation in fen-meadows, rush pasture and selected mire communities.

NVC	Sample depth	pH (H ₂ O)	Exch K	Exch Ca	Exch Mg	Exch Na	Exch acidity	Cation Exch Cap ^{ty}	Base satur ⁿ	Source
M22 <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow	0-7.5cm	6.5-7.5	See note ¹		See note ²					Chambers <i>et al.</i> , 1998a; Rodwell, 1991
M22b <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow, <i>Briza media-Trifolium</i> spp. sub-community	0-7.5cm	5.3-7.4	See note ³		See note ⁴					Chambers <i>et al.</i> , 1998c
M23 <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture	0-7.5cm		190							Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-7.5cm		350							Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-15cm 15-30cm	5.3 5.46		3992	352	40	21.2	134	81	Blackstock <i>et al.</i> , (1998)
M23b <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus effusus</i> sub-community	0-15cm 15-30cm	5.38 5.53		3808	218	31.3	10	116	88	Blackstock <i>et al.</i> , (1998)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-5cm	5.2	209	2828	1286	128				Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	5-15cm	5.3	153	1397	117	133				Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	15-30cm	5.5	88	1255	728	148				Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-7.5cm	6.5								Critchley <i>et al.</i> (2002)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow? (22 <i>Cirsium dissectum</i> sites throughout British Isles)	0-15cm	5.2	119	3185						de Vere (2007)
M24b <i>Molinia caerulea-Cirsium dissectum</i> , typical sub-community	0-15cm 15-30cm	6.03 6.64		12625	297	46	0.6	330	100	Blackstock <i>et al.</i> , (1998)

Table 2 continued:	depth	pH	Exch K	Exch Ca	Mg	Na	Ex acidity	CEC	Base satur ⁿ	Source
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-7.5cm	Min 4.7 Max 5.2	Min 152 Max 262	Min 871 Max 2682						Smith et al., BD1451 Appendix 5
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-7.5cm		190							Blackstock et al., (1998)
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-15cm 15-30cm	4.94 5.06		3707	338	43	34.6	143	65	Blackstock et al., (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum	0-15cm 15-30cm	5.16 5.37		2132	272	38	20	87	74	Blackstock et al., (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum (+ <i>C.dissectum</i> , + <i>Carex</i> spp) n= 11	0-15cm 15-30cm	5.08 5.29		2068		31	23.6		70	Blackstock et al., (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum (+ <i>C.dissectum</i> , - <i>Carex</i> spp) n = 12	0-15cm 15-30cm	4.97 5.14		1575		29	29.8		61	Blackstock et al., (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum (- <i>C.dissectum</i> , + <i>Carex</i> spp) n = 13	0-15cm 15-30cm	5.41 5.64		2697		53	9		88	Blackstock et al., (1998)
M25a <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Erica tetralix</i> sub-community	0-15cm 15-30cm	4.19 4.42		1210	253	46	55.5	99	47	Blackstock et al., (1998)
M25b <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Anthoxanthum odoratum</i> sub-community	0-15cm 15-30cm	4.65 4.94		1443	287	38	44.8	94	50	Blackstock et al., (1998)
M25c <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	0-15cm 15-30cm	4.89 4.92		2397	251	40	22.3	94	75	Blackstock et al., (1998)
M26 <i>Molinia caerulea-Crepis paludosa</i> mire	0-15cm 15-30cm	5.21 5.34		6653	443	56	5.1	192	97	Blackstock et al., (1998)
M26b <i>Molinia caerulea-Crepis paludosa</i> mire		6.8- 7.4								O'Reilly,
M27 <i>Filipendula ulmaria- Angelica sylvestris</i> mire		5 – 6								Rodwell, 1991
M28 <i>Iris pseudacorus-Filipendula ulmaria</i> mire										No information found

¹ Exchangeable K amount 81 & 130mg/l (Index 1), only 2 samples; ²exchangeable Mg amount 129 & 134 (Index 3), only 2 samples.

³ Exchangeable K amount 59 & 163mg/l (Index 1); ⁴exchangeable Mg amount 30 & 102 (Index 2)

Table 3. Values for total and extractable soil phosphorus (P) and herbage nitrogen (N) to phosphorus (P) ratio in fen-meadows, rush pasture and selected mire communities.

NVC Community	Sampling depth	Total P (total) mg kg ⁻¹	Olsen P mg kg ⁻¹	Herbage N:P ratio	Source
M22 <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow	0-7.5cm		See note ¹		Chambers <i>et al.</i> , 1998a
M22b <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow, <i>Briza media-Trifolium</i> spp. sub-community	0-7.5cm		See note ²		Chambers <i>et al.</i> , 1998c
M23 <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture	0-7.5cm	710	13	14.1	Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-7.5cm	1240	7.3	14.8	Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-15cm		31.5		Blackstock <i>et al.</i> , (1998)
M23b <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus effusus</i> sub-community	0-15cm		3.44		Blackstock <i>et al.</i> , (1998)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-5cm	511	8.8		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	5-15cm	368	3.6		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	15-30cm	264	2.6		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-7.5cm		5.8		Critchley <i>et al.</i> (2002)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-15cm		2.7		de Vere (2007)
M24b <i>Molinia caerulea-Cirsium dissectum</i> , typical sub-community	0-15cm		1.92		Blackstock <i>et al.</i> , (1998)
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-7.5cm	Min 496 Max 700	Min 2.5 Max 39.8	Min 15 Max 25	Smith <i>et al.</i> , BD1451 Appendix 5
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-15cm		3.51		Blackstock <i>et al.</i> , (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum	0-15cm		1.96		Blackstock <i>et al.</i> , (1998)

M25a <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Erica tetralix</i> sub-community	0-15cm	7.16	Blackstock <i>et al.</i> , (1998)
M25b <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Anthoxanthum odoratum</i> sub-community	0-15cm	3	Blackstock <i>et al.</i> , (1998)
M25c <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	0-15cm	3.46	Blackstock <i>et al.</i> , (1998)
M26 <i>Molina caerulea</i> - <i>Crepis paludosa</i> mire	0-15cm	6.6	Blackstock <i>et al.</i> , (1998)
M27 <i>Filipendula ulmaria</i> - <i>Angelica sylvestris</i> mire		No information found	
M28 <i>Iris pseudacorus</i> - <i>Filipendula ulmaria</i> mire		No information found	

¹Extractable P amount 7mg/l (Index 0); ²Extractable P amount 3 - 9mg/l (Index 0)

Table 4. Values for total soil nitrogen (N), dissolved inorganic N (DIN), ammonium N (NH₃-N), nitrate N (NO₃-N), inorganic N (inorg N = NH₃-N + NO₃-N), and N mineralization (N min) rate in fen-meadows, rush pasture and selected mire communities.

NVC	Sampling depth	Total N %	DIN	soil NH ₃ -N mg kg ⁻¹	Soil NO ₃ -N mg kg ⁻¹	Soil inorg N	N min mg kg ⁻¹ day ⁻¹	Source
M22 <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow	0-7.5cm	1.9 & 2.8						Chambers <i>et al.</i> , 1998a
M22b <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow, <i>Briza media-Trifolium</i> spp. sub-community	0-7.5cm	1.2-3.0						Chambers <i>et al.</i> , 1998b;1998c
M23 <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture	0-7.5cm	0.77	37.9	14.6				Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-7.5cm	0.55	41.8	11.8				Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-15cm					8.69	13.55	Blackstock <i>et al.</i> , (1998)
M23b <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus effusus</i> sub-community	0-15cm					9.35	0.36	Blackstock <i>et al.</i> , (1998)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-5cm	0.60		7.5	10.3	17.8		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	5-15cm	0.40		7.8	6.1	13.9		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	15-30cm	0.20		5	3.4	8.4		Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-7.5cm	1.93						Critchley <i>et al.</i> (2002)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-15cm	0.70						de Vere (2007)
M24b <i>Molinia caerulea-Cirsium dissectum</i> , typical sub-community	0-15cm					5.01	12.94	Blackstock <i>et al.</i> , (1998)
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-7.5cm	Min 0.66 Max 0.75	Min 13.5 Max 37.5	Min 1.7 Max 16.9	Min 4.9 Max 9.1			Smith <i>et al.</i> , BD1451 Appendix 5

M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-15cm	2.35	12.15	Blackstock <i>et al.</i> , (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum	0-15cm	4.07	11.87	Blackstock <i>et al.</i> , (1998)
M25a <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Erica tetralix</i> sub-community	0-15cm	2.68	9.66	Blackstock <i>et al.</i> , (1998)
M25b <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Anthoxanthum odoratum</i> sub-community	0-15cm	4.8	12.35	Blackstock <i>et al.</i> , (1998)
M25c <i>Molinia caerulea-Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	0-15cm	11.06	13.12	Blackstock <i>et al.</i> , (1998)
M26 <i>Molinia caerulea-Crepis paludosa</i> mire	0-15cm	20.32	10.98	Blackstock <i>et al.</i> , (1998)
M27 <i>Filipendula ulmaria- Angelica sylvestris</i> mire		No information found		
M28 <i>Iris pseudacorus-Filipendula ulmaria</i> mire		No information found		

Table 5. Values for soil carbon, soil carbon to nitrogen (C:N) ratio, soil organic matter and bulk density in fen-meadows, rush pasture and selected mire communities.

NVC Community	Sampling depth	Carbon %	C:N ratio	Organic Matter %	Bulk Density (g dry/ml)	Source
M22 <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow	0-7.5cm			33 & 55		Chambers <i>et al.</i> , 1998a
M22b <i>Juncus subnodulosus-Cirsium palustre</i> fen meadow, <i>Briza media-Trifolium</i> spp. sub-community	0-7.5cm			42-65		Chambers <i>et al.</i> , 1998c
M23 <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture	0-7.5cm	7.3	11.8		0.51	Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-7.5cm	11.9	10.3		0.51	Smith <i>et al.</i> , BD1451 Appendix 5
M23a <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus acutiflorus</i> sub-community	0-15cm			20		Blackstock <i>et al.</i> , (1998)
M23b <i>Juncus effusus/acutiflorus-Galium palustre</i> rush pasture, <i>Juncus effusus</i> sub-community	0-15cm			17		Blackstock <i>et al.</i> , (1998)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-5cm	7.5		19	0.41	Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	5-15cm	4.9		15	0.67	Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	15-30cm	2.1		8	0.93	Tallowin & Smith (2001)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-7.5cm		10	37		Critchley <i>et al.</i> (2002)
M24 <i>Molinia caerulea-Cirsium dissectum</i> fen meadow	0-15cm			31		de Vere (2007)
M24b <i>Molinia caerulea-Cirsium dissectum</i> , typical sub-community	0-15cm			32		Blackstock <i>et al.</i> , (1998)
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-7.5cm	Max 9.3 Min 7.3	Max 12.9 Min 11.8		Max 0.51 Min 0.37	Smith <i>et al.</i> , BD1451 Appendix 5
M24c <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, <i>Juncus acutiflorus-Erica tetralix</i> sub-community	0-15cm			39		Blackstock <i>et al.</i> , (1998)
M24x <i>Molinia caerulea-Cirsium dissectum</i> fen meadow, Welsh nodum	0-15cm			16		Blackstock <i>et al.</i> , (1998)

M25a <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Erica tetralix</i> sub-community	0-15cm	48	Blackstock <i>et al.</i> , (1998)
M25b <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Anthoxanthum odoratum</i> sub-community	0-15cm	27	Blackstock <i>et al.</i> , (1998)
M25c <i>Molinia caerulea</i> - <i>Potentilla erecta</i> mire, <i>Angelica sylvestris</i> sub-community	0-15cm	25	Blackstock <i>et al.</i> , (1998)
M26 <i>Molina caerulea</i> - <i>Crepis paludosa</i> mire	0-15cm	53	Blackstock <i>et al.</i> , (1998)
M27 <i>Filipendula ulmaria</i> - <i>Angelica sylvestris</i> mire			
M28 <i>Iris pseudacorus</i> - <i>Filipendula ulmaria</i> mire			

Biotic requirements for existence and restoration/creation

Regeneration requirement

A combination of low fertility soil conditions to maintain low competition by productive/highly competitive plant species, plus the introduction of seed/diaspores of target fen-meadow, rush pasture and mire community species, plus appropriate hydrological/hydrochemical conditions are all needed to optimise the chance of successful establishment of high nature conservation value wetland communities (Pfandenbauer & Grootjans, 1999; Verhagen *et al.*, 2001; Tallowin & Smith, 2001; Hölzel & Otte, 2003; Klimkowska *et al.*, 2007) For example, removal of competitive interactions with the established vegetation and removal of much of the seed bank of invasive/competitive species by turf or topsoil removal or smaller scale disturbance such as that created by cattle trampling are essential for seedling establishment and successful rhizomatous clonal spread of *Cirsium dissectum* (Jongejans *et al.*, 2008) and *Succisa pratensis* (Isselstein *et al.* 2002). The depth of topsoil removal that is designed to reduce soil fertility and severely deplete/eliminate the seed bank of invasive competitive species needs to take account of the position of the water table so that inappropriate hydrological conditions for the target wetland community are not inadvertently created (Hausman *et al.*, 2007). The depth of topsoil removal to reduce soil fertility should be based on prior soil sampling and soil chemistry analysis in order to identify the horizon where compatibility in soil fertility, particularly in extractable and/or total soil P, with the target wetland community exists (Tallowin & Smith, 2001). Lack of target fen-meadow, rush pasture and mire community species in the soil seed bank and poor dispersal opportunities at both local and landscape scales are major biotic factors limiting the restoration of fen-meadows today (Klimkowska *et al.*, 2007).

Mycorrhizal associations

Information on mycorrhizal associations with fen-meadow, rush pasture and mire plant species in the UK is scarce. The only specific relevant information was that obtained by Ross (1999) who found high colonization of young roots of *Cirsium dissectum* by arbuscular mycorrhiza. Studies by Fuchs and Haselwandter (2004) in Europe showed that the roots of *Serratula tinctoria* were regularly colonized by both arbuscular mycorrhiza and a dark septate endophyte. In light of the paucity of information on mycorrhization of PMGRP species, it is considered important that this knowledge gap is addressed, not least to identify the potential role of mycorrhiza for restoration of these communities.

Threats from fragmentation, isolation

Fragmentation and isolation of remaining habitats are ongoing threats to the UK's fen-meadow resource (<http://www.ukbap.org.uk/UKPlans>). Stevens *et al.* (2010) found that the average size of M24 sites in Wales was < 0.25 ha and, for the UK > 80 percent of purple moor-grass and rush pasture sites were <5 ha in extent (Bullock *et al.*, 2011). There is now clear ecological evidence of negative effects of habitat fragmentation, isolation and small site size on the characteristic species of fen-meadows, rush pastures and mire communities.

Vergeer *et al.*, (2003a; 2003b) found that plants from small populations of *Succisa pratensis*, a characteristic component of M24 communities (Rodwell, 1991) suffered more effects of eutrophication or acidification than plants from large populations. Population size effects on *S. pratensis* were closely related to measures associated with inbreeding, and it was postulated by Vergeer *et al.*, (2003a; 2003b) that the population size effect might be provoked by inbreeding. These results agree with the hypothesis that species are capable of responding to local selection pressures, provided there is enough genetic variation for these processes to take place (Ouborg & Van Treuren 1994; *ibid* 1995). This would indicate that low levels of genetic variation prevent small

Succisa populations from developing higher levels of tolerance. This 'selection hypothesis' relies on the assumptions that allozyme diversity reflects genetic variation at loci influencing plant performance and that there has been sufficient time for selection to increase the ecological amplitude of the large and genetically more variable populations. Vergeer et al. (2003b) were not able to test these assumptions; therefore, the actual mechanisms by which genetic erosion in small populations of *S. pratensis* affects plant performance under stressful conditions remains unclear. Vergeer et al. (2003b) also postulated that the expression of inbreeding depression in *S. pratensis*, arising from small population size, could increase with the amount of stress experienced by each individual. Whatever the reason, it seems that small, inbred populations of *S. pratensis* react differently to stress than large populations with lower levels of inbreeding.

de Vere et al. (2009) studied the interactions between population size, habitat quality, genetic diversity and fitness in 22 populations of *Cirsium dissectum* throughout the British Isles. These authors found that smaller populations of *C. dissectum* had lower genetic diversity which, in turn, had a negative impact on the survival of seedlings. This study and that of Jongejans et al. (2008) also showed the importance of creating habitat heterogeneity, a combination of taller vegetation, which allows flowering of *C. dissectum*, and patches of bare ground to provide regeneration niches for seedling recruitment. de Vere et al. (2009) also showed that in combination with the need to provide bare ground nutrient, particularly phosphorus (P), availability was important for seedling recruitment. These authors contended that higher levels of bare soil and phosphorus both had a positive relationship with genetic diversity, but probably for distinctly different reasons: bare soil provides safe sites for establishment, whilst phosphorus may promote flowering and improve seed germination. As discussed previously, M24 communities exist under very low soil P availability conditions. Nevertheless, de Vere et al. (2009) provide evidence that for the conservation of this species soil P availability should not be allowed to be severely depleted; we suggest that soil P should not be depleted much below the average found for existing *C. dissectum* sites; i.e. below ca. 3.0 mg /kg dry soil in the top 7 cm of soil. Where drastic restoration techniques such as top soil removal has been used, severe limitation of P could be a factor impeding establishment of some characteristic PMGRP species.

Habitat fragmentation and isolation has almost certainly compromised the probability of successful dispersal by both short and long distance dispersers in fen-meadows, as has been found generally for grassland forbs (Soons et al., 2005). Soons & Heil (2002) found that smaller populations of *C. dissectum* had lower colonization capacity due to the fact that they produced fewer seeds per capitulum, had lower percentage germination and a narrower range of seed dispersal distances. Soons and Heil (2002) also found that increasing site productivity changed colonization capacity. The capacity for colonization of nearby sites increased, due to higher seed production and seed germination ability, but the capacity for colonization of distant sites decreased, due to a lower long-distance dispersal ability. When habitat fragmentation results in a simultaneous decrease in population size and an increase in site productivity, both the local survival probability and the colonization capacity of remnant populations of wind-dispersed grassland forbs are likely to be severely reduced. The consequence of these processes is an increased regional extinction risk of these species.

The results of the studies on *S. pratensis* and *C. dissectum* are important in the context of conservation measures, especially when isolated, small populations with high levels of inbreeding are exposed to unfavourable habitat conditions. The identification of effects of reduced population size, genetic erosion and habitat deterioration on plant performance in a relatively common species, such as *Succisa pratensis* should be of considerable concern for PMGRP conservation management in the UK. The extent to which habitat fragmentation and isolation has caused genetic drift, genetic erosion and inbreeding in fen-meadow, rush pasture and mire species in the UK is largely unknown.

Therefore, any consequential reductions in the persistence of the surviving populations of wetland species through, for example, reduction in performance of established plants, even in the short term can only be speculated. Survival of small and declining populations suffering from unfavourable habitat conditions may, therefore, not be promoted by habitat restoration adjacent to existing sites, as the negative effects of genetic erosion will still continue unless genetic reinforcing from other distant sites occurs. Long-lasting, successful restoration of populations of fen-meadow, rush pasture and mire species will require a combination of habitat management to create/maintain conditions for flowering and seed production and regeneration niches for seed germination and seedling survival plus genetic reinforcement through the introduction of seed from a wide range of sites to prevent genetic erosion.

Landscape scale ecological studies aimed at providing space for fen-meadows, particularly to overcome the sustainability problems associated with isolation and small size of existing sites are needed.

Sustainable management practices

Agricultural improvement through drainage, cultivation and fertiliser application has been the major cause of loss of fen-meadows, rush pasture and mires in the past. This threat is now considered lower for the remaining habitats so long as agri-environmental payments provide financial incentives for their maintenance, although there are still isolated incidences of habitat damage and destruction. Groundwater abstraction may, however, pose a significant threat to the restoration potential of a site and to the long-term ecological integrity of fen-meadows and mires, particularly in the drier eastern regions of the UK. However, direct evidence of fen meadow degradation as a result of ground water abstraction may be obscured and/or confounded by other factors such as eutrication and/or management abandonment. An important monitoring tool for identifying unsustainable hydrological change is the response of indicator species sensitive to change in water-level flux (Wheeler and Shaw, 1992).

Under-management or abandonment of any management has been identified as the main cause of unfavourable condition of fen-meadows with extensive scrub encroachment and, in some sites, invasive species problems ([http://ukbars.defra.gov.uk/plans/national_plan - purple moor-grass and rush pastures](http://ukbars.defra.gov.uk/plans/national_plan_-_purple_moor-grass_and_rush_pastures)). Overgrazing and nutrient enrichment are, however, also still problems. Reluctance by livestock farmers to keep stock, particularly cattle, on fen-meadows is probably largely a consequence of current agricultural economics and policies exacerbated by concerns over animal health and disease risk. In addition the forage provided by fen-meadows appears to be widely perceived to have little nutritional value for productive livestock.

Anecdotal evidence suggests that there are a number of sites where conservation interest has been reduced (implicated in the loss of marsh fritillary at one site) due to a burning (no graze) regime (pers comm: P Burgess, Devon Wildlife Trust). This has not been due to frequency of burning *per se*, but by the homogeneity caused by using this one practice alone. However, where sites have heterogeneous structure caused by hydrology, soils etc burning alone can be an effective management tool.

In a survey of eleven fen-meadow sites in SW England and Wales all the sites were grazed by cattle in mid-summer but duration of grazing season and stocking density varied both within and between sites (Tallowin, Bullock, et al., 2000; Tallowin et al., 2002). However, caution has to be expressed in current perceptions of sustainable management practice, as the extent to which environmental changes such as atmospheric nutrient deposition, increased temperatures, shifts in rainfall and droughting patterns climate will interact with management practices to affect the composition of fen-meadows, rush pastures and mires. This is considered to be a key area requiring more research.

Predicted climate change threats

The extent to which climate change is affecting the composition of fen-meadow sites is largely an unknown quantity ([http://ukbars.defra.gov.uk/plans/national_plan - purple moor-grass and rush pastures](http://ukbars.defra.gov.uk/plans/national_plan_-_purple_moor-grass_and_rush_pastures)). However, as Rodwell (1991) points out the M24 community provides southern localities for a number of plant species which have a mainly northern distribution in the UK. Under climate change predictions there could be a northerly shift in the distribution of this community, provided that component species with a more southern distribution are able to disperse northwards. Active conservation measures, such as seed sowing and green “hay” strewing are likely to be needed to enable the more southerly floral elements of the community to move northwards. Current research by Mike Acreman and colleagues on behalf of the Wetland Vision project has sought to simulate future wetland hydrology using the latest UKCIP09 forecasts. The viability of wetlands over a 50-year projection is found to be highly dependent on geographic location and water source with sites that are either rain-fed or groundwater-fed in SE England being particularly vulnerable.

Threats from non native invaders

Himalayan Balsam (*Impatiens glandulifera*) is a significant and growing problem in some wetlands in south west England. Kismeldon Meadows SSSI (Torrige) in north Devon has a serious Himalayan Balsam problem throughout the site, which is associated with lack of management (pers comm: P Burgess, Devon Wildlife Trust). On managed sites the problem of invasion by Himalayan Balsam tends to be restricted to the river corridors and areas of wet flush. Many Culm sites exist in a neglected state so this species poses a significant threat.

Japanese Knotweed (*Fallopia japonica*) has established at Common Moor SSSI - East Putford (pers comm: P Burgess, Devon Wildlife Trust) and could, if uncontrolled, pose a threat to the integrity of the wetland community in at least part of this site.

Ecosystem Services

Evidence of water regulation value of fen-meadows

The presence of fen-meadows in catchments could be potentially important for moderating stream/river flow rates after high rainfall events, by absorbing substantial volumes of water particularly with humus-rich soils and fibrous peats, thus contributing significantly to aquifer/catchment re-charge after dry periods. These soils tend to be well structured with high infiltration rates (Gowing et al, 2002) and therefore can be very effective at absorbing and storing rainfall. The soil structure can be damaged by excessive drying (e.g. Spoor et al., 1999), by heavy machinery or by excessive poaching by heavy stock. The lateral flow of water that is thought to occur under fen meadows (e.g. de Mars and Garritsen., 1997) can act in much the same way as a water-treatment reedbed, filtering particulates, capturing nutrients and de-nitrifying nitrate under saturated/anaerobic soil conditions, thereby potentially improving outflowing water quality (e.g. Devito et al., 1989; Patrick and Reddy, 1976), but this service has not been directly tested under many of the communities under discussion here.

Evidence of carbon storage value

Data on soil carbon (C) amount and potential soil C storage by PMGRP communities were provided by project BD1451 (Smith *et al.*, 2010) and Tallowin & Smith (2001) (Table 5). From the data of Tallowin and Smith (2001) it is calculated that the M24 fen-meadow reference site contained about 77.1 t C per ha in the top 30 cm of soil, whereas a agriculturally semi-improved *Holcus lanatus*-*Juncus effusus* MG10 rush pasture (Rodwell, 1992) on the same soil type contained 57 t C per ha in the top 30 cm of soil. These soil carbon amounts were corrected for differences in bulk density between the two grassland types. The main difference between the fen-meadow and the

agriculturally semi-improved grassland was that the former had higher C amounts in the deeper soil levels than in the semi-improved soil: 32.8 t C per ha vs 20.1 t C per ha in the 5 – 15cm soil level and 29.3 t C per ha vs 19.5 t C per ha in the 15-30 cm soil level, respectively. The data from BD1451 provided similar values of total C amounts to Tallowin & Smith (2001), at 25.9 t C per ha in the top 7.5 cm of soil. Agriculturally improved, intensively managed grasslands sampled in BD1451 contained ca 48 t C per ha in the top 7.5 cm of soil. These data indicate that PMGRP communities may store more C at depth than agriculturally improved soils, but clearly more data to fully quantify the C storage value of PMGRP communities is required.

Biodiversity value,

The biodiversity value of PMGRP communities and M24 fen-meadows in particular has been extensively reviewed (HMSO, 1995; Moy et al., 2002; <http://www.ukbap.org.uk/UKPlans>). Fen-meadows are important habitats for a number of BAP priority species such as marsh fritillary butterfly (*Eurodryas aurinia*), narrow-bordered bee hawk-moth (*Hemaris tityus*), lesser butterfly orchid (*Platanthera bifolia*) and meadow thistle (*Cirsium dissectum*).

Provisioning service value

In a survey of eleven fen-meadow sites in SW England and Wales, the average weight of livestock carried and the output in terms of liveweight produced were up to 25% of the respective values achievable from grazed agriculturally improved (via the use of fertilizer and lime) permanent pastures (Tallowin, Bullock, *et al.*, 2000; Tallowin *et al.*, 2002). Average growth rate of cattle was 0.52 kg/day. Growth rates were particularly poor from mid summer onwards. The nutritional value of the forages and the contents of some minerals were sub-optimal for productive livestock (Tallowin, Bullock, *et al.*, 2000; Tallowin *et al.*, 2002).

GHG source/sink

Soil methane production is important in waterlogged systems, and so PMGRP habitats could be a source during periods of waterlogged ground conditions, which could be the case in many sites, particularly during the winter/early spring. Few data exist for these grasslands; most methane work has been done on peatlands. However, examination of patches of wet grassland within such peatlands has indicated high methane fluxes (Bullock *et al.*, 2011). More research is needed particularly where fen-meadows are established on stagnogley and stagnogley humic soils.

Nitrous oxide (NO_x) emissions are of greater concern in terms of GHG effect than methane. In general NO_x emissions are greater on clay-rich soils and positively correlated with nitrogen fertilisation rates. NO_x emissions from agriculturally unimproved grasslands are, however, considered to be generally low: only in the region of 1 – 10 percent of current day nitrogen deposition and equivalent to 1-2 kg.N.ha⁻¹.yr⁻¹ (Curtis *et al.*, 2006). Therefore, it is assumed that under the relatively infertile conditions of PMGRP habitats NO_x emissions will be very low. Nevertheless, research is needed to validate this assumption.

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Swamp communities

by

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Swamp communities review: Introduction

At the outset of the present review, the intention was to provide individual community accounts for each of the eleven communities of interest. However, as the review proceeded, it became apparent that for most of the communities, the published information was sparse. Consequently, following this preamble, the account is divided into two sections: the first dealing with reed-swamps (**S4**), for which there exists adequate material, and the second summarising information for the remaining ten *NVC* types. The foundation of the account is based on the description given in the *National Vegetation Classification (NVC; Rodwell 1995)*, using that work to provide the preliminary information on physiognomy and abiotic/biotic requirements of the community. Where possible the *NVC* information is supplemented from the review produced for the *Eco-hydrological Guidelines (Wheeler et al. 2004)*.

The communities described in this section are each overwhelmingly dominated by a single species and it was thus worthwhile to summarise the autecological information on these dominants in order to provide an insight into the ecology of the whole community. Information on comparative plant ecology was incorporated from Grime *et al.* (2007) and from the modified Ellenberg indicator values for the UK presented by Hill *et al.* (2004).

The reviews were then expanded as far as possible with information derived from the literature searches made in the course of the present project. Information from this literature review was especially important to provide an insight into issues such as ecosystem services and climate change impacts which were largely absent from the general works.

Although studies relevant to specific swamp communities and their dominant species exist for some factors such as hydrology and nutrients, other aspects of this review have to date largely been examined at the ecosystem level. For these factors, especially climate change and ecosystem services, it is necessary to examine studies with a wide focus. The literature for the different *NVC* communities and their dominant species varies greatly in quantity, with a wealth of material on *Phragmites* and to a lesser extent *Typha* spp, but most other types having meagre or almost no specific literature.

S4 *Phragmites australis* swamp and reed-beds

Summary of physiognomy

Reedbeds are readily characterised by the overwhelming dominance of *Phragmites australis*, although floristic variation (four sub-communities) and the polymorphic nature of reed itself (from 1-3m in height) results in **S4** having a highly variable appearance. The sub-communities vary in their species-richness and species composition depending on various environmental factors including water depth and nutrient availability, thus:

- **S4a** *Phragmites australis* sub-community: ca 3 species/sample and only Reed itself abundant
- **S4b** *Galium palustre* sub-community: more forb-rich with ca 8 species/sample and transitional to fen communities, *Galium palustre* in 61-80% of samples and *Mentha aquatica* with a constancy of III.
- **S4c** *Menyanthes trifoliata* sub-community: ca 6 species/sample and with three species having a constancy of IV (*Carex rostrata*, *Equisetum fluviatile* and *Menyanthes* itself), as well as *Comarum* and *Nymphaea* occurring in 41-60% of samples.
- **S4d** *Atriplex prostrata* sub-community: has considerable variation itself (3 variants described) and has a suite of halophytes present with ca 6 species/sample. Although *Atriplex prostrata* is the most widespread associate with reed, *Puccinellia maritima* and *Agrostis stolonifera* can be locally important, as well as less frequently *Aster tripolium*, *Juncus gerardii* and an algal mat.

Reed swamps have a canopy structure that is leafy *i.e.* with leaves of similar size fairly evenly spread up the stem (Grime *et al.* 2007). The canopy height is 1-3m (more in some warm temperate regions) and the lateral spread of 25-100cm.

Note: A detailed review of the biology of *Phragmites australis* has been undertaken by Engloner (2009) and includes much material that is relevant to an understanding of the abiotic and biotic requirements of the **S4** community. Where this information is included in the present review, it is cited as from Engloner (2009), who himself includes 190 references referring to growth and ecology of reed.

Abiotic requirements for existence and restoration/creation

In assessing the relative importance of water depth and nutrient status, Haslam (1970) judged that in the UK, reed growth was more limited by nutrient status in wetter habitats, and more by inter-specific competition at the drier reed-bed margins edge of reed-beds. In contrast, Clevering (1998) suggested that water depth could be a stronger selective force than availability of nutrients.

Soil type: **S4** reedbeds show few substrate preferences being recorded on substrata ranging from 1-97% organic content *i.e.* from almost purely mineral to deep peats, although in grazing marsh ditches, there is an apparent association with groundwater gleys (alluvial and humic-alluvial) – see Wheeler *et al.* 2004. Reed thrives in anaerobic soils provided that the rhizomes are aerated via dead aerial stems.

Soil chemistry: Reed occurs in sites with average to rich supplies of nitrogen (Ellenberg N value of 6), whilst the equivalent S indicator value is 2, indicating that *Phragmites* often grows in saline soils. Reed can occur in situations with low nutrient status (*e.g.* margins of dystrophic and oligotrophic tarns) but is typically short and sparse in such habitats. High soil fertility or high nitrogen availability lead to increased number, height, weight and diameter of reed shoots,

but also structural weakness through reduced production of sclerenchyma and aerenchyma (Engloner 2009), and this positive response of *Phragmites* growth to increased nutrients may be linked to the genetic origin of the plants. Excessive nutrient supply may be associated with reduced rhizome branching and lifespan of the rhizome, as well as shorter root length (Engloner 2009). Prolonged growth in eutrophic conditions weakens the structural tissue in the reed canes, leaving them liable to breakage (due to waves, wind or grazing) and eventual decay/death if the broken tips are immersed, thus preventing aeration of the rhizome. Oliveira *et al.* (1999) found that salinity, negative redox potential on the root system and high Cu, Na and Zn concentrations in soil did not affect the normal development of reed vegetation and its capability to recover after mechanical damage.

Hydro-chemistry: Reed is amphibious (Ellenberg F value of 10) occurring in standing water and in sites that are summer dry. The depth to which Reed can grow is limited primarily by nutrient unavailability *i.e.* for Reed to produce an effective photosynthesising canopy, then >35% of each stem must be emergent. The maximum water depth attained increases not only with nutrient availability but also with temperature. *Phragmites* has been recorded on sites with pH values from 4.5 upward, although preferred water pH values may be 6.1-7.0 (supported by Grime *et al.* (2007), Ellenberg and CEH studies of drainage channels). Reedbeds can be found from oligotrophic to eutrophic (even hypertrophic) situations, and both nitrogen and phosphorus are limiting for growth. The *Menyanthes trifoliata* sub-community (**S4c**) is characteristic of more mesotrophic conditions.

Reed tolerates salinities from 2-12(-22) gm Cl⁻/l, but salt may limit bud development in spring, meaning that reedbeds in brackish or tidal sites may be stunted or recede with saline incursions. Eid *et al.* (2010) and the literature reviewed by Engloner (2009) verify that height, diameter and shoot dry weight of *Phragmites* decreases with increasing salinity, whilst shoot density increases under mesohaline conditions.

Hydrology: (See Wheeler *et al.* 2004 for detailed summary of water regime variables). **S4** reedbed is widespread in open-water transitions around lakes and ponds, as well as in floodplain and basin mires, peat-cuttings, estuaries and along watercourses (*e.g.* drainage channels and along sluggish rivers). The water-supply mechanism is very variable, including riverine (or tidal) flooding, continual spring-fed supply and a range of artificial management regimes designed to conserve reedbeds or encourage commercial reed growth. **S4** occurs in permanently wet or waterlogged sites, where healthy growth depends on regularity of water-regime (*i.e.* always deep, always shallow, or regular seasonal fluctuations). Reedbeds are also often found beside water in topogenous mires, and in sites liable to winter flooding but which can be summer dry. Reed will grow in water-tables from 2m above substrate to >1m below, though there is variation between the sub-communities and the habitat:

- In open water transitions, the usual water depth for the **S4a** (typical sub-community) ranges from +0.5m above to -0.13m below (mean value +0.13m) the substrate, whilst **S4b** (*Galium palustre* sub-community) occurs from about +0.02m above to -0.40m below (mean value -0.1m) the substrate.
- In drainage channels, Reed stands (**S4a**) usually occur in 0.2-0.8m of water, though in some variants as much as 30% of samples may be summer-dry.
- In tidal situations, Reed has been recorded in the Netherlands growing from -1.5m below to +0.25m above mean high water (with greatest vigour between -1.0m and 0m). The **S4d** sub-community may also depend on surface seepage of fresh water from inland.
- In summer-dry situations, with the water-table well below the surface, **S4** should be in direct contact with open water situations via its rhizome.

Water usage by reedbeds may be calculated using crop coefficients for reed (Fermor *et al.* 2001) or detailed duty of evapotranspiration and surface energy fluxes (Kelvin in press). There have been numerous morphological analyses of reed stands growing in different water depths but they often appear to give contradictory results, although the growth of reed may be enhanced by moderately fluctuating water levels (Engloner 2009).

Biotic requirements for existence and restoration/creation

Ecology: The established strategy of *Phragmites* is clearly that of a competitor, and is generally found in well-lit sites, though occasionally in partial shade as in the understorey of fen carr. *Phragmites* appears to have a broadly stable distribution, though losses have been noted locally (e.g. die-back of reed-beds in Broadland since 1950). In contrast reed has also increased in some areas due to eutrophication, and where reed-beds have been created for breeding birds (Preston *et al.* 2002).

Mycorrhizal associations: *Phragmites* forms a vesicular-arbuscular mycorrhiza (Grime *et al.* 2007).

Regeneration requirement: *Phragmites* combines lateral vegetative spread (being a rhizomatous and stoloniferous herb) with widely-spread seeds that are dispersed by the wind. There is no persistent seed-bank as such, with all seeds shed during a growing season either germinating synchronously in that autumn or being lost. There are published examples of reed stands expanding by seed, but vegetative colonisation is overwhelmingly the main method of spread and both self-incompatibility (at least partial) and pollen limitation caused by the clonal behaviour of reed lead to reduced seed production and viability (Engloner 2009). The infrequent contribution from seed may result from the rarity of a suitable regeneration window. However when low water levels occur in the spring, colonisation by seed may occur, playing a key role in the pioneer stage of reedbeds (Alvarez *et al.* 2005). The rate of seed-set in reed ranges from 0.1-59.6% (mean 9.7%) and *P. australis* is at least partially self-incompatible, such that the addition of external pollen will increase the rate of seed set (Ishi and Kadono 2002). Seed weight is not related to climate, but depends on seed production and overall plant height, whilst high seed-set occurs in the UK when: (i) August rainfall is low; (ii) the combined rainfalls of September and October are high; and (iii) the combined temperatures of these months are high (McKee and Richards 1996). However other factors probably play a part in determining reed seed set.

Seed production is positively correlated with rainfall in September and October and with temperature, with germination normally following within 2-5 days but only where the water depth is <5cm and the oxygen concentration >2.5%. Early germination leads to higher rhizome biomass which in turn affects the water depth tolerance of juvenile reed plants. Salinity also affects reed germination, though there is some disagreement as to the maximum salt content that can be tolerated, with a reported 16% decrease in germination at 50mM NaCl concentration and complete inhibition at 500 mM. Salinity tolerance of reed also depends on temperature, with greater inhibition at high temperatures (Engloner 2009).

Experimental work in Japan suggests that reed germinates at a somewhat lower temperature than *Typha angustifolia*, though following moist chilling of the seeds, this pattern disappears (Nishihiro *et al.* 2004). More relevantly to the UK situation, Dutch research has shown that partial summer drawdown creates suitable conditions for germination and growth of *Phragmites australis* (Coops *et al.* 2004).

Within salt-marshes, invasion by *Phragmites* has been shown to have a number of stages (Bart and Hartman 2002) with the emergence of reed culms constrained by poor drainage and their survival constrained by salinity. In later stages of invasion, *Phragmites* is able to spread vegetatively into both anoxic and highly saline areas.

Threats from fragmentation and isolation: Fer and Hroudova (2009) investigated the genetic diversity and dispersal of reed in three small adjacent catchments, using microsatellite and spatial autocorrelation analyses. The results indicated both dispersal by water (or wind) along river corridors and via wind over longer distances between catchments. There was evidence for pollen and seed dispersal at distances of up to 1 km, but seed dispersal alone at distances up to 10 km, with a significant contribution from long-distance vegetative dispersal.

Management practices: The response of *Phragmites* growth and productivity to burning and harvesting treatments has been tested through many experiments as recounted by Engloner (2009), indicating that harvesting increases culm density and the amount of dead rhizomes, but decreases the relative growth rate, shoot length and diameter. If burned, reed density increases whenever during the year the burn occurs, and in summer alone, above-ground biomass declines. June cutting usually leads to reduced above-ground biomass and growth in the following year (although this may not occur on sandy soils), but no impact has been observed after a July/August harvest. Should the cutting occur below the water surface, re-growth of the culms is almost entirely inhibited. Winter cutting may possibly lead to increased subsequent biomass, probably through increased light intensity at the ground surface in spring. Winter harvesting may lead to *Phragmites* stems being denser but thinner, and reducing the damaging effects of parasites on growth.

Reed is very productive, with an annual biomass accumulation of 1(-2) kg m⁻² and annual above ground biomass as high as 5 kg DWm² in the Nile delta with the range in the temperate zone being 0.6–3.5 kg DW m² (Eid *et al* 2010). Increasingly, commercial output and biodiversity are both considerations in determining the form of management undertaken. Winter cutting combined with spring flooding of the Reed allows a commercial crop to be taken with minimal adverse effects on both biodiversity interest (except as a roost for migrant birds) and the growth of the Reed itself. Reed cutting not only reduces litter accumulation, but also stimulates production of new buds and slows down the spread of reedswamp into open water (should it be desired to maintain such a feature).

Growth of Reed can be suppressed directly by grazing or browsing, or indirectly through trampling, which may damage surface rhizomes. The occurrence of different **S4** sub-communities in drainage channels is related to management, with pure Reed stands (**S4a**) occurring primarily in ditches that are not subject to cleaning, or which are cleaned very infrequently (*e.g.* at intervals of 5 years and more). Forb-rich reedbeds (**S4b**) occur in drainage channels subject to annual or even more frequent management (*e.g.* cleaning, cutting), occurring in some IDB or EA drains. Reed can restore to full cover within three years of ditch cleaning (Boszke *et al.* 2005).

Management may be required to control the succession **S4** to other communities, and these transitions are heavily influenced by nutrient levels, management and chance factors. Amongst the factors that may lead to reedbed loss, Wheeler *et al* (2004) listed:

- Succession through to fen and carr woodland
- Erratic water-regime leading to accelerated succession, decay of litter and consequent release of nutrients - resulting in a eutrophic fen
- Eutrophication affecting the structural, photosynthetic and/or aeration tissues of the plant, resulting in weakened stems and regression of the reedbed (Kühl and Kohl 1992)
- Breakage or submergence of dead stems leading to aeration stress and reduction of Reed bud inception
- Grazing leading to regression of the community edge from landward and/or open water (e.g. by geese) margins. Shallow rhizomes are sensitive to trampling/poaching of livestock
- Unfavourable cutting season e.g. when green
- Intolerant of marked wave or current action (in tidal rivers reedbed is often protected by a fringe of bulrush (*Scirpus*) or reedmace (*Typha*)).

Predicted climate change threats: Although some research suggests that reed growth is controlled by “internal” factors rather than climate, but most studies emphasise that higher mean temperatures lead to higher and earlier increases of biomass and that the height of flowering stems is correlated positively with temperature (Englone 2009). Certainly reed stands at lower latitudes in Eurasia (e.g. Danube Delta or southern Anatolia) are markedly taller than those of northern Britain, though at least some of this variation may be due to ploidy levels (Pauă-Comănescu *et al.* 1999).

Populations of *Phragmites* show clinal variation in Europe (from northern Sweden to Spain) in a) the length of the growing season; b) flowering time; and c) morphology and biomass allocation (Clevering *et al.* 2001). Assessing how these reed clones might adjust to climate change, Clevering *et al.* (2001) predicted three stages: a) at first the local clones would survive through plastic responses; b) as climatic changes accelerated, such responses would be insufficient and reed populations would suffer and eventually die; and c) this die-back might provide suitable sites for the sexual recruitment of clones better adapted to the changed climate.

Where climate change leads to a shortened growing season, *Phragmites* may recede through reduced competitive ability caused by frosting. Higher summer temperatures and a longer growing season may lead to increased reed productivity and markedly higher evapotranspiration (Banaszuk and Kamocki 2008) with increased seed-set at higher latitudes and consequent greater potential to colonise new sites (McKee and Richards 1996). This process may in turn result in a reduced groundwater table and the decline of large sedge communities such as **S6** and **S7** which might thus require grazing and mowing regimes in order to achieve their effective conservation.

A modelling study on the Weser estuary of Germany (Osterkamp *et al.* 2001) predicted from a baseline of only 2% of the area under reed-dominated habitats in 2000 that sea level rise and altered hydrology would lead to *ca* 28% of reed habitat (divided roughly equally between scarcely and frequently flooded types) by 2050, although this was affected by the disposition of flood defences.

Threats from non native invaders: Although there are instances in the UK of neophytes invading reed-beds (e.g. *Aster x salignus* and *Crassula helmsii*), most of the apparently relevant literature refers to the invasive behaviour of Eurasian strains of reed in North America,

notably in salt-marshes, reducing both botanical species-richness and animal communities, especially birds.

Ecosystem Services

Evidence of water regulation and purification value: Lavrova and Koumanova (2008). Marshes may be sources as well as sinks for metal contaminants, and despite being an invasive species in the north-eastern USA, *Phragmites* sequesters more metals below-ground than the native *Spartina alterniflora* (which also releases more via leaf excretion) – information which could be potentially be used for either locating artificial wetlands for pollutant treatment or restoration schemes (Weis and Weis 2004). Reed is sometimes employed as the helophyte component of sludge treatment wetlands (Uggetti *et al.* 2010) and can remove $\geq 95\%$ of aluminium, barium and manganese (Marchand *et al.* 2010). Reed provides sites for arbuscular mycorrhizae, also aiding pollutant treatment and promotes sedimentation of suspended solids, by reducing flow (Marchand *et al.* 2010). A review by Mayes *et al.* (2009) recorded *Phragmites* growing in polluted sites that were either highly acid (coal and metallic mine waste) or alkaline (steel/lime leachate, Solvay (NaCO_3) waste and fly ash).

Reed and other macrophytes now have a long history in the effective treatment of eutrophic water and removal of nitrates from wetlands (Weisner *et al.* 1994). Reed is effective at denitrification in degraded fen soils (Rückauf *et al.* 2004) reducing nitrogenous runoff and correspondingly increasing N_2O emission and N_2 emission to the atmosphere via the *Phragmites* shoots from the soil. Reed can also be used to remove complex organic pollutants from the soil (Nepovim *et al.* 2005).

Evidence of carbon storage value: Following a review of research results and models, Brix *et al.* (2001) reported that reed wetlands could function as a source for greenhouse gases (and thus increase radiative forcing) if evaluated on the scale of decades, but if evaluated over centuries, *Phragmites* wetlands will act as a sink for greenhouse gases, attenuating radiative forcing. *Phragmites* wetlands could also be an essential sink for biogenic silica in the biogeochemical cycling of silicon (Struyf *et al.* 2005). In a comparative study of how wetland plants affected methane emissions, Koelbener *et al.* (2010) found that *Phragmites* had no effect distinct from peat cores without vegetation.

Biodiversity value: Large Reedbeds (S4) habitats support some of the most threatened birds and invertebrates in UK wetlands, although in North America establishment of reed has been shown to reduce plant diversity and litter accumulation in brackish systems can prevent tidal flushing out of NH_4^+ from the sediment (Meyerson *et al.* 2000). Indeed there is considerable disquiet about the invasion of salt-marshes along the Atlantic coast of North America (Silliman and Bertness 2004), and although *Phragmites* is native to that continent, this invasive behaviour has been attributed to the introduction of a non-native strains from Eurasia.

Provisioning service value: Reed provides a significant service through use in thatching, in building and furniture and for musical instruments, as well as increasingly as a source of bio-energy.

Other types of swamp

This section of the review deals with the following ten community types described in the *National Vegetation Classification (NVC: Rodwell 1995)*

- **S3** *Carex paniculata* swamp
- **S6** *Carex riparia* swamp
- **S7** *Carex acutiformis* swamp
- **S8** *Scirpus lacustris* ssp. *lacustris*¹ swamp
- **S10** *Equisetum fluviatile* swamp
- **S12** *Typha latifolia* swamp
- **S13** *Typha angustifolia* swamp
- **S14** *Sparganium erectum* swamp
- **S18** *Carex otrubae* swamp
- **S19** *Eleocharis palustris* swamp

Summary of the physiognomy of the swamp types and their sub-communities

The information presented here is derived from the *NVC* (Rodwell 1995) account, including the mean numbers of species per sample given in the floristic tables. All these swamp communities are species-poor, although some have slightly more diverse variants.

S3 *Carex paniculata* swamp has 8 species/sample and is dominated by large tussocks of *Carex paniculata*, where no other species have high constancy, though other swamp dominants or tall-herbs may occur at low cover. Tussocks usually emerge from standing water or wet peat/silt and may support some epiphytic growth.

S6 *Carex riparia* swamp has 5 species/sample and is dominated by tall *Carex riparia*, with no other species having high constancy, though other swamp dominants or tall-herbs may occur at low cover, often patchily.

S7 *Carex acutiformis* swamp is richer and more diverse than other sedge swamps (**S3** and **S6**), with a mean of 11 species/sample and *Juncus effusus* having a constancy of **III** (41-60% of samples). The *NVC* account is based upon a mere 5 samples, and the community is probably under-sampled with poor recognition of its variation e.g. survey data from *Natural England* and CEH suggest that rushy species-rich variants may be transitional to **M22** *Juncus subnodulosus-Cirsium palustre* meadow. *Carex acutiformis* is characterised by Grime *et al.* (2007) as an erect perennial helophyte, with a canopy >1m high and with the largest leaves near the base giving a lateral spread of about 1m per stem.

S8 *Scirpus lacustris* ssp. *lacustris* swamp is rather open, with only the bulrush itself having consistently high constancy. There are three sub-communities, two of which are typified by the high constancy of bur-reed (**S8b**) or *Equisetum fluviatile* (**S8c**) and with other species, notably *Carex rostrata* but also *Menyanthes* and *Potamogeton natans*, often accompanying the bulrush in **S8c**. The typical sub-community (**S8a**) is markedly species-poor (2 species/sample) but **S8b** and **S8c** are somewhat more diverse, resulting in a mean for the entire *NVC* type of 5 species/sample. Grime *et al.* (2007) characterise *Schoenoplectus l.*

¹ The nominate species of this community is now known as *Schoenoplectus l. lacustris*

lacustris as a perennial emergent aquatic forming swamps that are 1-3m tall and where each stem has a lateral spread of 25-100cm from its basal leaves.

S10 *Equisetum fluviatile* swamp has 6 species/sample and may be open or fairly closed, growing up to 50-100 cm high. *Equisetum fluviatile* is the only constant species and is usually the most abundant species too. There are two variants of this NVC type: **S10a** (*Equisetum fluviatile* sub-community) is more species-poor with little other than the horsetail itself but **S10b** (*Carex rostrata* sub-community) has constant *C. rostrata* and several other species with constancies of III or IV (*Menyanthes*, *Potentilla palustris* and *Galium palustre*). *Equisetum fluviatile* is a perennial aquatic species, with marked lateral spread (Grime *et al.* 2007).

S12 *Typha latifolia* swamp is dominated by the perennial aquatic *Typha latifolia* in an open or closed stand of stout shoots. *Typha latifolia* is leafy with lower leaves somewhat larger, a canopy at 1-3m high and lateral spread of >1m (Grime *et al.* 2007). No other species is frequent (only 4 species/sample overall) and no species has constancy of more than II (*i.e.* >40% of samples). Four sub-communities are described with *Mentha aquatica* (and *Galium palustre* and *Juncus effusus*) important in **S12b** (*Mentha aquatica* sub-community), *Alisma plantago-aquatica* (and *Sparganium erectum*) in **S12c** (*Alisma plantago-aquatica* sub-community) and *Carex rostrata* in **S12d** (*Carex rostrata* sub-community). Of these sub-communities, **S12b** is the most species-rich (*ca* 9 species/sample) – the typical sub-community (**S12a**) having only 3 species/sample.

S13 *Typha angustifolia* swamp broadly resembles **S12** but with *Typha angustifolia* as the overwhelming dominant. **S13** has no sub-communities and typically has only 4 species/sample with no species other than *T. angustifolia* having a constancy of >I. The swamp is made up of dense reed-mace stems to 2m tall.

S14 *Sparganium erectum* swamp is tall and generally dominated by the perennial aquatic *Sparganium erectum*, in open or closed stands. *S. erectum* itself is leafy with lower leaves somewhat larger, a canopy *ca* 1m high and lateral spread of 25-100cm (Grime *et al.* 2007). Although the overall species-richness of the swamp is low (6 species/sample), there are four sub-communities where species other than *S. erectum* may have high constancy:

- **S14a** *Sparganium erectum* sub-community has 2 species/sample, none with high constancy;
- **S14b** *Alisma plantago-aquatica* sub-community has 5 species/sample, with water-plantain occurring in >60% of samples;
- **S14c** *Mentha aquatica* sub-community has 14 species/sample, *Mentha aquatica* in >60% of samples and 10 other species having a constancy of III (in >41-60% of samples); and
- **S14d** *Phalaris arundinacea* sub-community has 6 species/sample and *Phalaris* in >80% of samples.

S18 *Carex otrubae* swamp is rather uncommon, tending to form narrow or fragmentary stands, where *Carex otrubae* is the commonest species forming an open cover of tufts. Although no other species is frequent in **S18**, there is a great variety of associated species. The mean number of species per sample is 7 but in the Sheffield region, Grime *et al.* (2007) found 14.1-18 species/m² associated with *Carex otrubae*. This variation in species-richness partly reflects the two sub-communities, where **S18a** *Carex otrubae* sub-community typically has 11 species/sample whereas **S18b** *Atriplex prostrata* sub-community only has 4 species/sample. *Carex otrubae* has most of the leaves nearer the stem base, with a canopy height of 60-100 cm and a lateral spread of 10-25cm in tussocks.

S19 *Eleocharis palustris* swamp is widespread and rather low, dominated by an open or closed cover of *Eleocharis palustris*. *Eleocharis palustris* has the leaves reduced to sheaths, a canopy height of 30-60 cm and a lateral spread of >1m through rhizomatous spread. **S19** has no consistently frequent associates, but there are three sub-communities where species of higher constancy are typical of **S19b** and **S19c** *i.e.*:

- **S19a *Eleocharis palustris* sub-community**: no other species with high constancy and a mean of 7 species/sample
- **S19b *Littorella uniflora* sub-community**: *L. uniflora* itself is found in 61-80% of samples and other species with frequency >40% are *Equisetum fluviatile* and *Juncus bufonius*. No summary is provided by the NVC on species richer per sample.
- **S19c *Agrostis stolonifera* sub-community** has *A. stolonifera* in >80% of samples, together with 3 species having a constancy of III (*Glaux*, *Potentilla anserina* and *Triglochin maritimum*)

Abiotic requirements for existence and restoration/creation of swamp types

Soil type: British swamp communities are mainly associated with anaerobic and waterlogged mineral soils on silty substrates, though certain types are found occasionally or primarily on peats. Thus the *Carex paniculata* swamp (**S3**) is found mainly on semi-fluid to firm peat (derived from reed or *Typha angustifolia*), and **S8** *Scirpus lacustris*, **S10** *Equisetum fluviatile* and **S14** *Sparganium erectum*, as well as the *Eleocharis palustris* sub-community of the *Eleocharis palustris* swap (**S19a**), all occur sporadically on peats. Within **S8**, there is some suggestion that the soil organic component is generally higher than in reed-beds (**S4**) and the upper layer of the substrate for **S6** *Carex riparia* swamp is described as “sloppy” sapropelic silt (*i.e.* very rich in organic matter).. The range of some swamp types extends onto sandy substrates or even fine gravels *e.g.* **S10** and especially the *Littorella* sub-community (**S19b**) of the *Eleocharis palustris* swamp, which can occur on stony substrates. Amongst the selected communities, **S18** *Carex otrubae* swamp stands out in normally being found on heavy clayey soils, although **S8** and **S14** will also occur on clay substrates.

More detailed information is available for the **S12** *Typha latifolia* swamp where Day *et al.* (1988) examined fertility and soil/water properties in riverine *T. latifolia* communities in eastern Canada and found the typical soil structural components to be (percentage mass) to be 0.4-2.3% gravel, 75.8-77.8% sand and 19.8-23.8% silt and clay, with a loss on ignition of 5.9-14.1%. The research literature suggests that the preferred situation for **S13** *Typha angustifolia* swamp is broadly similar to that of **S12**.

Soil chemistry: Although information on soil chemistry is unevenly available for the 10 NVC types, two fairly consistent sources of information are the species accounts of Grime *et al.* (2007) and the updated Ellenberg indicator values for Britain (Hill *et al.* 2004). These sources summarise the preferred soil chemistry for the dominant species of the swamps, and are presented in Table 6. Most swamp dominants have Ellenberg N indicator values of 7 (*i.e.* often found in richly fertile places) or 6 (showing situations between intermediately and richly fertile). However both *Eleocharis palustris* and *Equisetum fluviatile* have lower N indicator values of 4, showing a preference for sites that are between intermediately fertile and infertile. In terms of soil reaction, their Ellenberg indicator values are all either 6 or 7, corresponding to conditions that are circumneutral or transitional to mildly acidic. The equivalent information from Grime *et al.* (2007) largely confirms this pattern, though suggesting again that *E. palustris* and *E. fluviatile* locally occur on more acid soils.

Table 6: Ellenberg indicator values for nitrogen (N), reaction (R) and salt tolerance (S) for dominants of NVC swamp communities. Information on preferred pH of these species is included derived from *Comparative Plant Ecology*

Swamp community dominant species	Ellenberg Indicator Values (after Hill <i>et al.</i> 2004)			Grime <i>et al.</i> (2007) – pH
	Nitrogen (N)	Reaction (R)	Salt tolerance (S)	
<i>Carex paniculata</i> (S3)	6	6	0	ca 6.0 circum-neutral
<i>Carex riparia</i> (S6)	7	7	0	ca 6.5 circum-neutral
<i>Carex acutiformis</i> (S7)	6	7	0	ca 6.5 moderately variable -absent from acid soils
<i>Schoenoplectus lacustris</i> (S8)	6	7	0	ca 6.5 circum-neutral
<i>Equisetum fluviatile</i> (S10)	4	6	0	pH 4.0-7.5 but mainly on mildly acid soil
<i>Typha latifolia</i> (S12)	7	7	0	Mainly at pH >5.5
<i>Typha angustifolia</i> (S13)	7	7	1	ca 6.5 circum-neutral
<i>Sparganium erectum</i> (S14)	7	7	0	Mainly on pH 6.5-7.0 but scattered on all but most acid
<i>Carex otrubae</i> (S18)	7	7	2	ca 6.5 circum-neutral
<i>Eleocharis palustris</i> (S19)	4	6	1	Mainly confined to pH 5.0-7.5

The occurrence of these communities is often characterised in terms of their prevalence over a spectrum of fertility from dystrophic, though oligotrophic and mesotrophic to eutrophic and, exceptionally, hypertrophic. Both indicator values and other published data indicate that most of the NVC swamps are found in meso- to eutrophic situations, though **S10** and **S19** extend into oligotrophic sites. There is also some suggestion that **S13** *Typha angustifolia* swamp occurs in less eutrophic situations than **S12** *Typha latifolia* swamp, which itself is typical of mesotrophic to eutrophic, circumneutral to basic sites.

With regard to fertility and reaction, there is evidence that **S7** *Carex acutiformis* swamp occurs in more calcareous locations than **S6** *Carex riparia* swamp. *C. acutiformis* can grow in eutrophic fens where it has high productivity and is able to use a range of phosphorus sources, including not only KH_2PO_4 , aluminium phosphate and β -glycero-phosphate, but also sources such as ferric phosphate and calcium phosphate which were unavailable to those *Carex* species more typical mesotrophic fens (Corona *et al.* 1996). Other data on pH range suggest that **S10** *Equisetum fluviatile* is most prominent in sites with a sediment pH of 5.2-6.4, and that although most vigorous over pH 5.5, *Typha latifolia* (**S12**) can be found over a pH range of 4-8. Finally, both *Carex paniculata* (**S3** swamp) and *Equisetum fluviatile* (**S10**) are tolerant of high levels of ferrous iron in the soil (Lucassen *et al.* 2006).

The Ellenberg approach also provides guidance on the likely salinity tolerances of the dominant species for these ten NVC swamp types. On this basis, most swamp types would be absent from saline sites (S indicator value of 0). However, both **S13** *Typha angustifolia* swamp and **S19** *Eleocharis palustris* swamp are slightly more salt-tolerant, persisting in brackish situations, and with the *Agrostis stolonifera* sub-community of the latter (**S19c**) occurring in brackish situations by the upper edge of salt-marshes. The **S18** *Carex otrubae* swamp is recognised by Rodwell (1995) as well-distributed at the coast and in somewhat saline situations inland, and the S indicator of 2 suggests a community that can occur equally in saline and non-saline situations. The *Atriplex prostrata* sub-community (**S18b**) is characteristic of saline ditch and pool margins associated with the salt industry, and indeed **S18a** (and *Carex otrubae* itself) is frequent in coastal habitats, including upper salt-marsh grasslands, to which it is largely restricted in northern Britain. Although the indicator value for *Typha latifolia* show an intolerance of salinity, Rodwell (1995) NVC states that this reedmace may occur very rarely in salt-marshes *i.e.* rarely inundated inter-tidal stands, suggesting at least some tolerance of brackish situations.

Hydro-chemistry: Published sources are sparse that distinguish the chemistry of the waters from which the swamps emerge from the chemistry of the soil/substrate. However, **S3** *Carex paniculata* swamp is said to be associated with eutrophication of base-rich water but to be dominant in more mesotrophic calcareous base-rich water of pH 7.1-8.1 and calcium content of 71-74 mg/l.

More detailed work on reedmace (**S12**), bulrush (**S8**) and bur-reed (**S14**) swamps provides some refinement of the relevant community requirements. Thus for *Typha latifolia* swamp (equivalent to **S12**), Day *et al.* (1988) in a study of the water chemistry of the Ottawa River recorded a typical conductivity of 80.8-94.5 $\mu\text{S cm}^{-1}$, phosphorus content of 7.6-7.8 $\mu\text{g g}^{-1}$, magnesium of 134.2-163.6 $\mu\text{g g}^{-1}$, potassium of 48.6-56 $\mu\text{g g}^{-1}$ and pH of 5.9-7.1.

Results from River Habitat Surveys in Britain found that *Scirpetum lacustris* (*i.e.* **S8**) grew in waters with pH 8.3, mean conductivity of 602 $\mu\text{g S cm}^{-1}$, soluble reactive phosphorus of 369 $\mu\text{g P l}^{-1}$, total phosphorus of 389 $\mu\text{g P l}^{-1}$ and alkalinity of 4.6 meq l^{-1} (Dawson and Szoszkiewicz 1999). The same source indicates that the *Sparganium erecti* (*i.e.* **S14**) is found in waters with pH 8, mean conductivity of 666 $\mu\text{g S cm}^{-1}$, soluble reactive phosphorus of 392 $\mu\text{g P l}^{-1}$, total phosphorus of 554 $\mu\text{g P l}^{-1}$ and alkalinity of 3.9 meq l^{-1} (Dawson and Szoszkiewicz 1999). Although typical of mesotrophic to eutrophic waters, **S14** will occur where there is pollution by sewage and even industrial effluents.

There is evidence of variation between sub-communities within some swamp types. In the **S8** bulrush swamp, **S8b** (*Sparganium erectum* sub-community) occurs in more eutrophic sites on clay streams and silty drains, whilst **S8c** (*Equisetum fluviatile* sub-community) is found in nutrient- and base-poor waters. Correspondingly in the **S19** *Eleocharis palustris* swamp, the typical (**S19a**) sub-community occurs in mesotrophic waters, but **S19b** *Littorella uniflora* sub-community is the normal variant by Scottish lochs in more oligotrophic waters.

Hydrology: From the classic work of Spence (1964, 1967) to the NVC (Rodwell, 1995) and onward, attempts have been made to define the hydrological requirements of British swamp communities, often ordering the dominant species along an axis of water-depth range. The application of Ellenberg moisture indicator values (F) to the UK (Hill *et al.* 2004) also allows the tolerances of the communities to be grouped. On the basis of their nominate species,

many NVC swamp types are, as would be expected, typical of shallow-water sites that may lack standing water for long periods (F=10) *i.e.* **S10** *Equisetum fluviatile*, **S12** *Typha latifolia*, **S13** *Typha angustifolia*, **S14** *Sparganium erectum* and **S19** *Eleocharis palustris*. Most sedge-swamps reflect situations that are wet, often water-saturated and badly aerated, but with standing water transient (Ellenberg F=9) *i.e.* **S3** *Carex paniculata*, **S6** *Carex riparia* and **S7** *Carex acutiformis*. One “swamp” type in the NVC (**S18** *Carex otrubae*) is most typical of damp to wet sites that are very seldom inundated places (F=8). At the other end of the spectrum is **S8** bulrush swamp, where *Schoenoplectus l. lacustris* has an Ellenberg F value of 11, reflecting its requirement to grow always as an emergent and to be excluded from sites that are prone to drying out. Indeed *S. lacustris* also has a submerged aquatic form, though this is not the growth form that forms swamp vegetation.

Information on preferred water-depths also allows the NVC types to be ranked. Thus **S18** is found along the margins of standing or slow-moving waters, with no depth of surface water. Indeed *Carex otrubae* and the **S18** community it characterises will grow in ditches, swamps, wet lowland meadows and pastures, and at the upper edge of salt-marshes, as well as, less commonly, on damp roadsides, hedge banks and waste ground. Other sedge swamps (**S3**, **S6** and **S7**) will occur from saturated situations through to depths of up to 0.2 m of water, though **S3** *Carex paniculata* swamp in effect maintains a constant depth as the growth of tussocks depresses the peat surface. **S19** *Eleocharis palustris* will also be found where there is no surface water, but can extend to 0.5 m depth. Reedmace swamps (**S12** and **S13**) extend deeper still, to 0.6m and beyond (**S12a**, **S12d** and **S13**), and usually have some surface water throughout the year, though some examples of **S12a** are summer dry. **S12b** and **S12c** are more typical of shallower water where there are no marked seasonal fluctuations. Elsewhere in the Holarctic, stands equivalent to **S13** appear to tolerate generally deeper water than the *Typha latifolia* swamp (Inoue and Tsuchiya 2009), and such vegetation can be found on the deeper edge of reed stands in Broadland, although such deep water stands of **S13** swamp may occur as a floating marginal mat.

S14 bur-reed swamp normally occurs in shallower water than the reedmace swamps, but will tolerate depths of up to 1.0m. Distribution of the four sub-communities is related to depth *i.e.* **S14a** in deeper water, **S14b** in shallower water and **S14c/S14d** found where the ground may be exposed in mid-late summer. None of the sub-communities of the bur-reed swamp can tolerate a water-table >0.1m below ground surface for long periods. The community is tolerant of moderate currents and is thus frequent by lowland streams and rivers, though much preferring the negligible flow of ponds and ditches.

The *Equisetum fluviatile* swamp (**S10**) will also occur in up to 1 metre of water. As indicated by the Ellenberg F value, **S8** bulrush swamps are confined to permanently inundated sites up to 1.5 m deep and never with less than 0.25 m depth. Within this depth range, **S8b** bur-reed sub-community occurs in shallower waters, whereas **S8c** horsetail sub-community is typical of deeper waters. **S8** occurs at the deepwater limit of swamp vegetation in the UK.

Unlike fens, swamp communities have not been related to water-supply mechanisms, though some indication of the type of water-body within which they occur can be inferred. Most of the described swamp types grow in and by still and slow-moving water, in situations such as lakes, pools, canals and drainage channels or sluggish larger streams and rivers. Open-water transitions are typified by *Carex paniculata* and *Carex acutiformis* swamps. The **S3** swamp occurs more rarely in basin, flood-plain and valley mires, often where there is some seasonal water-movement. **S6** *Carex riparia* swamp sometimes develops in open areas within fen woodland. The *Equisetum fluviatile* sub-community of **S10** (*i.e.* **S10a**) can

occur where the **S9** *Caricetum rostratae* swamp is absent e.g. in the drawdown zone of reservoirs, by lowland pools and sluggish reaches of high-order streams. As well as tolerating deeper water, **S8** swamp can survive faster flows, especially as submerged leaves, but only where there is no spate that can damage the stems.

Biotic requirements for existence and restoration/creation of swamp types

Ecology: As with the abiotic requirements, certain key works can be used to make simple comparisons between the ecology of the dominants of the 10 *NVC* swamp types (Grime *et al.* 2007; Hill *et al.* 2004; Preston *et al.* 2002). Attributes that may be assessed include established strategy (CSR), tolerance of shade (as signified by the Ellenberg L indicator value) and trends in distribution.

Grime *et al.* (2007) do not ascribe an established strategy to certain swamp dominants: *Carex paniculata* (**S3**), *C. riparia* (**S6**) and *Typha angustifolia* (**S13**), although it may be inferred that the likely strategies for the last two are similar to *C. acutiformis* and *T. latifolia* respectively. Dominants with largely competitive strategies include *Typha latifolia* (C i.e. C:1; S:0; R:0), *Sparganium erectum* (C/CR i.e. C:0.75; S:0; R:0.25) and *Carex acutiformis* (C/SC i.e. C:0.75; S: 0.25; R:0). Both *Equisetum fluviatile* and *Schoenoplectus lacustris* have a competitor/stress tolerator strategy (SC i.e. C:0.5; S:0.5; R:0). The remaining two species have complex established strategies combining elements of competitor, stress-tolerator and ruderal. Thus *Carex otrubae* has a CR/CSR strategy (C:0.42; S:0.16; R: 0.42) and *Eleocharis palustris* is defined as SC/SCR (C:0.42; S:0.42; R: 0.16). Overall the swamp dominants are competitors, but with some trend toward stress-tolerator in bulrush, horsetail and spike-rush. Few species show any tendency toward a ruderal strategy.

Most of the swamp dominants are light demanding, with Ellenberg L indicator values of 8 for *Eleocharis palustris*, *Equisetum fluviatile*, *Schoenoplectus lacustris*, *Typha angustifolia* and *T. latifolia* (light-loving species rarely found where relative illumination in summer is <40%) or 7 for *Carex acutiformis*, *C. riparia* and *Sparganium erectum* (plants generally in well lit places, but also occurring in partial shade). Two sedge species (*C. otrubae* and *C. paniculata*) have an L value of 6 (more shade tolerant, though >10% relative illumination in summer) and the **S3** swamp in particular may be transitional to wet woodland.

The 10 dominant species of these *NVC* swamps are generally common with stable distributions in the UK over the past 50 years (Preston *et al.* 2002). There is some evidence of localised increases in three species, where both *Carex riparia* and *Typha angustifolia* may have gained from ornamental planting in ponds etc, although such changes would not constitute an increased distribution of the relevant communities. *Typha latifolia* (and **S12** swamp) may also have spread during the 20th century, although the cause of this spread is unclear. The general status of *Carex acutiformis* in the UK also seems stable, though possibly with declines in some locations and in contrast increasing in fen meadows that are managed less intensively than previously (Harding 2010) or prone to unseasonal summer flooding (Gowing 2012).

For five swamp dominants there is evidence of localised declines in frequency since 1960, and hence in the extent of the communities. *Carex paniculata* has been lost from many sites and is threatened in others e.g. in Broadland where “tussock-fens” have ceased to develop. Scattered losses of *Eleocharis palustris* stands can be demonstrated. More particularly,

there have been local losses of *Schoenoplectus lacustris* and *Equisetum fluviatile* in southeast England, with the decline of horsetail reflecting loss of small wetlands and the unsympathetic management of remaining sites. *Carex otrubae* has remained unchanged though drainage has led to local losses in some areas e.g. Dorset.

Rodwell (1995) describes the zonation of these communities and their tendency to succeed to other vegetation types. **S3** *Carex paniculata* may colonise open water directly or dynamically with reed (**S4**) or *Typha angustifolia* (**S13**), and gives way through richer fen vegetation to carr. **S6** *Carex riparia* generally occurs as part of the transition from open water but with the succession though to terrestrial habitat often curtailed by the agricultural management applied to many stands. **S7** *Carex acutiformis* swamp is found associated with reed-swamp (**S4**) and bur-reed swamp (**S14**), or in transition to tall-herb fen (e.g. **S24**) and fen-meadow (**M22**). Long-term competition studies in Japan between *Typha latifolia* and *T. angustifolia* (Tanaka *et al.* 2004) revealed a dependence on the ratio of net production between these two species and the initial biomass of *T. latifolia*. Due to its taller shoot height, *T. angustifolia* can dominate *T. latifolia* especially in systems constrained by nutrients. The occurrence and zonation of **S12** and **S13** in the UK may be partially determined by these factors.

Mycorrhizal associations: For most of the dominant species of NVC swamp types there is no apparent published information on the mycorrhizal associations: **S3, S6, S7, S8, S10, S18** and **S19**. However for both reed-maces and bur-reed, associations have been described. *Typha latifolia* is generally described as mycorrhizal (Stenlund and Charvat 1994), though some reports state that reedmace is non-mycorrhizal. Working in Idaho, Ray and Inouye (2006) investigated the colonisation of *Typha latifolia* by arbuscular mycorrhizae and found that there was mycorrhizae were formed in reedmace during both flooded and unflooded periods, but that drawdown periods reduced such colonisation, whilst Cornwell *et al.* (2001) noted that this reedmace was non-mycorrhizal in a phosphorus-poor site in New York, and suggested mycorrhizae did not provide improved phosphorus nutrition to *Typha latifolia*. In Florida (Ipsilantis and Sylvia 2007) either flooding or addition of phosphorus to freely-drained stands of *Typha latifolia* both almost eliminated mycorrhizal colonisation, but where colonisation did occur, this resulted in increased shoot- and root-concentrations of phosphorus, but without significant plant growth responses. Work on *T. angustifolia* is less extensive but experimental investigations of arbuscular mycorrhizal colonisation under a range of phosphorus concentrations found mycorrhizae could colonise lesser reedmace at up to 100 µM P (Tang *et al.* 2001). Finally, vesicular-arbuscular mycorrhizae have also been observed for *Sparganium erectum* (Grime *et al.* 2007).

Regeneration requirement: Grime *et al.* (2007) review the means whereby swamp dominant species spread and colonise new sites, as well the evidence for persistence of a seedbank. These results are summarised in Table 7. Most of the dominant species of swamps rely principally on lateral vegetative spread to regenerate, although longer distance dispersal by seed (or spores) can play a role in colonising new sites – this is particularly the case in *Typha* species and *Equisetum fluviatile*. None of the 10 species have a very persistent seed-bank, with most seeds germinating within the year following their shedding. Only for *Typha latifolia* (and by implication *Typha angustifolia*) is there evidence of slightly longer persistence of viable seed (Leck and Graveline 1979), an adaptation to colonisation of new and transient wetlands.

Table 7: Dominants of *NVC* swamp communities. Information on means of dispersal, regenerative strategy and seed-bank (Largely derived from *Comparative Plant Ecology*)

Swamp community dominant species	Means of dispersal	Main regenerative strategy	Evidence for and persistence of seed-bank etc
<i>Carex paniculata</i> (S3)	Fruits freely (in open)	Vegetative (especially in shade)	[Probably as <i>C. otrubae</i>]
<i>Carex riparia</i> (S6)	Some capacity to colonise new sites by seed	Vegetative (rhizomatous perennial)	[Probably as <i>C. acutiformis</i>]
<i>Carex acutiformis</i> (S7)	Seed dispersed by water – some dispersal of rhizome fragments (Reproduction by seed in UK poor)	Lateral vegetative spread (rhizomatous perennial)	Transient seedbank - present through winter but germinates synchronously in late winter & spring
<i>Schoenoplectus lacustris</i> (S8)	Seed (and plant fragments) mainly dispersed by water, and probably also by animals (Coops & van der Verde 1995)	Lateral vegetative spread via rhizomes (rate of spread can be rapid). Sometimes seasonal regeneration by seed	Possibly with transient seed bank during summer but germination occurs synchronously in the autumn
<i>Equisetum fluviatile</i> (S10)	Widely wind-dispersed spores	By spores and by lateral vegetative spread	Spores remain viable through growing season but no over-winter persistence
<i>Typha latifolia</i> (S12)	Wind-dispersed seed	By seed for new sites but lateral vegetative spread via rhizomes where established	Small amount of the seed may persist in soil (occasionally for >5 years) but seed-bank only well-stocked immediately after shedding of seed
<i>Typha angustifolia</i> (S13)	[As <i>T. latifolia</i>]	[As <i>T. latifolia</i>]	[As <i>T. latifolia</i>]
<i>Sparganium erectum</i> (S14)	Fruit dispersed by water or by animals	Lateral vegetative spread through rhizomes	Transient seed bank during summer after fruit-shedding, but germination occurs synchronously in the autumn
<i>Carex otrubae</i> (S18)	Water-dispersed	[Assume both by seed and vegetative]	Transient seed-bank surviving winter before germinating synchronously in late winter and spring
<i>Eleocharis palustris</i> (S19)	Seed dispersed by animals (some spread from detached plantlets)	Lateral vegetative spread through rhizomes	Transient seed-bank surviving winter before germinating synchronously in late winter and spring

Other information on regeneration by these swamp dominants is scattered. Within the more terrestrial species, the viability of seed of *Carex acutiformis* buried for one or two years is markedly reduced (Bekker *et al.* 1998), although such viability problems may be of only occasional importance since the main regenerative strategy vegetative. The seeds of *Typha latifolia* floats for a day or more (up to 3 or 4 days) and normally germinates on submerged soil, with seedlings also showing best growth when inundated (Coops and van der Velde 1995). In contrast, *T. angustifolia* seed seldom floats for more than a day and will germinate under water where seedling growth is also more rapid than when exposed (Coops and van der Velde 1995). In addition, increased germination in *T. angustifolia* may occur at rather higher temperatures than *Phragmites*, though this effect is eliminated following moist chilling of the seed (Nishihiro *et al.* 2004). For *Sparganium erectum*, Piquot *et al.* (1998) indicate that clonal propagation is favoured at the population level while selection will favour sexual reproduction at the metapopulation level because seeds produced by sexual reproduction are the only means for long distance dispersal. Finally in the most aquatic of these species, *Schoenoplectus l. lacustris*, seed floats for <1 hour and experiments on the viability of seed ingested by wildfowl indicate that small seed size favoured survival in the gut, and that germination of seed from faeces was highest where the retention time in the gut was short (Figueroa *et al.* 2010). Seedlings show most rapid growth in shallow water.

Threats from fragmentation and isolation: Although information that can be unequivocally applied to particular swamp communities is sparse (especially in the cases of **S3, S6, S7, S8, S10, S14, S18** and **S19**). However, more generalised trends can be demonstrated. Thus non-marine aquatic vascular plants (*e.g.* *Phragmites australis*, *Schoenoplectus lacustris* and *Typha latifolia*) generally show broad distributional ranges and climatic factors seem to have limited effects on their distributions (other than major zones *i.e.* tropical–temperate–subarctic). Hence the *NVC* communities included in this review of swamp types are often dominated by species that are well-spread through the Palaearctic and sometimes the entire Holarctic – witness the preponderance of references in the entire review drawn from the North American literature. Santamaria (2010) suggested that the reason for this generality of broad distributions and low differentiation among the inland aquatic flora is best explained by a combination of:

- (1) selection for stress-tolerant taxa with broad tolerance ranges
- (2) The selective advantages provided by clonal growth and multiplication, which increases plant tolerance to stress, genet survivorship and population viability
- (3) Long-distance dispersal of sexual propagules and high local dispersal of asexual clones
- (4) The generality of broad plastic responses, promoted by the combination of clonal growth, high local dispersal, small-scale spatial heterogeneity and temporal variability

More specific information is available for the dominants of reed-mace swamps (**S12** and **S13**). Studies of gene flow in both reedmaces were conducted by Tsyusko *et al.* (2005) who found high variation among *Typha* populations probably due to their high selfing rates and to extensive vegetative reproduction (reducing gene flow among populations). Pair-wise population-genetic distances in both *Typha* species were relatively high, as is expected with such limited gene flow. Combining population differentiation and gene flow normally produces positive correlation between genetic and geographic distances *i.e.* evidence for isolation by distance. The correlation between genetic and geographic distances was relatively low for *T. latifolia* (though significant) and even lower and non-significant for *T. angustifolia*.

Management practices:

In contrast to reed-swamps (**S4** and other communities dominated by *Phragmites australis*), there is remarkably little published information on the typical management practices applied to other swamps and their response to management. **S3** *Carex paniculata* can tolerate light grazing by cattle and poaching of soil, and *Carex acutiformis* (and probably *C. riparia*) may be favoured where intermittent grazing reduces the vigour of other potential swamp dominants (Wheeler 1983). Similarly, the **S18** *Carex otrubae* community will tolerate light grazing and cutting and is often a feature of lower-lying parts of grazing marshes and salt-pastures. **S19** *Eleocharis palustris* swamp may also be favoured by some disturbance of the habitat that limits taller swamp dominants. However, both **S14** *Sparganium erectum* swamp and those dominated by *Typha* species (**S12** and **S13**) do not survive repeated summer cutting or heavy grazing by stock.

Predicted climate change threats:

There has been very little work on the impact of climate change on the distribution of particular swamp communities, or the species that dominate them. To some extent, this lack of attention appears to stem from such species-poor single-dominant swamps being extremely widespread in the Palaearctic. Hence the predicted climatic changes within the UK and especially within England will not create conditions outside the “bio-climatic envelope” occupied by most swamp communities. However, some limited research has focussed on Finnish communities clearly related to the **S10** *Equisetum fluviatile*. There experiments conducted by Ojala *et al.* (2002) have tested the effect of elevated CO₂ (doubled to 600–700 ppm) and temperature (increased by 2.5–3°C) on the growth of *E. fluviatile*, finding that temperature effects were more distinct than those down to CO₂, with no interactions observed. Increased temperatures positively affected emergence, growth, maximum length and biomass of shoots. Elevated CO₂ had a negative effect on the maximum length of shoots, though possibly with some positive impact on the belowground biomass. Whilst speculating that climate change would lead to faster growth and greater shoot biomass in stands of horsetail, this was a laboratory experiment, whose relevance to wild stands of **S10** is not demonstrated.

Threats from non native invaders

Work on the threat of invasive alien species on the particular swamp types of interest to this review is essentially non-existent, and the threats posed by such invaders must be surmised rather than demonstrated from the literature. Reviewing British government policy and the advice given by its agencies (*e.g.* the Environment Agency) as well as the campaigns of NGOs such as Plantlife suggests that swamp communities per se are not particularly threatened by non-native invaders.

Most invasive plant species of concern colonise disturbed ground and especially aquatic systems (*Azolla filiculoides*, *Crassula helmsii*, *Elodea spp*, *Hydrocotyle ranunculoides*, *Lagarosiphon major*, *Myriophyllum aquaticum* etc) and river margins (*Fallopia japonica*, *Heracleum mantegazzianum* and *Impatiens glandulifera*). There are no apparent cases of any of these species becoming pestilential within swamps although there is anecdotal evidence that *C. helmsii* will invade the transition between open water and tall emergent swamps. *I. glandulifera* can sometimes be frequent where tall-herb vegetation along watercourses gives way to sedge and reed swamp, but only where the swamp has no surface water during the summer. There are instances of *Fallopia baldschuanica*

spreading from scrub and hedges into the edge of swamps, and in such cases there is potential for the invasive vine to shroud and out-compete the native swamp components. Other invasive species are more typical of wet woodland (e.g. *Lysichiton americanus*) or heaths and woodland (e.g. *Rhododendron ponticum*) and do not appear to pose a threat in swamps.

Some non-native plants do occur within fens and swamps, but the evidence suggests that these are almost entirely non-aggressive and have not posed a conservation problem e.g. *Aster x salignus* at Wicken Fen and *Lysimachia terrestris* in reed-swamps within the Lake District. Locally some goldenrod species (mainly *Solidago canadensis*) are also found in the margins of swamps. On mainland Europe, certain other species have become locally problematic in swamps and tall-herb margins to watercourses, and may pose a future problem in the UK, especially with climate change (e.g. *Amorpha fruticosa*, *Echinocystis lobata* and *Sicyos angulatus*) but these too are more likely to become a pest on river banks and in waste ground than in reed and sedge swamps.

Finally, some introduced herbivores do use swamps for foraging. Muntjac (*Muntiacus reevesi*) certainly occurs in land adjacent to native swamps, but makes most use of woodlands for cover and drier ground (including crops) within which to feed. The Chinese Water-deer (*Hydropotes inermis*) is locally frequent in wetlands in eastern England, but there is no suggestion that their grazing is having an unduly damaging impact on swamp communities.

Ecosystem Services:

Evidence of water regulation and purification value: Several tall helophytes have potential for the removal of pollutants, and the communities that they dominate should contribute this service. In the case of heavy metals etc, *Typha latifolia* (equivalent to **S12** swamp) is effective in removing metallic pollutants, though it is less widely used as *Phragmites* (Marchand *et al.* 2010). A review by Mayes *et al.* (2009) recorded *T. latifolia* growing well in polluted sites that could be either highly acid (coal and uranium mine waste, and copper smelting drainage) or alkaline (steel slag leachate and fly ash). This review also cited *T. angustifolia* (equivalent to **S13** swamp) in highly acid polluted sites (uranium mine drainage and mining lakes). *Schoenoplectus* species are also proven as efficacious in removing metallic pollutants, though they are not widely used (Marchand *et al.* 2010) and the review by Mayes *et al.* (2009) recorded *S. lacustris* growing in highly polluted acid lakes, as well as *Equisetum fluviatile* growing in highly alkaline polluted sites from steel slag or lime leachate.

With eutrophication and organic pollution, *Typha latifolia* can be used to remove complex organic pollutants from the soil (Nepovim *et al.* 2005) and to remove nitrates from wetlands (Weisner *et al.* 1994). Martin *et al.* (2003) report experimental evidence that increased macrophyte transpiration in *T. latifolia* contributes to nitrogen removal from wetlands, and supports their use in treatment systems. Where these wetlands are harvested (e.g. for bio-fuels) there is a corresponding negative impacts on the potential improvement of water quality. Soto *et al.* (1999) and Zimmerman (1973) recorded the value of *Schoenoplectus lacustris* in removing bacteria and nutrients from eutrophic water.

The broad contribution of such swamps to ecosystem services may be inferred from work in the US Upper Midwest region, where Zedler (2003) suggested that three such services (flood abatement, water quality improvement and biodiversity support) declined when ca 60% of the historical wetland area was drained for agriculture etc, though noting that some of these lost services could potentially be regained through measures for wetland restoration.

Evidence of carbon storage value: The main contribution of swamp communities to carbon storage lies not in locking up carbon within living plant tissue but rather in the accumulation of organic matter within the developing peat under such vegetation. The classic hydrosereal change through an emergent swamp phase to tall-herb fen and carr producing an autochthonous peat. Much research has been published on the sequestration of carbon within swamp forests, such as those dominated by *Taxodium* and *Nyssa aquatica*, and there is less on the accumulation under herbaceous swamps. A recent critical review by Kayranli *et al.* (2010) concluded that wetlands as such could act as carbon sources or as sinks "...depending on their age, operation, and the environmental boundary conditions such as location and climate". The review included examples of carbon accumulation in sediments of different wetland types, measured as $\text{kg C m}^{-2} \text{ year}^{-1}$. Examples quoted for temperate peatlands in Finland (Turunen *et al.* 2002) suggest 0.01-0.046 $\text{kg C m}^{-2} \text{ year}^{-1}$ accumulation per square metre annually, whilst results from North American peatlands give a summary figure of 0.29 $\text{kg C m}^{-2} \text{ year}^{-1}$. However, none of the examples in this detailed review are unequivocally applicable to specific swamp types within the NVC. Rather they provide a broad indicative range of carbon accumulation rates for such wetlands that may be relevant for those examples of these 10 types where both water management and grazing/cutting do allow the gradual build-up of peat – an uncommon situation in the lowlands of England.

Work on greenhouse gas fluxes within herbaceous swamps is more frequent. For example, continuously inundated wetland zones emitted methane from summer through fall, while in edge zones methane fluxes were only substantial in spring and summer (Altor and Mitsch 2008). Other studies of methane emissions from swamps suggested varied patterns with different dominants. In a *Typha angustifolia* wetland in eastern Canada (related to **S13**) analyses of CO_2 fluxes for a complete year showed that the wetland was a net CO_2 sink for each month from June to September but and a source of CO_2 to the atmosphere for the remaining autumn and winter months (Bonneville *et al.* 2008). Although the study referred to a boreal lake rather than the more typical situation for **S10** *Equisetum fluviatile* swamp in the UK, Hyvonen *et al.* (1998) calculated that the total annual emission of methane from the area covered by horsetail was 5000 kg, reflecting a seasonal pattern (but with no daily pattern). These emissions appear to be more related to turnover of detritus in the anaerobic sediment (affected by temperature) and less to seasonal variation in plant growth dynamics (Kankaala and Bergstrom 2004). Comparing unvegetated peat cores with those on which *Carex acutiformis* was grown, Koelbener *et al.* (2010) found that the sedge increased methane emissions five-fold. Studies of wetland where *Carex paniculata* and *Typha latifolia* were prominent Paludan and Blicher-Mathiesen (1996) strongly suggested that NO_3 loading of such freshwater wetlands disturbs the carbon balance of such areas, resulting in an accelerated loss of inorganic carbon in both gaseous and dissolved forms.

Evidence of Biodiversity value: Most of the attention on the nature conservation and biodiversity importance of swamp communities in Europe has focussed on reed-dominated vegetation (**S4** etc). Reedmace swamps will partially share the role in providing bird and invertebrate habitat, but the less contribution of the sedge-swamps is rather different. Within the south and southeast of England, floodplain stands of **S6** and **S7** (as well as the **S5** *Glyceria maxima* swamp) are the major refuge for the BAP priority species *Vertigo moulinsiana* as well as further uncommon molluscs and other invertebrates. Any role of sedges in biodiversity provision can be reduced where there is increased nitrogen input to mesotrophic fens, since the higher nitrogen use efficiency of *Carex acutiformis* compared to, for example, *Carex*

diandra and *C. rostrata* can lead to rapid expansion of *C. acutiformis* and reduced conservation value for the fen vegetation (Aerts and Decaluwe 1994; Aerts *et al.* 1992). Overall the markedly species-poor composition of the 10 swamp types and the general absence of specifically dependent animals and plants have meant that their role in biodiversity provision has not been regarded as markedly significant. However, their position within wetland successions, transitions and mosaics means that their presence, together with more highly valued communities, can be taken to suggest intact wetland structure and function.

Provisioning service value: Most of these swamp communities are not now exploited for provisioning, although expert reviews on behalf of the Global Environment Facility has suggested real potential for the use of tropical *Typha* swamps in biogas production, biomass pellets, combustion and gasification, traditional housing and the production of containers, baskets *etc.* Traditional uses of *Typha* in some parts of the world include consumption of the rhizomes or employing the down surrounding the seeds as soft linings and stuffing for clothes. In parts of England, stands of **S8** *Schoenoplectus* swamp are still exploited for weaving into baskets and seat bottoms. Many of the dominant species have had traditional culinary or medical uses, and several are currently used for horticultural and amenity purposes around urban wetlands.

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Section 3.

Mires and tall-herb fen communities

by

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M6: *Carex echinata* –*Sphagnum recurvum/auriculatum* mire.

Physiognomy.

The guidelines for the selection of biological SSSI's (1989) characterise the community as containing small sedges or rushes with dominance of more oligotrophic *Sphagna* with a variable contribution from higher plants; of medium species richness and regarded as poor fen. The community is said to be associated with slopes within M17 and M19 mire systems and sometimes over mineral ground, virtually ubiquitous in the upland fringes. Mainly on peats and peaty gleys irrigated by rather base-poor but not excessively oligotrophic water (SSSI Guidelines 1989).

M6, the *Carex echinata* –*Sphagnum recurvum (fallax)/auriculatum* mire (Rodwell 1991) is the commonest of the four British communities of the poor sedge fens of the *Caricion nigrae* alliance and is widespread across the northern and western sub-montane areas of the British Isles: at higher altitudes (>650m) in the Central Highlands of Scotland it is replaced by either the *Carex curta* – *Sphagnum russowii* mire (M7) or, in slightly less base poor situations, the *Carex rostrata-Sphagnum warnstorffii* mire (M8).

Although recognised as a coherent community, M6 in reality brings together a variety of poor fens; its subcommunities being dominated by small sedges as in the *Carex echinata* and *Carex nigra-Nardus stricta* subcommunities (M6a and M6b respectively) or by rushes in the bulkier types of vegetation seen in the *Juncus effusus* and *Juncus acutiflorus* units (M6c and M6d).

M6 is not as important for uncommon plant species as are base-rich flushes such as the *Carex dioica-Pinguicula vulgaris* mire (M10). The oceanic *Wahlengbergia hederacea* is occasional in rushy stands and another oceanic plant, *Carum verticillatum*, can be abundant in examples of the community from southwest Wales (Stevens *et al.* 2010). In the more westerly stands of the community there is a stronger representation of *Molinia caerulea*, *Succisa pratensis* and the moss *Aulacomnium palustre*.

M6a is an open sedge-rich subcommunity characterised largely by a lack of preferentials for the other subcommunities rather than by positive floristic markers. *Sphagnum auriculatum* tends to be more typical of this unit than is *S.fallax*. The combination of mosses, sedges and rushes marks M6 as a very distinctive and characteristic form of flush: the other widespread flush community, M10, is calcareous and its 'brown moss' dominated layer is strikingly different in colour and appearance.

M6 is unusual amongst British plant communities in that due to the level of floristic variation between stands of the recognised subcommunities there are, apart from *Carex echinata* no genuine community constants. The majority of stands however feature *Polytrichum commune*, *Sphagnum recurvum (fallax)*, *Agrostis canina*, *Potentilla erecta*, *Viola palustris* and *Molinia caerulea* and these may be regarded as the characteristic species of the community as a whole.

The *Carex echinata* subcommunity (M6a) is the most impoverished form of the community (mean species/sample=13) and the one likely to support the highest cover of *Molinia*. It is low growing and usually contains the densest carpets of *Sphagnum recurvum* and/or *S.auriculatum*; the latter species tending to become more prominent in the more Atlantic climate of the west of Britain.

M6a is usually a very open vegetation with bare areas colonised by *Drosera rotundifolia* and *Vaccinium oxycoccus*, both differential species for the subcommunity.

Cover of small sedges reach their peak in M6b, the *Carex nigra-Nardus stricta* unit, with both *C.nigra* and *C.panicea* being prominent in addition to very frequent *Eriophorum angustifolium*. This vegetation is closer to a flushed grassland than the other units of the community with frequent records for *Nardus stricta*, *Festuca ovina* and *Anthoxanthum odoratum*. *Sphagnum* cover is generally relatively low and often patchy but the stands tend to be relatively species rich.

The *Juncus effusus* subcommunity (M6c), is a taller, more tussocky, vegetation type and more often encountered on gleyed mineral soils though it not infrequently occurs as a zone between M6a or M6b and surrounding acidic pasture land. In such situations it may grade into M23a rush pasture. *Juncus effusus* is the only strong preferential species for the subcommunity.

M6d, the *Juncus acutiflorus* subcommunity, is, like M6c, a tall rush-dominated vegetation type but one which tends to be associated with wet heaths and within *Juncus-Molinia* meadows and rush pastures rather than with the blanket mires within which stands of the other types of the *Carex echinata* mire are most usually encountered. M6d is also a more lowland and more oceanic mire than are the other subcommunities.

Abiotic requirements for existence and restoration.

(a) Landscape.

M6 more closely resembles other communities when its *Sphagnum* layer is patchy. In such cases the distinction between M6 and slightly flushed examples of *Juncus-Galium palustre* rush pasture (M23) or *Molinia-Potentilla erecta* mire (M25) is far from clear cut. Most M6 flushes are set within a matrix of marshy grassland or heathland, typically including M23 and M25 on the one hand (Prosser and Wallace 2010) and M15 on the other. M6b, the *Carex nigra-Nardus* unit is often found in association with U4 (*Festuca ovina-Agrostis capillaris-Galium saxatile* grassland). The distinction between the two is sometimes very blurred as the *Sphagnum* cover increases gradually along a hydrological gradient. At higher altitudes the association may be with the *Nardus-Galium saxatile* grassland, U5 (Wallace and Prosser 1999, 2005).

M6 does not feature prominently in conservation literature, this is likely to be due to a combination of its widespread distribution allied to its lack of associated species of rarity or of otherwise conservation importance.

Some sites subject to agricultural modification through drainage support large species-poor areas of the *Juncus effusus* subcommunity (Stevens *et al.* 2010). These authors also note that a combination of heavy grazing and nutrient enrichment can lead to a diminution, or even loss, of *Sphagnum* cover. They note that the largest recorded area of the community in Wales is at Egel Valley in Glamorgan with almost 20ha, mostly of the *Juncus effusus* unit. Sizeable stands have also been recorded in North Wales, e.g. Llanycil Common (Wallace and Prosser 1999) where the largest continuous stands are again of the *Juncus effusus* subcommunity.

On Fox Tor, South Dartmoor SSSI, 38ha of the community were mapped (Wallace and Prosser 2005). Mainly the *Carex echinata* subcommunity (22.88ha) which formed extensive linear bands on gentle slopes within U5 grassland; in contrast the *Juncus*-dominated subcommunities occupied ± flat ground in the centre of the mire system grading to blanket mire (M17) above and *Carex rostrata* mire (M4) in the wetter hollows.

(b) Soil type.

Mainly on peats and peaty gleys irrigated by rather base-poor but not excessively oligotrophic water (SSSI Guidelines 1989).

Stands of the *Juncus effusus* unit vary greatly in size from a few m² to >20ha. The water table varies seasonally in the drier sites but is permanently high in many stands. These drainage differences are shown floristically through an abundance of *Polytrichum commune* over gleyed podzols compared to the abundance of *Sphagna* over wetter peaty gleys (McVean and Ratcliffe 1962).

(c) Soil Chemistry.

Wheeler and Procter (2000) classify M6 as 'mesotrophic bog' rather than sedge poor-fen; they restrict the term 'fen' to sites generally having a pH >5.5 and irrigated by calcium-rich water. Procter's values for 193 mire water samples from Britain and Ireland show the M6 stands to have a mean pH around 5.0 with calcium concentration generally <1mg l⁻¹.

M6a is, in general, irrigated by less acidic water than are the other subcommunities; the stands sampled for the NVC having a mean pH of 4.9 (Rodwell 1991). The mean pH, for M6b, at 3.9, is lower than for the other three subcommunities.

In a study of 26 *Sphagnum fallax*-dominated mires in western Poland, Gąbka and Lamentowicz (2008) found all sites to be poor in calcium with a mean of 4.5 mg Calcium litre⁻¹ but relatively rich in nutrients with NH₄-N at 2.2 mg l⁻¹ and PO₄P 1.7 mg l⁻¹. The sites had quite high conductivity at 134 µS and an unusually high DOC concentration at 58 mgC l⁻¹. These workers found no correlation between calcium concentration and pH: this contrasts with the findings of Wheeler and Procter (2000) and others.

Hájek *et al.* (2002) studied the poor-rich fen gradient in the western part of the Carpathian flysch zone. Calcium and magnesium concentrations, pH, conductivity, and soil organic carbon content all showed strong correlations with the main vegetation gradient. The poorest spring fens supporting *Sphagnum fallax*, *S. auriculatum* and *S. magellanicum* were poor in calcium, iron, sodium and potassium, findings supported by Malmer (1986) and Økland *et al.* (2001). These Czech and Slovak poor fens feature *Sphagnum fallax*, *Sphagnum flexuosum* (formerly *S. recurvum* spp *anblyphyllum*), *Polytrichum commune* and *Drosera rotundifolia* in a community they placed in the *Carici echinatae-Sphagnetum recurvi* and so these fens are virtually identical to the British M6. However, they also feature a mean pH of 5.5 and a mean calcium concentration of 7.0 mg l⁻¹ which makes them overall less acidic and less base poor than their British counterparts though, on the other hand, they were also recorded as occurring on moderate slopes of 2 – 3 degrees, a feature common of most British stands. Hájek *et al.* note that when the *Sphagnum recurvum* aggregate is not restricted by a high calcium level it grows rapidly and forms dense carpets eliminating calcitolerant *Sphagnum* species. They consider rich *Sphagnum* fens in their study area to be critically endangered vegetation types since they are often replaced by *Sphagnum flexuosum* poor fens if the phosphate and sulphate inputs increase.

Sphagnum-dominated, mostly unmown, poor fens such as M6 accumulate potassium which under aerobic conditions is strongly bound in soils (Heikkilä 1987).

(d) Hydro-chemistry.

Proctor *et al.* (2009), studying fen sites at Abernethy, found statistically significant associations between species distribution and the division of ombrotrophic from telluric-influenced sites. In the latter, species most significantly associated with this mineral input included *Carex echinata*, *Sphagnum recurvum s.l.*, *Potentilla erecta*, *Agrostis canina*, *Juncus effusus*, *Polytrichum commune*, *Carex nigra* and *Narthecium ossifragum*, all M6 species, confirming the influence of inflow of water from mineral soils on the composition of the community.

(e) Hydrology

M6 is characteristically to be found on gently slopes and follows the channelling of soligenous waters. M6 usually forms relatively narrow linear features often of considerable length though some *Juncus effusus* stands may be much more extensive. Both are fed by groundwater and runnels are frequent, often supporting M6a or M6b with wider fringes of M6c and M6d more distant from the surface flow. The community may be found on shallow peat or on mineral-enriched peat; deep peats and purely mineral soils are much less frequent substrates.

Although not covered in WETMEC's it seems most probable that M6 would be associated with WETMEC 10, 15 or 17 (Wheeler *et al.* 2009a and b). WETMEC 10 is associated with permanent seepage slopes and the stands of poor fen here are typically small, <0.5ha, and WETMEC 17 represents groundwater flushed slopes, again small in extent it often occurs in association with WETMEC 10. WETMEC 15 encompasses seepage flow tracks.

Biotic requirements.

Many of the biotic requirements of the community are covered in detail in the management issues section. Of particular importance is the maintenance of high water tables and continuous water flow.

The level of grazing is also important; some grazing may be indicated to prevent invasion especially by *Betula pubescens* whereas intensive grazing may give rise to a degree of eutrophication and a reduction in the cover of *Sphagnum*. Short term eutrophication may lead to conversion from the more species-rich *Sphagnum*-dominated subcommunities (a & b) to the rush-dominated forms of the community (c & d). On the less wet areas of M6 long periods of grazing are likely to convert the flush to a *Juncus-Galium* mire (M23) or even to acidic grassland with only fragmentary remains of the M6 flush.

Species diversity may be enhanced through rush control so as to favour the development of M6b from M6c.

Liming without drainage could result in the conversion of stands of the M6 b,c, and d subcommunities to *Carex rostrata-Sphagnum squarrosum* mire (M5) which occupies a median position in the sequence of communities ranging from the oligotrophic and calcifuge vegetation of these M6 subcommunities to the *Carex*-rich basic flushes of M10.

Management Issues.

M6 flushes are mostly managed as pasture, grazed mainly by cattle, especially in the lowlands. Long continued grazing on drier soils probably converts this vegetation to either the *Juncus-Galium palustre* mire (M23) or to acidic grassland dominated by *Nardus stricta* and *Juncus squarrosus* communities, U5 and U6 respectively (Rodwell 1991).

Some sites subject to agricultural modification through drainage support large species-poor areas of the *Juncus effusus* subcommunity (Stevens *et al.* 2010). These authors also note that a combination of heavy grazing and nutrient enrichment can lead to a diminution, or even loss, of *Sphagnum* cover.

Bobbink *et al.* (2002) give 5 – 10 kg Nitrogen ha⁻¹ year⁻¹ as the critical load for base poor fens which would include M6. Exceedence of this value and negative effects on the moss layer become rapidly apparent.

Negative indicator species for M6 are given as *Phragmites australis*, *Phalaris arundinacea*, *Glyceria maxima*, *Typha latifolia*, *Urtica dioica* and *Epilobium hirsutum* (JNCC 2004).

Hájek *et al.* (2002) consider rich *Sphagnum* fens in their study area to be critically endangered vegetation types since they are often replaced by *Sphagnum flexuosum* poor fens if the phosphate and sulphate inputs increase.

Limpens *et al.* (2003) concluded that *Sphagnum fallax* will gradually colonise an increasing number of new habitats in areas with low but increasing N deposition but will only grow to dominate when phosphorus supply is adequate. An increase in the observed frequency of *S.fallax* coincided with an historical increase in N deposition in the Netherlands.

The vegetation of a Belgian drained species-poor fen of the *Caricetum nigrae* was dominated by *Juncus effusus* and *Agrostis canina*, a form of 'rump' M6. The vegetation was found to be K-limited. A re-wetting greenhouse experiment was conducted, the results of which showed the K-deficiency to be maintained, thus highlighting the potential problem with fen restoration in that simply rewetting is unlikely to be effective (Van Duren *et al.* 1997).

De Mars *et al.* (1996), working on a former floodplain in northeast Poland, suggested that the drainage of peat soils causes a sharp decrease in potassium availability due to leaching. Once leached K will not be easily available after rewetting since the concentration of potassium in ground water and rain water is usually very low.

A study of environmental variables on wet meadows and fens in Belgium and the Netherlands (Venterink *et al.* 2001) included six *Caricetum nigrae* sites. These had a mean pH of 5.9 compared with 5.6 for *Junco-Molinion* and *Calthion* meadows. They found biomass increasing with increasing N mineralisation; this was particularly true for graminoids. Also, 42% of variation in species density was explained by variations in biomass with increased biomass associated with a decrease in threatened species. Similar effects were shown for phosphorus availability: P-limited fens have more threatened species but as P increases threatened species decline.

In simple terms, the results of these and other studies suggest that were a conservation objective to be the transformation of poor fen to more species-rich fen mowing, liming and nutrient stripping are all indicated.

A fertilisation experiment (Verhoeven and Schmitz 1991) on three Dutch mesotrophic fens in an area of high N input from precipitation included one with dominant *Sphagnum fallax* as the ground layer.

This fen also features *Carex echinata* but the water inflow is base rich and the general floristics suggest the equivalent of a British M9 of the *Caricion daviallianae* rather than an M6. The findings are however likely to be relevant to this community. The addition of P resulted in a significant increase in biomass whereas no such effect was found following N addition. This situation contrasted with that in younger *Carex rostrata* and *Phragmites/Juncus subnodulosus* fens which remained N limited even in the high N input area.

In an area of low atmospheric N deposition (central Ireland), Verhoeven *et al.* (2011) have shown that vascular plant biomass and bryophyte biomass in a spring-fed bog were not affected when N was added as nitrate but were affected when ammonium-N was used. Vascular plant biomass was significantly higher in NH₄ treatments whilst bryophyte biomass significantly decreased. Similarly, vascular plant species diversity was not affected by N-dose or N-form treatments whereas bryophyte diversity declined greatly with NH₄ application. As in other studies, N-limitation is lifted and turned into P limitation with nitrogen-only additions. Graminoides increased with NH₄-N addition at this site, *Carex spp* biomass was largely unchanged but herbaceous species showed a decline.

Similar results to those of Verhoeven *et al.* (2011) have previously been found by Risager (1998) who showed that growth of *Sphagnum fallax* was significantly stimulated by the application of NH₄ but that NO₃ additions did not influence the growth of the species.

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M13 *Schoenus nigricans*–*Juncus subnodulosus* mire

(Account largely based on Wheeler *et al.*, 2009 and Rodwell, 1991)

Summary of physiognomy

Typically dominated by *Schoenus nigricans* and *Juncus subnodulosus*, although sometimes one or other is absent. *Phragmites australis* and *Molinia caerulea*, and sometimes *Cladium mariscus*, may be important, sometimes dominant. Species-poor stands with *Schoenus* and *J. subnodulosus* are usually better referred to as M22 (or M24) rather than M13. Stands of M13 provide some of the most diverse fen vegetation in Britain, a wide range of sedges, rushes, grasses, herbs and bryophytes occurring amongst the dominants, associated with the varied microtopography and environmental conditions provided by the tussocks and hummocks, interspersed with small runnels or pools. The community is important in supporting several rare and infrequent fen species (SEE Biodiversity value).

M13a *Festuca rubra*–*Juncus acutiflorus* sub-community (Rodwell, 1991)

Generally the most impoverished stands of M13, where species such as *Juncus subnodulosus* and *Molinia caerulea* tend to be more important than *Schoenus*, which is sometimes much reduced or even absent. Characteristic herbs and bryophytes are also generally reduced in number, while some grasses can make a more major contribution to the vegetation cover.

M13b *Briza media*–*Pinguicula vulgaris* sub-community (Rodwell, 1991)

Typically dominated by mixtures of *Schoenus*, *Juncus subnodulosus* and *Molinia* with a wide variety of associates (especially low-growing herbs and a variety of orchids) and a well-developed runnel flora, often with a high cover of bryophytes; vegetation often particularly species-rich.

M13c *Caltha palustris*–*Galium uliginosum* sub-community (Rodwell, 1991)

Also mostly dominated by mixtures of *Schoenus*, *Juncus subnodulosus* and *Molinia*, but often occurring in a mosaic with other monocots such as *Cladium mariscus*, *Carex rostrata*, *Carex diandra*, *Carex elata* and *Phragmites australis*. Runnel flora not so diverse as in M13b, and taller dicotyledons more common.

Species which are particularly characteristic of M13 (although not necessarily confined to M13), and which help separate it from other communities were identified by Wheeler, Shaw & Tanner (2009) – see Table M13-1. The number of these species recorded from a vegetation sample gives an indication of how well it ‘fits’ M13 (the more, the better), and, usually, the more characteristic M13 species present, the greater the representation of rare and regionally rare species.

Table M13-1 Species characteristic of M13 (after Wheeler *et al.*, 2009).

Characteristic species		
<i>Anagallis tenella</i>	<i>Dactylorhiza traunsteineri</i>	<i>Pedicularis palustris</i>
<i>Aneura pinguis</i>	<i>Drepanocladus lycopodioides</i>	<i>Pellia endiviifolia</i>
<i>Bryum pseudotriquetrum</i>	<i>Drosera longifolia</i>	<i>Philonotis calcarea</i>
<i>Campyliadelphus elodes</i>	<i>Eleocharis quinqueflora</i>	<i>Philonotis fontana</i>
<i>Campylium stellatum</i>	<i>Epipactis palustris</i>	<i>Pinguicula vulgaris</i>
<i>Carex dioica</i>	<i>Eriophorum latifolium</i>	<i>Plagiomnium elatum</i>
<i>Carex hostiana</i>	<i>Euphrasia pseudokernerii</i>	<i>Plagiomnium ellipticum</i>
<i>Carex pulicaris</i>	<i>Fissidens adianthoides</i>	<i>Potamogeton coloratus</i>
<i>Carex viridula</i> ssp	<i>Gymnadenia conopsea</i>	<i>Preissia quadrata</i>
<i>brachyrrhyncha</i>	<i>Hamatocaulis vernicosus</i>	<i>Riccardia chamedryfolia</i>
<i>Cladium mariscus</i>	<i>Listera ovata</i>	<i>Riccardia multifida</i>
<i>Dactylorhiza incarnata</i>	<i>Moerckia hibernica</i>	<i>Sagina nodosa</i>
<i>Dactylorhiza praetermissa</i>	<i>Palustriella commutata</i>	<i>Schoenus nigricans</i>
	<i>Parnassia palustris</i>	<i>Scorpidium</i>
		<i>cossonii/revolvens</i>
		<i>Scorpidium scorpioides</i>

Abiotic requirements for existence and restoration/creation

(a) Landscape

Most stands occur in valleyhead fens, on sloping ground, typically near the headwaters of small streams, but can also be found on soligenous slopes around small basins and sometimes at the upland margins of floodplains. The community can occasionally be found in topogenous sites, usually where there is particularly strong groundwater inflow, and sometimes forming trails along flow lines rather than large stands.

(b) Soils and geology

Can be found on a wide range of soil types and geological substrata, but usually found on a shallow (< 50cm) organic substratum, occasionally in old peat pits, and sometimes on very skeletal mineral soils; a few examples occur on deeper peat and marl. Occasionally found directly upon the bedrock, but most examples overlie permeable sands and gravels, or sandy silt. Examples over less permeable basal substrata tend to be drier than other examples.

Normally associated with calcareous bedrocks, primarily Chalk, or Carboniferous or Jurassic Limestones. A few examples are associated with Crag deposits (in Norfolk), or with areas of base-rich drift (sand and gravel).

(c) Soil chemistry

Most high-grade M13 stands occur on a base-rich substratum and are flushed by groundwater discharge across sloping ground. The substratum is typically of low fertility, as reflected in the low vegetation productivity reported by Wheeler & Shaw (1991) (mean increment (April to September) in dry weight of above ground standing crop of 200 g dry wt m⁻²).

Boyer and Wheeler (1989) showed that the low productivity of some examples of the community was mainly caused by P limitation, and that where this is the case, high concentrations of N have little influence on substratum fertility. However, Shaw and Wheeler (1991) did find a significant positive correlation between species density and substratum fertility – the likely cause being an increase in the occurrence of fen-meadow species. Thus, whilst in the absence of P, N enrichment may have little effect on stand floristics, an increase in P may lead to the development of fen meadow (M22) vegetation, where managed.

(d) Hydro-chemistry

M13 stands are mostly flushed by groundwater discharge across sloping ground, so accumulation and stagnation of water are not usually encountered. Irrigating waters are typically oligotrophic, base-rich/high pH [Tables M13.2 and M13.3 after Wheeler *et al.*, 2009], P-limited (in some cases due to adsorption of P onto calcite particles (Boyer and Wheeler, 1989)), and often supersaturated with calcium carbonate. Calcite precipitation is generally visible, either locally, or sometimes forming large tufaceous concretions ('tufa mounds'). The rare occurrence of ochre usually indicates that there is some contribution to the water supply from a drift aquifer. Concentrations of soluble reactive phosphorus (SRP) are often very low but those of N can be variable, and sometimes high; for example, Boyer and Wheeler (1989) measured > 30 mg l⁻¹ NO₃-N in some seepage waters.

Table M13.2 pH, conductivity and substratum fertility measured in stands of M13 (after Wheeler *et al.*, 2009).

Variable	Mean	Range
Water pH	7.0	5.7–8.3
Soil pH	7.1	5.4–7.5
Water conductivity (K_{corr} $\mu\text{S cm}^{-1}$)	565	301–928
Substratum fertility ² (mg phytometer)	7.0	2–18

Note: Experience has shown that N and P data derived from soil analysis has only limited use in assessing fertility of wetlands. Consequently the technique of phytometry (measuring the biomass of test species (phytometers) grown on soil samples) was developed. Typical phytometer yields (dry wt.); low fertility = <8mg, high fertility >18mg.

Table M13.3 Mean ion data for interstitial water samples for a limited selection of sites recorded by Boyer and Wheeler (1989) and Wheeler *et al.*, 2009)

Limits	pH	Ca ²⁺	Mg ²⁺	K ⁺	HCO ₃ ⁻	SRP*	NH ₄ ⁺	NO ₃ ⁻	SO ₄ ²⁻
Lower	7.0	97.0	3.0	1.4	285.0	5.0 x10 ⁻³	0.13	0.85	17.0
Upper	7.4	146.0	38.0	3.0	406.0	27.0 x10 ⁻³	0.32	32	73.0

All figures (apart from pH) are in mean concentration mg l⁻¹.

* Soluble reactive phosphorus

Note: Rodwell (1991) gives 60–200 mg l⁻¹, for calcium, quoting Wheeler 1975 and 1983

(e) Hydrology

[See Wheeler *et al.*, 2009 for detailed summary of water regime variables].

M13 communities are mostly associated with strongly soligenous conditions, often with visible springs, typically fed by lateral or vertical groundwater discharge from a semi-confined or unconfined aquifer (principally chalk or limestone, but sometimes from calcareous drift). Drier stands may be associated with an intermittent water supply. Sometimes found in topogenous situations, for example at the edge of a basin mire system, but fed by surface water from springs and seepages upslope or by direct groundwater outflow from an aquifer. M13 is occasionally found over low-permeability mineral deposits, on slopes flushed by groundwater outflow above the stand (such as Banc y Mwldan (Cardiganshire), Nantisaf (Ynys Môn)), although this is more often the case with M10 stands.

Of the three M13 sub-communities, the *Festuca rubra*–*Juncus acutiflorus* sub-community (M13a) tends to be associated with the wettest conditions, and the *Caltha palustris*–*Galium uliginosum* sub-community (M13c) with the driest.

Wheeler *et al* (2009) identified almost half of their M13 samples as occurring within WETMEC 10 (Permanent Seepage Slopes), and almost 30% within WETMEC 13 (Seepage Percolation Basins). “Most of the remainder occurred within WETMECs 9 (6%), 11 (7%), 15 (2%) and 17 (5%)”.

Water regime requirements are difficult to specify quantitatively for M13 because different versions of the community are associated with rather different water regimes, and particularly because the microtopographical variation, which is a typical feature of the community, leads to different regimes within individual stands. “(Wheeler and Shaw (2000) provide some details in Table M13.4 for stands in Eastern England. Consequently, mean water-table values have limited value, are potentially misleading and should be interpreted with caution”.

Table M13.4 Mean rainfall, potential evaporation and summer water table for M13 (after Wheeler *et al.*, 2009)

	Mean	Range
Rainfall (mm a ⁻¹)	724	558–1,050
Potential evaporation (mm a ⁻¹)	613	564–646
Mean summer water table (cm agl or bgl) (all sites)	–4.6	–38.6–8.4
Mean summer water table [Eastern England] (cm agl or bgl)	–9.5	–38.6–5.0

Wheeler *et al.* (2009) discussed the compass and syntaxonomy of M13, and the floristic overlaps between M13 and other communities such as M24 and M22, which mean that it is difficult to specify spatial limits of ‘pure’ stands and limits for associated environmental conditions such as water tables. For example, the species diversity of examples of M13 is often a consequence of the mosaic-like structure, where drier niches (tussock and hummock tops) tend to be occupied by plant species of drier (and sometimes more acidic) habitats, whilst low spots between usually provide wetter conditions and can support more aquatic species. Thus for example, stands with a greater proportion of higher, drier niches can have closer affinities to M24 than to M13, even though the associated water table may be within the range of optimal development of M13.

Wheeler *et al.* (2009) provide comments on optimal and sub-optimal (or damaging) water levels for M13 stands. Although due to the tussocky and mosaic nature of the vegetation structure, water levels experienced by different plant species can vary considerably within a stand, in general, most examples of M13 are found where water tables are at or close to the ground surface (–5 to +1 cm), the most species-rich examples occurring in locations where this is the case in both summer and winter. The sloping nature of the ground on which most stands are found means that surface water accumulation is usually prevented, other than in small, shallow pools, which may in any case experience considerable throughflow of water. This also means that there is frequently little difference between summer and winter water levels, except in particularly dry conditions. Stands occurring in situations where seepages are more intermittent, with seasonally sub-surface water tables, or where summer water tables are deeper than 30 cm bgl in non-drought years, tend to be less species-rich, particularly in the rarer bryophyte species, and a long term reduction in summer water table can be expected to lead to a reduction in diversity. Conversely, sites where the summer water table is above the surface between tussocks also tend to be less species-rich, and prolonged inundation or scouring can also be expected to lead to species losses, whilst drainage could be expected to lead to an increase in species diversity. However, it appears that examples of the community can withstand, or recover from, periodic summer droughts (of at least three years duration) when water tables may be 30 cm bgl.

If the contribution of groundwater flow is reduced, floristic changes may result, even if a high water table is maintained by other sources, due to such factors as reduced base supply, increased fertility and stagnation.

(f) Geographic distribution / climate

M13 is not a common vegetation type, but examples can be found scattered across England and Wales. It is essentially a lowland and southern community, being largely absent from upland

locations and Scotland (where comparable habitats are generally occupied by M10). Distribution is centred on two main locations, East Anglia and North Wales (especially Ynys Môn), but there are important outliers elsewhere (such as Cothill basin, Oxfordshire; North Yorkshire).

Rodwell (1991) considered that the climate, particularly summer warmth, plays an important part in restricting the range of the community. It includes some of the more Continental species which are very scarce in northern Britain, although some northern mire plants occasionally occur. Rodwell (1991) also highlights the complex interactions between climatic and edaphic factors which appear to determine the distribution of *Schoenus* (as, for example, described by Sparling (1968) and Proctor (2008)). Hydrological regime and substratum characteristics (including fertility) are also important in determining the distribution of the community, reflecting its association with conditions of continuous irrigation by base-rich and calcareous waters (and hence with lime-rich aquifers), conditions which are more prevalent in the south.

Regeneration requirements

The community is of quite local occurrence in Britain, being associated with a quite narrow range of edaphic conditions, and largely restricted to the warmer, drier southern lowlands of Britain (see Abiotic requirements for existence and restoration/creation). The likely success of restoration/regeneration activities depends on the starting conditions, and the ease with which conditions appropriate for the community can be provided, or re-development over the longer term facilitated, as well as the availability of appropriate plant material/seed sources.

It may be possible to restore damaged M13 stands by simple corrective management measures, providing damage is recent and not intensive; restoration of severely damaged stands or regeneration in 'new' sites is likely to be much more difficult. Removal of scrub and re-instatement of an appropriate management regime (normally mowing or grazing), should be sufficient to restore a stand that has been left unmanaged for a while, if other conditions have not changed irreversibly.

Removal of top soil from a partly-drained fen surface, followed by irrigation with calcareous water has been used to induce the spread of M13-like vegetation at Cors Erddreiniog, Anglesey, and it may be possible to use this approach to expand the area of M13 onto surfaces which have not naturally supported this community. However, rewetting of dry stands through raising water levels by blocking outflows could be detrimental if through-flow of water is prevented and strongly stagnant and reducing conditions are created.

Wheeler et al (2009) indicate that at Smallburgh Fen (Norfolk), there is some stratigraphical evidence (Wheeler, Shaw and Wells, 2003) to suggest that the current patches of M13-like vegetation have developed fairly recently from former shallow swamp and wet fen (e.g S2 and M9). This may be due to a slight natural drying of the surface in response to autogenic peat accumulation, or may represent a response to slight drainage of the fen basin as a result of the excavation of dykes and interception of spring flow.

At Dry Sandford Pit, Cothill, M13-like vegetation has developed spontaneously in appropriate, newly created groundwater-fed habitats, where a suitable source of species occurs nearby.

Vegetation management may increase the representation of certain M13 species in drier stands.

Threats from fragmentation, isolation

Many stands have been left isolated and much modified within intensive agricultural landscapes (Rodwell, 1991). Similar ecological issues and constraints on restoration, such as dispersal barriers and restrictions, to those discussed in relation to the fen-meadow and rush pastures almost certainly apply to M13.

Management practices

Some form of management, such as occasional burning, summer mowing or periodic light grazing, is generally important for the maintenance of species diversity; grazing and trampling in particular help to produce the microtopographical variation provided by a pronounced tussock/runnel system, which provides a variety of niches for different plant species to thrive. Bryophyte cover tends to be highest in tussocky stands, where the vegetation is kept quite open.

Lack of management or overgrazing can be detrimental. However, the effects of management may also depend on other factors such as substratum fertility and water table regime, as well as the identity of the associated species. Management is generally least important in low fertility, summer-wet stands and it is possible that some of these are largely self-maintaining, but where tussocks are tall and dense, or much litter accumulates, growth of lower-growing associates around the tussock bases and in runnels can be restricted. Management may be more significant in supporting species richness in more fertile, drier situations.

Lack of management can sometimes lead to the coalescence of *Schoenus* and *Molinia* tussocks, such that they merge to form an elevated 'platform' occupied largely by *Molinia* species, to form a stand lacking many typical M13 species. The stand may then develop floristically towards M24, even though the absolute level of the water table has not been reduced.

Predicted climate change threats

The M13 community does appear to have climatic, as well as edaphic and hydrological, constraints on its distribution (see Abiotic requirements for existence and restoration/creation), which will limit responses to climate change.

Threats from non native invaders

No information available.

Ecosystem Services

Evidence of water regulation value

Most high-grade M13 stands occur on a base-rich, low fertility substratum and are flushed by groundwater discharge across sloping ground (see Abiotic requirements for existence and restoration/creation). Such areas would not be appropriate for flood storage, sediment trapping or water quality enhancement.

Evidence of carbon storage value

Typically, but not always, found on an organic substratum, although this may be shallow (< 50cm); a few examples occur on deeper peat.

Biodiversity value

M13 stands are typically species-rich (Table M13.5) and the community is important in supporting many rare and uncommon fen plant species, particularly orchids and bryophytes, in some parts of lowland Britain. The community is thus of high conservation importance, and many sites are protected under national and international designations: examples of the M13 community have been included within the 'calcium-rich spring water-fed fens' SAC interest feature; some also fit the 'chalk-rich fen dominated by saw sedge' SAC interest feature, as indicated in Wheeler *et al.*, (2009). Even some degraded examples can have regional significance.

Table M13.5 Number of plant species recorded from stands of M13 (after Wheeler *et al.*, 2009)

	Total	Mean	Range
All species (spp 4 m ⁻²)	367	30.9	7–65
Mire species (spp 4 m ⁻²)	154	22.2	3–53
Rare mire species* (spp 4 m ⁻²)	39	2.3	0–13

* These include: *Calamagrostis canescens*, *Calamagrostis stricta*, *Calliargon giganteum*, *Campyliadelphus elodes*, *Carex appropinquata*, *Carex diandra*, *Carex elata*, *Carex lasiocarpa*, *Cladium mariscus*, *Dactylorhiza praetermissa*, *Dactylorhiza traunsteineri*, *Drepanocladus vernicosus*, *Drosera longifolia*, *Eleocharis uniglumis*, *Epipactis palustris*, *Eriophorum latifolium*, *Liparis loeselii*, *Moerckia hibernica*, *Oenanthe lachenalii*, *Peucedanum palustre*, *Philonotis calcarea*, *Pinguicula lusitanica*, *Plagiomnium elatum*, *Plagiomnium ellipticum*, *Potamogeton coloratus*, *Preissia quadrata*, *Primula farinosa*, *Pyrola rotundifolia*, *Ranunculus lingua*, *Rhizomnium pseudopunctatum*, *Selaginella selaginoides*, *Sphagnum contortum*, *Sphagnum russowii*, *Sphagnum subsecundum*, *Sphagnum teres*, *Thalictrum flavum*, *Thelypteris palustris*, *Thuidium deliculatum*, *Utricularia minor*.

Provisioning service value

Maintenance of species diversity depends on management (mostly grazing or mowing) but stands occur on low-fertility substrata with low productivity (mean increment (April to September) in dry weight of above ground standing crop was 200 g dry wt m⁻² (Wheeler & Shaw, 1991), and the vegetation probably provides fairly poor nutritional value.

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M14, *Schoenus nigricans*–*Narthecium ossifragum* mire

(Account largely based on Wheeler et al 2009 and Rodwell, 1991)

Summary of physiognomy

As with the M13 community, vegetation assigned to M14 is usually dominated by *Schoenus* (and often with *Molinia caerulea*), but here typically with fewer associated species, and including some species (such as *Eleocharis multicaulis*, *Pinguicula lusitanica*, *Rhynchospora alba*) which do not occur in M13. Species of bog moss (*Sphagnum* spp) are also usually much more prominent in M14 than in M13, but some of the basiphilous bryophytes (such as *Scorpidium scorpioides*, *Campylium stellatum*) are more patchily represented.

The community is only moderately-rich in plant species (5–38 spp per sample), but is important in supporting a wide range of rare mire species (see Biodiversity value).

Wheeler *et al.* (2009) discussed the compass and syntaxonomy of M14, and suggested that although it is a valuable unit, there are uncertainties about its compass and how it relates to some other communities. This means that there may be inconsistencies in the allocation of vegetation samples to this unit by different surveyors, which is critical to the specification of appropriate environmental regimes.

Abiotic requirements for existence and restoration/creation

(a) Landscape

Stands of M14 mostly occur on sloping sites with a strong input of telluric water, for example in valleyhead fens where they may occupy small flushes, seepages or soakways, sometimes within wet heath. Examples are known in Scotland where the community is found in soakways at the mineral edges of some blanket mires.

(b) Soils and geology

Found on firm peaty surfaces, but also on sloppy muds over more solid peat or mineral soil (especially in soakways), and occasionally forming a buoyant vegetation raft. Where peat is present, this is typically quite shallow (< 1m deep). Usually associated with lime-poor basal substratum, including sands, gravels, silts and clays.

(c) Soil chemistry

Most stands of M14 are found where a base-enriched water supply has ameliorated an otherwise acidic environment and are mostly associated with substrata of low fertility and moderate to high base status. Mean pH values are significantly lower than in the closely-related M13 community (Table 16.3).

Stands can be found where there are high concentrations of N, but there is some evidence for P-limitation, and also an increase in substratum fertility being associated with an increase in species density and number of rare fen species. However, this may have also been a response to an increase in base richness rather than to nutrients, and in general nutrient enrichment is likely to be detrimental (Shaw & Wheeler, 1991). The community can be found on some substrata with high

concentrations of toxic metals, which is surprising in view of the relatively high pH. Some particularly high Mn concentrations were found in some of the Scottish samples (Shaw & Wheeler, 1991).

(d) Hydro-chemistry

Characteristically found in locations with a relatively base-rich water supply (Table M14.1) with fairly low concentrations of bicarbonate and which is weakly buffered. It usually occurs as patches within the context of more acidic conditions, reflecting variations in the local hydrogeology. The base-enrichment may be derived, for example, from water draining over a base-rich aquitard or more directly by a localised groundwater outflow from a (weakly) calcareous aquifer³.

The tussocky structure of the vegetation means that a variety of conditions are provided; conditions on the tussock-tops tend to be more acidic and drier than on the ground in between, and thus provide appropriate conditions for calcifuges, whereas calcicoles are confined to the inter-tussock spaces where conditions are more influenced by the base-rich irrigating waters.

The association with relatively base-rich but weakly buffered water supply means that M14 may be particularly vulnerable to acidification in the surrounding catchment, and for the same reason, Wheeler et al (2009) suggested that it may be amongst the most sensitive of all mire communities to acid deposition. Acidification is likely to lead to the development of *Nartheccium ossifragum*–*Sphagnum papillosum* mire (M21).

It is also likely to be sensitive to enrichment by nutrients (either dissolved or in silt), particularly in surface-water fed examples, which is likely to lead to the development of a less species-diverse, taller, more productive sward, and eventual replacement by wet fen meadow or tall herb fen.

Table M14.1 pH, conductivity and substratum fertility measured in stands of M14 (after Wheeler et al, 2009)

Variable	Mean	Range
Water pH	5.5	4.6–6.5
Soil pH	5.6	4.4–6.8
Water conductivity (K_{corr} $\mu\text{S cm}^{-1}$)	170	59–470
Substratum fertility ⁴ (mg phytometer)	4.8	4–7

Rodwell (1991) quotes dissolved calcium concentrations of 5–35 mg l^{-1} and pH of 5 to just over 7.

(e) Hydrology

[See Wheeler et al. 2009 for more detailed summary of water regime variables].

³ There seems to be little evidence for the proposition of Rodwell (1991) that the base enrichment encountered within M14 is a function of a flow-induced increase in pH and calcium (see Wheeler et al, 2009)

⁴ Experience has shown that N and P data derived from soil analysis has only limited use in assessing fertility of wetlands. Consequently the technique of phytometry (measuring the biomass of test species (phytometers) grown on soil samples) was developed. Typical phytometer yields (dry wt.); low fertility = <8mg, high fertility>18mg.

M14 is mostly found in soakways and on soligenous slopes where there is a consistent throughflow of telluric water, fed either directly or indirectly by base-enriched groundwater outflow, although surface water may be significant in a few locations.

Wheeler et al (2009) identified almost half (48%) of samples as occurring within WETMEC 15 (Seepage Flow Tracks), 24 per cent within WETMEC 10 (Permanent Seepage Slopes) and 16 per cent within WETMEC 17 (Groundwater-Flushed Slopes). A few examples occurred within WETMECs 11, 13 and 19.

Water regime requirements are difficult to quantify for M14 because the microtopographical variation, which is a typical feature of the community, leads to different regimes within individual stands. Consequently, mean water table values have limited value, are potentially misleading and should be interpreted with caution. Values measured by Wheeler et al (2009) are provided in Table M14.2.

Table M14.2 Mean rainfall, potential evaporation and summer water table for M14 (after Wheeler et al, 2009).

	Mean	Range
Rainfall (mm a ⁻¹)	863	639–1,548
Potential evaporation (mm a ⁻¹)	597	534–620
Mean summer water table (cm agl or bgl)	1.4	–12 to +13.4

Wheeler et al (2009) provide comments on optimal and sub-optimal (or damaging) water levels for M14 stands, although few data are available. The community requires continuous irrigation; water levels appear to be near the surface in the runnels between tussocks year round, although levels are probably a little higher in winter than summer, which may lead to some inundation.

Strongly sub-surface water levels are not typical, and a prolonged lowering of water tables, either through drainage or reduction in water supply, can be expected to lead to a loss of wetland species and increase in dryland species, with development of rank fen and then woodland if unmanaged. Conversely, prolonged, deep inundation, especially if associated with stagnation of water in spring or summer, is likely to lead to species losses and development of less diverse vegetation types.

Even if appropriate water levels are maintained overall, a change in water source or a reduction in base-rich water inflow could be detrimental; an impact which may originate in changes to groundwater or surface water sources some considerable distance from the mire.

(f) Geographic distribution / climate

Mainly occupying only small areas and largely confined to the more oceanic south of England (occurring locally in Cornwall, Devon, Dorset and the New Forest). However, although Rodwell (1991) only includes southern examples (and considers examples in north-west Scotland to be *Schoenus*-dominated stands of the *Scirpus–Erica* wet heath (M15)), there appear to be some outliers of similar vegetation in Norfolk, Shropshire, Yorkshire, Cumbria and Wales, as well as associated with some of the flushed blanket mire and patterned fens of Northern Scotland (Shaw & Wheeler, 1991). The distribution of the community and differences in the floristics of the northern and southern stands are likely to be influenced by climatic as well as edaphic factors (Rodwell, 1991). However,

the poor-representation of Continental species in M14 may be co-incidental as some of these species are calcicolous and mesophytic (Rodwell, 1991).

Biotic requirements for existence and restoration/creation

Mycorrhizal associations

See *Ecoflora*. (ecoflora.co.uk)

Regeneration requirements

The community is of quite local occurrence in Britain, apparently being associated with a quite narrow range of edaphic and climatic conditions (see Abiotic requirements for existence and restoration/creation). The likely success of restoration/regeneration activities depends on the starting conditions, and the ease with which conditions appropriate for the community can be provided, or re-development over the longer term facilitated, as well as the availability of appropriate plant material/seed sources. It may be possible to restore M14 stands by simple corrective management measures, providing damage is recent and not intensive, but restoration of severely damaged stands or regeneration in 'new' sites is likely to be much more difficult.

One of the best and most extensive examples of M14 (at Hartland Moor, Dorset) occurs in a location which *may* be a former turbarry. This suggests that in an appropriate hydrogeological, valleyhead context, it may be possible to recreate M14 in a dry site by removal of turf to create wetter conditions (Wheeler et al, 2009). However, rewetting of dry stands through raising water levels by blocking outflows could be detrimental if through-flow of water is prevented and strongly stagnant and reducing conditions are created.

Threats from fragmentation, isolation

Most stands are small in extent, and the community is very local, partly because suitable habitats are naturally scarce, but also due to a reduction in their extent by human activity (Rodwell, 1991). Thus, it is probable that the community is likely to be particularly vulnerable to further fragmentation.

Management practices

Most stands of M14 occupy only small areas and thus management (typically grazing or occasional burning) is usually dependent on the context of the surrounding habitats (e.g. heathland).

Maintenance of species diversity appears to require some grazing pressure, but heavily grazed stands had lower species numbers, and fewer rare species, than the more lightly grazed stands (Shaw and Wheeler, 1991). Heavy grazing can also tend to fragment the sward. Unmanaged stands tend to have lower species diversity and numbers of typical fen species than those that are managed (Shaw & Wheeler, 1991), and absence of management can be expected to lead to scrub invasion and the eventual development of a type of wet woodland. Some wet examples appear to be self-maintaining if unmanaged, but as stands are usually small, development of scrub/woodland on adjoining habitats may lead to overgrowth and shading and a change in the community anyway.

Apart from lowering water levels, ditching could lead to the complete destruction of examples that are particularly narrow.

Predicted climate change threats

The distribution of the community and differences in the floristics of the northern and southern stands appear to be influenced by climatic as well as edaphic and hydrological factors, which will limit responses to climate change (see Abiotic requirements for existence and restoration/creation).

Threats from non native invaders

No information available

Ecosystem Services

Evidence of water regulation value

Most M14 stands occur on a moderately base-rich, low fertility substratum with constant irrigation (but without deep inundation) (see Abiotic requirements for existence and restoration/creation). Such areas would not be appropriate for flood storage, sediment trapping or water quality enhancement.

Evidence of carbon storage value

Often, but not always, found on an organic substratum, although this may be quite shallow (< 1 m).

Biodiversity value

Moderately-rich in plant species (5–38 spp per sample), and particularly important in supporting a wide range of rare mire species (Table M14.3). The community is thus of high conservation importance, and many sites are protected under national and international designations: examples of the M14 community have been included in the “chalk-rich fen dominated by saw sedge” and “transition mire and quaking bog” SAC interest features. [See Tables 3.1 and 3.3 in Wheeler et al, 2009]

Table M14.3 Number of plant species recorded from stands of M14 (after Wheeler et al, 2009).

	Total	Mean	Range
All species (spp 4 m ⁻²)	154	18.5	5–38
Mire species (spp 4 m ⁻²)	106	16.4	5–34
Rare mire species* (spp 4 m ⁻²)	22	1.3	0–5

* These include: *Calliergon giganteum*, *Cladium mariscus*, *Drosera intermedia*, *Drosera longifolia*, *Epipactis palustris*, *Erica ciliaris*, *Eriophorum gracile*, *Eriophorum latifolium*, *Hammarbya paludosa*, *Hypericum undulatum*, *Osmunda regalis*, *Philonotis calcarea*, *Pinguicula lusitanica*, *Rhizomnium pseudopunctatum*, *Selaginella selaginoides*, *Sphagnum contortum*, *Sphagnum molle*, *Sphagnum pulchrum*, *Sphagnum subsecundum*, *Thelypteris palustris*, *Utricularia intermedia*, *Utricularia minor*.

Provisioning service value

M14 often occurs in grazed sites (and is sometimes damaged by heavy grazing) (see above) but on low-fertility substrata, so the vegetation probably provides fairly poor nutritional value.

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M21, *Narthecium ossifragum*–*Sphagnum papillosum* mire

(Account largely based on Wheeler et al 2009 and Rodwell, 1991)

Summary of physiognomy

Both *Narthecium ossifragum* and *Eriophorum angustifolium* are constant and often abundant in this fairly species-poor, poor-fen community, and can give it a striking and colourful appearance, but it is the extensive carpets of *Sphagna* (in particular *S. papillosum*) that are particularly characteristic. A variety of leafy liverworts and scattered herbs and sub-shrubs (such as *Calluna vulgaris*, *Erica tetralix*, *Myrica gale*) also occur, but small sedges and rushes tend to be infrequent. *Molinia caerulea* is frequently found, but does not generally form large tussocks. Calcicolous species are mostly lacking, but occasionally species such as *Anagallis tenella*, *Cirsium dissectum* and *Schoenus nigricans* can be found.

The community is fairly species-poor (5–39 spp per sample), although overall it supports over 20 rare mire species (see Biodiversity value).

M21a *Rhynchospora alba*–*Sphagnum auriculatum* sub-community (Rodwell, 1991)

The most frequent type of M21, with a *Sphagnum* carpet generally dominated by mixtures of *S. papillosum* and *S. auriculatum* (now called *S. denticulatum*). Liverworts, for example, *Odontoschisma sphagni*, *Kurzia pauciflora* and *Aneura pinguis*, are often abundant, as are the vascular constants of the community, and frequently *Rhynchospora alba* and *Myrica gale*.

M21b *Vaccinium oxycoccos*–*Sphagnum recurvum* sub-community (Rodwell, 1991)

S. recurvum tends to be more abundant in M21b than M21a, and *S. papillosum* more patchy, whilst *S. auriculatum*(*denticulatum*) is much reduced in frequency. The liverwort component is generally less rich than in M21a. *Vaccinium oxycoccos* and *Potentilla erecta* are more frequent, but *R. alba* scarcer than in M21a.

Wheeler *et al.* (2009) discussed the compass and syntaxonomy of M21, and showed that (a) it shares some floristic similarities with certain types of ombrogenous mire (for example showing much overlap with *Sphagnum cuspidatum/recurvum* bog pool community (M2) (especially the M21b sub-community); (b) some stands also have strong affinities with *Schoenus nigricans*–*Narthecium ossifragum* mire (M14); (c) some atypical, species-poor stands, rich in *Molinia caerulea* and with a rather limited development of *Sphagnum*, are difficult to place.

Abiotic requirements for existence and restoration/creation

(a) Landscape

Characteristically found in valleyheads and troughs, where the ground may be strongly or quite gently sloping, but in permanently waterlogged, soligenous situations.

(b) Soils and geology

Mostly associated with acidic substrata, such as Eocene clays, sands and gravels and Lower Greensand deposits in southern England, and occurring on shallow (20–150 cm) acid and oligotrophic peats. In Cumbria and Wales some examples are associated with Silurian deposits which may support local minor aquifers, with fracture flow within superficial fracturing.

(c) Soil chemistry

Although some examples have been found on soils with a pH greater than 6, most stands are found in base- and nutrient-poor conditions [Table M21.1], and are therefore likely to be particularly vulnerable to increases in base status or eutrophication. There is some evidence for an increase in soil fertility to be related to a significant decrease in the number of rare species present in the vegetation, but no overall relationship was found between soil fertility and the number of mire species (Shaw & Wheeler, 1991). In some situations, nutrient enrichment may cause a coarsening of the vegetation, for example expansion of such species as *Molinia caerulea*; in others, it may encourage the establishment of atypical species and development of rank fen, especially if accompanied by a reduction in water levels.

Available data suggest that mean extractable substratum concentrations of Fe and Al are high, but this reflects the inclusion of some stands with extremely high concentrations, for example Dersingham Bog (Norfolk), although the numbers of species present (other than rare species) did not seem to be adversely affected. However, Mn concentrations were typically moderate to low.

(d) Hydro-chemistry

Typically associated with base-poor groundwaters, with an increase in base status being associated with an increase in species richness and base enrichment may be associated with the development of M14 (Shaw & Wheeler, 1991). These authors also found that stands of M21b could be found in some sites of higher base status than M21a.

In situations where the community occurs alongside streams and soakways, the community may be vulnerable to enrichment from these.

Table M21.1 pH, conductivity and substratum fertility measured in stands of M21, *Narthecium ossifragum*–*Sphagnum papillosum* mire (after Wheeler et al 2009)

Variable	Mean	Range
Water pH	4.7	3.4–6.8
Soil pH	4.9	3.3–6.6
Water conductivity (K_{corr} $\mu\text{S cm}^{-1}$)	133	31–536
Substratum fertility ⁵ (mg phytometer)	5.6	1–12

(e) Hydrology

Although most, if not all stands, appear to be dependent on a groundwater supply, little is known about groundwater sources for many M21 sites. In southern England, the water supply to M21 stands in valleyheads appears to be mainly base-poor groundwater, but in wetter northern and

⁵ Experience has shown that N and P data derived from soil analysis has only limited use in assessing fertility of wetlands. Consequently the technique of phytometry (measuring the biomass of test species (phytometers) grown on soil samples) was developed. Typical phytometer yields (dry wt.); low fertility = <8mg, high fertility>18mg.

western areas (e.g. Wales and Cumbria), where rainfall and surface water run-off probably provide a greater contribution, groundwater outflow may be less important.

Wheeler et al (2009) identified 24% of M21 samples as occurring within WETMEC 10 (Permanent Seepage Slopes), 22% in WETMEC 14 (Seepage Percolation Troughs), 19% in WETMEC 15 (Seepage Flow Tracks), 13% in WETMEC 16 (Groundwater-Flushed Bottoms), and 11% in WETMEC 17 (Groundwater-Flushed Slopes). A few examples occurred within WETMECs 2, 11, 13 and 19. The examples from WETMECs 2 and 13 are all rheo-topogenous, representing basins supplied with a throughflow of weakly minerotrophic water (WETMEC 2c) or small, wet sumps embedded within examples of WETMECs 14 or 16.

Mean values for annual rainfall and potential evaporation for the sites examined by Wheeler et al (2009) are given in Table M21.2 together with mean recorded values for summer water table associated with stands of M21.

Table M21.2 Mean rainfall, potential evaporation and summer water table for *Narthecium ossifragum*–*Sphagnum papillosum* mire (M21) (after Wheeler et al, 2009)

	Mean	Range
Rainfall (mm a ⁻¹)	883	627–2,101
Potential evaporation (mm a ⁻¹)	593	474–620
Mean summer water table (cm agl or bgl)	–0.6	–23 – +15

Wheeler et al (2009) provide comments on optimal and sub-optimal (or damaging) water levels for M21 stands, although few data are available. Most stands occur in situations that are permanently waterlogged. Water levels in summer are typically at or just below surface level and appear to be relatively stable year-round, which favours the growth of peat-building *Sphagna* (Rodwell, 1991) such as *Sphagnum papillosum*. Shaw and Wheeler (1991) found that mean water levels were higher in the M21a sub-community than M21b, as reflected in the greater abundance of *Sphagnum auriculatum* (*denticulatum*) and *Rhynchospora alba*.

Stands occurring away from the main point of groundwater discharge, or where seepages are weaker, often support more tussocky *Molinia* (although this may also relate to a change in substratum conditions such as nutrient availability).

Strongly sub-surface water levels are not typical, and prolonged lowering of water tables (whether by drainage or reduction in supply), can be expected to lead to a loss of wetland species and increase in dryland species, with development of rank fen or wet then dry heath (turning to woodland if not managed). Partial drainage, with seasonal or intermittent waterlogging, is also likely to lead to the replacement of the typical *Sphagnum* species complement with those more tolerant of drier conditions, with development towards wet heath and/or increase in *Molinia* dominance (particularly where water levels strongly fluctuate). The latter may also increase in situations where there is a reduction in groundwater outflow; stands which are less consistently wet than typical may also be more prone to damage by burning and grazing (including poaching). Drying may also make stands more vulnerable to damage by burning, as well as permitting greater access to, and possible damage by, grazing animals.

Deep inundation, especially if associated with stagnation of water in spring or summer, is also likely to lead to species losses, and may lead to the development of bog-pool vegetation types, unless the vegetation can form a buoyant raft.

A change in water source on its own may not have much effect unless there is also a significant change in water quality (e.g. eutrophication).

(f) Geographic distribution / climate

The community can be found in Cumbria and North Yorkshire and scattered in Wales, but is largely restricted to the warmer, drier southern lowlands of Britain, being particularly characteristic of the acidic valley mires of Southern and South-Western England, especially in the New Forest (Hampshire) and Dorset. Rodwell (1991) maps no records for Scotland, but stands in some Scottish mires (mainly in the Borders and the Hebrides) have been identified as this community (Wheeler et al, 2009).

The two sub-communities of M21 show a difference in distribution, with the *Rhynchospora alba*–*Sphagnum auriculatum* sub-community (M21a) mostly occurring in the south, and *Vaccinium oxycoccus*–*Sphagnum recurvum* sub-community (M21b) to the north and west (Rodwell, 1991). This difference may relate to climatic, as well as edaphic factors.

Biotic requirements for existence and restoration/creation

Mycorrhizal associations

See Ecoflora. (ecoflora.co.uk)

Regeneration requirement

The community is of quite local occurrence in Britain, largely restricted to the warmer, drier southern lowlands of Britain, and apparently associated with a quite narrow range of edaphic and climatic conditions (see Abiotic requirements for existence and restoration/creation). The likely success of restoration/regeneration activities depends on the starting conditions, and the ease with which conditions appropriate for the community can be provided, or re-development over the longer term facilitated, as well as the availability of appropriate plant material/seed sources. It may be possible to restore M21 stands by simple corrective management measures, providing damage is recent and not intensive, but restoration of severely damaged stands or regeneration in ‘new’ sites is likely to be much more difficult.

Spontaneous regeneration of M21 seems to have occurred on former turbary sites, suggesting that removal of peat may be an appropriate restoration measure in mires that are becoming dry.

Some M21 sites in the New Forest have been adversely affected by drainage and erosion; restoration initiatives have attempted to reverse the impacts, for example by the use of heather bales and gabions.

Threats from fragmentation, isolation

‘Ecoflora’ has a few relevant details (on dispersal) for individual species.

Management practices

There is some evidence that managed stands support more species, and more rare species than unmanaged stands, but in general management did not have a major impact on stand floristics (Shaw & Wheeler, 1991). Stands are typically grazed, and management probably helps to maintain species diversity and retard successional processes (although the wet conditions mean that in the absence of management the community would probably be slow to change). In the New Forest and Dorset, most stands occur within the open grazing land, and can be heavily grazed (especially during dry periods); this may cause damage including fragmentation of the *Sphagnum* carpets, although not necessarily loss of species.

Although the low fertility probably helps to retard invasion by 'coarse' species, drainage is detrimental and leads to loss of species (particularly *Sphagna*), increased likelihood of damage from grazing or burning, and likely development towards wet heath/ scrub/woodland (see above (e) Hydrology).

Some mires have been damaged by peat-cutting, but sometimes this has led to a diversification of the surface patterning, and in dry sites may produce areas suitable for regeneration of M21.

Predicted climate change threats

The M21 community does appear to have climatic, as well as edaphic and hydrological, constraints on its distribution (see Abiotic requirements for existence and restoration/creation), which will limit responses to climate change.

Threats from non native invaders

No information available

Ecosystem Services

Evidence of water regulation value

Most M21 stands occur on a base-poor, low fertility substratum with constant irrigation (but without deep inundation) (see Abiotic requirements for existence and restoration/creation). Such areas would not be appropriate for flood storage, sediment trapping or water quality enhancement.

Evidence of carbon storage value

Mostly occurring on shallow (20–150 cm) acid and oligotrophic peats.

Biodiversity value

Stands are typically only moderately rich in plant species (5–39 spp per sample) although important in supporting a wide range of rare mire species (see Table M21.3). The community is thus of high conservation importance, and many sites are protected under national and international designations, for example some are included in the "depressions on peat substrates (*Rhynchosporion*)" SAC feature (though this community rarely occurs in such situations, nor is it referable to the *Rhynchosporion* (Wheeler et al, 2009)).

Table M21.3 Number of plant species recorded in stands of M21 (after Wheeler et al, 2009)

	Total	Mean	Range
All species (spp 4 m ⁻²)	244	16.9	5–39
Mire species (spp 4 m ⁻²)	125	13.7	5–29
Rare mire species* (spp 4 m ⁻²)	24	1.2	6

* These include: *Andromeda polifolia*, *Carex lasiocarpa*, *C. limosa*, *C. magellanica*, *C. pauciflora*, *Cephalozia loitlesbergeri*, *C. macrostachya*, *Cladium mariscus*, *Cladopodiella fluitans*, *Dactylorhiza praetermissa*, *Drosera intermedia*, *Drosera longifolia*, *Erica ciliaris*, *Eriophorum gracile*, *Hammarbya paludosa*, *Osmunda regalis*, *Pinguicula lusitanica*, *Sphagnum contortum*, *Sphagnum molle*, *Sphagnum pulchrum*, *Sphagnum subsecundum*, *Sphagnum teres*, *Sphagnum warnstorffii*, *Utricularia intermedia*, *Utricularia minor*.

Provisioning service value

M21 mostly occurs in grazed sites (and is sometimes damaged by heavy grazing) (see above) but on low-fertility substrata, so the vegetation probably provides fairly poor nutritional value.

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M29, *Hypericum elodes*–*Potamogeton polygonifolius* soakway

(Account largely based on Wheeler et al 2009 and Rodwell, 1991)

Summary of physiognomy

The *Hypericum elodes*–*Potamogeton polygonifolius* soakway community is generally quite distinctive and readily identified, because both the soakway habitat in which it usually occurs and both *Hypericum* and *Potamogeton* are easily seen. The vegetation is characteristically low-growing, with mats comprising these two species, often with a submerged carpet of *Sphagnum denticulatum*, and a limited range of vascular associates (such as *Ranunculus flammula*, *Juncus bulbosus*). *Phragmites* can be prominent in stands which are not closely grazed. M29 can be variable in species composition, but is often moderately species-rich (see Biodiversity value).

Abiotic requirements for existence and restoration/creation

(a) Landscape

Characteristically found in shallow soakways, pools and water tracks in valleyhead wetlands, but can also occur in hillslope, basin and floodplain wetlands, where it may pick out zones of greater lateral water flow, or occasionally forming isolated, shallow seasonal pools on heathlands.

(b) Soils and geology

The substratum usually consists of a mixture of very loose peat, water and liquid muds over a more solid peat (mostly shallow) or over silt or clay (Wheeler et al, 2009); sometimes in flushed former peat pits or seasonally-flooded pools. Basal material ranged from sands and gravels to silts and clays.

(c) Soil chemistry

Rodwell (1991) indicates that calcium concentrations are probably low in most cases and the character of the vegetation suggests that low availability of phosphorus and relatively slow turnover of nitrogen limit growth. Shaw & Wheeler (1991) found some examples with high substratum values of N, P or K, but substratum fertility values were generally low, and there was no direct relationship between fertility and species density (grazing may help to prevent the coarsening of the vegetation). However, these authors found that increases in calcium and bicarbonate concentrations were associated with increase in species richness and sites with higher conductivity and magnesium supported more rare species.

(d) Hydro-chemistry

M29 is typically found in low fertility, base-poor conditions (Table) but perhaps slightly higher fertility than *Schoenus nigricans*–*Narthecium ossifragum* mire (M14) (Wheeler et al, 2009). Substantial enrichment of the substratum, whether as a result of drying-induced mineralisation or direct nutrient inputs, is likely to lead to the replacement of M29 by more rank vegetation, especially in the absence of grazing.

Potamogeton polygonifolius is characteristically found in conditions ranging from oligotrophic to mesotrophic (Preston & Croft, 1997)

Table pH, conductivity and substratum fertility measured in stands of M29 (after Wheeler *et al*, 2009)

Variable	Mean	Range
Water pH	5.2	4.5–6.4
Soil pH	5.3	4.5–6.4
Water conductivity (K _{corr} , $\mu\text{S cm}^{-1}$)	131	40–691
Substratum fertility ⁶ (mg phytometer)	6.9	2–13

(e) Hydrology

Mostly found in soakways and water tracks, in locations with at least gently flowing water; examples in more topogenous locations (including peat cuttings) have water flowing through. Over half (56%) of the samples examined by Wheeler *et al* (2009) occurred within WETMEC 15 (Seepage Flow Tracks), and 25 per cent within WETMEC 19 (Flow Tracks). A few examples occurred within WETMEC 10: Permanent Seepage Slopes, WETMEC 17: Groundwater-Flushed Slopes and WETMEC 20: Percolation Basins.

Mean values for annual rainfall and potential evaporation for the sites examined by Wheeler *et al* (2009) are given in Table M29.2, together with mean recorded values for summer water table associated with stands of M29.

Table M29.2 Mean rainfall and potential evaporation for M29 stands (after Wheeler *et al*, 2009)

	Mean	Range
Rainfall (mm a^{-1})	1,253	627–2,101
Potential evaporation (mm a^{-1})	572	524–614
Mean summer water table (cm)	2.5	–10 to +15

Wheeler *et al* (2009) provide comments on optimal and sub-optimal (or damaging) water levels for M29 stands, although few data are available. Shallow flooding, with some water moving through, is characteristic and possibly essential, at least during part of the year, although summer water levels are variable, and may be well below the surface in some soakways and hollows, leaving moist mud. Stands often occupy areas of increased lateral water movement or vertical fluctuation in water level, forming a narrow, but distinct zone within other vegetation types.

Strongly sub-surface water levels, particularly in winter, are not typical, although some stands experience low levels in summer. Prolonged lowering of water tables can be expected to lead to a loss of wetland species and increase in dryland species, as well as damage due to increasing grazing pressure, with scrub invasion if unmanaged. Conversely, prolonged, deep inundation is likely to lead to species losses.

A change in water source on its own may not have much effect unless there is also a significant change in water quality (e.g. eutrophication) or flow rate, although it should be noted that the ecological requirements of M29 are particularly poorly understood (Wheeler *et al*, 2009).

⁶ Experience has shown that N and P data derived from soil analysis has only limited use in assessing fertility of wetlands. Consequently the technique of phytometry (measuring the biomass of test species (phytometers) grown on soil samples) was developed. Typical phytometer yields (dry wt.); low fertility = <8mg, high fertility>18mg.

(f) Geographic distribution / climate

M29 is confined to western Britain, being mainly found in the South-West, New Forest, Surrey, and throughout Wales, extending north into Southern Cumbria and into western Scotland (Rodwell, 1991, Wheeler et al, 2009). It is characteristic of the warm, oceanic parts of the country where February minima are usually at least a degree above freezing (Rodwell, 1991).

Biotic requirements for existence and restoration/creation

Mycorrhizal associations

Ecoflora www.ecoflora.co.uk: *Potamogeton polygonifolius*: Mycorrhizal type: absent, Frequency: never mycorrhizal (Harley & Harley, 1987).

H. elodes: No UK data available

Regeneration requirement

Ecoflora www.ecoflora.co.uk: *Potamogeton polygonifolius* reproduces by seeds and vegetatively (turions and rhizomes), it is also wind pollinated (Clapham, Tutin & Moore, 1987).

The community is of quite local occurrence in Britain, being associated with a quite narrow range of edaphic conditions, and largely restricted to the warmer, more oceanic parts of Britain (see Abiotic requirements for existence and restoration/creation). The likely success of restoration/regeneration activities depends on the starting conditions, and the ease with which conditions appropriate for the community can be provided, or re-development over the longer term facilitated, as well as the availability of appropriate plant material/seed sources. It may be possible to restore M29 stands by simple corrective management measures, providing damage is recent and not intensive, but restoration of severely damaged stands or regeneration in 'new' sites is likely to be much more difficult.

Rewetting of dry areas through raising water levels by blocking outflows could be detrimental if through-flow of water is prevented, but if shallow pools are created, M29 may colonise, or even expand into adjoining communities, such as M21.

Threats from fragmentation, isolation

Rodwell (1991) comments that the habitats supporting this community are often found in small, fragmented and isolated situations, which probably has an influence on the considerable floristic variation between stands, due to differences in environmental conditions as well as chance influencing colonisation.

Management practices

Conservation management involves ensuring low fertility and relatively base-poor conditions, possibly coupled with some grazing (Wheeler et al, 2009). Most stands of M29 occupy only small areas and thus management (typically grazing) is usually dependent on the context of the surrounding habitats. Shaw & Wheeler (1991) found that lightly grazed sites had more species (including fen and rare fen species) than heavily grazed sites, and heavy grazing may lead to fragmentation of the sward (especially the *Sphagnum* carpet) (see also Ratcliffe & Hattey, 1982 and Alcock et al, 1984), although both *Hypericum elodes* and *Potamogeton polygonifolius* appear to be resistant to close grazing (and thus the community may be promoted by grazing). Some wet

examples appear to be self-maintaining if unmanaged, but as stands are usually small, development of scrub/woodland on adjoining habitats may lead to overgrowth and shading and a change in the community anyway.

Lack of management may not necessarily be detrimental, although this may depend on the wetness of the substratum. In summer-dry sites, grazing may help to prevent scrub invasion.

Predicted climate change threats

The strongly oceanic distribution of this community in the UK (which reflects that of *Hypericum elodes*) suggests that there is some climatic control on its distribution (Wheeler *et al*, 2009). There are also edaphic and hydrological constraints on its distribution (see Abiotic requirements for existence and restoration/creation), which will also limit responses to climate change.

Ecoflora [www.ecoflora.co.uk]:

Potamogeton polygonifolius:

Altitudinal range: max recorded 780m (Preston & Croft, 1997).

Max depth of leaves: < 0.5m. Floating to submerged (Clapham *et al* 1987)

Jan mean temperature: 3.3°C (Hill, Preston & Roy, 2004)

July mean temp: 13.9°C (Hill, Preston & Roy, 2004)

Annual ppt. 1254 mm (Hill, Preston & Roy, 2004)

Threats from non native invaders

Report of invasion by *Crassula helmsii* at Woolmer Forest SSSI, Hants. (Cox and Pincombe, 2011)

Ecosystem Services

Evidence of water regulation value of M29

Most M29 stands occur on a base-poor, low fertility substratum with constant irrigation (but with only shallow flooding) (see Abiotic requirements for existence and restoration/creation). Such areas would not be appropriate for flood storage, sediment trapping or water quality enhancement.

Evidence of carbon storage value

Often, but not always, found on an organic substratum, although this may be quite shallow.

Biodiversity value

A moderately species-rich community (7–32 plant spp per sample), which is important in supporting a range of rare mire species (Table M29.3), including the nationally rare *Eriophorum gracile*. The community is thus of considerable conservation importance, and many sites are protected under national and international designations; for example, some stands have been included in the “transition mire and quaking bog” SAC interest feature. [See Tables 3.1 and 3.3 in Wheeler *et al* 2009]

Table M29.3 Number of plant species recorded from stands of M29 (after Wheeler *et al*, 2009)

	Total	Mean	Range
All species (spp 4 m ⁻²)	139	19.3	7–32
Mire species (spp 4 m ⁻²)	101	17.5	6–28

Rare mire species (spp 4 m ⁻²)	14	0.9	0–5
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* These include: *Calliergon giganteum*, *Carex elata*, *Carex lasiocarpa*, *Carex limosa*, *Drosera intermedia*, *Eleocharis uniglumis*, *Eriophorum gracile*, *Osmunda regalis*, *Parentucellia viscosa*, *Philonotis calcarea*, *Sphagnum contortum*, *Sphagnum subsecundum*, *Utricularia intermedia*, *Utricularia minor*

Provisioning service value

M29 stands often occur in grazed sites (and are sometimes damaged by heavy grazing) (see above) but they are typically small in extent and on low-fertility substrata, so the vegetation probably provides fairly poor nutritional value.

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M35: *Ranunculus omiophyllus*-*Montia fontana* rill.

A vegetation type which has attracted little attention in the literature of British plant communities (Rodwell 1991). Butcher (1933), in his early account of the vegetation of the different types of stream bed, provided a list of the flowering plants most frequently encountered in channels with rapid flows: *R. lenormandi* (= *R. omiophyllus*) is recorded as 'frequent' as is *Ranunculus fluitans* whilst *Glyceria fluitans*, *Montia fontana* and species of *Potamogeton* are characterised as 'locally abundant'. *Philonotis fontana* is also included as an abundant moss. This collection bears a close resemblance to the composition of a typical stand of M35.

M35 is not included as a running water habitat (Codes 3210-3290) in the Natura 2000 Interpretation Manual of European Union Habitats (EU 1999). This omission is somewhat surprising given the relative rarity of streams supporting *R. omiophyllus* in Europe.

Syntaxonomy of M35

The M35 Ranunculus omiophyllus-Montia fontana rill community falls within the Cardamino-Montion alliance (Rodwell 1991). The alliance covers spring vegetation of base-poor waters and the British representatives span six communities, four of which are high altitude vegetation types:

M34: *Carex demissa-Koenigia islandica* flush (Birks 1973). This is confined in the UK to the Isle of Skye with a mean altitude of 625m (Rodwell 1991) with similar vegetation recorded elsewhere in Scandinavia.

M31: *Anthelia julacea-Sphagnum auriculatum* spring (Shimwell 1972). A local but widespread community throughout much of Scotland with a few outliers in the Lake District and Snowdonia, having a mean altitude of 712m.

M32: *Philonotis fontana-Saxifraga stellaris* spring (Nordhagen 1943). A high altitude community having a similar geographic distribution to that of M32 also found in suitable locations in mainland Scandinavia, Iceland and the Faroe Islands. Rodwell gives a mean altitude for the British releveés of 701m.

M33: *Pohlia wahlenbergii* var. *gracilis* spring (McVean and Ratcliffe 1962). The most high altitude (mean 992m) of the British communities; also found in Norway (Nordhagen 1943).

The alliance has a single low altitude representative in M36, lowland springs and stream banks of shaded situations, this community, not separately sampled in the NVC, features *Cardamine flexuosa* and *Chrysosplenium alternifolium* and is based on the *Cardaminion* of Westhoff and den Held (1969) and is similar to the *Cardaminion montion* of Schaminée *et al.* (1995).

The *Ranunculus omiophyllus-Montia fontana* rill (M35) completes the series as an intermediate community of moderate altitudes in southwestern England, the Welsh Marches, Wales and the Lake District. No altitude range is given for M35 in the published tables but most samples are likely to be found between 250m and 450m on Dartmoor, Bodmin Moor, Ceredigion and the Lake District though good examples also occur in Snowdonia, sometimes at higher elevations e.g. c.600m on the Glyders (Prosser pers.obs.) whilst the distribution of *Ranunculus omiophyllus* itself can extend to 1005m as on Carnedd Llewelyn, also in Snowdonia (Preston *et al.* 2002).

Habitat.

Ranunculus omiophyllus is an oceanic west European plant which although found on damp soil of e.g. gateways and tracks is more usually associated with flowing water. The term rill refers to water trackways in channels often formed through erosion and it is in such a situation within tracts of blanket bog or heathland over acidic rocks that the M35 community is most frequently encountered. Such rills are usually shallow (<25cm), with a reasonable rate of flow and with oxygen levels close to saturation. The community is irrigated by usually quite oligotrophic waters; these are typically base- and nutrient-poor with pH values ranging from 4.5 to 6.5 (Elkington *et al.* 2001). JNCC monitoring guidance for the community indicates that at least 90% of vegetation cover should be made up of *R. omiophyllus*, *Montia fontana* and *Potamogeton polygonifolius* with <50% of cover showing evidence of grazing (JNCC 2008).

Cook (1966) makes the observation that the limits of the British distribution of the species 'follow extremely closely the August 3 inch isohyet'.

At lower elevations and with slower flows M35 may grade into the *Hypericum elodes*-*Potamogeton polygonifolius* soakaway community (M29).

European distribution.

Flora Europaea (Tutin *et al.* 1964) gives the distribution of *Ranunculus omiophyllus* as restricted to Great Britain, Ireland, France, Spain, Portugal and Italy; the species was formally found in the Netherlands but has been extinct there since 1980. Salisbury (1934) compared the distribution of *Ranunculus omiophyllus* with that of *R.hederaceus* and highlighted the 'Atlantic' nature of the former. This early work also showed *R.omiophyllus* to have been present in Belgium at that time.

A distribution map of the species appears in Cook (1966) and demonstrates western Britain and southern Ireland to be the principal loci for the species in Europe. Given this limited range on the continental mainland it is unsurprising that associations in which the species is prominent are scarce in the literature.

Rivas-Martínez *et al.* (2002) in their comprehensive syntaxonomical checklist of the vascular plant communities of Spain and Portugal recognise a *Montia-Ranunculus hederaceus/R. omiophyllus* community which is floristically very close to M35. This association is very species poor, the nominate species being principally accompanied by *Callictriche* species, and occurs in shallow (5-15cm) water of small pools associated with springs or rivulets of cold, fresh oligo- or mesotrophic water. The type location given is the Sierra de Avila in central Spain.

Further to the west the same authors provide relevé data for a *Myosotis stolonifera-R.omiophyllus* community dominated by the Crowfoot but also with *Montia fontana*, *Potamogeton polygonifolius* and *Glyceria fluitans*, all taxa characteristic of M35. These stands have typically even shallower water (5-10cm) and are more oligotrophic than the preceding association.

A *Ranunculetum omiophyllii* is reported further north, at the northern end of the Sistema Berico range (Navarro *et al.* 2001). This occurs at higher altitudes (c.1000m), at what is described as the eastern border for Atlantic plant communities.

Molina (2007) has separated the Iberian *Ranunculetum omiophyllii* community from the *Myosotido stoloniferae-Ranunculetum omiophyllii* association on a geographical basis with the former

occupying areas, especially in the Galician-Asturian range, with more Atlantic temperate climate and the latter more widespread in the central Spanish ranges having a sub-Mediterranean climate but occurring at higher altitudes where the effects of summer drought are ameliorated.

The *Myosotis-Ranunculus omiophyllus* community is also recorded from southern Portugal (Pereira *et al.* 2010). Despite the name, *Myosotis stolonifera* is scarce in an association dominated by *R. omiophyllus* with *Glyceria declinata*, *Myosotis laxa*, *Callitriche spp.* *Juncus bufonius* and *Isolepis cernua*.

Julve (1993) records a *Ranunculetum lenormandii* (= *omiophyllus*) association in his synopsis of the vascular plant communities of France but here the community is placed within the *Hydrocotylo-Baldellion* order rather than the *Montion*, an approach rejected by Rodwell (1991) who limits British expressions of the *Baldellion* to the poorly defined, only seasonally inundated, M30 community; the *Montion* being restricted to permanent, if shallow, running water normally fed by springs.

R. omiophyllus is also recorded from the Madonie mountains in Sicily and from the extreme toe of mainland Italy where it occurs in the Appennino Caledrese (Cook 1966) but no information on its associates in either of these locations has come to light.

Environmental parameters.

The M35 community is normally associated with cool, well oxygenated, oligotrophic water flowing at a reasonable rate through peatland communities developed over acidic bedrock.

Beyond this generalisation it is difficult to proceed with confidence since data specific to the community is elusive. However, a body of data is available for another *Batrachium* species of similar habitats to that of *R. omiophyllus*. *R. penicillatus* var. *penicillatus* is a plant of base-poor rivers and streams flowing over Paleozoic or Igneous rocks whose distribution in Britain (Preston *et al.* 2002) closely parallels that of the M35 community. It occurs in Cumbria, north and south Wales and the southwest peninsula. *R. penicillatus* var. *pseudofluitans* is, in contrast, a species of base-rich rivers and streams and is the more common variety but one with a more easterly distribution in Britain.

Mony *et al.* (2006) studied the floristic and ecological diversity of aquatic *Ranunculus* habitats in the sub-Atlantic range. Their work, centred on uplands in NE France, included the comparison of four species groups, one of which was dominated by *R. pedicellatus pedicellatus* with *Glyceria fluitans*, *Potamogeton polygonifolius*, *Lemna minor* and *Callitriche platycarpa* in a species-poor association. The association was characterised by water depths of 12-35cm, a current velocity in the range 0.3-0.6ms⁻¹ with conductivity ranging from 50-200 μScm⁻¹, a mean pH of 6.8 and low levels of available phosphate. Apart from the rather high pH these conditions would seem to be relatable to the environment of M35. Webster (1988) cites a similarly low conductivity (30-200 μS cm⁻¹) for *R. penicillatus* var. *penicillatus* from British sites and notes its southwesterly distribution in England and Wales.

Lumbreras *et al.* (2009), studying aquatic *Ranunculus* communities in the Iberian Peninsula, distinguished *R. penicillatus* associations thus: water depth 25-35cm, oxygen concentration 90-110% with appreciable flow. They describe *R. pedicellatus* as a submontane species inhabiting narrow rivers with acid and weakly mineralised waters.

There have been a number of studies on European spring vegetation including some specific to the *Montio-Cardaminetia* order, Zechmeister and Mucina (1994), Molina (2001) and some more wide ranging (Sekulová *et al.* 2011). However, this body of work has concentrated on high altitude, arctic-alpine associations beyond the altitudinal limit for associations relatable to M35. Molina (2001) does however draw a useful distinction between members of the *Cardamino-Montio* alliance, which can contain *R. omiophyllus*, which he describes as an Iberio-Atlantic vegetation of low pH streams contrasted with higher elevation peat bog streams with much more *Montia fontana*.

Conservation.

Although the published description of M35 does not include any rare species of vascular plant or bryophyte, *Bryum weigelii* and *Hamatocaulis vernicosus* have been reported to occur in stands of the community in Shropshire (Iain Diack, *pers. comm.*) Although the community is not listed in Annex I of the Habitats Directive as a running-water vegetation type of conservation importance and whilst the association is scarce (though probably under-recorded) in the UK, the British Isles provide the stronghold of *R. omiophyllus* in Europe and, as such, the community is worthy of preservation.

Heavy grazing and poaching, especially where the M35 rills flow through heathland, is likely to have an adverse effect both directly through a reduction in cover of *R. omiophyllus* and indirectly through eutrophication of the, usually small, runnels which if dunging is severe may increase Biological Oxygen Demand and result in a lowering of oxygen saturation levels. Such effects could rapidly lead to the community assuming unfavourable condition.

In some upland situations grips may be deliberately blocked to assist the re-wetting of bogs which have suffered a decline in *Sphagnum* cover. Any such changes to the drainage should be carefully managed to ensure that they do not result in a significant diminution of flow rate in the rills – this may lead to a conversion of the M35 to a less desirable M6 (*Carex echinata-Sphagnum auriculatum/recurvum*) flush: a similar succession may occur if surrounding areas of rush are allowed to expand into the channel.

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S24, *Phragmites australis*–*Peucedanum palustre* fen

(Account largely based on Wheeler et al 2009 and Rodwell, 1995)

Summary of physiognomy

The major structural component of this tall herbaceous fen community is provided by monocotyledons, primarily *Phragmites australis* and *Cladium mariscus*. Species richness can vary from very low to very high, and there is a wide range of associates, although certain species, for example, *Calamagrostis canescens*, *Carex elata*, *Peucedanum palustre* and *Thelypteris palustris*, occur regularly and as a whole the community supports many rare or infrequent species (see Biodiversity value).

Rodwell (1995) recognises seven sub-communities of S24:

S24a *Carex paniculata* sub-community

Dominated by large tussocks of *Carex paniculata* with most of the characteristic associated tall herbaceous species (e.g. *Lysimachia vulgaris*, *Peucedanum palustre*) and woody species growing on the tussock tops. There may be a patchy mat of bryophytes around the shoot bases. *Phragmites australis* and other tall swamp helophytes and sedges occur patchily in the wet hollows between the tussocks.

S24b *Glyceria maxima* sub-community

Can be quite variable in composition, but *G. maxima* is usually the most prominent species, often dominant, amongst other tall fen species such as *P. australis*, *Epilobium hirsutum* and *Urtica dioica*. Where *G. maxima* is less prominent, a wider range of sedges, rushes and small herbs can occur.

S24c *Symphytum officinalis*

Symphytum officinalis is a particularly distinctive component amongst the tall herbs of this sub-community, although there is much local variation and the dominants may vary between such species as *P. australis*, *C. mariscus*, *Calamagrostis canescens* and *C. epigejos*. The sedge/rush layer is also variable, and usually species-poor, although may be quite extensive. *Molinia caerulea* tussocks are a distinctive feature of some stands.

S24d Typical sub-community

Usually dominated by *P. australis* (although *C. canescens* and *C. mariscus* can be locally prominent) with a variety of tall dicotyledon associates, and often a prominent understorey of *J. subnodulosus*. *Thelypteris palustris* sometimes forms a thick cover, but sedges are infrequent and the small herb element species-poor.

S24e *Cicuta virosa* sub-community

Tall herbs, especially Apiaceae (Umbelliferae) such as *Cicuta virosa*, *Berula erecta*, *Sium latifolium* and *Peucedanum palustre* are characteristic, but otherwise similar to the Typical sub-community in the prominence of *P. australis*, although *C. mariscus* may dominate and *C. canescens* is less common. A variety of sedges, rushes and small herbs help to make this the most species-rich of the S24 sub-communities.

Two variants of this sub-community have been identified: Typical variant and *Carex lasiocarpa* variant.

S24f *Schoenus nigricans* sub-community.

Normally dominated by *C. mariscus* or *P. australis*, but poorer in helophytes and tall herbs than the other sub-communities and with a distinctive sedge/rush layer, in particular *S. nigricans* with *Carex elata* and *J. subnodulosus* and a characteristic small herb component.

S24g *Myrica gale* sub-community.

The presence of scattered, leggy bushes of *Myrica gale* is the most distinctive feature of this typically quite species-poor sub-community, dominated by *P. australis*, *C. mariscus* or *C. canescens*, with a few tall herbs, sedges and rushes.

Wheeler *et al.* (2009) discussed the syntaxonomy of S24, and concluded that (a) a re-consideration, and possible revision, of the status and compass of S24 in relation to similar units is required; (b) the ecological range of S24 as currently constituted is wide; and (c) it has limited value as an ecological unit for which meaningful environmental thresholds can be specified. For example, in Broadland there are some examples of vegetation with strong affinities to both S24 and *Carex rostrata*–*Potentilla palustris* tall herb fen (S27); and also there is much floristic overlap between S24 and *Phragmites australis*–*Eupatorium cannabinum* fen (S25).

Abiotic requirements for existence and restoration/creation

This section summarises the key abiotic requirements of S24 communities and provides information, where available, on tolerance limits to variation in these abiotic variables.

(a) Landscape

Most often found on floodplains, including in Fenland and the Somerset Levels, but particularly characteristic of the Broadland fens where they form the main herbaceous vegetation. Some examples are found in basins and troughs.

(b) Soils and geology

Found on solid peat or sometimes forming a semi-floating raft within a turf pond on fen peat, which in some locations is more than 4m deep. In some locations in Broadland the alluvial infill contains a layer of estuarine clay some 50–100 cm below ground level. The community may develop hydroserally over considerable depths of lake muds and occasionally marl. In Broadland, sites occur over a bed-rock of Norwich Crag.

(c) Soil chemistry

Soil pH provided in Table S24.1.

There appears to be a complex interaction between historical influences, management regime and edaphic conditions which is reflected in the sub-community type which develops (Rodwell, 1995), and, given its restricted distribution, the community can be found over a surprisingly wide range of environmental conditions.

Generally occurs in conditions of moderate to high substratum fertility, as reflected in the relatively high vegetation productivity reported by Wheeler and Shaw (1991): mean increment (April to September) in dry weight of above-ground standing crop was 681 g dry wt m⁻² (range: 381 to 1,097 g dry wt m⁻²). *Cladium*-dominated examples tend to occur in locations of relatively low fertility, whilst examples with much *Glyceria maxima* are consistently associated with eutrophic soils and stands dominated by *Phragmites* can occupy a very wide fertility range. The Yare valley fens (e.g. Woodbastwick Fen) tend to support the more fertile examples of the community compared to the northern Broadland valleys.

Enrichment may be due to such influences as periodic river flooding, drying-induced mineralisation, mud pumping onto the fen surface and burning, and can result in a change in sub-community and loss of characteristic and rare species, and potentially conversion to another herbaceous vegetation type (such as S25 or S26). However, regular management may mitigate the effects of enrichment to some extent.

Some Broadland stands occur in oligohaline conditions (with high Na, Mg and conductivity values), perhaps derived from the presence of estuarine clay, but the community is also found in freshwater sites and it is in these that most of the richer examples are found (Shaw & Wheeler, 1991). These authors also found that species density and number of mire species were negatively related to conductivity and K concentrations, indicating the fewer species can tolerate extremely high conditions of ionic strength, and that the higher fertility sites supported significantly fewer rare species.

(d) Hydro-chemistry

Typically found in base-rich conditions, although sometimes found where the pH is low, for example near or at the margins of fens in the Ant and Thurne valleys in Broadland, where this may be related conditions in the adjoining mineral ground, or a result of acidification due to drying.

The very high conductivity values that have been recorded in some Broadland sites (e.g. Thurne valley) could be due to inundation by brackish river water or to the presence of estuarine clays at shallow depths beneath the peat surface.

Table S24.1 pH, conductivity and substratum fertility measured in stands of S24 (after Wheeler et al 2009).

Variable	Mean	Range
Soil pH	6.45	5.3–7.9
Water pH	6.45	3.7–7.9
Water conductivity (µS cm ⁻¹)	1,418	87–7,200
Soil fertility ⁷ (mg phytometer)	12.0	5.0–92.0

Rodwell quotes Wheeler (1983)⁸ in giving dissolved calcium levels range of 60–120 mg l⁻¹.

⁷ Experience has shown that N and P data derived from soil analysis has only limited use in assessing fertility of wetlands. Consequently the technique of phytometry (measuring the biomass of test species (phytometers) grown on soil samples) was developed. Typical phytometer yields (dry wt.): low fertility < 8 mg, high fertility > 18 mg.

⁸ published as Wheeler 1984 (British Fens)

(e) Hydrology

[See Wheeler et al. 2009 for detailed summary of water regime variables].

Mean values for annual rainfall and potential evaporation for the sites examined are given in Table S24.2, together with together with mean recorded values for summer water table associated with stands of S24.

Table S24.2 Rainfall, potential evaporation and water table data for S24 stands (after Wheeler *et al.*, 2009)

	Mean	Range
Rainfall (mm a ⁻¹)	611	539–1,140
Potential evaporation (mm a ⁻¹)	622	562–627
Mean summer water table (cm)	–16.7	–78.4 – +3.8

The S24 community mostly occurs in locations on floodplains and hydrosereal areas within them, primarily irrigated by periodic flooding by river water, although can also be found in groundwater-fed sites. Wheeler *et al* (2009) identified almost half of their S24 samples as occurring within WETMEC 5 (Summer-Dry Floodplains) and 41 % within WETMEC 6 (Surface Water Percolation Floodplains). A few examples occurred within WETMECs 7, 8, 13, 15, 16 and 20.

Wheeler *et al* (2009) provide comments on optimal and sub-optimal (or damaging) water levels for S24 stands, although few data are available. However, water regime requirements are difficult to specify quantitatively for S24 because different versions of the community are associated with rather different water regimes, and particularly because the microtopographical variation, which is a typical feature of the community when tussocky, leads to different regimes within individual stands. In addition, the variability of the floristic composition of S24 stands mean that it is difficult to know how factors such as water source and regime interact with others such as management and substratum fertility.

A change in water source on its own may not have much effect on the *community*, even with some change in water quality, but may affect the floristic composition (Wheeler *et al*, 2009).

Water levels are typically below ground in summer (< 15 cm) and well above ground in winter. The depth of inundation in winter is probably inconsequential to the vegetation, unless exceptionally deep and prolonged (in which case a less diverse swamp vegetation is likely to develop), but stands that are inundated for a long time in summer are likely to be less species-rich than those where the summer water table is sub-surface. Stands (particularly S24e) on rafts in turf ponds, where the water table is at or near the surface year-round were found to support the most rare fen species. However, rare species also occur where the substratum fertility is low, and the vegetation is well managed.

Summer water tables can be quite low (e.g. –75 cm bgl), especially on solid peat and where stands are located some distance from dykes and watercourses, in which case the water regime may be strongly influenced by rainfall events and evapotranspiration between flooding episodes. Indeed, in highly managed floodplains, where flooding is closely controlled and infrequent (or no longer occurs), the surface of the peat may now be fed primarily by precipitation, and thus prone to acidification. However, strongly sub-surface summer and winter water levels are not typical, and

prolonged lowering of water tables can be expected to lead to a loss of wetland species and increase in dryland species, with development of rank fen, rapidly becoming wooded without management, especially when drying is associated with substantial nutrient release as a result of mineralisation.

Lowest summer water tables tend to occur in stands on solid peat, whilst stands on turf pond infills or forming buoyant rafts experience higher water tables, due to their lower surface level or accommodation of the raft, but also higher rates of water recharge through the more transmissive sub-surface peat infill. Wheeler et al (2009) found the mean summer water table associated with examples of S24 in reflooded peat workings was -9.1 cm, whilst that of examples on solid peat was -23.3 cm. These differences are also reflected in the different sub-communities found in different conditions.

In addition to between-site variation, summer water tables can also vary considerably between years, and a site may be saturated one year but experience water levels well below ground in another. However, surface flooding in winter is characteristic, and water depths of 50 cm above ground can sometimes persist for quite long periods.

The impact of water table drawdown is likely to depend on the initial water and management regimes, as well as substratum fertility (Wheeler et al, 2009). For example, drying of stands where the initial summer water table is above ground may lead to an increase in species diversity. Where the initial summer water table is at or within c. 10cm of the ground surface, a reduction in water table may lead to a loss of rare species in particular, although some of the drier, managed stands on low-fertility, solid peat are known to be species-rich, including rare species.

Drier (S24c) and tussocky (S24a) stands are likely to be more prone to scrub invasion than others (Rodwell, 1995).

(f) Geographic distribution / climate

A very localised community, with its main distribution in East Anglia, particularly Broadland where it is widespread and extensive. Fragmentary stands occur in the Somerset Levels. Similar vegetation occurs elsewhere, e.g. Crymlyn Bog (Glamorgan), Test valley (Hampshire), and West Midlands, but their status has not yet been clarified.

Biotic requirements for existence and restoration/creation

Mycorrhizal associations

No information found

Regeneration requirement

The community is of very local occurrence in Britain, being largely restricted to East Anglia. The likely success of restoration/regeneration activities depends on the starting conditions, and the ease with which conditions appropriate for the community can be provided, or re-development over the longer term facilitated, as well as the availability of appropriate plant material/seed sources. It may be possible to restore S24 stands by simple corrective management measures, providing damage is recent and not intensive, but restoration of severely damaged stands or regeneration in 'new' sites is likely to be much more difficult.

Many S24 stands are particularly prone to scrub invasion and woodland development when management is relaxed or abandoned. If scrub has spread fairly recently, its removal coupled with reinstatement of a regular management regime is likely to improve stand quality. However, the effectiveness and desirability of clearance of mature fen woodland is much less clear.

The effects of re-wetting sites that have dried out are largely untested, although some trials are ongoing. Where drying has resulted in enrichment of the surface layer of peat, it may be necessary to remove this in order to re-establish appropriate conditions for the re-establishment of S24.

McBride et al (2011) give a detailed Case Study for the Bure Marshes, which includes S24 (see page 134 – 137)

Threats from fragmentation, isolation

No specific information available

Management practices

It appears that most examples of the S24 community are largely an 'artificial' product of management, being secondarily derived by management following such activities as clearance of fen woodland, drainage of swamps, or peat cutting. Ongoing management, for example mowing for litter, or reed and sedge harvesting (see Provisioning service value), is therefore considered to be essential for the maintenance of its character and abandonment of these traditional activities has led to a reduction in the extent of S24 stands and development of scrub and fen woodland over much of Broadland.

The degree to which abandonment leads to significant floristic changes depends upon the sub-community type, particularly as many of the characteristic S24 species (e.g. *Carex elata*, *Peucedanum palustre*, *Thelypteris palustris*) grow as well in shaded conditions as open fen, although it is likely to lead to the development of a tall, rank and botanically impoverished sward (which may sometimes be mistaken for evidence of dehydration). Conservation management of S24 may therefore be aimed at general maintenance of a diverse stand and/ or for uncommon species that are not especially characteristic of the community (such as *Schoenus nigricans*).

The timing and frequency of management activities is crucial (Wheeler and Giller, 1982), for example the regrowth of *Cladium* can be inhibited if the cut stems become submerged by winter floods following mowing, and there appears to be a complex interaction between historical influences, management regime and edaphic conditions which is reflected in the sub-community type which develops (Rodwell, 1995). In addition, some mowing regimes may be detrimental to certain species, as found for example, for *Peucedanum palustre* at Wicken Fen (Harvey & Meredith, 1981).

Replacement of mowing by grazing is likely to lead to a reduction in tall herbs, and possible change in community, for example towards fen meadow (M22), although some of the characteristic species (e.g. *Peucedanum*) may remain.

The S24a (*Carex paniculata*) sub-community is particularly prone to invasion by woody species such as willow and alder on the tussock tops. S24c tends to be found in drier locations than other types of the community, and is also prone to scrub invasion (Rodwell, 1995).

[McBride et al (2011) give a detailed Case Study for the Bure Marshes, which includes S24.(see page 134–137)]

Predicted climate change threats

Rodwell (1995, p224): “Although it was certainly more extensive in the past (e.g. Pallis, 1911) it is probably essentially a vegetation type of those areas to the south and east where once extensive floodplains with calcareous catchments occur in a more continental climate.” It includes several species with a Continental or Continental Northern distribution, which are generally limited to habitats away from the west of the country. There are also edaphic and hydrological constraints on distribution which will also limit responses to climate change.

Threats from non native invaders

No specific threats found

Ecosystem Services

Evidence of water regulation value

Surface flooding in winter is characteristic, and water depths of 50 cm above ground can sometimes persist for quite long periods, suggesting that some stands may be able to accommodate a degree of flood storage. Some stands are found on high fertility substrata, but higher fertility sites support significantly fewer rare species, and therefore flooding of high grade stands with enriched water would be undesirable (although in some circumstances regular management may mitigate the effects of enrichment to some extent).

Evidence of carbon storage value

Found on solid peat or sometimes forming a semi-floating raft within a turf pond on fen peat, which in some locations is more than 4m deep.

Biodiversity value

S24 stands are typically moderately species-rich although there is a wide range (TABLE 23.1). The community is important in supporting many rare and uncommon fen plant species, particularly in Broadland, although the notable species of S24 are not necessarily associated with particularly species-rich vegetation. The community is thus of high conservation importance and many sites are protected under national and international designations: examples have been included within the ‘chalk-rich fen dominated by saw sedge’ SAC feature (although not all stands of S24 necessarily support *Cladium mariscus*).

S24 stands in Broadland are well known for their associated rich invertebrate fauna, including butterflies, moths and spiders (Rodwell, 1995), for example, providing the main habitat for *Peucedanum palustre* (Milk parsley), the food plant for the indigenous race of the swallow-tail butterfly (*Papilio machaon britannicus*).

Table S24.1 Number of plant species recorded in samples of S24 (after Wheeler et al, 2009)

	Total	Mean	Range
All species (spp 4 m ⁻²)	384	17.4	2–46
Mire species (spp 4 m ⁻²)	147	14.5	1–43
Rare mire species* (spp 4 m ⁻²)	30	3.4	0–13

* These include: *Calamagrostis canescens*, *Calliargon giganteum*, *Campyllum elodes*, *Campyllum polygamum*, *Carex appropinquata*, *Carex diandra*, *Carex elata*, *Carex lasiocarpa*, *Cicuta virosa*, *Cinclidium stygium*, *Cladium mariscus*, *Dactylorhiza praetermissa*, *Dryopteris cristata*, *Eleocharis uniglumis*, *Epipactis palustris*, *Lathyrus palustris*, *Oenanthe lachenalii*, *Osmunda regalis*, *Peucedanum palustre*, *Plagiomnium elatum*, *Plagiomnium ellipticum*, *Potamogeton coloratus*, *Pyrola rotundifolia*, *Ranunculus lingua*, *Rhizomnium pseudopunctatum*, *Sium latifolium*, *Sonchus palustris*, *Stellaria palustris*, *Thalictrum flavum*, *Thelypteris palustris*.

Provisioning service value

Traditionally used for four types of crop: “*Phragmites* for reed thatch, *Cladium* for sedge thatch, *G. maxima* for green fodder, winter hay or litter, and more mixed vegetation, often with abundant *Juncus subnodulosus* and/or *Molinia caerulea*, also for litter.” Each involves a different mowing regime. Rodwell (1995, p226)

Wheeler and Shaw (1991) reported a relatively high vegetation productivity: mean increment (April to September) in dry weight of above-ground standing crop was 681 g dry wt m⁻² (range: 381 to 1,097 g dry wt m⁻²).

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Section 4

Effects of ammonium and nitrate deposition on fen bryophytes

Earlier experimental studies in the UK have confirmed that application of fertilisers to lowland wet grasslands on peaty soils result in rapid and significant declines in the cover of pleurocarpous mosses (Mountford *et al.* 1993). These grasslands (a mosaic of **MG8** and its variants, **S6**, **MG10/11** and **MG13**) were closely related floristically to rush pastures (**M22** and **M23**), and significant declines in mosses were observed after a single year at levels of 200 kg N ha⁻¹ year⁻¹, and after 4-5 years at 25 kg N ha⁻¹ year⁻¹. Although these impacts were largely due to competition and increased litter production from grasses, evidence has also been presented that in meadows fertilisers can behave as muscidicides (Rabotnov, 1977).

The main modern sources of information of relevance to this review were from the Netherlands.

In terms of biomass and species diversity, bryophytes are very important in rich fens in the Netherlands (Kooijman, 1992; Vitt, 2000). Brown mosses, including members of the genera *Scorpidium*, *Calliergon* and *Campylium*, dominate the bryoflora of rich fens (Kooijman, 1992).

Paulissen *et al.* (2004) provided evidence that that high NH₄⁺ inputs pose a serious threat to the brown moss flora of rich fens. Paulissen *et al.* (2005) showed that, at an external pH of 5.5, NH₄ is potentially toxic to brown mosses. NH₄ toxicity generally increases as the external pH decreases. Therefore, it is likely that the NH₄ stress experienced by the typical brown moss vegetation of rich fens further increases as *Sphagnum* and *Polytrichum* species invade and the external pH decreases to values as low as 4 (Paulissen *et al.*, 2004). Moreover, as Paulissen *et al.* (2005) suggest the frequent occurrence of P limitation under field conditions may exacerbate NH₄ toxicity to fen bryophytes through the occurrence of internal nutrient imbalance.

Recent studies by Verhoeven *et al.* (2011) indicated that enhanced atmospheric inputs of N mainly in the form of NH₃ will seriously damage the bryophyte community of mesotrophic vegetation, with vascular plant vegetation showing an increased biomass production and dominance by *Carex* and herb species shifting to dominance by grasses and shrubs. Studies of more calcifuge grassland vegetation show a significant decline of *Hylocomium splendens* and other bryophytes at high levels of atmospheric N deposition although *Hypnum cupressiforme* exhibited higher cover at high levels and appears to be more tolerant of air pollution than most bryophytes (Stevens *et al.* 2004).

The studies by Mitchell *et al.*, (2005) on effects of atmospheric N on the epiphytic communities of Atlantic oakwoods, indicate that even in the relatively unpolluted areas of western UK, elevated N inputs could be affecting sensitive bryophytes of PMGRP and other wetland communities.

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Section 5

Gaps in ecological knowledge - research needs

The quantity, quality and distribution of wetland community types in the UK

The full extent and quality of the Natura 2000 **6410** *Molinia* meadows and the other equivalents of UK Purple Moor-grass and Rush Pasture across Europe are at present uncertain (EEA 2008; JNCC 2007). The same is also true for some of the mire and swamp communities. There is, therefore, a need to collate existing data from the Republic of Ireland and across Europe together with information from the UK. Within the UK, our database on wetland communities appears to be deficient for the upland fringe zone for which a comprehensive inventory is needed.

Abiotic constraints on wetland community restoration

Enhanced site fertility and soil drainage are the two key constraints to the restoration or creation of high nature value wetlands in the UK. The ubiquity of direct (via drainage, cultivation and fertilizer application) or indirect (via upstream drainage, aquifer abstraction, altered hydro-chemistry due to groundwater pollution/fertilizer run-off) land improvement for agriculture throughout lowland UK coupled with atmospheric N enrichment has made the targeting of wetland community restoration on appropriately infertile and wet sites extremely difficult. Remediation techniques to reduce fertility such as topsoil removal although of proven value can produce disappointing results despite careful targeting based on soil chemical analysis. For example, where topsoil removal exposes clay subsoil this substrate is vulnerable to severe compaction by heavy rain and it becomes a particularly hostile environment for seed germination and establishment, as experience in north Devon has shown. Further study of soil surface ameliorative strategies coupled with topsoil removal such as the use of finely chopped fen or fen-meadow litter on restoration sites to facilitate establishment of early successional species should be undertaken.

The extent to which soil and water acidification is a major factor impeding the restoration and maintenance of more basophilic fen-meadow and rich fen communities in the UK is difficult to gauge, due to paucity of systematic monitoring of soil and hydrochemistry of sites. General acidification of soils in marginal agricultural land, which includes most of the UK's semi-natural grassland and wetlands such as those in the upland fringe zone, has probably been exacerbated by the removal of the liming subsidy in the 1976 (Tallowin, 1998). The leaching of calcium carbonate from limed soils almost certainly contributed to localised elevation of base richness in flush zones. Acidity inhibits nitrification and the resultant high ammonium concentrations in the soil (exacerbated by high atmospheric deposition of reduced nitrogen in some areas) have been found to reduce germination and seedling survival of some characteristic fen-meadow species. Increased ammonium concentrations have been found where turf/sod removal was used at some sites in Europe. There was some evidence that turf stripping could have removed the nitrifying bacteria that exist in the topsoil layers. Recovery of the nitrifying bacterial population took several months. Whatever the mechanism behind the increase in NH_4^+ concentration with turf or topsoil removal, these findings have implications for fen-meadow restoration in the UK. Insufficient is known about the effects of elevated ammonium levels on the recruitment of fen-meadow and wetland species in the UK. At the very least, NH_4^+ concentration in the soil should be monitored at fen-meadow restoration sites. Measurements of soil base status using pH will provide an edaphic criterion on

which to assess the likely outcome of any restoration programmes. Research both at site and catchment scale on use of liming for the maintenance and restoration of more basophilic fen-meadow communities in the UK is merited.

Nitrate-N enrichment of ground and surface water flows into wetlands can inhibit the restoration/creation of species-rich fen, mire and swamp communities due largely to the competitive advantages provided to dominant/invasive species, as demonstrated by Green and Galatowitsch (2002). There is, therefore, little room for compromise between the restoration/creation of wetlands for the Ecosystem Service of water quality enhancement and biodiversity enhancement, unless the two functions can be placed in series in a landscape so that **former** enables the latter. Success would depend upon the extent of N enrichment of the source water, which would determine the scale of the filtration wetland upstream from the biodiversity restoration/creation site and upon controlling invasion of the latter by competitive species. The practicality and ecological sustainability of such multifunctional wetland systems requires more long-term studies.

Stagnation of surface water and sulphate enrichment were identified as key factors impeding the restoration of fens at sites in Europe. This would represent a problem where the restoration target for a particular site is rich fen type vegetation. The extent to which sulphate enrichment is likely to affect the use of ponding of water for rich fen restoration in the UK has probably diminished in light of the large reductions in sulphate concentrations in rainwater (Defra, 2012). Nevertheless, prior to implementing ponding likely constraints for rich fen restoration such as sulphate enrichment of the water need to be assessed.

The hydrological processes that underpin the existence of fen meadows are poorly understood. Most authors suggest lateral water movement in the root zone to be a typical characteristic of this vegetation type, but the soil-water regime has rarely been fully quantified at a site, such that the tolerances of different communities can be understood. Hydrological monitoring data have been collected for some fen-meadow communities in the UK by the Environment Agency, but much of these data are yet to be analysed by ecohydrologists. This information will expand our knowledge base on the hydrological conditions that are likely to be required for successful restoration/creation of these communities.

Biotic drivers of unsustainable changes in wetland communities

There are severe gaps in knowledge on the scale of genetic erosion and the consequences for regeneration and resilience to environmental change in fragmented, isolated small populations of wetland species. There is a need for long-term manipulative experiments to allow us to examine interactions between habitat management, dispersal processes and population dynamics. There is an urgent need for evidence to support or otherwise, genetic reinforcement through the periodic introduction of seed of rare/declining species from a wide range of sites to prevent continued genetic erosion.

Gaps in knowledge on the autecology of several wetland species were identified. For example, the individual swamp communities examined in this review are overwhelmingly dominated by single species, and hence a review of research needs should focus primarily on the autecology of these swamp dominants. With the exception of reedbeds (S4) and to some extent Typha swamps (S12 and S13), many of the abiotic and biotic requirements and the impact of management are relatively poorly known. The soil and water chemistry requirements of *Carex paniculata* (S3) and *C. riparia* (S6) were identified as particular knowledge gaps, which require research. To some extent, the research

needs that exist for wetland species can be addressed through targeted effort in the *Biological Flora of the British Isles*. There is a paucity of information on mycorrhization of species in wetland communities. It is considered important that this knowledge gap be addressed, not least to identify the potential role of mycorrhiza in the restoration of these communities.

Data on the threats to the integrity of wetland communities through invasion by alien species was found to be fragmentary and often anecdotal. There is a need for a comprehensive study/quantification of the risks posed by alien species to the different wetland community types in the UK.

Management and climate change effects on wetlands

Management studies of fens, fen-meadows, mires and swamp communities are extensive and detailed. However, for some wetlands such as (S3 *Carex paniculata*, S8 *Schoenoplectus lacustris* and S14 *Sparganium erectum*) these have only been partially researched, and for many swamp communities the information is anecdotal at best.

Under climate change predictions, there is likely to be a northerly shift in the distribution of some wetland community types, provided that component species with a more southern distribution are able to disperse northwards and the appropriate hydrological and edaphic conditions exist in more northerly environments. Active conservation measures, such as seed sowing and green “hay” strewing are likely to be needed to enable the more southerly floral elements of the community to move northwards. Close attention will need to be paid to maintaining good hydrological conditions in more northerly sites to ensure resilience to climate change, which may mean removing pressures such as abstraction and blocking drainage ditches. Current research by Mike Acreman and colleagues on behalf of the Wetland Vision project has sought to simulate future wetland hydrology using the latest UKCIP09 forecasts. The viability of wetlands over a 50-year projection is found to be highly dependent on geographic location and water source with sites that are either rain-fed or groundwater-fed in SE England being particularly vulnerable.

The effects of climate change on swamp communities have been well researched for reed and to some extent for *Equisetum fluviatile*, but otherwise data are fragmentary for most of the reviewed wetland communities. The extent to which environmental changes such as atmospheric nutrient deposition, increased temperatures, shifts in rainfall and droughting patterns are likely to affect wetland community structure and interact with management practices such as timing of mowing or grazing is largely unknown. Research to examine long-term effects of manipulated changes in the above environmental drivers and their interaction with management practices is considered to be a priority.

Ecosystem-service value knowledge gaps

In order to mitigate the risks to existing wetlands from climate change and to offset ecological sustainability problems associated with isolation and small size there is a clear need for expansion and connection of existing sites, plus the restoration - creation of new wetland community sites. Restoration/creation of high ecological value wetlands should be closely linked to future landscape scenarios for the UK not least to integrate their Ecosystem Service values within catchments. This landscape scale ES optimisation of restored/created wetlands is likely to be particularly challenging given likely future pressures on land for food security provisioning. Therefore, robust quantification of the Ecosystem Services provided by different wetland types is urgently needed in order to provide a more comprehensive socio-economic valuation of these habitats than is currently available.

Quantification of intrinsic values of fen, mire and meadow would assist policy makers in assessing trade-offs between values. These communities as well as being important repositories of biodiversity also hold considerable aesthetic, cultural and recreational value in many areas of the UK.

The provisioning, biodiversity and cultural values of the reviewed wetlands have largely been adequately quantified. Information on the regulatory services such as water quality and storage, GHG emissions and carbon storage provided by many of the reviewed wetlands was found to be patchy.

With regard to the water regulation value of mires, fen-meadows, rush pastures and some swamp communities such as S3, S6, S7, S18 and 19, more information is required.

Soil methane production is important in waterlogged systems, and so many wetland communities are likely to be a source of this important greenhouse gas (GHG.) Most methane emission studies have been done on peatlands. Examination of patches of wet grassland within such peatlands has indicated high methane fluxes. More research is needed particularly where fens, mires, swamps and PMGRP communities are established on stagnogley and stagnogley humic soils. In particular the role played by the plants themselves in facilitating methane release appears to merit further study.

Nitrous oxide (NO_x) emissions are of greater concern in terms of GHG effect than methane. However, it is assumed that NO_x emissions will be very low for swamps, mires, fens and PMGRP communities due to the infertile conditions under which most of these communities exist. Nevertheless, research is needed to validate this assumption.

In terms of carbon sequestration, there is a good evidence base for the value of mire communities on peat. For some swamp communities such as the S3 and S8 there is some data on C storage, but for other swamp communities such as S3, S6, S7, S18 and 19 there is a paucity of C storage data. There is also evidence that wetland communities such as PMGRP store more carbon at depth than agriculturally improved soils, but more data are required to quantify the carbon-storage potential of these communities and the hydrological management required to maximise this service.

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Section 6

A field-based programme to characterise the state/condition of a range of restoration sites and compare with reference site conditions.

The following field-based programme is based on the gaps in knowledge summarized in Section 5 and the need for improved characterisation of existing fens, 'purple moor-grass and rush pastures'. In order to achieve improved characterisation of existing communities and of targeted restoration/re-creation projects, a sample of sites including those undergoing restoration need to be examined. Where possible, restoration sites representing a time series (chronosequence) should be selected for sampling in order to determine successional processes and likely timescales of restoration success. It is also envisaged that some large-scale restoration field sites will be included in this programme. We suggest using a two-tiered sampling system, with some sites receiving a botanical survey and a basic description of environmental variables, whilst others receive more intensive instrumentation and monitoring.

Envisaged monitoring

Each site will first be stratified into different vegetation communities using vegetation mapping techniques adapted from the HLS monitoring project (Mountford *et al.*, 2010a; *ibid* 2010b). A number of vegetation types characteristic of fen/mire, swamp and PMGRP habitats will be selected for detailed sampling to enable meaningful comparisons between sites and to ensure the cost-effectiveness of the survey:

Botanical composition

Cover of all vascular and non-vascular plant species, litter and bare ground will be visually estimated within each of 5 standard-sized quadrats placed in homogeneous stands of the distinctive vegetation types at each site. Standard quadrat sizes are expected to be 2 m x 2 m, but larger quadrats will be used where taller or relatively species poor stands are being examined to capture on record the presence of plant species typical of the vegetation. Stands of vegetation smaller than the standard sample size will be recorded in their entirety, e.g. for flushes, soakways, rills *etc.*

Soil chemistry

Five soil cores 0-10 cm deep will be taken and bulked within each depth category for each sampled homogeneous vegetation stand. Soil samples will be analysed for soil total C, total N, total P, extractable P, exchangeable K, Ca, Mg, Na, and pH analyses using standard approaches. Soil organic matter content by ignition at 550°C, soil moisture content and bulk density will also be measured on each bulked sample. Soil type and profile description including, for example, presence of gleyed horizon will be carried out at each homogeneous vegetation stand. Underlying geology at each of the sampled sites will also be obtained.

Hydro-chemistry

A full characterisation of the water chemistry of a site is very time consuming and expensive and not necessarily a priority at many sites where soil chemistry is the more dominant determinant of

community composition. Therefore, water chemistry characterisation will be carried out at selected sites where there is clear groundwater or surface water interaction with the root zone. It is suggested that 4 water samples per year would be adequate for water chemistry characterisation*. Teflon sampling tubes, for example, would be used for sampling groundwater. The water samples would be analysed for macro-nutrient concentration, pH and conductivity.

*Where flood waters are involved water chemistry monitoring would need to be carried out over several years in order to establish relationships between flood-pulse nutrient supply and vegetation dynamics.

Hydrological regime

Some data are already available with respect to water-table depths below fen and PMGRP sites, so only selected communities would require additional monitoring to improve our understanding of this variable. However, it has often been observed in these communities, in contrast to mesotrophic grasslands, that water movement and particularly water source (e.g groundwater versus surface water) can be a stronger determinant of plant community composition than water-table depth *per se* (e.g. Grootjans *et al.*, 1988). It is therefore necessary to characterise the hydrological system at some key sites to determine how variations in water movement give rise to different plant associations. To achieve this, it would be necessary, at a small number of selected sites where interesting juxtapositions of contrasting communities occur, to instrument the system sufficiently to determine flow paths and velocities. Automatic logging would avoid the need for repeated site visits and soil hydraulic properties could be established at a single visit during instrumentation. The data would be analysed after a full annual cycle to estimate the flux of water through the root zone within each distinct stand of vegetation.

Landscape/topographical context of site

The position of each site will be located on a GIS and buffered with a 1 km edge buffer. Slope and aspect will be recorded along with upslope and adjacent land uses. Land use adjacent to each site will be determined from analysis of the New Land Cover map supplemented by OS Mastermap, Google earth if required. The Natural England Habitat Inventory will be used to determine the location and connectivity of fen and PMGRP habitat in the landscape. This spatial analysis will provide information on the potential effects of adjacent land use on each habitat patch, including eutrophication (arable, improved grassland), transpiration water loss (woodland), and colonisation by desirable species (adjacent patches of priority habitat).

Light Detection and Ranging (LiDAR) data is now available for many PMGRP and fen sites. These data will be used to produce sub-metre (typically 0.2-0.5 m vertical accuracy) digital elevation models (DEMs) for each site using the last re-turn lidar signal. Aerial photogrammetry will be used to calculate DEMs in the few cases where LiDAR data is absent. Construction and analysis of high resolution DEMs for each site will inform our understanding of the likely hydrological constraints on successful restoration.

Where selected sites fall within areas of high resolution soil survey, we would seek access to records held by Cranfield University, within their LandIS database, should defra be able to facilitate access to these data at reasonable cost. Association between vegetation type and soil type would be sought and the results used to analyse which edaphic variables are likely to be driving plant community composition.

Information on peat depth within England and Wales may be obtained from the British Geological Survey (BGS). The information is held in a variety of forms with the two main sources being, firstly,

recent and historical geological mapping (down to 1:10 000 scale in many areas), with associated geological memoirs and, secondly, in the form of borehole lithological logs, of which BGS hold around 1 million for the UK. The BGS also have a national superficial deposits thickness model; however this includes all types of superficial deposits, including peat, which lie above bedrock.

In addition to the above national datasets and model, the Survey hold numerous reports which may contain information concerning peat thickness in specific areas, and, depending on location, have a number of detailed geological models and other data concerning superficial deposits thickness and lithology.

In the light of the above, it is considered that the most cost-effective way of using the BGS data to determine peat thickness at a given location will be to use relevant BGS geological staff to provide assessments based on the most appropriate data for the site in question.

Past and current land management

Details of site management ideally covering at least the previous ten years will be sought from site owners and/or associated stakeholders.

Statistical analysis

The relationship between biophysical and vegetation variables will be investigated using multivariate analysis techniques, such as Redundancy techniques and Correspondence Analysis. The positioning of the plant community of the sampled sites in ordination space and the influence of environmental variables such as hydrology, hydro-chemistry, soil macro-nutrient status (corrected for bulk-density differences), soil base status, climatic region, soil pH will provide a powerful correlative analysis of what factors are influencing the character of different mire and fen-meadow rush pasture plant communities. Partitioning of variance will be used to identify the strength of correlations between measured variables and characteristics of the different plant communities. Cluster/nearest neighbour analysis will be used to rank restoration sites in relation to reference plant community types under similar environmental conditions. Ordination approaches have been used extensively by the proposers to examine relationships between vegetation and soil variables.

Deliverables

The dataset for selected reference and targeted restoration sites should allow us to generate a quantitative "proximity" scale i.e. an index of "restorability" for targeted fen and PMGRP restoration elsewhere.

Section 7.

Decision support system

The successful restoration or re-creation of fen and PMGRP systems requires a clear understanding of the biophysical and biological constraints on achieving these goals, and a suite of proven, cost-effective techniques to overcome them, together with likely timescales associated with their success (Fig. 1).

Fig. 1 Flow diagram of the restoration process for fen and PMGRP communities

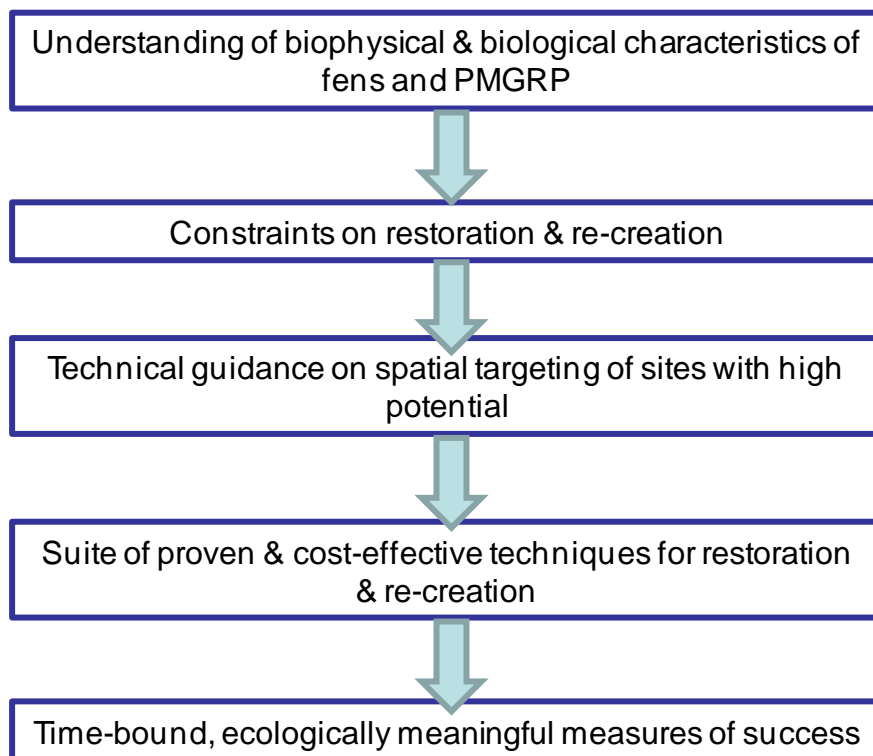


Fig. 2 Draft decision support system for wetland restoration/re-creation

