Systematics

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Section A—Systematics

I. General introduction

In large parts of Central Europe grasslands are important to the agricultural economy. Many of the permanent grasslands are very old and have received similar management for generations. This paper describes ecological investigations on certain types of hay meadows. These were hygro-mesophilous grasslands of alluvial areas and valleys and lowlands which are fertilised. They are anthropogenic, i.e. they represent a secondary man-made climax.

The different grassland communities have been well described by the phytosociologists. In order to delimit the communities for experimental purposes it is necessary to consider the classification of fertilised grasslands. Although the author does not agree in whole with the methods and the classification of the sociologists, he admits that it is a useful tool in ecological research. Moreso since the "Classes" of vegetation are essentially these which are agreed upon by ecologists of other schools' of thought. The meadows and pastures occurring in Europe are included in the Class *Molinio-Arrhenatheretea.* This class is sufficiently distinct from the more reed-like communities on the one hand and the dry steppe-like grasslands on the other to be a useful ecological entity. Although the community is an abstract vegetation unit distinguished by floristic, ecological, physiognomic and structural criteria, the association is a community identified by its characteristic species composition including one or more character or differentiating species. The association is described after analysing a number of selected stands and floristically similar plots being grouped into the abstract unit according to species fidelity. The associations are classified into a hierarchy, e.g. the poor quality straw meadows form the alliances *Molinion* and *Filipendulo-Petasition*, the pastures form the alliances *Cynosurion* and *Poion alpinae*, and the fertilised meadows form the alliances *Calthion*, *Arrhenatherion* and *Polygono-Trisetion.* This basic division according to the management of the grassland appears sensible. The important associations of wet fertilised meadows are shown in Table 1.

In general the wet fertilised meadows are typified by the *Cirsium oleraceum* grasslands ("Kohldistelwiesen" in German) and the *Arrhenatherum elatius* grasslands ("Glatthaferwiesen") when growing in damp places. TÜXEN in 1937 described the *Cirsium oleraceum* grasslands as the *Cirsium oleraceum-Angelica silvestris* Association and listed several subassociations. This association he subdivided in 1955 into:

Cirsium oleraceum-Polygonum bistorta-Assoc.
Bromus racemosus-Senecio aquaticus-Assoc.
Poa palustris-Lathyrus palustris-Assoc.

Table 1 The systematics of the European meadows
(Synonyms in brackets) M = montane
* = associations of particular relevance to this discussion

Class	**Molinio-Arrhenatheretea Tx. 37**	
Order 1	**Molinietalia Koch 26**	
Alliance A.	*Calthion* Tx. 36 (*Bromion racemosi* Tx. 51, *Juncion acutiflori* Br.-Bl. 47, in part)	
Assoc. (a)	*Juncetum subnodulosi* Koch 26	
(b)	*Trollio-Juncetum subnodulosi* (Koch 26, Vollm. 47) Oberd. 57	M
(c)	*Crepido-Juncetum acutiflori* (Br.-Bl. 15) Oberd. 57 (includes *Epilobio-Juncetum effusi* Oberd. 57, acc. to Passarge 64)	M
(d)	*Senecio-Juncetum acutiflori* Br.-Bl. Tx. 52	
(e)	*Juncetum filiformis* Tx. 37 (*Filiformi-Scirpetum* [Tx. 37] Oberd. 57)	M
* (f)	*Polygono-Scirpetum* (Schwick. 44) Oberd. 57 (*Angelico-Scirpetum silvatici* Pass. 55, *Scirpetum silvatici* Knapp 46)	(M)
* (g)	*Deschampsio-Brometum (racemosi)* Oberd. 57	(g)–(j): (*Bromo-Senecionetum* Tx. 51)
* (h)	*Achilleo-Brometum (racemosi)* Oberd. 57 (*Holcetum lanati* Issler 36)	
* (i)	*Silao-Brometum (racemosi)* Oberd. 57 (*Sanguisorbo-Silaetum* Klapp 51)	
* (j)	*Polygono-Brometum (racemosi)* Oberd. 57 (*Angelico-Cirsietum* Klapp 51, *Bistortae-Brometum* Oberd. 56)	
* (k)	*Polygono-Cirsietum oleracei* Tx. 51	
* (l)	*Thalictro-Cirsietum oleracei* Pass. 55	
* (m)	*Trollio-Cirsietum* (Kuhn 37) Oberd. 57 (*Cirsio-Valerianetum* Kuhn 37, *Cirsietum rivularis* Ralski 31)	M
(n)	*Chaerophyllo-Ranunculetum aconitifolii* Oberd. 52	
Alliance B.	*Filipendulo-Petasition* Br.-Bl. 47	
	e.g. Assoc. *Filipendulo-Geranietum* Koch 26	M
Alliance C.	*Molinion* Koch 26	
	e.g. Assoc. (a) *Molinietum* Koch 26	
	(b) *Polygonetum bistortae* Kovacevic 59	
Order 2	**Deschampsietalia caespitosae Horvatić 56**	
Alliance A.	*Deschampsion caespitosae* Horv. 35	
* Assoc.	*Deschampsietum caespitosae* Horv. 30	
Alliance B.	*Alopecurion pratensis* (*Agrostion albae* Sóo [33] 40)	
* Assoc. (a)	*Alopecuretum pratensis* Eggler	
(b)	*Galio-Alopecuretum* Hundt 58	
Order 3	**Arrhenatheretalia Pawl. 28**	
Alliance A.	*Arrhenatherion* (Br.-Bl. 25) Koch 26	
* Assoc. (a)	*Arrhenatheretum medioeuropaeum* (Br.-Bl. 19) Oberd. 52	
(b)	*Arrhenatheretum subatlanticum* Tx. (37) 55	
(c)	*Arrhenatheretum montanum* Oberd. 52 (*Arrhenatheretum holcetosum* Oberd. 38, *Centaureo nigrae-Arrhenatheretum* Oberd. 57)	M
(d)	*Trifolio-Festucetum rubrae* Oberd. 57	M
* (e)	*Poa-Trisetetum* (Knapp 51) Oberd. 57	M
* (f)	*Melandrio-Arrhenatheretum* (Kuhn 37) Oberd. 57	M

Alliance B.	*Polygono-Trisetion* Br.-Bl. 47	M
Assoc. (a)	*Trisetetum hercynicum* Tx. (37) 55	M
(b)	*Astrantio-Trisetetum* Knapp 52	M
(c)	*Geranio-Trisetetum* Knapp 51	M
Alliance C.	*Poion alpinae* (Gams 36) Oberd. 50	M
Alliance D.	*Cynosurion* Tx. 47	

To these were added an additional form by PASSARGE: *Thalictro-Cirsietum oleracei*. OBERDORFER (1957) in his monograph on the vegetation formations of southern Germany retained the *Polygono-Cirsietum oleracei*, but distinguished four further associations, equivalent to the *Bromo-Senecionetum* of TÜXEN. These were the *Deschampsio-Brometum (racemosi)*, the *Achilleo-Brometum*, the *Silao-Brometum* and the *Polygono-Brometum*. There appeared to be some basis for this distinction. The *Senecio aquaticus* meadows are most typical in the northern parts of Germany and are associated with poor and more or less acid soil conditions. OBERDORFER described the various *Brometum* associations from mineral soils lacking $CaCO_3$ and the *Cirsio-Polygonetum* from calcareous soils. The numerous associations were re-ordinated by PASSARGE (1964). He described suballiances in the *Calthion:*

(a) Suballiance *Holco-Juncion*
  Assoc. 1. *Scirpetum silvatici* (= *Polygono-Scirpetum* Schwick. 44)
  2. *Brometum racemosi*
  3. *Holcetum lanati* (= *Achilleo-Brometum* Oberd. 57)
  4. *Juncetum acutiflori*
(b) Suballiance *Cirsion oleracei*
  Assoc. 1. *Cirsietum oleracei*
  2. *Juncetum subnodulosi*

The *Cirsietum* grassland also has montane representatives which have been distinguished as the association *Trollio-Cirsietum*. This association replaces the *Cirsietum* on calcareous soils above ca. 500–600 m, and OBERDORFER suggested that the *Brometum* was replaced by *Polygono-Scirpetum* and *Crepido-Juncetum*.

The wetter forms of the *Arrhenatherum elatius* meadows are not so confused in the systematic classification. The *Arrhenatheretum* is of wide distribution and montane variants are represented by the *Trisetetum*.

The confused nomenclature poses the problem whether these associations of wet fertilised meadows are in reality ecological entities or whether some represent the purposeful selection by the sociologist. This question is further examined in the next section.

II. Characterisation of the community

1. Synthesis of stand descriptions

A less subjective approach to the description of the vegetation seems to be that of "ecological indicators" developed by ELLENBERG (1952). He evaluated sites in terms of moisture, pH, nitrogen, temperature, etc., by giving from ecological experience a value to each species for each important factor. He has stressed that in Central European grasslands dominance types are weak indicators of environments and classification must be based on total floristic composition.

All available descriptions of wet fertilised meadows from C. and S. Germany, E. France, and Switzerland were gathered and the constancies of each species for each area described listed. A large amount of the data came from a survey of grasslands carried out by Professor ELLENBERG and his students in S. Germany. Their intention was to characterise the grasslands and use this as an advisory basis. Stand descriptions were made whithout any prior subjective selection of the site and then the data ordinated into tables and differentiated according to the presence or absence of groups of ecological indicator species. All likely material was taken for the analysis.

The species were ordinated into groups according to their F value[1] (humidity), 5, 4, 3.5, 3, 0, and the others were put into a class 2.5. Each group was subdivided according to the N value of the species putting together N 1–2, N 3–5, N 0. Then all data was entered[2].

The cover-abundance values of the original stands were denoted by a system of underlining, e.g. Braun-Blanquet scale +, 1–5 and Klapp scale in %; mean values of 4 or 5, or > 50% were underlined twice, 3 or 25–50% underlined once, less than 2 or less than 5% underlined with dots. The other values, i.e. 2–3, 5–25% had no underlining.

It was immediately apparent that many species were present throughout the table, others were not. Mean F and N values were calculated for each column and any column with an F value of less than 3.3 was rejected, since lower values pointed to stand descriptions of typical *Arrhenatheretum*.

$$\text{Mean F value} = \frac{5\,(SF_5) + 4\,(SF_4) + \text{-----}\ 2.5\,(SF_{2.5})}{SF_5 + SF_4 + \text{-----}\ SF_{2.5}}$$

$$\text{Mean N value} = \frac{5\,(SN_5) + 4\,(SN_4) + \text{-----}}{SN_5 + SN_4 + \text{-----}}$$

where F_5, F_4, N_5, N_4, etc., is the F and N value and S represents the sum of.

The columns emphasised that no two lists of constancies were the same, but the same combination of species occurred repeatedly, even in different geographical regions.

[1] F values range from 1–5 (6), N values from 1–5. In each case the higher number represents higher indication for the factor. F0 and N0 represent species which are indifferent to the factor (see ELLENBERG 1952, 1956 or 1963).

[2] The table is not printed here.

Table 2 Main vegetation variants from Appendix Table 1 and their mean N and F values (+ = presence, – = absence of the differential species group, (+) = weak presence)

Variant unit		Column	Group *Trag.*	*Arrh.*	*Carex*	*Alch.*	*Calth.*	*Sanguis.*	Mean F value	Mean N value
Dry	I	1–9	+	+	–	–	+, –	+, –	3.37	3.13
	II	10–23	+	+	–	+	+, –	+, –	3.39	3.04
Int.	III	24–40	(+)	(+)	(+)	(+)	(+)	(+)	3.47	3.10
Wet	IV	41–49	–	+	+	+	–	+, –	3.49	3.06
	V	50–57	–	+	+	+	+	+, –	3.73	2.96
	VI	58–67	–	–	+	+	+	–	3.73	2.89
	VII	68–95	–	–	+	+	+	(+)	3.78	2.75
	VIII	96–98	–	–	+	+	–	–	3.78	2.89

The *Cirsium oleraceum* group was present throughout the table. The species of this group are typically present in the wet fertilised meadows. The main subdivision was formed by the *Tragopogon orientalis* group and the *Carex acutiformis* group. These divided the data into a "wet" unit and a "dry" unit, and there were some columns forming an "intermediate" unit. Species of the *Arrhenatherion* (*Arrhenatherum elatius* group) were present in the dry units and in some columns of the wet; these indicate good fertilisation. Species of the *Calthion* (*Caltha palustris* group) were present in most of the wet and in some of the dry units. There was some overlap of these differential groups. The dry unit was subdivided by the presence or absence of *Alchemilla vulgaris*, *Luzula campestris*, *Colchicum autumnale*, etc., which indicate poor management and poor fertilisation. *Sanguisorba officinalis*, *Succisa pratensis*, etc., also indicate poor management in the wetter groups (also the presence of *Caltha palustris* and *Bromus racemosus* indicates poor fertilisation). *Sanguisorba officinalis* and *Molinia coerulea* are species of the *Molinietum*, but they are not so faithful to it. The *Dactylis glomerata* group contains species more usually present in the drier well-fertilised meadows and it was significant that at the "wettest end" of the table these species were not always present. The major factor differentiating the data was humidity and secondarily nitrogen. The synthesis in the (not published) table showed a large number of grassland species were constant with few exceptions in all areas described. Other species had the tendency to be present only when a certain differentiating group was present, e.g. *Mentha aquatica* with the *Carex acutiformis* group and *Orchis majalis*, *Carex fusca* and *C. davalliana* with the *Caltha* group; but they were not frequent enough to be used with reliability.

That the vegetation variants represented a gradient in humidity was demonstrated by the mean F values. An increase in the F value was usually accompanied by a fall in the N value. Thus the wettest meadows seem to have been fertilised the least. Loss of nitrogen by denitrification might be another reason for this negative correlation with soil humidity.

To examine which sociological association the variants belonged to the columns of the (not published) table were examined to see whether they belonged to the *Molinietalia* or the *Arrhenatheretalia*. All the columns of the dry units showed affinities to the *Arrhenatheretalia*. In the intermediate and the wet units with the *Arrhenatherum* group but not the *Caltha* group, some lists corresponded to the *Arrhenatheretalia*, some to the *Molinietalia*. The four wettest variants belonged with the *Molinietalia*. This posed the question whether the dry units belonged to the *Arrhenatheretum* wet subassociation (e.g. with *Cirsium oleraceum*) or to the *Cirsietum oleracei* dry subassociation (e.g. with *Tragopogon pratensis*). The two driest variants of the tabulated meadows agree with published descriptions of wet *Arrhenatheretum*. The intermediates then represent intermediates between the *Cirsietum* and the *Arrhenatheretum*, but these communities grade uniformly into one another. The sociological hierarchy is too rigid and obviously artificial, because the *Arrhenatheretum* and the *Cirsietum* cannot be well separated in the field. Until this problem is resolved it will depend on the individual author to which association he ascribes his stand descriptions. Examples such as this, which show that there is a continuum in the vegetation as well as environmental conditions underlines the high degree of subjectivity of the phytosociological classification.

The constancies of the species in the eight major variants ordinated in the original table[1] are shown in Table 3. Apart from the differential species, the remaining species were very constant. Most of the species showed similar constancies in all the variants although *Bromus mollis*, *Heracleum sphondylium* and *Vicia sepium* had higher constancies in the drier variants.

TÜXEN (1937) described three subassociations of the *Cirsietum:* (a) *caricetosum* (diff. spp. *Carex fusca*, *C. panicea*, *C. gracilis*, *Juncus articulatus* and *Valeriana dioica*), (b) *filipenduletosum* (later put into the *Filipenduletum*), and (c) *heracleetosum* (diff. spp. *Achillea millefolium*, *Heracleaum sphondylium*, *Lolium perenne*, *Chrysanthemum leucanthemum* and *Bromus mollis*). The *caricetosum* differentials correspond with the *Carex acutiformis* group of the synthetic table and the *heracleetosum* with the dry variants containing the *Arrhenatherum* group. The subassociations of most meadow associations are differentiated by a "fertile drier" group, or a "wetter" *Carex* group and there may be several variants differentiated by different *Carex* species, e.g. *C. davalliana*, *C. fusca*, *C. gracilis*, etc. Similarly the subassociations of the *Arrhenatheretum* usually correspond to humidity, e.g. the wet forms: subassociation with *Cirsium oleraceum* or *Colchicum autumnale* or *Alopecurus pratensis*, e.g. the dry forms: subassociation with *Salvia pratensis*. Many subdivisions represent local differences only. A good example of typical subdivisions is that of HUNDT (1954). PIETSCH (1962) has calculated the mean N and F values of several associations and this pointed out how useful were the ecological indicator concepts in separating grassland communities (see Table 4).

[1] Not published because of its large size. Available in the library of the Geobotanical Institute, CH-8044 Zürich, Zürichbergstrasse 38.

Table 3 The mean constancies of species in 8 variants of lowland wet fertilised meadows in southern Central Europe[1]

(M-A = character species of the class *Molinio-Arrhenatheretea*). The character species of orders, alliances etc. see page 81/82)

Variant number	Dry		Int.			Wet		
	I	II	III	IV	V	VI	VII	VIII
Cirsium oleraceum group								
Cirsium oleraceum	4	4	3	4	3	4	4	4
Angelica silvestris	2	2	2	3	3	4	3	2
Lathyrus pratensis	2	3	3	4	4	4	4	3
Lychnis flos-cuculi	4	2	3	4	4	4	3	3
Deschampsia caespitosa	3	2	3	4	3	4	4	4
Tragopogon pratense group								
Tragopogon pratense	1	2	1	+	+	+	+	
Medicago lupulina	2	1	+	+	+	1	1	
Melandrium diurnum	2	2	1	+	+	1	+	
Daucus carota	2	1	+	1	1	1	+	+
Knautia arvensis	2	1	1	1	1	+	+	
Leontodon hispidus	1	1	1	1	1	+	+	+
Arrhenatherum elatius group								
Arrhenatherum elatius	5	4	2	3	2	1	+	+
Anthriscus silvestris	3	2	1	2	1	1	+	+
Crepis biennis	3	2	2	3	2	+	+	+
Geranium pratense	2	+	1	3	1	+	+	+
Carex acutiformis group								
Equisetum palustre	1	+	1	2	2	3	2	2
Carex panicea	+	+	+	1	2	2	2	+
Carex gracilis	+	+	1	1	3	4	2	3
Scirpus silvaticus	+	+	1	3	2	3	2	2
Galium palustre	+	+	+	2	1	2	2	2
Galium uliginosum	+	+	+	1	1	2	2	1
Carex acutiformis	1	+	1	3	3	2	2	3
Alchemilla vulgaris group								
Alchemilla vulgaris	+	3	2		1	1	1	
Luzula campestris	+	2	1	+	1	+	1	
Colchicum autumnale	+	2	2	2	3	2	1	1
Filipendula ulmaria	1	2	2	4	3	3	4	4
Plantago media	1	1	1	1	1	1	1	+
Caltha palustris group								
Caltha palustris	+	+	+	1	3	3	3	1
Valeriana dioica		1		1	3	2	3	1
Polygonum bistorta	1	2	2		3	2	2	
Bromus racemosus	1	1	1		1	1	1	
Senecio aquaticus	+	+	+	+	1	2	1	

[1] 5 = species present in more than 80% of the relevés;
4 = in 60–80%, 3 = in 40–60%, 2 = in 20–40%;
1 = in less than 20%, + = in less than 5%.

Variant number	Dry		Int.	Wet					
	I	II	III	IV	V	VI	VII	VIII	
Sanguisorba officinalis group									
Sanguisorba officinalis	1	2	2	1	2	+	3	1	
Trollius europaeus	+	1	1		1	+	2	+	
Succisa pratensis	+	1	1	1	1	+	1	+	
Ranunculus auricomus	+	+	+	1	1	+	1		
Molinia coerulea	+		+	+		+	+		
Dactylis glomerata group									
Dactylis glomerata	5	4	3	3	1	1	1	1	
Galium mollugo	5	4	4	5	3	1	2	2	
Heracleum sphondylium	4	4	3	4	3	2	1	+	
Chrysanthemum leucanthemum	4	5	4	4	3	3	2	2	
Bellis perennis	3	3	3	3	3	3	2	+	
Pimpinella major	3	3	4	3	2	3	2	2	
Achillea millefolium	3	3	2	2	1	1	1		
Others									
Holcus lanatus	4	4	4	5	5	4	4	3	M-A
Ranunculus acer	4	5	4	5	5	5	4	3	M-A
Plantago lanceolata	4	5	4	5	3	3	3	3	M-A
Festuca pratensis	4	4	4	5	4	5	4	3	M-A
Poa trivialis	4	4	4	4	4	4	3	3	M-A
Cardamine pratensis	3	3	3	4	4	3	4	3	M-A
Rumex acetosa	4	5	4	4	4	4	3	4	M-A
Trifolium pratense	4	5	4	5	5	4	4	3	M-A
Ajuga reptans	3	4	3	4	4	4	3	3	
Ranunculus repens	4	3	4	4	5	4	3	4	
Taraxacum officinale	4	4	4	4	3	3	2	2	
Cerastium caespitosum	4	3	3	4	4	3	2	1	M-A
Alopecurus pratensis	4	3	4	3	4	3	3	2	M-A
Trifolium repens	3	3	3	3	4	3	3	2	
Anthoxanthum odoratum	2	3	2	2	4	3	3	+	
Centaurea jacea	3	3	3	3	2	2	2	2	M-A
Trisetum flavescens	3	4	3	2	3	2	2	1	
Veronica chamaedrys	3	4	2	3	3	2	2	2	
Avena pubescens	2	3	2	2	2	2	2	1	
Myosotis palustris	2	2	3	1	4	3	3	1	
Bromus mollis	3	3	1	1	2	1	1		
Prunella vulgaris	1	1	1	2	1	2	2	2	M-A
Lysimachia nummularia	3	2	3	4	3	3	3	3	
Poa pratensis	4	4	2	3	3	2	2	1	M-A
Geum rivale	4	3	3	1	2	3	3	2	
Glechoma hederaceum	2	2	2	2	1	1	1	2	
Vicia sepium	2	1	2	2	1	1	1	1	
Agrostis alba	1	1	1	2	1	2	1	2	
Rumex crispus	2	1	2	2	1	2	1	1	
Festuca rubra	3	3	3	4	3	2	2	3	M-A
Cynosurus cristatus	1	2	2	+	2	1	1		
Silaum silaus	1	1	1	2	1	+	1	+	
Briza media	+	1	+	1	1	1	2	+	
All other species with very low constancy									

Table 4 The mean F and N values of different meadow types according to PIETSCH (1962)

		N	F
Molinietum	subass. *Ranunculus repens*	2.1	4.1
	subass. *Trifolium dubium*	2.6	3.7
Cirsietum oleracei	typical	3.1	3.7
	subass. *Carex fusca*	3.3	3.8
Arrhenatheretum	subass. *Alopecurus pratensis*	a) 3.3	3.4
		b) 4.0	3.3

It seemed that most of the subassociations represented different ecological conditions. Many of the variants described in Table 3 may be equated with those named in the literature.

Apart from the main variants, some of the species had an irregular distribution in the table (unrelated to geographical region). Some of these are discussed.

Veronica arvensis is a dry indicator, but high constancy of this species did not always ally with the dry group selected for differentiating. In these meadows it is a relict of arable land.

Alopecurus pratensis was often present in large quantities. More than 25% abundance represents good management. In other areas it is completely absent despite high N status. This is seen sometimes in the Swiss lowlands, and might be due to intensive cutting.

Daucus carota, although a dry indicator, may establish as a result of disturbance. Disturbance caused by amelioration accounted for large quantities in the wet end of the table. This was also the case for *Medicago lupulina*.

Carex acutiformis, *C. panicea* and *C. gracilis* often cohabited in the same fields. Their local abundance in the wet variants was due to less cutting. Like *Filipendula ulmaria* they succumb to cutting and drainage, though may persist for several years after drainage. Whereas large quantities of *C. gracilis* indicate more fertile sites, *C. fusca* indicates poorer sites.

Bromus racemosus and *Senecio aquaticus* were not evenly distributed. This was because they are usually found on more acid soils (also *Achillea ptarmica* and *Cirsium palustre*) contrasting with the distribution of *Plantago media*, *Silaum silaus*, and *Geranium pratense*, etc., which are usually found on calcareous or base rich soils.

2. The complex of related "associations"

a. Lowland communities

It was not possible to divide the data used in the synthetic table into the distinct units *Cirsio-Polygonetum* and *Brometum*. Nor was it possible to separate the *Senecio aquaticus* meadows. It appears that these forms were just varieties of the community. *Cirsium oleraceum*, *Polygonum bistorta*, *Scirpus silvaticus* and *Bromus racemosus* were the character species originally used for the *Cirsietum*. When *Bromus racemosus* and *Senecio aquaticus* were optimal, on more acid soils, the vegetation was named *Brometum*. The important species used to characterise the hierarchy are (after OBERDORFER, 1957, and PASSARGE, in: SCAMONI, 1963):

Species of the *Molinietalia:*

Equisetum palustre, *Colchicum autumnale*, *Orchis latifolia*, *Trollius europaeus*, *Lychnis flos-cuculi*, *Filipendula ulmaria*, *Lathyrus palustris*, *Sanguisorba officinalis*, *Silaum silaus*, *Stachys officinalis*, *Angelica silvestris*, *Cirsium oleraceum*, *Cirsium palustre*, *Galium uliginosum*, *Des-*

champsia caespitosa, Carex panicea, Juncus effusus, J. conglomeratus, Achillea ptarmica, Lotus uliginosus, Selinum carvifolia, Taraxacum palustre.

Species of the *Calthion:*

Bromus racemosus, Scirpus silvaticus, Polygonum bistorta, Crepis paludosa, Caltha palustris, Myosotis palustris, Senecio aquaticus, Geum rivale, Trifolium hybridum, Cirsium salisburgense, Fritillaria meleagris.

Species of the *Arrhenatheretalia:*

Dactylis glomerata, Trisetum flavescens, Anthriscus silvestris, Pimpinella major, Veronica chamaedrys, Taraxacum officinale, Bellis perennis, Chrysanthemum leucanthemum, Tragopogon pratensis, Crepis capillaris, Daucus carota, Heracleum sphondylium, Lotus corniculatus, Achillea millefolium, Bromus hordeaceus (mollis).

Species of the *Arrhenatherion:*

Arrhenatherum elatius, Galium mollugo, Crepis biennis, Knautia arvensis, Pastinaca sativa, Geranium pratense, Campanula patula.

The wet fertilised meadows contain most of these species in many cases in sufficient numbers to denote both the *Arrhenatheretalia* and the *Molinietalia*. It is clear that no sharp boundary can be drawn between the *Arrhenatheretum* and the *Cirsietum*. They are sufficiently distinct from the other associations of the *Calthion* (*Juncetum*, etc.) in species composition. The meadows receive similar management, i.e. they are fertilised and cut. From an ecological viewpoint they represent wet fertilised meadows and drier fertilised meadows and are therefore two facets of the same community. Other closely related groups are the *Deschampsietum* and the *Alopecuretum*, which have been put into a separate order by HORVATIĆ, although the *Deschampsietum* could be put into the *Calthion* and the *Alopecuretum* into the *Arrhenatherion*. The *Deschampsietum* indicates poor fertilisation and is more typically found in E. Europe. The *Deschampsietum* usually contains plants indicative of changing water conditions. Flooding occurs at some period (see SCAMONI, 1956). A wet *Arrhenatheretum* may contain ca. 10–25% species indicating changing water conditions and only ca. 3% indicating flooding. Comparative figures for the *Cirsietum* are 25–30% and 3–6%. Constancies of the lowland variants are shown in Table 3.

b. Montane communities

The montane form of the wet fertilised meadows was described by K. KUHN (1937) from southern Germany. This was called *Cirsio (oleracei)-Valerianetum*. It has since been renamed *Trollio-Cirsietum*. The character species is *Cirsium rivulare (C. salisburgense)*. KUHN described the following subassociations:

Subass. with *Carex davalliana*
Subass. typical
Subass. with *Succisa pratensis*
Subass. with *Arrhenatherum elatius*

The association has been described from several parts of S. Germany (e.g. GÖRS, 1959; RODI, 1959; BENZING, 1954) and Switzerland (e.g. MOOR, 1958, and *Scirpo-Cirsietum* Br.-Bl. 49 of the Swiss forealps near Fribourg). Apart from the high constancy of *C. rivulare* this association has *Trollius europaeus* and several other plants indicative of montane conditions, e.g. *Chaerophyllum hirsutum*, *Crocus albiflorus*, *Geranium silvaticum*, etc.

The montane wet fertilised meadows have floristic affinities with the wetter forms of the montane *Arrhenatherum* meadows. These include:

Assoc.	Wet subass.
Arrhenatheretum montanum	*polygonetosum bistortae*
Melandrio-Arrhenatheretum	*cirsietum oleracei*
	polygonetosum
	alopecuretosum
Poa-Trisetetum	*polygonetosum*

In the subalpine regions are found the associations of the *Polygono-Trisetion* (see Table 1). The *Trisetetum* tends to replace the *Arrhenatheretum* above ca. 800 m. The character species are the same but in addition the following are more typical of the *Trisetetum:*

Alchemilla vulgaris, Stellaria graminea, Phyteuma nigrum, P. spicatum, P. orbiculare, Crepis mollis, Geranium silvaticum.

The wet subassociations often contain *Polygonum bistorta* and *Trollius europaeus*. Material from montane examples of these wet variants and data of the more typical wet fertilised meadows were ordinated in a table in a similar manner to that of the lowland meadows. The final ordination is presented in a second large table.[1]

The constancies of the important species are shown in Table 5. The dry group was better represented than in the lowland types. Included with the differential montane species were the dry indicators *Stellaria graminea*, *Thymus serpyllum* and *Saxifraga granulata*. These are more or less absent in lowland types. The wet group and the *Arrhenatherum elatius* group contained the same species in both the lowland and montane forms although *Geranium pratense* is of low constancy in the montane. Species of the *Calthion* were present in all variants. *Cirsium rivulare*, the character species of *Trollio-Cirsietum*, was not very constant. The montane examples differred from the lowland ones chiefly in the higher presence of *Alchemilla vulgaris*, *Crepis mollis*, *Geranium silvaticum* and *Phyteuma nigra*. These are essentially species of the *Trisetetum*. It was seen at the dry end of the table that the variants merged into the *Trisetetum* (variant II) and the montane *Arrhenatheretum* (variant I). In no great respect did the montane forms differ from the lowland ones. The retention of a separate association does not appear to be useful. Apart from the montane species the community appears to be a variant of the lowland types.

The montane meadows showed large variations in the mean F values, e.g. the mean F values for the columns of Table 5 were: I 3.53, II 3.39, III 3.24, IV 3.73, V 3.67, VI 3.83, VII 3.74. Individual columns in the original table did not show

[1] Also not published, but available in the library of the Geobotanical Institute, Zürich.

a regular change in the F value when ordinated according to the indicator values of the species. Similarly the mean N values varied. This could be due to the fact that many of the montane meadows are on slopes and the water and nitrogen relations are more subject to change.

3. Distribution

a. Geographical distribution

Variability in stand descriptions may be unlimited. This does not, however, signify that the variation is by chance. DUVIGNEAUD (1946) contended that the variation was subject to rules. Variation in a community which has a wide area of distribution may be due to geographical variants. Such variants are usually more apparent on dry soils. PASSARGE studied the distribution of three units of the *Cirsietum (Angelico-*, *Polygono-*, and *Thalictro-Cirsietum)* in N.E. Germany. It seemed that their distribution was conditioned partly by soil factors (this is the case for the true *Cirsietum* and the *Brometum*) and partly climatically; they were called respectively subatlantic, subboreal and subcontinental. The *Cirsium oleraceum* meadows obtain their maximum development in Germany. They extend as far south as Savoie and as far north as S. Sweden (GILLNER, 1960). It appears that their distribution is chiefly within the oceanic climatic region (Fig. 1).

Similar meadows are also recorded from N. Spain. These variants contain *Polygonum bistorta* and *Narcissus pseudonarcissus* (TÜXEN and OBERDORFER, 1958).

In the same area occurs the *Senecio-Juncetum acutiflori* which contains most of the characteristic species of the *Calthion* and approaches in floristic composition the *Senecio aquaticus* meadows *(Brometum)* of N. Germany. This association is also found in W. France and Ireland (BRAUN-BLANQUET and TÜXEN, 1951), and its atlantic character is marked by such species as *Cirsium dissectum*,

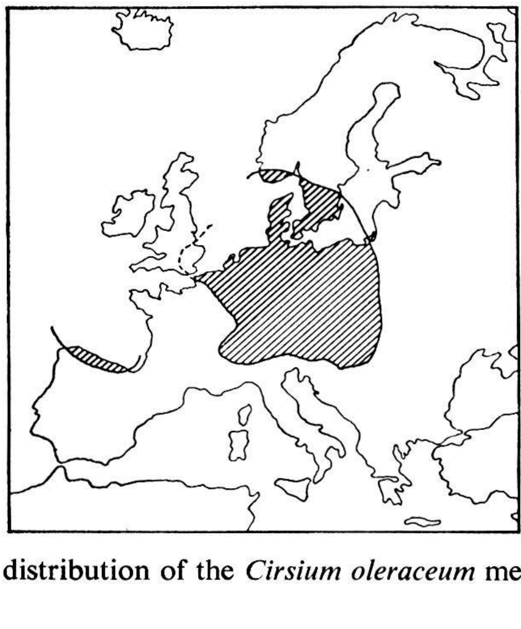

Fig. 1 The geographical distribution of the *Cirsium oleraceum* meadows.

Hypericum elodes, *Anagallis tenella*, etc. It is strange that an association floristically so similar to the *Cirsium oleraceum* meadows should be found outside their distributional area. The reason for this must be the management. In Central and Southern Germany, Switzerland and neighbouring areas the meadows are subjected to the same treatment of intense fertilisation with liquid manure and cutting. Different agricultural practises have virtually excluded these meadows from France. Similar meadows are described from Holland (LEEUWEN, 1958; MEISEL, 1960), but in N.W. Germany and the Low Countries permanent

Table 5 The mean constancies of species in seven variants of montane wet fertilised meadows in southern Central Europe

Variant number	Dry		Int.	Wet			
	I′	II′	III′	IV′	V′	VI′	VII′
Cirsium oleraceum group							
Cirsium oleraceum		2	1	2	2	1	3
Angelica silvestris	+	1	+	1	2	1	2
Lathyrus pratensis	3	4	3	2	4	3	3
Lychnis flos-cuculi	2	2	2	3	1	3	3
Deschampsia caespitosa	1	1	1	2	1	3	3
Trollius europaeus group							
Trollius europaeus	1	2	2	1	2	2	1
Stellaria graminea	1	1	1	+	1	+	+
Geranium silvaticum	1	2	1	1	1	1	1
Thymus serpyllum	+	+	1	+	1	+	+
Crepis mollis	1	2	1	+	+	2	+
Phyteuma nigrum	1	2	1	+		+	
Saxifraga granulata	+	1	+			1	
Cirsium rivulare			1	1	+	2	2
Tragopogon pratense group							
Tragopogon pratense	3	2	2	+	2	1	+
Medicago lupulina	1	+	1	+	1	1	
Melandrium diurnum	2		1	+	+	+	+
Daucus carota	2	1	1	+	1	+	+
Knautia arvensis	1	1	1	1	2	1	1
Leontodon hispidus	1	2	2	+	2	1	1
Arrhenatheretum elatius group							
Arrhenatheretum elatius	4	2	1	1	2	1	1
Anthriscus silvestris	3	4	1	1	1	+	1
Crepis biennis	3	2	1	+	1	+	+
Geranium pratense	1	+		+	+	+	+
Carex acutiformis group							
Equisetum palustre				+	2	1	2
Carex panicea			+	1	2	3	2
Carex gracilis						+	2
Scirpus silvaticus			+	+	1	2	2
Galium palustre			+	1	1	1	1
Galium uliginosum		1	+	+	1	2	1
Carex acutiformis					1	+	2

Variant number	Dry		Int.	Wet			
	I′	II′	III′	IV′	V′	VI′	VII′
Alchemilla vulgaris group							
Alchemilla vulgaris	2	4	3	1	2	2	+
Luzula campestris	2	4	1	2	+	2	1
Colchicum autumnale	3	3	2	1	3	2	1
Filipendula ulmaria		2	+	1	3	3	3
Plantago media	2	2	1	+	1	1	+
Caltha palustris group							
Caltha palustris		+	1	1	3	2	3
Valeriana dioica			+	+	2	2	1
Polygonum bistorta	3	3	3	2	2	3	4
Bromus racemosus	+	+		+	1	+	+
Senecio aquaticus			+	+	1	+	1
Sanguisorba officinalis group							
Sanguisorba officinalis	1	2	2	2	1	3	2
Succisa pratensis	1	+	+	1	+	+	1
Ranunculus auricomus	+	+		+	1	+	+
Molinia coerulea		+	+	+		+	+
Dactylis glomerata group							
Dactylis glomerata	2	3	4	3	3	+	1
Galium mollugo	5	2	2	2	1	2	1
Heracleum sphondylium	3	4	3	2	2	1	1
Pimpinella major	3	2	2	2	1	1	1
Achillea millefolium	4	3	2	2	+	+	1
Chrysanthemum leucanthemum	5	4	4	3	2	2	2
Bellis perennis	2	1	1	2	+	1	1
Other species							
Ranunculus acer	5	5	4	3	4	3	4
Trifolium pratensis	5	4	4	3	5	3	4
Anthoxanthum odoratum	4	4	3	3	3	3	3
Trisetum flavescens	5	5	4	3	2	2	2
Festuca rubra	3	4	3	2	3	2	3
Poa pratensis	4	4	2	2	2	1	3
Rumex acetosa	4	4	2	3	3	3	4
Cerastium caespitosum	3	4	2	2	2	2	3
Festuca pratensis	4	3	3	3	2	3	3
Holcus lanatus	3	4	2	4	4	3	4
Cynosurus cristatus	3	3	2	3	2	2	1
Plantago lanceolata	4	4	3	3	3	2	2
Trifolium repens	3	2	3	3	3	2	3
Taraxacum officinale	4	4	3	2	4	1	1
Veronica chamaedrys	3	4	3	1	1	1	2
Alopecurus pratensis	3	2	2	3	2	2	2
Vicia sepium	3	2	1	1	1	1	+
Myosotis palustris	1	3	3	3	2	3	4
Geum rivale	1	2	1	1	2	3	3
Ajuga reptans	2	3	2	2	2	3	2
Prunella vulgaris	2	2	2	2	2	2	1
Centaurea jacea	2	2	2	2	2	2	2

Variant number	Dry		Int.	Wet			
	I′	II′	III′	IV′	V′	VI′	VII′
Poa trivialis	2	2	2	2	1	1	2
Cardamine pratensis	2	4	2	2	2	3	3
Briza media	1	2	2	1	2	3	2
Vicia cracca	1	2	2	1	3	1	2
Avena pubescens	2	2	1	2	2	2	2
Lotus corniculatus	2	1	1	+	2	1	1
Agrostis tenuis	1	1	2	+	2	1	1
Primula elatior	1	1	1	1	1	1	1
Ranunculus repens	+	1	1	2	2	1	3
Bromus mollis	1	1	1	2	1	+	1
Carum carvi	1	3	2	1	1	1	
Rhinanthus minor	+	1	1	+	3	+	+
Plantago media	2	2	1	+	1	1	+
Phleum pratense	1	1	1	1	1	+	1
Potentilla erecta	+		1	+	1	1	1
Lolium perenne	2	1	2	1	1	1	+
Lysimachia nummularia		2	+	1	1	+	1
Agrostis alba	1	1	1	1	1	1	1
Crepis paludosa	+	+	+		2	+	1
Campanula patula	2	1	1	1		+	
Carex fusca				+	+	+	2
All other species with very low constancy							

grasslands are pastured rather than mown; or they are cut some years and pastured others. Alluvial meadows described from Britain have some affinities to the wet fertilised meadows (BAKER, 1934), but again different management has resulted in a differing community. In the more northern countries large amounts of inorganic fertilisers are used in contrast to the liquid manure of C. Europe. From the relict areas of N. Spain and S. Scandinavia it is probable that the essential climatic limits are the highly oceanic regions.

The eastern distribution of the meadows is related to the climate. In N.E. Germany the *Thalictro-Cirsietum* (characterised by *Thalictrum flavum*, *Potentilla anserina*, *P. reptans* and *Festuca arundinacea*) described by PASSARGE, reflects the more continental climate, and in Poland the community contains continental species such as *Arabis arenosa* and *Mentha verticillata* (BARYLA, 1962). In the Ukraine *Cirsium oleraceum* is replaced by *C. canum* (LOHMEYER, 1941) and in the Carpathians continental species, e.g. *Gladiolus imbricatus* and *Leontodon hastilis*, are found (PAWLOWSKI, 1961, cited in PASSARGE, 1964). In S. Moravia and S. Slovakia the wet *Arrhenatheretum* is represented by *Arrhenatheretum* subass. with *Cirsium canum*. The more continental the area the fewer *Calthion* species are present. Meadows more like the *Holcetum lanati* are found and in the eastern parts of Europe meadows of the alliance *Agrostion albae* partially geographically replace those of the *Calthion*. This partial replacement is correlated with the soil conditions. The plant communities of the *Agrostion albae* are confined to salt soils. Constantly present are *Lotus corniculatus* ssp. *tenuifolius*, *Trifolium fragiferum*, *T. bonannii*, *Melilotus dentatus*, *Achillea millefolium* ssp. *aspleniifolia*, *Juncus gerardi*, *Cirsium brachycephalum* (Dr. J. VICHEREK, personal communication). The replacement by the *Deschampsietum* in S. E. Europe, e.g. S.E. Croatia (HORVATIĆ, 1934), is seen in Austria where the main wet fertilised meadows are represented by the *Alopecuretum pratensis*, *Holcetum lanati*, and *Deschampsietum caespitosae* (EGGLER, 1933). These types are also found in northern parts of E. Europe. Some meadows of the *Alopecurion (Agrostion)* are found in mid-Sweden, Holland, E. Prussia and the Baltics besides the east part of Europe. REGEL (1936) has described various wet meadows from Lithuania, the drier belonging to *Caretum carvi*, the wetter to *Deschampsietum* and *Alopecuretum*. In these regions as in Austria the fertilised meadows are comparatively young, and in many eastern parts not managed intensively, e. g. in Silesia (Poland) many species of the *Molinietum* are present. This is reflected in the mean N and F values of the stands. HUNDT (1954) described *Alopecuretum* and *Deschampsietum* from Westbrandenburg. They had similar F values, but the N value was much less in the *Deschampsietum*.

Although typical *Cirsietum* has been listed from Belgium other meadows showing poor management, e.g. association with *Deschampsia caespitosa* and *Polygonum bistorta*, are described as well as a *Filipendulo-Cirsietum* (LEBRUN *et al.*, 1949; GÉHU, 1961).

The main geographical variants are, therefore, conditioned by climate. Thus variants in the experimental region of S. Germany and Switzerland would not be expected apart from the distribution of individual species being modified by local conditions. This was demonstrated in the *Arrhenatheretum* by SCHREIBER (1962) in S. Germany. The rather uniform floristic composition of the meadows in the same region are shown by stand descriptions from Switzerland.

The eight variants of the lowland wet fertilised meadows described in Table 3 contained species of very similar geographical affinities. All species with a constancy of > 2 were used to give a geographical spectrum. This gave the following mean percentages (Table 6).

The *Arrhenatheretum* appears to be of subatlantic origin (cf. *Fagus*), and it is widely distributed throughout Western Europe but is limited by a continental

Table 6 Geographical spectrum of the Cirsietum (area-type after OBERDORFER)

	%	Range %
Eurasian (wide distribution)	56.6	52.2–62.8
Eurasian (suboceanic)	26.2	22.4–32.6
Eurasian (subatlantic)	14.1	10.6–18.3
Submediterranean	1.8	0.0– 2.2
Continental	1.3	0.0– 2.2

And there were 1–2% prealpine species.

climate and is not found in e.g. E. Poland, Yugoslavia, etc. The *Arrhenatheretum* shows some variation geographically, e.g. *Malvo-Arrhenatheretum* in Spain, *Gaudinio-Arrhenatheretum* in S. France, etc. The *Trisetetum* of more montane conditions has been described from the Pyrenees, central French mountains, the Vosges, central German mountains, the Carpathians and the Alps. The geographical area of the *Trisetetum* probably corresponds more or less to that of the *Arrhenatheretum*. The montane *Cirsietum* has been described from Germany, the Juras and the Alps. It occurs in the Swiss, French, German, Austrian and Italian alps. The smaller distribution must be due to the geographical range of the differential species. *Trollius europaeus* is widely distributed in prealpine regions but has an essentially northern distribution. *Cirsium rivulare* tends towards a more continental range.

b. Natural distribution of typical components

The wet fertilised meadows are semi-natural communities due to their anthropogenic origin (ELLENBERG, 1963). However, some species typical of the *Calthion* are found naturally in seral stages bordering lakes and on alluvial areas liable to flooding. Species typical of the *Arrhenatheretum* especially depend on fertilisation or inundation bringing nutrients. In the "Spülsaum" bordering rivers there is deposited an organic band where ammonification is rapid. It is in such zones that nitrogen indicators, e.g. *Cirsium oleraceum*, *Anthriscus silvestris*, *Heracleum sphondylium*, have their natural home. These species are found bordering woods where the meadow is mixed with scrub ("Laubwiesen") and on slopes representing nutrient flushes. These habitats all have one thing in common and that is the nutrient status (and nitrification) is high. The wet fertilised grasslands represent grades of nitrophily. This factor is examined experimentally in Section B.

4. Aspect and life forms

a. Aspect

The different aspects depend on the seasonal development and on the vegetation unit. This in turn depends on the management. Structurally important in the wet units of the wet fertilised meadows are the large sedges (e.g. *Carex gracilis*, *C. acutiformis*), *Cirsium oleraceum*, *Caltha palustris*, *Filipendula ulmaria*, *Poa trivialis*, *Holcus lanatus*, and in the drier units the legumes *Trifolium pratense*, *Lathyrus pratensis*, *Vicia cracca*, and the good fodder grasses, e.g. *Alopecurus pratensis*, *Festuca pratensis*, *Arrhenatherum elatius*, *Trisetum flavescens*, *Dactylis glomerata*, *Poa pratensis*. In most of these species of the drier units, growth is promoted by manure or N, P, K fertilisers. Especially characteristic of the liquid manure are *Heracleum sphondylium*, *Anthriscus silvestris*, *Taraxacum officinalis*, *Crepis biennis* and *Rumex obtusifolius*. Many of the herbs which are important fodder plants occur in most variants of the meadows, e.g. *Plantago lanceolata*, *Achillea millefolium*, *Silaum silaus*. Cutting selectively eliminates those plants which do not ripen their seed before cutting unless they vigorously reproduce vegetatively. Most of the important agricultural grasses are fruiting before the first cut is made, and some species flower twice, e.g. *Taraxacum officinale*, *Anthriscus silvestris*, *Ranunculus acer* and *Lychnis flos-cuculi*.

The chief aspects represented in Switzerland are:

(1) Spring (April–May)

(a) Wet: *Cardamine pratensis*, *Taraxacum officinale*, *Ranunculus acer*, *Lychnis flos-cuculi* and *Rumex acetosa*. In the very wet units *C. pratensis*, *L. flos-cuculi* and *Caltha palustris*.

(b) Dry: *T. officinale*, *R. acer*, *Anthriseus silvestris*, *Melandrium dioicum* and *Symphytum officinale*.

(2) Late summer (July–August)

(a) Wet: *Filipendula ulmaria* and *Cirsium oleraceum* following the flowering of the large *Carex* spp. and *Senecio aquaticus*. In autumn the fruiting aspect is marked.

(b) Dry: *Crepis biennis* and *Heracleum sphondylium* following the flowering of *Tragopogon pratensis* and *Knautia arvensis*.

The growth of the individual species of grasses varies through the year. In *Anthoxanthum odoratum*, *Alopecurus pratensis*, *Festuca rubra*, *Carex panicea* growth is highest in the spring, in *Cynosurus cristatus*, *Bromus racemosus*, *Dactylis glomerata*, *Poa trivialis*, *Deschampsia caespitosa* and the large carices in early summer. *Festuca pratensis*, *Poa pratensis*, *Holcus lanatus* and *Molinia coerulea* develop later, although it is difficult to generalise because the growth depends on the fertilising regime and the soil type, e.g. *Festuca rubra* and *Holcus lanatus* may have low competitive powers on clay soils but may become agressive with high N on lighter soils.

b. Life forms

Raunkiaer described his life forms for use in distinguishing plant-climatic regions, but they may be used in characterising plant communities in terms of their total flora. Western and Central Europe is a "hemicryptophyte region" and about a half of the native species are hemicryptophytes. A biological spectrum was prepared for the community and compared to the *Arrhenatheretum* and the region as a whole (Table 7).

Highly constant species may be totally insignificant for the aspect when they occur in small quantities or are small in size. Apart from the very wet sedge-rich variant and the *Alopecurus* type, the wet fertilised meadows are not dominated by any single species. Rather they are poly-dominant communities. GIMINGHAM (1951) suggested that the relation between structure and environment may be explained by the life form of the species and the ratio of the life form types and the distribution of the species. Of the fairly large group of species contributing to the physiognomy of the community the species differed in their distribution within the community. Some are "overdispersed", i.e. they tend to grow in

Table 7 Biological spectra of fertilised meadow communities taking into account only the presence of the species

	H	Ch	G	T	P
Wet fertilised meadows	79.8	11.1	7.8	1.3	–
Arrhenatheretum					
I. Zürich (SCHNEIDER, 1954)	74	9	8	9	–
II. Central Switzerland (BRAUN-BLANQUET, 1951)	50	5	15	20	10

H = hemicryptophytes, Ch = chamaephytes, G = geophytes, T = therophytes, P = phanerophytes

clumps ("contagious"), others are underdispersed. Species such as *Cirsium oleraceum* and *Holcus lanatus* show contagious distribution, whereas species not showing this type of distribution are distributed more or less randomly.

Taking into account the dominance of the species the individual variants previously described were examined and life form spectra produced (Table 8).

It was noticeable that the wetter variants contained proportionately more geophytes than the drier variants. The quantity of chamaephytes was similar, but the proportion of hemicryptophytes decreased as the proportion of geophytes increased.

III. Discussion

It was seen that the wet fertilised meadows vary in floristic composition according to the geographical region, altitude, soil conditions, and the intensity of their management. Their present classification is complex and many associations have been described. These appear too detailed for general purposes. It is suggested that for ecological purposes the meadows should be called collectively

Table 8 Life form spectra of different variants of the *Cirsietum* taking into account the dominance of the species

Units	Variants	H	Ch	G	T
Dry	I	83.7	11.6	–	4.7
	II	84.3	11.6	2.2	2.3
Intermediate	III	85.3	12.2	2.5	–
Wet	IV	79.9	10.6	10.5	–
	V	75.0	11.3	11.3	3.4
	VI	76.0	10.8	13.2	–
	VII	78.4	10.8	10.8	–
	VIII	75.6	12.2	12.2	–
All types		79.8	11.1	7.8	1.3

the Association group[1] *Cirsietum oleracei medio-europaeum* and the types such as those that grow on poor soil delegated as variants according to their ecological relationships. The Association group is controlled by the same ecological factors. The name *Cirsietum oleracei* should be retained. Association tables showed that there was a gradient of vegetation types from the wet poorly fertilised forms to the drier more fertilised *Arrhenatheretum*. These forms may exist in a successional relation.

The present hierarchy of the *Molinio-Arrhenatheretea* should be re-ordinated from ecological and successional data to produce a more generic classification. In the following experimental section the vegetation units are arbitrarily distinguished as "wet", "typical" and "dry". These corresponded more or less to the subassociations *caricetosum*, *typicum* and *heracleetosum*. The latter was compared to a wet subassociation of the *Arrhenatheretum*.

The montane association which has been described as the *Trollio-Cirsietum* appears to be very similar to the *Cirsietum oleracei*. There is a group of montane differential species, but it would be better to consider it as a variant of the lowland association.

The meadows have a subatlantic distribution tendency and they are limited by a continental climate. The variants in relation to climate are not so distinct as those of the *Arrhenatheretum*. The disjunct distribution is due to agricultural practises and site conditions.

Examination of the structure of the meadows showed that rarely was any one plant dominant. The important species contributing to the physiognomy of the community coexist in comparative equilibrium. The equilibrium appeared to be mainly controlled by anthropogenic factors. Natural distribution of the species combinations in nitrophilous habitats suggested that nitrogen was an important factor controlling the stability of the meadows. In section B the nitrogen relations are examined and in section C the agricultural yield is assessed.

Section B—Soil factors

I. The importance of the nitrogen factor

Floristic analyses and phytosociological investigations have demonstrated that the wet fertilised meadows are communities showing great overall stability. In different parts of Europe these have come into existence in various ways. Some have developed from alluvial vegetation on the flood plains of rivers, or from natural seral vegetating bordering lakes, and some were originally sown. Most have originated from forests especially after the destruction of alder, ash

[1] Hauptassoziation *sensu* KNAPP, Assoziationsgruppe *sensu* TÜXEN.