

# **Phytosociology informs the conservation of species-rich meadows in hydrologically dynamic habitats: an example from British floodplains in a wider European context**

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## **Abstract**

Nature conservation requires classification of vegetation types for site assessment and assignment. Species-rich floodplain meadows are a declining habitat in Britain and Europe yet their classification in Britain has been based on just a few samples and fails to describe community response to environmental change adequately. European classification, in opposite, has been based on samples from the wide geographical range with no environmental data/analysis supporting the choices. We propose a revised classification of the lowland meadow *Alopecurus pratensis-Sanguisorba officinalis* community of the British National Vegetation Classification (NVC) linked to variation in local water-table depth. Data have been collated from 58 British floodplain meadows. Based on botanical and hydrological data, four subcommunities within the *Alopecurus-Sanguisorba* community have been defined. Assessment of conservation sites at the subcommunity level allows temporal and spatial evaluation of the trends and suggests hydrological management towards desirable vegetation. This approach, developed on data from the British meadows, has much wider geographical applications if compared with European plant communities. Seventy-two British and European plant associations were compared *via* Canonical Correspondence Analysis (CCA). Species ordinations were used to study the coherence of floodplain syntaxonomic alliances across Europe from Ireland to Bulgaria. CCA confirmed the spread of the British subcommunities of the *Alopecurus-Sanguisorba* community along a strong hydrological gradient and highlighted their lower fertility compared to their Dutch counterparts. The hydrological gradient separating the British subcommunities should help inform site management for the conservation of the species-rich communities, especially where hydrological control is possible.

**Keywords:** Deschampsion (*Alopecurion*); floodplain meadows; hydrological gradient; British National Vegetation Classification; wet grassland

## **Introduction**

Nature conservation survey programmes require a robust vegetation classification to form the basis of site selection and management (Havlova *et al.*, 2004). In Europe many countries have developed their own phytosociological or other classifications

which have been used as the basis for site designations and the interpretation of international definitions such as those of the Habitats and Species Directive (Council of the European Union, 1992). Recently a unified system for vegetation of Europe, based on hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities, has been produced (Mucina *et al.*, 2016). Importance of land management to the classification of lowland meadows in Europe was highlighted by Rodríguez-Rojo *et al.* (2017).

Lowland floodplain meadows are recognised as a threatened habitat in the EU and listed in Annex I of the Habitat Directive as 6510 Lowland hay meadows (*Alopecurus pratensis*, *Sanguisorba officinalis*). In the UK, the definition of the category has been taken very narrowly with only one community of the British National Vegetation Classification (NVC) being assigned to this category, the *Alopecurus pratensis*-*Sanguisorba officinalis* community (MG4 of Rodwell, 1992). Other countries have taken a broader perspective and included vegetation of the syntaxonomic alliances *Cynosurion cristati* Tüxen 1947 and *Calthion palustris* Tüxen 1937 emend. Balátová-Tuláčková within this category. Member States differ in which Annex I categories they include in such broad habitats; this partly reflects climatic variation across the region such that vegetation types, which in Britain are largely confined to upland areas beyond the limit of enclosure, occur more widely on the lowlands elsewhere in Europe (Rodwell *et al.*, 2007).

The *Alopecurus pratensis*-*Sanguisorba officinalis* community is an iconic part of the English landscape and, in common with other European countries (Joyce & Wade, 1998; Soons *et al.*, 2005; Rodwell *et al.*, 2007; Krause *et al.*, 2011), is a threatened habitat. In Britain, although present on more than 120 sites many of these are small and fragmented (Jefferson & Pinches, 2011) and the total estimated area is between 485 ha (Blackstock *et al.*, 1999) and 1500 ha (Rodwell *et al.*, 2007). Situated on fertile floodplains, the community has traditionally been managed for hay with aftermath grazing (Jefferson & Pinches, 2011). The fertility of the sites makes them vulnerable to conversion to silage cropping, whilst urban development and extraction of underlying minerals have resulted in substantial loss of habitat. More recently abandonment of agricultural management and summer flooding are threatening this species rich community (Gowing *et al.*, 2002a).

Conservation organisations rely on vegetation classification for monitoring and evaluation of these rare plant communities. The threatened *Alopecurus pratensis*-*Sanguisorba officinalis* grassland was poorly defined in the NVC, with the floristic tables based on only 22 relevés (Rodwell, 1992). Thus, the range of floristic variation relative to soil moisture, soil fertility and management has been poorly understood and this has hampered effective management and conservation. A full review of the vegetation communities of damp meadows in Britain is needed (Rodwell *et al.*, 2000) together with a reassessment of their placement within a broader European context (Rodwell *et al.*, 2007). The dynamic nature of the *Alopecurus*-*Sanguisorba* community in Britain gives the impression that it straddles three alliances: the *Cynosurion*, *Arrhenatherion* and *Molinion* alliances (Rodwell, 1992). Page (1980) who first described this vegetation as a *Fritillario-Sanguisorbetum* placed it within the *Molinion*, but accepted that it appears to occupy a position intermediate between the *Molinion* and *Arrhenatherion*. A similar community from base-rich alluvial meadows in Belgium (Le Brun *et al.*, 1949), is characterised by *Sanguisorba officinalis*, *Colchicum autumnale* and *Anthriscus sylvestris* though these hay meadows, unlike

the British *Alopecurus –Sanguisorba* community, are not grazed in winter. They place the community in the Arrhenatherion. Indeed, communities featuring a high frequency of both *Alopecurus pratensis* and *Sanguisorba officinalis* have been placed in a wide range of alliances *vis* Alopecurion (Passarge, 1964; Kovar, 1981; Schaminée *et al.*, 1996), Arrhenatherion (Le Brun *et al.*, 1949; Meisel, 1960; Julve, 1993), Calthion (Dierschke, 1994), Cynosurion (Rodwell, 1992), Deschampsion (Kuyper *et al.*, 1978; Botta-Dukát *et al.*, 2005) and Molinion (Page, 1980; Balátová-Tuláčková, 1991). This is explained partly by the variation in ecological amplitude of *Alopecurus pratensis* and *Sanguisorba officinalis* in different parts of their range. Thus, *Alopecurus* is constant and *Sanguisorba* very frequent in the summer dry meadows of eastern Austria and western Slovakia (Botta-Dukát *et al.*, 2005); these meadows are not aftermath grazed and in summer the water level often drops to >1 m below ground level. Elsewhere in Austria *Sanguisorba* is constant in a much damper Deschampsietum cespitosae (Kuyper *et al.*, 1978) which features *Caltha palustris*, *Jacobaea aquatica*, *Carex panicea* and *Cirsium rivulare*. The ecological range of *Alopecurus pratensis* and *Sanguisorba officinalis* is getting even wider in the floodplains of non-regulated rivers in Eastern Europe and Siberia (Kucherov *et al.*, 2020).

A detailed study of the hydrological requirements of floodplain meadow species using floristic data and hydrological models (Silvertown *et al.*, 1999; Gowing *et al.*, 2002b; Garcia-Baquero Moneo *et al.*, 2022) demonstrated that the dominant factor in determining community distribution and composition in Britain was soil moisture; with communities clearly segregated by their tolerance to both soil aeration (waterlogging) and soil-drying stress using the sum exceedence values approach (SEV; Sieben, 1965). Data for this study were restricted to 18 sites with relevés systematically arranged across the hydrological gradient at the site. Additionally, conservation agencies have commissioned many vegetation surveys of sites supporting floodplain meadows, and these have provided relevés spanning the full hydrological spectrum of the floodplain communities.

The aim of this study is to use all available floristic data to describe the variation within the *Alopecurus-Sanguisorba* community in Britain and establish subunits. The tolerance of the community to different soil-moisture regimes will be described using modelled hydrological data and Ellenberg indicator values (Ellenberg, 1998), which showed a strong linear relationship (Gowing *et al.*, 2002b).

The placement of the British variation within a broader European framework was investigated using floristic data from published studies by workers in continental Europe, where vegetation unit assignment is still ongoing (e.g. Maciejewski *et al.*, 2020).

### **Data Sources**

Relevés were gathered from three sources. Firstly, the systematic survey and hydrological modelling of floodplain meadows in England (Gowing *et al.*, 2002b). 2330 relevés were selected from 16 sites. All these relevés have modelled hydrological data for SEV aeration and drying stress. The second source of relevés was also from grids of plots established to monitor long-term vegetation change. 972 quadrats from 10 sites (underlined in Fig. 1) were added; these did not have hydrological data. The third source was phytosociological surveys commissioned from the authors and others by various organisations. The survey of these relevés

involved the initial mapping of homogeneous stands of vegetation with relevés then sampled either randomly, or in the case of small stands or scarce units placed in 'typical' areas. 1444 quadrats from 32 sites were added.



**Figure 1.** Location of study sites supporting the *Alopecurus pratensis-Sanguisorba officinalis* community. 1 Ashleworth Ham, 2 Aughton Ings, 3 Besthorpe, **4 Blackthorn**, 5 Brighton Meadows, **6 Broaddale**, 7 Bubwith Ings, 8 Cassington Mead, 9 Chaceley Meadow, 10 Clifton Ings, 11 Coombe Hill Canal, **12 Cricklade**, **13 Dancing Gate**, 14 Ducklington Mead, 15 Eakring, **16 East Cottingwith**, 17 Ellerton Ings, 18 Elmlea, 19 Eskhamhall Meadows, 20 Far Hall Meadow, 21 Gunby Ings, 22 Hucclecote Meadow, 23 Ing Marsh, 24 Long Herdon, 25 Menthorpe Ing, 26 Mill Crook, **27 Mottey Meadows**, **28 Nethercote**, 30 North Duffield Carrs, 31 North Duffield Ings, 32 Oxey Mead, 33 Oxley Mead, 34 Pixey Mead, **35 Portholme**, 36 Rectory Farm, 37 Sherbourne Meadows, 38 South Duffield Ings, 39 Storwood Ings, 40 The Low Grounds, 41 Thorganby Ings, 42 Thornton and Melbourne Ings, **43 Upton Ham**, **44 Upwood**, 45 West Carr Ings, 46 Wheldrake Ings, 47 Wolvercote meadows, 48 Yarnton Mead. Not all sites supported vegetation of the *Alopecurus-Sanguisorba officinalis* community and these are omitted from the figure for clarity.

In BOLD = First source of data: 18 sites with systematic survey and hydrological modelling.  
 UNDERLINED = Second source of data: 10 sites where grids of plots established to monitor long-term vegetation change (Gowing *et al.*, 2002b)

In all cases the relevés were 1x1 m in size. The species record involved the listing of all vascular plants (Tutin *et al.*, 1964 *et seq.*, with names now updated to follow Stace [2019]) and bryophytes (Corley & Hill, 1981), species abundance was recorded using visual estimates of percentage cover.

### **Data analysis**

The 4746 relevés were analysed using the Juice software (v.6.3, Tichý & Holt, 2006) incorporating the modified version of TWINSpan from the PC-Ord software (v.5. McCune & Mefford, 1999). Species cover data were used with five cut levels (0, 1, 2, 5 and 33) and no downweighting of rare species. To avoid the problem of outliers and chaining preventing a satisfactory division of the central, most homogeneous, section of the data set, the analysis was run to six divisions producing 64 end groups. These groups were progressively amalgamated to produce units that appeared to be homogeneous with respect to species frequency. The Czekanowski co-efficient of similarity was used *via* the software program MATCH (Malloch, 1998) to test the goodness of fit of the successive amalgamations of TWINSpan end groups to units of the NVC.

The floristic distinctness of the groups derived from TWINSpan was tested against environmental data through ANOVA; using SEV for soil drying and waterlogging where available and also mean Ellenberg scores calculated from the Ellenberg scores for the species in each quadrat.

Soil chemical data were available for some relevés. These comprised pH and available phosphorus values, measured using the Olsen extraction method (Gilbert *et al.*, 2009). These were used to interpret the full range of variation within the *Alopecurus-Sanguisorba* grassland.

The second objective of the paper is to place the subsections of the British *Alopecurus pratensis-Sanguisorba officinalis* community into a broader European context. The associations selected for this comparison are in published papers (see Appendix 1 at end of paper) and were chosen so as to cover the major damp and circumneutral grassland associations in which the indicator species *Alopecurus pratensis*, *Sanguisorba officinalis*, *Trisetum flavescens*, *Caltha palustris* and *Carex panicea* are well represented. Differing data sources presented species data as either percentage frequency or as constancy classes: for consistency in this analysis, all species frequency data are expressed using the five standard constancy classes; Constancy Class I= 1-20% frequency, Class 2= 21-40%, Class 3=41-60%, Class 4 =61-80% and Class 5 = 81-100%. Species present at <5% frequency in any synoptic table have been omitted. The comparison between the 11 groups arising from the analysis of the 4746 relevés from this research, other similar British groups, and 46 continental groups was studied *via* a Canonical Correspondence Analysis (CCA; PC-Ord, v.5. McCune & Mefford, 1999). The main matrix comprised 72 groups with a total species complement of 395.

A second matrix of six proxy environmental variables included mean Ellenberg scores for soil reaction (R), fertility (N) and moisture tolerance (F) using the original scores (Ellenberg, 1988) (rather than the various regional lists now available), longitude as a measure of continentality, species number per relevé and a categorical variable for the published alliance of each group. The CCA was run using Centred and normalised data optimised for row (sample) scores. Diagrams of the distribution

of species and groups against axis scores are presented. For the groups row (samples) scores were derived from the columns (species) and are equivalent to the weighted averages of the species scores (WA scores of Palmer, 1993). Bioplots (McCune & Mefford, 1999) were used to investigate the strength of relationships with the environmental parameters in the second matrix using inter-set correlations whilst overlays of the relative frequency of selected species were used to assess their discriminating power between the different alliances.

## Results

### *Community description*

The TWINSpan analysis of the 4669 relevés produced 11 groups that appeared distinct in their floristic composition. Seventy-seven samples were not assigned and were omitted from further analyses. These outlying groups of samples consisted of relevés referable to the following NVC communities; *Juncus effusus/acutiflorus-Galium palustre* rush pasture, *Holcus lanatus-Deschampsia cespitosa* coarse grassland, *Holcus lanatus-Juncus effusus* rush pasture, the *Epilobium hirsutum* and *Agrostis stolonifera-Ranunculus repens* communities.

The 11 groups spanned five recognised NVC communities; *Lolium perenne-Cynosurus cristatus* grassland (1 group), the *Alopecurus pratensis-Sanguisorba officinalis* community (4 groups), the *Caltha-Cynosurus cristatus* community (3 groups), the *Lolium perenne-Alopecurus pratensis-Festuca pratensis* grassland (1 group), the *Agrostis-Carex spp.* grassland (1 group) and a group intermediate between the *Alopecurus-Sanguisorba* and *Caltha-Cynosurus* communities.

The geographic spread of the 48 sites supporting the *Alopecurus-Sanguisorba* community in England and Wales shows clear concentrations along the River Thames in the south and the River Derwent in the northeast (Fig. 1).

A Synoptic table is presented (Table 1) for the four proposed subcommunities of the *Alopecurus-Sanguisorba* grassland, (a) *Dactylis glomerata*, (b) Typical, (c) *Holcus lanatus* and (d) *Agrostis stolonifera*. The (a) and (b) subcommunities are relatively species-rich (with 25 and 22 species m<sup>-2</sup> respectively) whilst the (c) and (d) ones are less rich (16 and 15 species m<sup>-2</sup> respectively).

**Table 1. Synoptic table for the proposed subcommunities of the *Alopecurus pratensis-Sanguisorba officinalis* (MG4) grassland in Britain. Values are percentage frequency of species in 1 x 1 m quadrats. Species present at >5% frequency in any subcommunity are included**

<b>Subcommunity</b>	<b>4a</b> <i>Dactylis glomerata</i>	<b>4b</b> <i>Typical</i>	<b>4c</b> <i>Holcus lanatus</i>	<b>4d</b> <i>Agrostis stolonifera</i>	<b>MG4</b>
CCA group	61	62	64	63	
Number of samples	604	933	624	257	2410
Mean species / sample	25	22	16	15	21
<b>Constants</b>					
<i>Ranunculus acris</i>	87	90	81	45	82
<i>Festuca rubra</i>	92	91	50	49	77
<i>Rumex acetosa</i>	74	79	77	56	75
<i>Sanguisorba officinalis</i>	75	77	61	61	71

<i>Holcus lanatus</i>	90	79	65	4	70
<i>Lolium perenne</i>	85	72	63	39	70
<i>Poa trivialis</i>	51	66	85	86	70
<i>Alopecurus pratensis</i>	35	65	83	82	64
<i>Cynosurus cristatus</i>	89	73	41	2	62
<i>Anthoxanthum odoratum</i>	69	78	58	15	64
<i>Lathyrus pratensis</i>	63	61	52	51	58

#### **Preferential to a & b**

<i>Centaurea nigra</i>	81	66	22	11	53
<i>Plantago lanceolata</i>	80	66	18	14	52
<i>Trifolium pratense</i>	76	72	17	6	52
<i>Taraxacum officinale</i>	69	66	38	28	54
agg.					
<i>Trifolium repens</i>	60	56	24	19	45
<i>Bromus racemosus</i>	44	40	19	15	33
<i>Cerastium fontanum</i>	47	45	15	4	33
<i>Agrostis capillaris</i>	27	29	14		22
<i>Fritillaria meleagris</i>	15	7	1	1	3
<i>Succisa pratensis</i>	12	10	2	2	7
<i>Ophioglossum vulgatum</i>	14	6	2	3	7
<i>Carex flacca</i>	13	10	2	1	8
<i>Bellis perennis</i>	13	7	1		6

#### **Preferential to a only**

<i>Dactylis glomerata</i>	88	29	8	1	35
<i>Trisetum flavescens</i>	81	17	3	1	28
<i>Rhinanthus minor</i>	60	44	4	11	34
<i>Leucanthemum vulgare</i>	64	15			22
<i>Arrhenatherum elatius</i>	60	15	7	2	23
<i>Lotus corniculatus</i>	56	37	11	18	33
<i>Ranunculus bulbosus</i>	51	18	4		21
<i>Prunella vulgaris</i>	52	24	3	3	23
<i>Heracleum sphondylium</i>	32	3	2		9
<i>Brachythecium</i>	29	16	7	3	16
<i>rutabulum</i>					
<i>Tragopogon pratensis</i>	23	1			6
<i>Leontodon hispidus</i>	24	9			10
<i>Galium verum</i>	17	10	3	2	9
<i>Linum catharticum</i>	15				4
<i>Medicago lupulina</i>	9				2
<i>Briza media</i>	33	6			11
<i>Bromus racemosus</i>	23	12	19	3	16
<i>Leontodon saxatilis</i>	14	2			4
<i>Primula veris</i>	12	3	1		4
<i>Eurhynchium</i>	14	9	4		8
<i>praelongum</i>					
<i>Anthriscus sylvestris</i>	6				2

#### **Preferential to c and d**

<i>Deschampsia cespitosa</i>	8	19	23	23	18
<i>Oenanthe silaifolia</i>		5	12	16	7

<i>Elymus repens</i>	1	3	22	13	9
<i>Phalaris arundinacea</i>			6	15	3
<i>Rumex crispus</i>	2	2	7	16	5
<b>Preferential to d only</b>					
<i>Agrostis stolonifera</i>	29	50	72	87	54
<i>Filipendula ulmaria</i>	54	56	48	74	56
<i>Cardamine pratensis</i>	4	34	54	79	36
<i>Carex acuta</i>	1	3	7	34	7
<i>Persicaria amphibia</i>	5	2	14	20	8
<i>Carex disticha</i>	0	3	10	29	7
<i>Lysimachia nummularia</i>	2	5	7	22	7
<i>Achillea ptarmica</i>		4	2	21	4
<i>Myosotis laxa</i>		1	1	14	2
<i>Galium palustre</i>		1	1	13	2
<i>Stellaria palustris</i>			1	11	1
<i>Carex acutiformis</i>	1	4	3	10	4
<b>Associates</b>					
<i>Silaum silaus</i>	46	43	20	49	39
<i>Scorzoneroides autumnalis</i>	35	47	17	51	37
<i>Vicia cracca</i>	33	30	24	39	30
<i>Hordeum secalinum</i>	33	27	26	26	28
<i>Phleum pratense</i>	28	36	25	34	31
<i>Potentilla reptans</i>	14	11	14	2	11
<i>Schedonorus pratensis</i>	12	29	14	37	22
<i>Ranunculus repens</i>	10	34	48	42	32
<i>Carex hirta</i>	9	10	7	9	9
<i>Equisetum palustre</i>	8	6	4	7	6
<i>Calliergonella cuspidata</i>	6	8	6	12	8
<i>Filipendula vulgaris</i>	5	6	5		5
<i>Luzula campestris</i>	4	11	4		7
<i>Silene flos-cuculi</i>	1	7	2	2	4
<i>Juncus acutiflorus</i>	2	5	4	3	4
<i>Trifolium dubium</i>	3	14	8	1	8
<i>Cirsium arvense</i>	2	4	8	2	4
<i>Carex panicea</i>	1	5	2	2	3
<i>Stellaria graminea</i>	1	2	5	1	2
<i>Vulpia bromoides</i>		5	1		2
<i>Alopecurus geniculatus</i>		2	2	6	2
<i>Jacobaea aquaticus</i>		1	3	11	2
<i>Caltha palustris</i>		1	2	6	2
<i>Carex nigra</i>	3	5	4	5	4
<i>Agrostis canina</i>		2	4	5	2
<i>Carex riparia</i>			7	4	2

In addition to the community constants (*Ranunculus acris* to *Lathyrus pratensis* in Table 1) the *Dactylis glomerata* and Typical subcommunities share a suite of preferential species which are scarce in both the *Holcus lanatus* and *Agrostis stolonifera* subcommunities (*Centaurea nigra* to *Bellis perennis*).



The *Dactylis glomerata* subcommunity is the richest subcommunity and is characterised by having constant *Dactylis glomerata* and *Trisetum flavescens* plus very frequent *Leucanthemum vulgare*, *Arrhenatherum elatius* and *Rhinanthus minor*. It is also distinguished from the Typical subcommunity by the presence of a suite of Mesobromion species, which include *Galium verum*, *Tragopogon pratensis*, *Leontodon saxatilis*, *Linum catharticum* and *Medicago lupulina* whilst *Avenula pubescens*, *Polygala vulgaris* and *Bromopsis erecta* are also encountered occasionally. It is further distinguished by a second group of calcicolous species including *Briza media*, *Bromus racemosus*, *Leontodon hispidus* and *Primula veris*, which are either absent or scarce in the other subcommunities. It should be noted that *Alopecurus pratensis* is often sparse and patchy in this subcommunity.

The Typical subcommunity, as its name implies, represents those stands closest to the constancy table of the published NVC (Rodwell, 1992). These stands are less species rich than those of the NVC in which the classic sites for this kind of floodplain meadow were over-represented. The expansion of the range of sites sampled here has led to the lower frequency of *Fritillaria* and *Bellis perennis*. The subcommunity lacks any strong preferential species.

The *Holcus lanatus* subcommunity is widespread being recorded at 35 of the sites in this analysis. It is characterised by the low frequency of species common to the (a) and (b) subcommunities (*Centaurea nigra* to *Bellis perennis* in Table 1) and lacks strong preferential species.

The *Agrostis stolonifera* subcommunity is the most floristically impoverished. Again, lacking those species that characterise the (a) and (b) subcommunities, it shares with the (c) subcommunity the high frequency and cover of *Alopecurus pratensis*. However, it displays a suite of preferential species which include taxa characteristic of damper soil conditions: *Agrostis stolonifera*, *Cardamine pratensis*, *Carex disticha*, *Carex acuta*, *Filipendula ulmaria* and *Lysimachia nummularia*. In addition, *Achillea ptarmica*, *Myosotis laxa* and *Stellaria palustris*, though present at low frequencies, are differential for this group. In general, the (c) and (d) subcommunities feature species of more fertile substrates than those preferential to the (a) and (b) subcommunities.

#### *Community – Environment relationships*

The soil aeration and soil-drying stress (Table 2) show a clear progression of increasing aeration stress and decreasing soil drying across the groups. The *Dactylis glomerata* subcommunity experiences considerable periods of soil drying during the growing season, as indicated by the high SEV<sub>d</sub> value, but is rarely exposed to waterlogged soil (hence low SEV<sub>a</sub>), i.e. water tables remain low throughout the season. This contrasts with the *Agrostis stolonifera* subcommunity where soils are less prone to soil drying (lower SEV<sub>d</sub>), but experience long periods of waterlogged soil during the growing season (higher SEV<sub>a</sub>). The *Holcus lanatus* and Typical subcommunities occupy intermediate areas in terms of summer drought, but the spring inundation of the Typical subcommunity is significantly less than both the *Holcus* and *Agrostis* units.

**Table 2. Waterlogging and soil drying stress. Values are based on 5-year average sum exceedence values for aeration stress (SEV<sub>a</sub>) and soil drying (SEV<sub>d</sub>). Values are means, units are metre.weeks, ± one standard error of the mean. n= number of samples for each vegetation unit. ANOVA between vegetation units SEV<sub>d</sub>  $p < 0.001$  and SEV<sub>a</sub>  $p < 0.001$ . Means not significantly different indicated by the same letter**

Vegetation unit	n	SEV <sub>a</sub>	SEV <sub>d</sub>
<i>Alopecurus pratensis</i> - <i>Sanguisorba officinalis</i> community			
<i>Dactylis</i> subcommunity	383	0.48±0.03	8.70±0.13
Typical subcommunity	587	1.03±0.04	5.40±0.11 <sup>a</sup>
<i>Holcus lanatus</i> subcommunity	344	1.77±0.05	5.10±0.06 <sup>a</sup>
<i>Agrostis stolonifera</i> subcommunity	64	2.71±0.17	2.99±0.24

Comparison of mean Ellenberg indicator scores (Table 3) demonstrates that the soil-moisture index (F) follows the same pattern illustrated by the SEV scores. All four groups have mean Ellenberg F scores that are significantly different to each other (Anova  $p < 0.001$ ). The *Agrostis stolonifera* subcommunity of *Alopecurus-Sanguisorba* grassland contains the highest proportion of flood-tolerant species, a fact that is emphasised by the list of preferential and differential taxa (Table 1). It is also the form of the community that seems to be associated with soils having the highest levels of available phosphorus (Table 4). If Ellenberg N is considered as an indirect reflection of soil fertility, then the significant differences between the subcommunities confirm that the *Holcus* and *Agrostis* subcommunities occupy the naturally more fertile sites where sediment deposition is high; the *Holcus* subcommunity is concentrated on extensive sites on the wider floodplains of the larger river systems subject to frequent, if not prolonged inundation, whilst the *Agrostis* subcommunity tends to occupy sites with impeded drainage where flood waters sit for longer. In contrast, the *Dactylis glomerata* subcommunity is characteristic of the least fertile soils amongst the *Alopecurus-Sanguisorba* subcommunities, probably attributable to a combination of leaching and to a lower frequency and duration of inundation.

#### *Comparison with European vegetation types*

The groups used in the CCA have been partitioned according to the alliance into which each was placed by the author(s). Different authors have different understandings of the scope of any particular alliance. In the case of lowland meadows, some organise assemblages of communities into broad alliances, particularly the Molinion and Arrhenatherion, whilst others prefer to work with units of narrower definition. Thus, the Alopecurion of Passarge (1964) is subsumed within the Molinion by Dierschke (1994) and into an Agrostition albae Soó 1930 alliance by Kovács & Máthé (1967). The Deschampsion cespitosae Horvatic 1930 is retained by Page (1980), Stančić (2008) and Hájek et al. (2008) but is placed in the Agropyro-Rumicion Nordhagen 1940 emend. Tüxen 1950 by Westhoff & den Held (1969) or the Calthion by Rodwell (1992) and Raman & de Becker (2012). It has to be accepted that the traditional classification system was created by different authors, each of them using different criteria. The consequence of this is that many of the earlier described alliances are very general whilst others are very specific and

geographically constrained. A unified approach was recently applied at the European scale (Mucina *et al.*, 2016).

**Table 3. Mean Ellenberg scores for reaction (R), fertility (N) and moisture tolerance (F). ANOVA for differences between vegetation units R  $p<0.001$ , N  $p<0.001$ , F  $p<0.001$ . Reaction (R) values not significantly different denoted by the same letter, for N and F all values significantly different from each other. n=number of samples for each unit**

Vegetation Unit	n	R	N	F
<i>Alopecurus-Sanguisorba</i> community				
<i>Dactylis</i> subcommunity	604	<sup>a</sup> 6.12 ±0.01	5.01 ±0.02	5.54 ±0.01
Typical subcommunity	1018	5.87 ±0.01	5.12 ±0.01	5.79 ±0.01
<i>Holcus</i> subcommunity	624	<sup>a</sup> 6.07 ±0.02	5.49 ±0.02	6.24 ±0.02
<i>Agrostis</i> subcommunity	257	<sup>a</sup> 6.13 ±0.03	5.38 ±0.02	6.76 ±0.04

**Table 4. Soil chemistry for the subcommunities of *Alopecurus pratensis-Sanguisorba officinalis* and *Caltha-Cynosurus, Sanguisorba* subcommunity. (Based on data from Gowing *et al.*, 2002b). Values are means, ± one standard error of the mean, n=number of samples for which data were available. ANOVA for pH  $p=0.013$  and Olsen P  $p=<0.001$ . Pairwise comparisons indicated, for pH, *Alopecurus-Sanguisorba* Typical subcommunity > *Caltha-Cynosurus* whilst for Olsen P values denoted by the same letter were not significantly different from each other**

Vegetation unit	n	pH	n	Olsen P mg/kg
<i>Alopecurus-Sanguisorba</i>				
<i>Dactylis</i> subcommunity	12	5.89 ±0.27	33	7.65 <sup>bc</sup> ±1.18
Typical subcommunity	33	5.98 ±0.15	55	9.54 <sup>b</sup> ±0.62
<i>Holcus</i> subcommunity	16	5.46 ±0.14	21	12.51 <sup>ab</sup> ±1.63
<i>Agrostis</i> subcommunity	8	5.60 ±0.20	16	16.22 <sup>a</sup> ±2.78

CCA analysis was used to assess the major gradients of species distribution. Of the 395 species recorded in the 72 groups, 109 were recorded in a single group and a further 52 occurred in only two groups. A selection of species having a wide range of values for Ellenberg indices for R, F and N are plotted against their axis scores (Figs. 2 and 3).

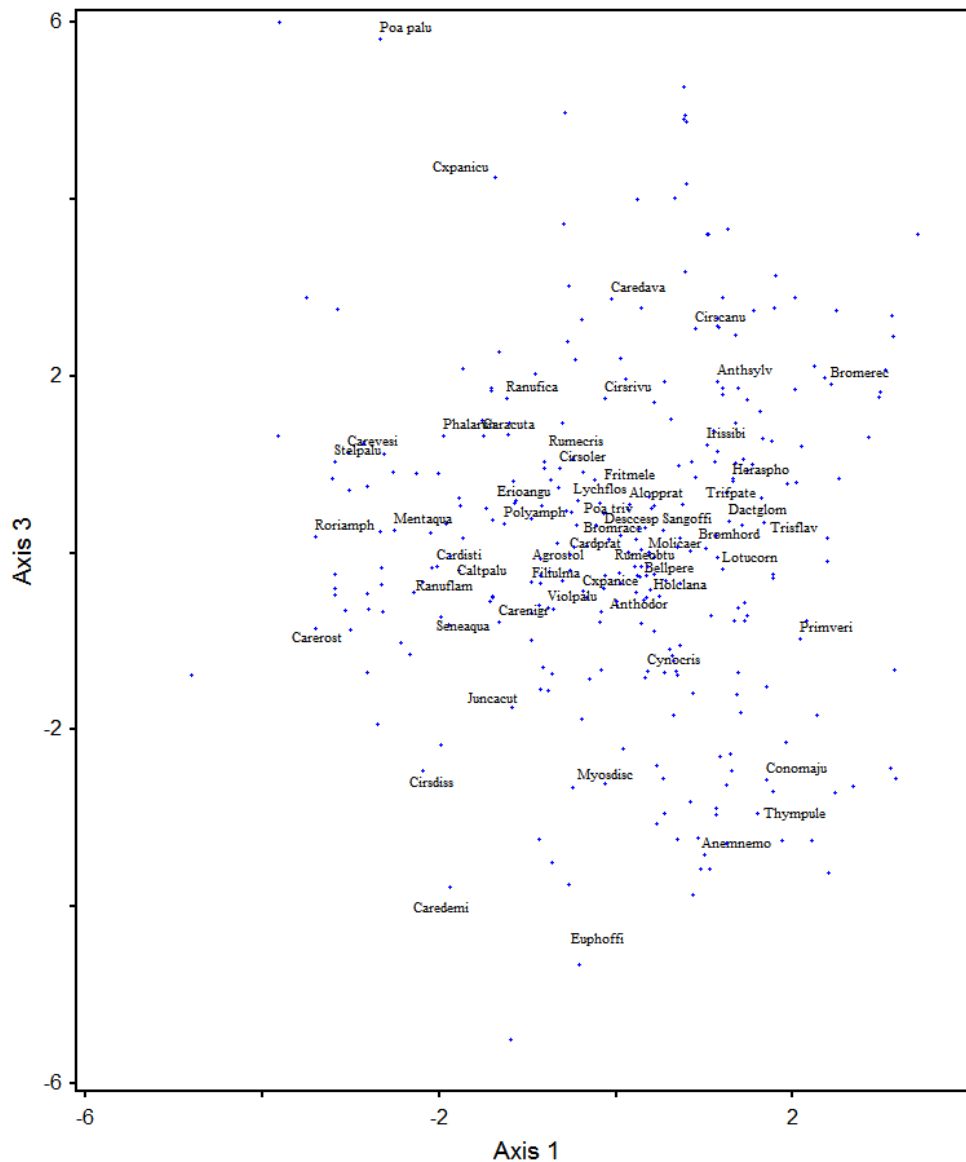
A suite of species with low F values have high CCA scores on Axis 1: *Bromopsis erecta* (3), *Primula veris* (4), *Trisetum flavescens* (4), *Heracleum sphondylium* (5) in contrast to species with high F values and low CCA Axis 1 scores: *Rorippa amphibia* (10), *Carex vesicaria* (9), *Stellaria palustris* (9), *Mentha aquatica* (9), *Ranunculus flammula* (9), *Carex disticha* (9) and *Phalaris arundinacea* (8). Axis 1 therefore appears to reflect a hydrological gradient with species of high flood tolerance being replaced by more drought-tolerant taxa along the axis.

On Axis 2 species of low fertility (low N) habitats have low axis 2 scores; *Carex davalliana* (2), *Molinia caerulea* (2), *Iris sibirica* (2), *Eriophorum angustifolium* (2), *Carex panicea* (3) and *Viola palustris* (5) whilst those with high N scores occur at the

upper end of the axis; *Rumex obtusifolius* (9), *Anthriscus sylvestris* (8), *Heracleum sphondylium* (8) and *Ficaria verna* (formerly *Ranunculus ficaria*) (7). Axis 2 therefore seems to indicate a gradient of increasing soil fertility.



**Figure 2. Species distribution on the CCA plot: Axis 1 versus Axis 2**

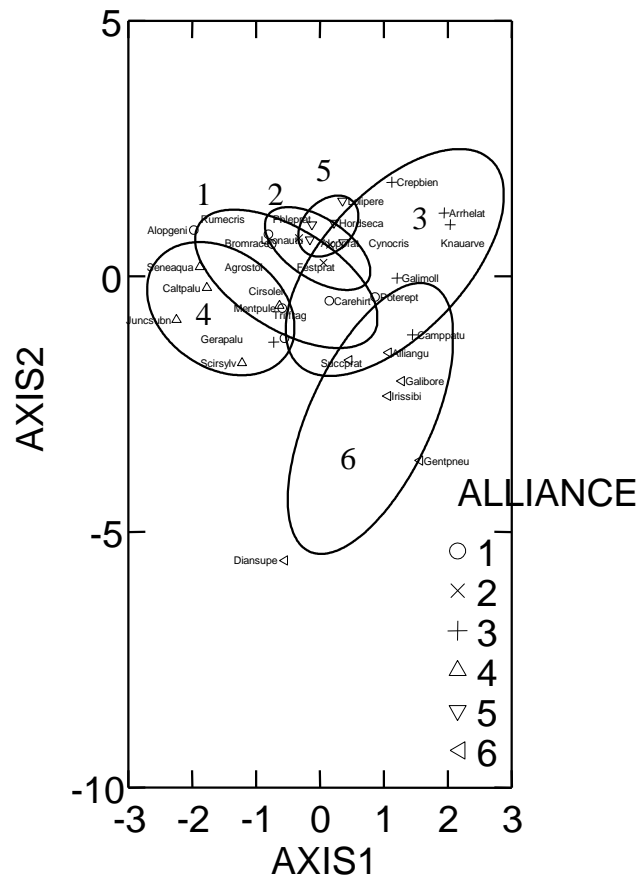


**Figure 3. Species distribution on the CCA plot: Axis 1 versus Axis 3**

On Axis 3 species of low R value have low CCA scores; *Carex demissa* (4), *Cirsium dissectum* (4), *Myosotis discolor* (4), *Conopodium majus* (4), *Anemone nemorosa* (5) and *Juncus acutiflorus* (5). In contrast high scoring species are evident at the positive end of the axis; *Poa palustris* (8), *Carex davalliana* (8), *Cirsium canum* (7), *Carex paniculata* (6), *Cirsium rivulare* (8), *Bromopsis erecta* (8), *Ficaria verna* (7) and *Anthriscus sylvestris* (7). Thus, this axis seems to feature a gradient from species of acidic to those of alkaline soils. The position of *Thymus pulegioides* appears anomalous here as, at least in England, it is a species of chalky substrates.

Fig. 4 shows the position in hyperspace of a selection of species characteristic of different alliances. The species are taken from the lists of Ellenberg (1988) except for the Alopecurion (Schaminée et al., 1996). A clear segregation is evident; Molinion species tend to occupy the dry (high Axis 1) infertile (low Axis 2) segment of the ordination whilst those characteristic of the Arrhenatherion are tightly clustered in the driest, fertile quadrant (high Axis 1, high Axis 2). Species of the Cynosurion and

Alopecurion are also tightly clustered being of similar fertility to the Arrhenatherion but of higher soil moisture tolerance (i.e. lower Axis 1 scores) whilst the suite of Calthion species are clustered at the wet end of Axis 1 at slightly lower fertility. Species of the Potentillion anserinae Von Rochow 1948 ( $\equiv$  *Elymo-Rumicion*) are less concentrated on Axis 1 but do occupy a zone of moderate fertility.



**Figure 4. Selected species representative of different alliances. Bivariate ellipses for each alliance are based on species mean axis scores. Ellipses axes are determined by sample deviation and orientation between x and y using covariance between axis 1 and 2. Ellipse probability set at 0.60. Alliances (1) Potentillion, (2) Alopecurion, (3) Arrhenatherion, (4) Calthion, (5) Cynosurion, (6) Molinion**

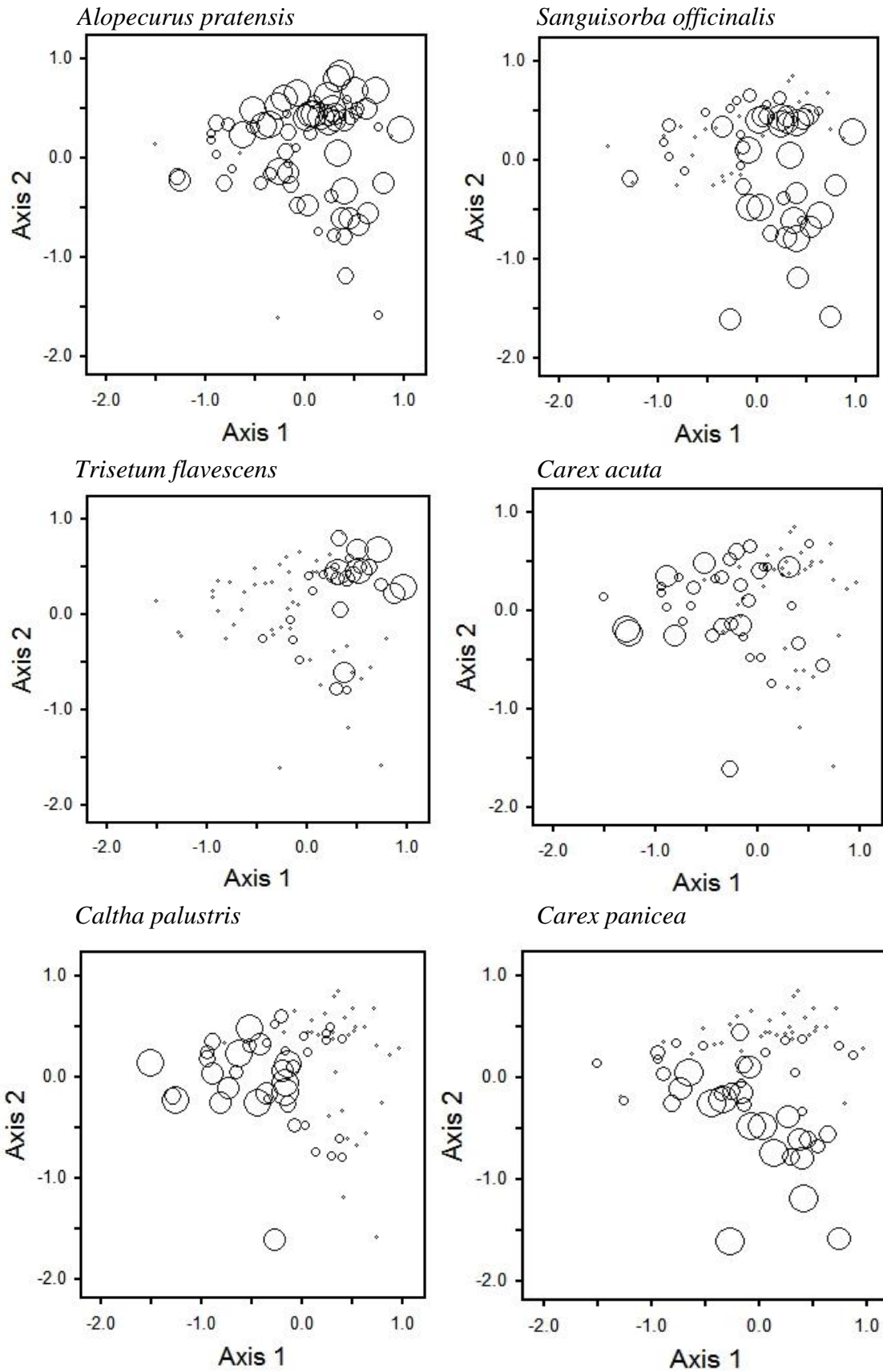
A number of species occupy anomalous positions: *Cirsium canum* and *Cirsium rivulare*, both listed as Calthion species by Ellenberg, fall near the centre of the Molinion group, which also accommodates *Inula britannica*, given as characteristic of the Agropyro-Rumicion. *Phleum bertolonii* of the Cynosurion appears with a cluster of

Arrhenatherion species whilst *Cirsium dissectum*, given as a species of the Molinion, appears to fit more comfortably with the Calthion species.

The diagnostic value of species can be considered through their distribution and relative frequency across the alliances (Fig. 5). The size of the circle is scaled by constancy class. The cosmopolitan nature of *Alopecurus pratensis* is clear since although those groups where the species occurs at high frequency tend to be clustered towards the drier and more fertile section of the ordination, the species is present in all but six of the 72 groups presented. *Sanguisorba officinalis* occurs only very sparsely in the Calthion stands, but it is quite evenly distributed across the right-hand side of the diagram, demonstrating that the species can be prevalent in vegetation units found over a wide range of soil fertility. *Trisetum flavescens* in contrast, is much more closely associated with dry sites having a high reaction value and moderate to high fertility in terms of floodplain meadow vegetation: it must be appreciated that the groups selected do not include the grass-dominated communities of the Lolio-Plantaginion that receive considerable artificial fertiliser, hence the use of fertile in this context is a relative term. *Carex panicea* has been included as an example of a frequently encountered species which can be widespread over much of the hydrological gradient, but its presence is strongly skewed to soils of low fertility. *Caltha palustris* occurs across the groups, but the presence of this species at high constancy is restricted to the wetter end of the gradient. *Carex acuta* (= *C. gracilis* Curtis of most continental authors) is similarly associated with the wetter meadows, but this species can invade less inundated habitats and thus its distribution across the moisture gradient is less confined than is that of *Caltha palustris*.

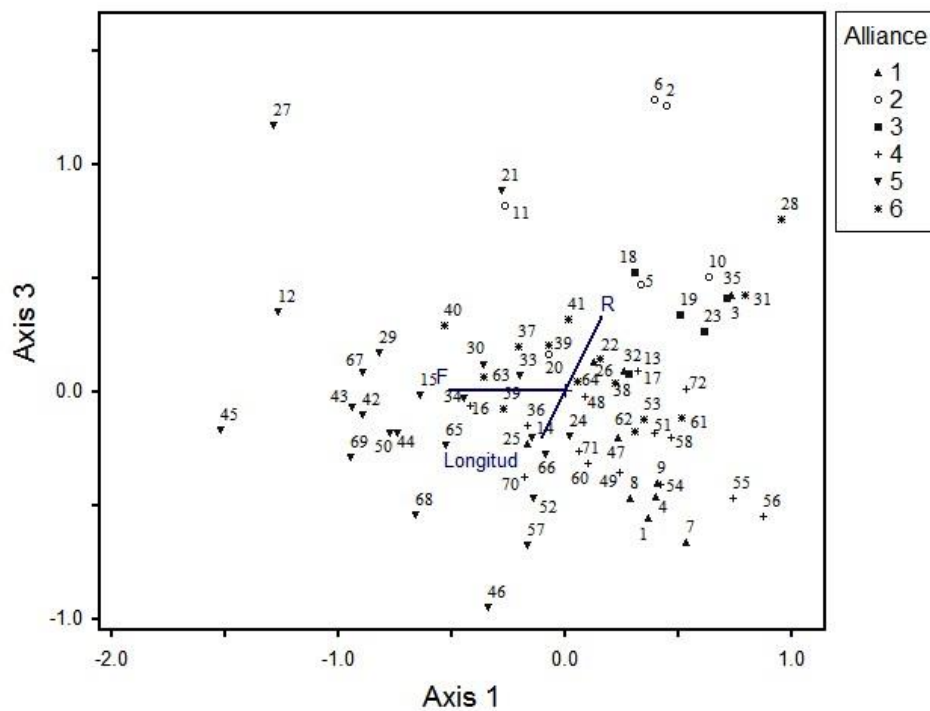
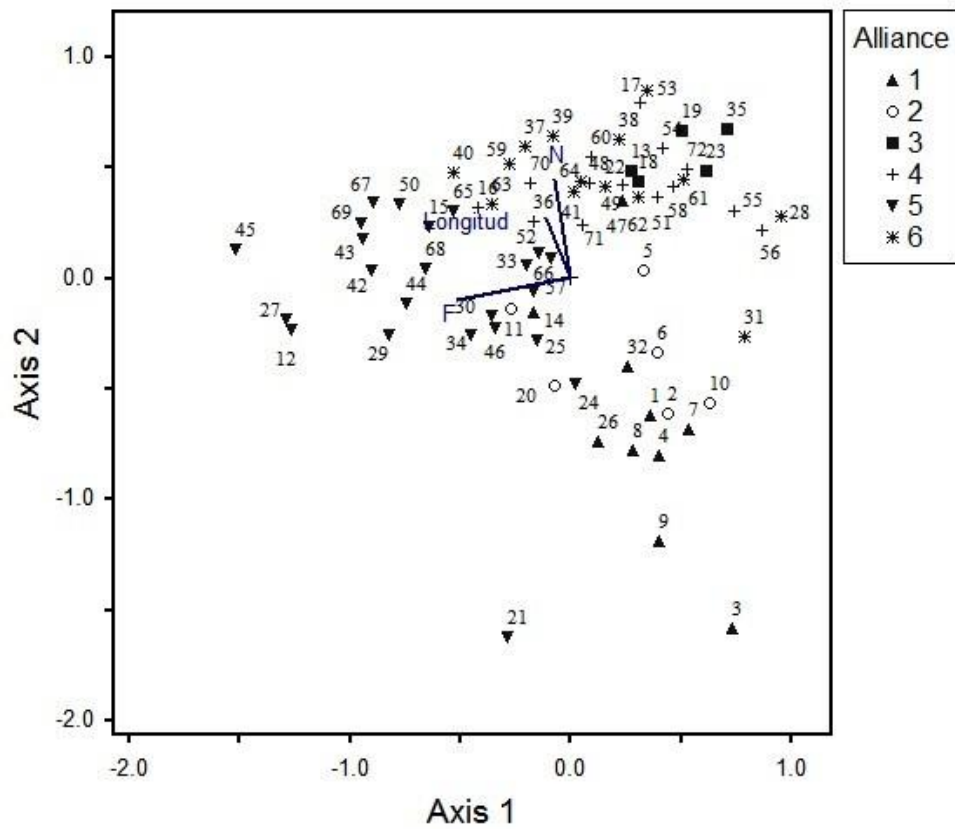
The inter-set correlations shown on the CCA diagram of the 72 groups (Fig. 6) confirms a strong negative correlation between Axis 1 and Ellenberg F (-0.957), a positive correlation between Axis 2 and Ellenberg N (0.85) and Longitude (0.52) whilst Axis 3 shows a weaker correlation with both Ellenberg R (0.75) and longitude (-0.47).

On the first axis of the ordination vegetation groups having a high proportion of drought-tolerant species are clustered towards the right-hand margin compared to those dominated by flood-tolerant taxa, such as the *Caricetum gracilis* typicum (Kovar 1981) [group 27 on the DCA plot] at the left-hand margin. The second axis, related to soil fertility, has the groups widely dispersed with the Arrhenatherion meadows grouped at the fertile end of the spectrum (high Axis 2 scores) and associations, such as the unmanured Molinion meadows from central Europe, displaying the lowest Axis 2 scores. The pair of communities from western Europe placed by their authors in the Molinion [14, 47] are separated from those of central Europe in having similar mean Ellenberg F scores but much higher mean Ellenberg N values. This is the first indication from the analysis that alliances across Europe may have quite dissimilar floristic compositions.



**Figure 5. Distribution of species across the stand ordination. Circles are scaled relative to species frequency using 5 constancy classes**





**Figure 6. Distribution of the 72 groups on the first three axes of the CCA analysis; Top: Axis 1  $\nu$  2 and Bottom: Axis 1  $\nu$  3. Numbers refer to group number (see Appendix 1). Eigenvalues Axis 1=0.275, Axis 2=0.244, Axis 3=0.168. Alliances distinguished by different symbols: 1 *Molinion*, 2 *Deschampsion*, 3 *Arrhenatherion*, 4 *Cynosurion*, 5 *Calthion*, 6 *Alopecurion***

The Cynosurion and Arrhenatherion communities form a tight group with high Axis 1 and 2 scores. This corresponds to the close grouping of the diagnostic species for these alliances (Fig. 4).

The communities of the Deschampsion described from central Europe are widely dispersed along the fertility axis, four of them have similar mean Ellenberg F scores; however, even in this geographically constrained set of central European groups there are two outliers with much higher F scores; the *Oenanthe silaifolia-Alopecurus pratensis* community from Croatia [11] (Stančić 2008) and the *Deschampsietum cespitosae* community from Austria [20] (Kuyper *et al.*, 1978).

The Calthion communities are spread widely across the hydrological gradient from the relatively dry *Junco-Molinietum* (Dierschke, 1994) [24] from the Czech Republic to the Irish *Carex nigra-Ranunculus repens* community (Heery, 1991) [45] from the Shannon Callows. There is no segregation related to geographic location on Axes 1 and 2: the Irish *Carex panicea-Festuca rubra* community having an almost identical score to those of the *Circetum oleracei* of Passarge (1964) from north-east Germany. However, there is separation on Axis 3; the Irish community occurring on much more base poor substrates than its German counterpart.

The third axis of the CCA, principally correlated with pH values, also shows a weak separation associated with continentality, as measured by longitude. The British, Irish and Dutch groups being segregated from the most continental groups of Bulgaria, Slovakia and Croatia. The groups of the Molinion from the Czech Republic form a discrete grouping. There is a suggestion that the more continental stands are also those with higher soil base status, as indicated by the positive association between axis 3 score and mean group Ellenberg R.

The four subcommunities of the British *Alopecurus-Sanguisorba* grassland identified in the current analysis [61-64] are spread widely along Axis 1 but are within a relatively narrow band on Axis 2. This is in accordance with the mean Ellenberg F and N scores (Table 3) and the soil phosphorus values (Table 4). It is of interest to compare the positions of these groups with those of the five Dutch Alopecurion associations (Schaminée *et al.*, 1996) which display a very similar spread along the soil-moisture axis, but four of which are elevated on the soil fertility axis; the fifth, the *Sanguisorbo-Siletum* community lies adjacent to the proposed *Holcus lanatus* subcommunity of the *Alopecurus pratensis-Sanguisorba officinalis* community, but appears to be an association of rather more base-rich substrates.

## Discussion

The proposed subcommunities of the NVC *Alopecurus pratensis-Sanguisorba officinalis* grassland community MG4 fit into four different alliances of the Molinio-Arrhenatheretea class in the current European classification (Mucina *et al.*, 2016). The *Dactylis* subcommunity would fit into Arrhenatherion alliance; the *Typical* subcommunity in the Cynosurion alliance; the *Holcus lanatus* subcommunity in the Deschampsion (Alopecurion); and the *Agrostis stolonifera* subcommunity in the Potentillion anserinae alliance (A. Kuzemko, personal communication). The changing classification of damp meadows in Europe, and the hydrological sensitivity of the British *Alopecurus-Sanguisorba* grassland, in part accounts for why British meadows seem to straddle a number of different alliances.

The Alopecurion alliance was established by Passarge (1964) to include meadows of moderately to very nutrient rich soils, located in floodplains and

dominated by graminoids. Dierschke (1997) described *Alopecurus pratensis* meadows and produced a table of 24 groups from across northern Europe, which may be interpreted as forming three subcommunities of an *Alopecurus pratensis-Ranunculus repens* community. These meadows were relatively species poor and were seen by Dierschke as semi-improved recent derivatives of the original floodplain grassland communities. Adopting a conservative approach, Dierschke did not recognise an Alopecurion alliance on the grounds that no convincing set of characteristic species could be produced for the alliance, a view shared by Balátová-Tuláčková (1994).

Many other workers have however accepted the reality of the alliance (Kovar, 1981; Schaminée *et al.*, 1996; Kuzemko, 2011). Julve (1993) also recognises an Alopecurion alliance, which includes an *Alopecuretum pratensis* community with *Fritillaria meleagris* and *Sanguisorba officinalis* amongst its characteristic species. The Alopecurion has also been recognised and included in Annex I of the Habitats Directive (EU 2007) in Austria, Slovenia, Lithuania, Latvia and Bulgaria (Rodwell *et al.*, 2007). In more recent vegetation reviews, the Alopecurion is treated as a synonym of Deschampsion (Kuzemko, 2016; Mucina *et al.*, 2016).

The *Alopecuretosum* of Kovar includes, in addition to *Alopecurus* and *Sanguisorba*, *Dactylis glomerata*, *Trisetum flavescens*, *Heracleum sphondylium* and *Arrhenatherum elatius* as community constants and hence bears a close resemblance to the proposed *Dactylis glomerata* subcommunity of the British *Alopecurus-Sanguisorba* community. Among Dutch groups of the alliance (Schaminée *et al.*, 1996), the *Sanguisorbo-Silaetum* has an affinity with both the proposed *Agrostis stolonifera* and *Holcus lanatus* subcommunities of *Alopecurus-Sanguisorba*, though the Dutch group is a more species-rich assemblage. The *Fritillario-Alopecuretum-Cynosuretosum* contains more drought-tolerant species and is quite similar to the *Dactylis* subcommunity, whilst the Dutch *Fritillario-Alopecuretum* typicum has a species complement intermediate between the *Agrostis stolonifera* and the proposed *Holcus* subcommunity of the *Alopecurus pratensis-Sanguisorba officinalis*. The Dutch members of the Alopecurion occur on more fertile sites than their British counterparts (Fig. 6). Though the proposed subcommunities of *Alopecurus-Sanguisorba* are associated with somewhat less fertile floodplains it seems reasonable to suggest their inclusion within the Alopecurion alliance.

Although some Alopecurion vegetation types from Central Europe are drier and develop on soils of higher pH, for example those of Kovar [28] and Passarge [31], similar mixtures of grass-dominated, species-poor groups and forb-rich groups can be found from Poland to Great Britain. In contrast the Deschampsion, which appears to represent a distinctive group of communities of relatively dry substrates of generally low fertility in central and eastern Europe, seems to lose its identity towards the Atlantic fringe. Although recognised by Page (1980) and used by that author to place the *Deschampsietum cespitosae* community, considered to be part of the Calthion by Rodwell (1992), the western examples feature prominently species characteristic of the *Agropyron-Rumicion crispi* ( $\equiv$  *Potentillion anserinae*) and are placed in that alliance (Westhoff & den Held, 1969).

The position of the Molinion Koch 1926 is similar. Its characteristic species (Ellenberg, 1988) are dominated by taxa absent from the native British flora. Communities of the alliance from Bulgaria [3], Slovakia [9], Slovenia [7] and the Czech Republic [4 and 8] have little in common with a French example [14] and occupy similarly dry infertile sites as do communities of the Deschampsion from that

region. In western Europe, the alliance has been replaced by a new entity, the *Junco (subuliflori)-Molinion* Westhoff (Westhoff & den Held, 1969), differentiated from the eastern Molinion by species such as *Carex pulicaris*, *Carex echinata*, *Agrostis canina* and the rushes *Juncus articulatus* and *Juncus acutiflorus*. In Britain there are no Molinion meadows, the sole representative of the alliance, the *Molinia caerulea-Crepis paludosa* mire (Rodwell, 1991) is a local community of the marginal uplands.

Changes in Calthion across the continent are more subtle and are discussed in a separate paper (Wallace & Prosser, 2017).

Differences within communities of the Arrhenatherion across Europe seem to relate mainly to differences in rainfall. Towards the Atlantic margin where rainfall is generally high, the Arrhenatherion is usually unmown and ungrazed since abundant hay crops can be taken from other sources, but in regions with drier summers these communities have been widely mown as an important source of hay (Rodwell *et al.*, 2007.) There is therefore considerable variety and variation in species richness across communities of the alliance; the core of the alliance is nonetheless clearly recognisable throughout the temperate European lowlands.

Regional variation in the Cynosurion cristati Tx. 1947 has been exhaustively analysed with seven types of Cynosurion vegetation recognised, occupying five geographical areas from Ireland to Romania (Zuidhoff *et al.*, 1995). Differences in the composition of the component communities principally reflect a transition from lowland to submontane habitats as the climate changes from the high rainfall and moderately low temperatures of the Atlantic fringe to more extreme conditions in southern and eastern Europe.

Coenological differences of the British *Alopecurus pratensis-Sanguisorba officinalis* lowland grassland community from its European and Asian counterparts are explained by its geographic location in the Atlantic fringe (Kucherov *et al.*, 2020).

The four proposed subcommunities of MG4 form an interchangeable gradient on British floodplains with heavily regulated rivers. The maintenance of species richness in the floodplain vegetation of Central Europe appears to be due to a combination of regular inundation and the maintenance of hay making. Thus, meadows of the *Oenanthe silaifolia-Alopecurus pratensis* community which flood regularly are mown two, or even three times a year for hay, but not for silage (Stančić, 2008,) whereas the swards described as degraded *Deschampsia* meadows are no longer flooded even though situated on a floodplain (Řezníčková, 2007). Some Molinion meadows, also in the Czech Republic, have been abandoned as hay yield became so low; others are now cut only every other year (Havlová *et al.*, 2004).

On the larger floodplains in the UK, where there is sufficient hydrological gradient to accommodate both the drought-tolerant *Dactylis* and the much more flood-tolerant *Agrostis* subcommunities, it is not unusual for all four subcommunities to be found at a single site. The hydrological ranges of the subunits suggest they are separated by relatively small differences in summer water table as measured by the SEV tolerances. Monitoring of permanent quadrats on some sites over time periods of 3 - 13 years has demonstrated rapid transitions between the units associated with extreme flood events and also with variation in cutting times. Studies at North Meadow (Wiltshire) and at East Cottingwith (Yorkshire) following the wettest 36 months on record in the UK (1999-2001) demonstrated migration of relevés from the species-rich *Dactylis* and Typical subcommunities to the *Holcus* and *Agrostis* subcommunities of up to 60% in a single year. Data from nine sites ranging from

Cumbria to the floodplain of the River Severn (Gowing *et al.*, 2002b) showed the number of relevés classified in the species-rich subcommunities declined by 38% per year when aeration SEVs exceeded 1.1 m.weeks, whilst transitions from the *Agrostis* back to the drier Typical subcommunity, when water tables fell, were much slower averaging only 5% p.a. (Gowing, 2005) which would imply a recovery period to the richer subcommunity of approximately 20 years. Similar structural and functional responses of the floodplain meadows to flooding were also shown in temperate Europe (Baattrup-Pedersen *et al.*, 2018).

Flooding not only affects water-table depth, but also fertility through sediment deposition. The *Dactylis* subcommunity occupies the driest margins of many sites that are rarely flooded and hence where fertility levels are low. Extreme flood events, with high sediment deposition, can affect both fertility and pH resulting in transition from the *Dactylis* to the Typical subcommunity with the loss of many of the smaller characteristic herb species. On the Oxford meads, summer flooding in 2007 increased both pH and available phosphorus with a 50% shift from the Typical to the *Holcus* subcommunity and 45% shift from the *Holcus* subcommunity to *Lolium perenne-Alopecurus pratensis-Festuca pratensis* grassland (Wallace *et al.*, 2008). *Carex acuta* commonly spreads into the *Alopecurus pratensis-Sanguisorba* grassland following summer-flood events and without regular mowing reduces the quality of the resultant hay.

Climate change may lead to more extreme weather events. The probability of increased summer flooding has implications for site management since this can lead to an increase in waterlogging stress and a very rapid shift from the species rich *Dactylis* and Typical subcommunities to the less species rich *Holcus* and *Agrostis* expressions of the community. Thus, maintenance of effective internal water-management systems is essential for the removal of excess flood water since, once established, the species poor swards are slow to revert, even under ideal hydrological conditions. An indirect consequence of prolonged summer flooding is the loss of the hay crop and, in the retained biomass, an increase in fertility, which again results in a decline in species richness. The four subcommunities of the rare *Alopecurus pratensis-Sanguisorba officinalis* mesotrophic grassland community, reflect its dynamism along the frequently changing environmental gradient. Conservation efforts can be informed by the recorded transition between the subcommunities. Additional hay cuts and improved drainage may help to minimise negative effects of occasional prolonged floods on the vegetation.

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**Appendix 1.** Groups used in the analysis of floodplain meadow communities *Alopecurus pratensis-Sanguisorba officinalis* and *Caltha palustris-Cynosurus cristatus*. Numbers in the first column refer to group numbers on the CCA and are indicated in square brackets when referred to in the text

	Author	Unit	Alliance	Location	Comment
1	Balátová-Tuláčková (1991)	Sanguisorbo-Festucetum commutatae	Molinion	Czech Republic	
2	Hájeck <i>et al.</i> , (2008)	Deschampsion	Deschampsion	Bulgaria	(Cluster 3)
3	Hájeck <i>et al.</i> , (2008)	Molinion	Molinion	Bulgaria	(Cluster 4)
4	Havlová (2006)	Molinetum caeruleae var. Scorzonera humilis	Molinion	SW Czech Republic	
5	Botta-Dukát <i>et al.</i> , (2005)	Deschampsion (Cluster 1.3)	Deschampsion	Slovakia	Sub-oceanic Deschampsion meadows
6	Botta-Dukát <i>et al.</i> , (2005)	Deschampsion (Cluster 1.2)	Deschampsion	Austria and Slovakia	Summer-dry, continental Deschampsion meadows
7	Zelnik & Čarni (2008)	Sanguisorbo-Festucetum commutatae	Molinion	Slovenia	
8	Havlová <i>et al.</i> , (2004)	Molinion (Cluster 4)	Molinion	Czech Republic	Unmanured, intermittently wet meadows
9	Řezníčková (2007)	Molinetum caeruleae var. Scorzonera humilis	Molinion	Slovakia	
10	Řezníčková (2007)	Degraded Deschampsion meadows	Deschampsion	Slovakia	Degraded Deschampsia meadows
11	Stančić (2008)	Oenanthe silaifolia-Alopecurus pratensis association	Deschampsion	NW Croatia	
12	Géhu (1961)	Filipenduleto-Cirsetum oleracea	Bromion racemosi	Northern France	Table 11
13	Géhu (1961)	Arrhenatheretum elatoris colchicetosum	Arrhenatherion	Northern France	Table 21
14	Géhu (1961)	Filipenduleto-Schorzoneretum	Molinion	Northern France	Table 12
15	Géhu (1961)	Brometo-Senecietum	Bromion racemosi	Northern France	Table 13
16	Géhu (1961)	Lolio-Cynosuretum uliginosi	Cynosurion	Northern France	Table 15
17	Géhu (1961)	Lolio-Cynosuretum	Cynosurion	Northern France	Table 16
18	Eskuche (1955)	Carex-Arrhenatherum meadow	Arrhenatherion	South Germany	In Ellenberg 1988
19	Meisel (1960)	Alopecurus pratensis-Arrhenatherum meadow	Arrhenatherion	South Germany	In Ellenberg 1988
20	Kuyper <i>et al.</i> , (1978)	Deschampsietum cespitosae	Deschampsion	Austria	Group 9

21	Kuyper <i>et al.</i> , (1978)	Valeriana dioicae-Caricetum davallianae: Calthetosum palustris	Calthion	Austria	Group 20
22	Fijalkowski & Chojnacka-Fijalkowski (1990)	Ranunculus repens-Alopecurus pratensis community: Trifolium pratense variant	Alopecurion	S.W. Poland	Group 4 In: Dierschke (1997)
23	Dierschke (1994)	Arrhenatheretum, Northern race	Arrhenatherion	Germany	Group 23
24	Dierschke (1994)	Junco Molinietum	Calthion	Czech Republic	Group 49
25	Dierschke (1994)	Sanguisorba officinalis-Polygonum bistorta community	Calthion	Germany	Group 35
26	Spanikova (1983)	Molinietum caeruleae	Molinion	Slovakia	Group 59 In: Dierschke (1994)
27	Kovář (1981)	Caricetum gracilis typicum	Caricion gracilis	Czech Republic	
28	Kovář (1981)	Alopecuretosum	Alopecurion	Czech Republic	
29	Passarge (1964)	Holcetum lanati	Calthion	N.E Germany	Table 57 Column G
30	Passarge (1964)	Circetum oleracei	Calthion	N.E. Germany	Table 59 Column D
31	Passarge (1964)	Alopecuretum pratensis	Alopecurion	N.E. Germany	Table 65 Column D
32	Tüxen (1937)	Molinietum caricetosum panicae (typicum)	Molinion	Germany	
33	Tüxen (1937)	Cirsium oleraceum-Angelica sylvestris community	Calthion	Germany	
34	Tüxen (1937)	Cirsium oleraceum-Angelica sylvestris community, subass. Carex fusca	Calthion	Germany	
35	Tüxen (1937)	Arrhenatheretum elatioris subass. Alopecurus pratensis	Arrhenatherion	Germany	
36	Schaminée <i>et al.</i> , (1996)	Lolio-Cynosuretum Lotetosum uliginosi	Lolio Cynosurion	Netherlands	Table 16 column 8
37	Schaminée <i>et al.</i> , (1996)	Fritillario-Alopecuretum pratensis	Alopecurion	Netherlands	Table 16.4 column 1
38	Schaminée <i>et al.</i> , (1996)	Fritillario-Alopecuretum Cynosuretosum	Alopecurion	Netherlands	Table 16.4 column 2
39	Schaminée <i>et al.</i> , (1996)	Fritillario-Alopecuretum Typicum	Alopecurion	Netherlands	Table 16.4 column 3
40	Schaminée <i>et al.</i> , (1996)	Fritillario-Alopecuretum Calthetosum	Alopecurion	Netherlands	Table 16.4 column 4
41	Schaminée <i>et al.</i> , (1996)	Sanguisorbo-Silaetum	Alopecurion	Netherlands	Table 16.4 column 5
42	Schaminée <i>et al.</i> , (1996)	Ranunculo-Senecionetum aquatici	Calthion	Netherlands	Table 16.3 column 6
43	Schaminée <i>et al.</i> , (1996)	Ranunculo-Senecionetum Juncetosum articulati	Calthion	Netherlands	Table 16.3 column 7

44	Schaminée <i>et al.</i> , (1996)	Ranunculo-Senecionetum Caricetosum paniceae	Calthion	Netherlands	Table 16.3 column 8
45	Heery (1991)	Carex nigra-Ranunculus repens community: Eleocharis sub- variant.	Calthion	Ireland	Table 1 Column 4
46	Heery (1991)	Carex panicea-Festuca rubra community: Carex flava variant.	Calthion	Ireland	Table 1 Columns 12+13 amalgamated
47	Page (1980)	Fritillario-Sanguisorbetum	Molinion	England	
48	Gowing <i>et al.</i> , (2002b)	Alopecurus pratensis-Sanguisorba officinalis grassland. Species poor type	Cynosurion	England	Endgroup 4
49	Stevens <i>et al.</i> , (2010)	Alopecurus pratensis-Sanguisorba officinalis grassland. Welsh Variant	Cynosurion	Wales	
50	Cox & Leach (1996)	Agrostis stolonifera-Carex spp grassland	Calthion	England	
51	Rodwell <i>et al.</i> , (1992)	Alopecurus pratensis-Sanguisorba officinalis grassland	Cynosurion	England	MG4
52	Rodwell <i>et al.</i> , (1992)	Cynosurus cristatus-Caltha palustris	Calthion	England	MG8
53	Rodwell <i>et al.</i> , 1992	Lolium perenne-Alopecurus pratensis-Festuca pratensis	Lolio-Plantaginion	England	MG7C
54	Rodwell <i>et al.</i> , 1992	Lolio-Cynosuretum cristati	Cynosurion	England	MG6b
55	Rodwell <i>et al.</i> , 1992	Centaureo-Cynosuretum cristati	Cynosurion	England	MG5a
56	Rodwell <i>et al.</i> , 1992	Centaureo-Cynosuretum cristati	Cynosurion	England	MG5b
57	Prosser (1990)	Northern Caltha meadow community	Calthion	England	
58	Gowing <i>et al.</i> , (2002b)	Alopecurus pratensis-Sanguisorba officinalis grassland	Cynosurion	England	Endgroup 2
59	Gowing <i>et al.</i> , (2002b), revised	Lolium perenne-Alopecurus pratensis-Festuca pratensis	Lolio-Plantaginion	England	
60	Prosser & Wallace (Unpubl 2010)	Lolio-Cynosuretum cristati	Cynosurion	England	
61	Prosser & Wallace (Unpubl 2010)	Alopecurus pratensis-Sanguisorba officinalis: Dactylis glomerata	Alopecurion	England	
62	Prosser & Wallace (Unpubl 2010)	Alopecurus pratensis-Sanguisorba officinalis: Typical	Alopecurion	England	
63	Prosser & Wallace (Unpubl 2010)	Alopecurus pratensis-Sanguisorba officinalis Agrostis stolonifera subcomm	Alopecurion	England	
64	Prosser & Wallace (Unpubl 2010)	Alopecurus pratensis-Sanguisorba officinalis: Holcus lanatus subcomm	Alopecurion	England	
65	Prosser and Wallace (Unpubl 2010)	Cynosurus cristata-Caltha palustris grassland: Typical	Calthion	England	

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66	Prosser & Wallace (Unpubl 2010)	Cynosurus cristata-Caltha palustris grassland: Sanguisorba officinalis	Calthion	England
67	Prosser & Wallace (Unpubl 2010)	Cynosurus cristata-Caltha palustris grassland: Carex acuta	Calthion	England
68	Prosser & Wallace (Unpubl 2010)	Cynosurus cristata-Caltha palustris grassland: Agrostis canina	Calthion	England
69	Prosser & Wallace (Unpubl 2010)	Agrostis stolonifera-Carex spp	Calthion	England
70	Prosser & Wallace (Unpubl 2010)	Lolium-Filipendula community	Cynosurion	England
71	Zuidhoff <i>et al.</i> , (1995)	Junceo-Cynosuretum	Cynosurion	Pan European
72	Zuidhoff <i>et al.</i> , (1995)	Lolio-Cynosuretum	Cynosurion	Pan European

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