The nitrogen relations and other ecological investigations on wet fertilised meadows

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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.

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

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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	
*	(h)	*Achilleo-Brometum (racemosi)* Oberd. 57 (*Holcetum lanati* Issler 36)	
*	(i)	*Silao-Brometum (racemosi)* Oberd. 57 (*Sanguisorbo-Silaetum* Klapp 51)	(*Bromo-Senecio-netum* Tx. 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 $\quad\quad\quad\quad\quad$ (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

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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*.

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

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

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.

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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						Mean F value	Mean N value
			Trag.	*Arrh.*	*Carex*	*Alch.*	*Calth.*	*Sanguis.*		
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).

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[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%.

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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

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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 differed 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

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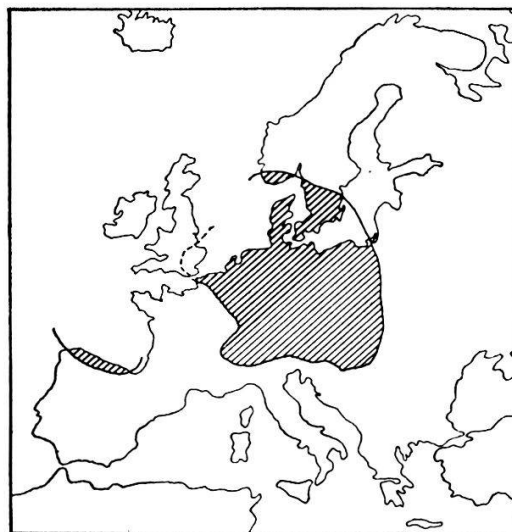
Fig. 1   The geographical distribution of the *Cirsium oleraceum* meadows.

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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 pratense	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. *tenui-folius*, *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.

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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, Anthriscus 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. GIMING-HAM (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

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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.

or oak-hornbeam woodlands. Many show evidence in the soil profile of phloughing. Yet the same community is present on land with differing histories, and even the original nature of the soil parent material has made little difference. Besides the humidity of the soil the dominant controlling factor has been, and still is, their agricultural management. These grasslands represent a biotic plagioclimax vegetation and their stability is in equilibrium with their treatment. Fertilised grasslands are either mown for hay (meadows) or grazed (pastures) and on this dichotomy rest the floristic variations between the associations. Grazing with animals excludes certain species which may reach their optimum in meadowlands and other species take their place, especially those grasses which produce a turf by lateral tillers.

Many of the species of the *Cirsium oleraceum* grasslands are also indicators of the soils. Some *Calthion* meadows *(Cirsium oleraceum* Assoc. *sensu lat.)* are intermittently fertilised though the better managed ones and the wetter forms of the *Arrhenatheretum* may be fertilised up to three times a year. They are cut at least once (the wettest variants) and maybe three times (drier variants) a year.

The fertilising regime has a decisive selective effect on the floristic composition of the grassland, whether it is long ley or permanent grassland. Most of the meadows are fertilised with liquid manure made from the farm garbage and spread by means of a large tank. KLAPP (1956) cites a typical analysis of "Jauche" or "Gülle". In each litre there was 4.0 g N, 1.0 g P_2O_5, 8.4 g K_2O, 1.9 g CaO and 120 g organic matter giving a ratio of $N:P_2O_5:K_2O:CaO$ of 10:2.5:21:4.7. Many of the species present are indicators for nitrogen, in contrast to those nitrophilous species of dung heaps, and the presence of many of the species depend on the inherent capacity of the soil for nitrification.

The nitrogen is not only supplied by the fertilisation but soluble nitrogen substances are produced in the soil by the activity of the ammonifying and nitrifying bacteria. Nitrification takes place in two stages:

$$2\,NH_3 + 3\,O_2 \rightarrow 2\,HNO_2 + 2\,H_2O + 79\,\text{Cal.}$$
$$2\,HNO_2 + O_2 \rightarrow 2\,HNO_3 + 43\,\text{Cal.}$$
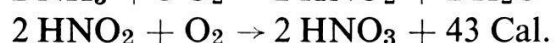
and the second takes place at a faster rate than the first. The N source is provided by ammonium which is split off from organic N compounds by heterotrophic microorganisms. During denitrification the reverse process occurs. The atmospheric nitrogen is replaced by the O of the nitrate ion in oxidising respiratory substrates, and organic compounds such as organic acids, etc., act as hydrogen donors in different denitrifying bacteria, though some can utilise inorganic substances such as molecular hydrogen, sulphur, thiosulphate, etc. Since the ammonium or nitrate content of the soil at any one time is not an indication of the nitrogen available for plants experiments were carried out to follow the pattern of ammonification and nitrification in the field throughout the year and the ammonification and nitrification in the laboratory with a constant temperature of 20 °C. Since the supply of ammonium or nitrate is of prime importance to plant growth, factors determining the accumulation of ammo-

nium or nitrate in the soil also determine productivity. Factors affecting the rate and amount of nitrification were also studied.

There has not been a lot of work on the nitrogen supply of grasslands. Most of the published work relates to arable land or woodlands. RICHARDSON (1938) examined the nitrogen contents of a short ley and a pasture 59 years old, and a pasture 200 years old in Britain and found that a greater proportion of their mineral N was ammonium which remained fairly constant at 3–9 p.p.m. throughout the year, but after the addition of an ammonium or nitrate fertiliser this N disappeared and was taken up by the plants. It was inexplicable why the ammonium was not totally nitrified in sites when it was incubated.

MEYER (1957) examined the nitrogen pattern in grasslands on alluvium subjected to flooding near Hamburg. The associations were *Phragmitetum, Glycerietum, Cirsium oleraceum* meadows and *Arrhenatheretum.* Nitrification was measured in Winogradsky's medium. The associations showed characteristic patterns of nitrification, e.g. the *Glycerietum* showed the lowest values and a typical *Arrhenatheretum* nitrified better than the wet and showed maxima in autumn, winter and a prolonged one in spring. The lowest values were reached in July. The wetter forms of wet fertilised meadows parallelled this. MEYER also made determinations of ammonification and denitrification.

There also is a relative paucity of data on nitrogen supply in other natural or seminatural communities. HARMSEN and VAN SCHREVEN (1955) emphasised that mineralisation of nitrogen was optimal in spring and decreased gradually during the summer. This spring optimum may result from a partial sterilisation effect of freezing during the winter. In uncropped soil the nitrogen content was lowest during the winter, then there was the spring flush of nitrates and high levels were maintained during the summer. On cropped land a second minimum in midsummer was caused by absorption of mineral nitrogen by plants. Most of the other literature which deals with nitrification in arable soils chiefly emphasises the spring release of nitrates. HESSELMAN (1917) compared the nitrogen relations of various woodlands in Sweden and suggested that the vegetation types showed great constancy in regard to nitrogen supply. He found that nitrogen supply in different communities distinguished them ecologically, e.g. nitrogen supply in Alder wood > Beech wood > mixed dicot. wood > coniferous wood. (Most soils HESSELMAN investigated had ammonium and not nitrate.) Other literature relating to the nitrogen budget of the soil is reviewed in the sections describing experimental work, e.g. ELLENBERG (1964), KOCH (1911), OLSEN (1921), QUASTEL (1946), RUSSELL (1914), and AMER and BARTHOLOMEW (1951).

Other edaphic factors besides nitrogen were investigated, especially the seasonal changes in phosphorus content and pH. Water is also an important factor controlling the stability of the communities studied. This is implied in the term "wet meadow" ("Feuchtwiesen"). The soil water was studied by recording the seasonal fluctuations in water table, the content of water in the surface soil and the water potentials developed by the soils.

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II. Experimental sites

1. Swiss Midlands

In order to provide contrasting soil conditions three experimental areas, containing ecological variants were selected. Twelve sites were chosen in the Cantons of Aargau and Zürich. The descriptions of the stands are given in the Appendix Table. The soils were all loams or clay loams with the exception of plots S 11 and S 12, which were silts (Table 9). The two latter represented a flush vegetation and water was supplied from an underground source. Site S 11 was on a slope near the water supply and site S 12 at the bottom. Water tended to accumulate at the bottom and the vegetation was invaded by *Caltha palustris* and other hygrophytes. Plots S 4 and S 1 were wetter types characterised by the high presence of *Carex acutiformis* and *C. gracilis*. Plot S 2 was close to plot S 1, but there were differing water relations, and it appeared also that this part of the field has been continually better fertilised. Plot S 5 was a wet type but differed from the others in its affinities to a *Filipenduletum*, probably because it had not been cut so often. Plot S 10 was a true *Arrhenatheretum* taken to provide a comparison between the associations. The other plots were true *Calthion* meadows, all with typical floristic composition. Plot S 6 differed because the soil water was considerably less and the soil of plot S 9 contained high quantities of iron salts. This bordered a stream and was occasionally flooded in winter. The differences between plots are well illustrated by the mean N and F values of the stands (Table 10).

Table 10 Mean F (humidity) and N (nitrogen) values of experimental plots (Swiss Midlands)

	Plot No.	F	N	Remarks
Wet	S 1	3.94	3.19	Same area, differing
	S 2	3.42	3.80	management
	S 3	3.57	2.63	
	S 4	4.02	2.37	
	mean	*3.74*	*2.99*	
Typical	S 5	3.55	3.21	
	S 6	3.39	3.50	
	S 7	3.56	3.00	
	mean	*3.50*	*3.24*	
Dry	S 8	3.41	3.13	
	S 9	3.50	3.14	
	mean	*3.45*	*3.14*	
Arrhenatheretum	S 10	3.20	3.84	
Wet slope	S 11	3.53	2.90	Top
	S 12	3.91	2.64	Bottom
	mean	*3.72*	*2.77*	

Table 9 next page.

Table 9 Soil characteristics of the experimental plots in Switzerland (surface soil)

Plot No.	Soil texture	sand	gravel	coarse sand* 2–0.2 mm	fine sand* 0.2–0.02 mm	silt* 0.02–0.002 mm	clay* 0.002 mm	% loss on ignition		Dry weight of 1 litre g	Volume of 100 g dry soil cm³	CaCO₃ %	pH (mean 1963)
S 1	heavy		+	3.4	31.7	47.5	17.5	20.1	(19–22)	812.1	123.1	0	5.7
S 2	wet			0.7	31.9	45.0	22.5	17.0	(19–19)	576.4	173.5	0	6.0
S 3	loams			0.6	57.0	17.5	25.0	16.0	(12–17)	1040.2	96.1	0	6.2
S 4				1.4	36.1	39.3	23.2	37.0	(24–55)	823.7	115.8	0	6.0
S 5				0.9	19.1	65.0	15.0	15.3	(12–17)	905.8	108.4	0	7.0
S 6	loam	+		2.3	37.5	42.5	17.7	15.7	(14–18)	517.0	193.4	0	5.7
S 7				0.4	34.7	50.0	15.0	21.2	(20–21)	793.6	126.0	0	6.3
S 8				0.5	30.0	57.5	12.5	24.0	(23–25)	672.6	148.7	0	6.3
S 9	red-brown loam	+		0.9	41.7	40.0	17.5	27.1	(24–28)	941.5	106.2	0	6.5
S10	loam			1.0	40.8	45.5	12.7	16.5	(16–17)	712.5	146.3	0	6.8
S11	light loam	+	+	5.6	57.0	30.0	7.5	17.3	(16–18)	684.7	208.9	2.50	7.0
S12	and sand	+	+	8.3	44.2	40.0	7.5	14.4	(14–17)	728.2	137.3	0.20	6.8

*Measured by Esenwein's method

2. Alsace, France

The sites in France were in the locality of Blotzheim, close to the Swiss border. The past history of this area has had an important effect on the vegetation and systems of management. Firstly there have been oscillations of political affinities and these have variously affected the agricultural emphasis. Secondly the sites were in the valley of the Rhine and since the early eighteen hundreds (especially 1817–1874), there have been corrections made and canals built, which have affected the water levels of the soil. (The Grand Canal d'Alsace and the Canal de Huningue were built 1928–1932.) The sites were on true alluvium, and the fact that they were on an old bed of the Rhine is shown not only by the topography, but by the absence of villages in a corresponding band (see the figure in SPECKLIN, 1962). The soils were chiefly silt though in texture they approximated to sandy soils. However, the usual limit taken for sandy soils is > 30% sand (Table 11). The soils were also calcareous and had high pH values. Despite variations in soil composition in the area, the sandy fractions dominate. DIRRIG (1959) quotes a typical mechanical analysis from Village-Neuf as: clay 8.6, silt 14.0, fine sand 41.9, large sand 12.1, calcium 21.6 and organic matter 1.8%. The unfavourable drying tendencies of this type of soil are not apparent because the ground water table is high and the soil water lost at the surface by evaporation is replaced by capillary rise. The high water table is made obvious by the many small "Piscineries" in the area.

It is certain that these meadows are fragmentary and were formerly much more extensive. The agriculture now is chiefly arable and a thriving vegetable industry is being established. The management of the meadows is not good and not always consistent and there is a tendency to revert to reed. Charcoal remains in the soil profiles show that at one stage the vegetation has been burnt and firing is still used to control *Phragmites* in the area.

High water in the river Rhine is in early June, but the levels of the small drainage ditches remain high. In spring there is some flooding depositing organic debris and iron salts on to the soil surface.

Nine plots were selected. Three supported the wet type of vegetation with *Carex acutiformis*, *C. gracilis*, *C. tomentosa* and *Juncus effusus*. Three supported intermediate vegetation, and three the dry containing several indicators of drier conditions (*Daucus carota*, *Tragopogon pratensis*, *Picris hieracioides*, *Medicago lupulina*, etc., Table 12). The N and F values were calculated, and though the series of stands showed distinct differences in their indicators for humidity, the differences in indicators for nitrogen were not so marked. The typical and dry vegetation types gave similar N values (in the range 3.3–3.8) and this points to the less intensive management (Table 13).

3. Baden-Württemberg, S. Germany

The Nature Reserve at the Federsee, at Buchau, has wet meadows growing on a predominantely black organic soil. Several centuries ago the Federsee was

Table 11 Soil characteristics of the experimental plots in France (surface soil)

Plot No.	Soil texture	sand	gravel	coarse sand 2–0.2 mm	fine sand 0.2–0.02 mm	silt 0.02–0.002 mm	clay 0.002 mm	% loss on ignition		Dry weight of 1 litre g	Volume of 100 g dry soil cm³	CaCO₃ %	pH (mean 1963)
F 1	clay-silt	+	+	2.8	47.2	20.0	30.0	25.0	(22–27)	708.1	141.2	18.6	7.3
F 2	silt (heavy)	+	+	6.0	66.8	22.2	5.0	21.0	(17–22)	703.9	142.1	23.2	7.3
F 3	silt (dry)	+	+	2.0	48.1	42.4	7.5	21.0	(19–24)	622.5	160.6	24.3	7.3
F 4		+	+	2.3	62.7	32.5	2.5	20.3	(19–22)	841.4	118.9	26.7	7.2
F 5	silt	+		6.4	30.4	53.6	9.6	21.7	(17–24)	842.3	118.7	31.4	7.2
F 6	sandy loam	+		9.1	27.2	50.5	13.2	18.0	(17–20)	893.3	112.0	36.8	7.3
F 7	+ clay	+	+	22.8	26.8	35.4	15.0	9.70	(8–11)	1204.8	83.0	24.9	7.3
F 8	sandy	+	+	16.8	25.0	42.5	5.7	13.3	(12–14)	1085.6	92.1	25.8	7.2
F 9	loam—clay	+	+	16.2	29.6	48.9	5.3	20.0	(20)	1050.5	95.2	33.5	7.3

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Table 12 Stand descriptions of field plots in Alsace
(May 1963, figures are cover values according to the Braun-Blanquet scale)

Plot number	F	1	2	3	4	5	6	7	8	9
Trisetum flavescens	+	+			1	1	2	1	2	1
Arrhenatherum elatius	+			+	+	1	1	2	1	3
Anthriscus silvestris	2	3	2		1	3	2	2	2	2
Heracleum sphondylium	+	1			2	+	+	1	1	2
Galium mollugo			+	+	+	1	1	2	2	1
Pimpinella major	+				+	2	2	2	1	1
Daucus carota	+				+			+	2	2
Chrysanthemum leucanth.	+	+	+		1	+	1	+	1	1
Melandrium diurnum							+	+		1
Tragopogon pratensis					+			1	1	+
Leontodon hispidus								1	1	2
Lotus corniculatus						2			2	
Veronica arvensis					1			1		+
Cirsium oleraceum	2	2	1		2	3	3	1	2	2
Deschampsia caespitosa	2	1	2		1		1	+	+	
Bromus racemosus	2	2	2			1		1		+
Geum rivale			+							
Filipendula ulmaria	2	2	+		2	2	3	+	+	+
Galium uliginosum	1	+			1	1	1	+		+
Lychnis flos-cuculi	1	2	2					1	1	+
Crepis paludosa	1	+	+						+	
Succisa pratensis		2								
Cirsium palustre	2			1		+		+		+
Lotus uliginosus		2				1				
Myosotis palustris	1	1	2		+		+	+	+	
Agrostis alba	+	2	1		1					
Festuca arundinacea	2	1	1				+	+		
Angelica silvestris	2			2	2	1	2	2	1	2
Equisetum palustre	2	1	2		+	1	+	1	1	+
Senecio aquaticus	1									
Lysimachia nummularia	1				+					
Carex acutiformis	1	1	3		2	2	+		+	1
Carex gracilis	2	2			1	1	+			
Carex flacca	1	1	1						+	+
Carex panicea	1	2	2		1			+	+	
Carex tomentosa	2	1	+		2	+			+	+
Festuca rubra	1	+		1		1	1	+		+
Medicago lupulina					1	+		1	1	1
Dactylis glomerata	2	+	1		1	+	1	2	2	2
Ranunculus acer	1	+	1		2	1	1	3	2	1
Rumex acetosa	2	1	2		1	+	+	2	1	2
Poa pratensis ssp. latifolia	1	2	1		1	2	1	+	+	1
Poa trivialis	1	2	2		1	2	3	1	2	2
Plantago lanceolata	1	1	+		2	1		2	1	+
Cerastium caespitosum	1	+	+		+	1	1	+	+	+
Holcus lanatus	2	2	3		2	3	2	1	1	1
Festuca pratensis		+			1	+	+	2	1	2

Plot number	F 1	2	3	4	5	6	7	8	9
Lathyrus pratensis	1	+	1	1	+	1	1	+	+
Centaurea jacea					1		2		
Taraxacum officinale	1	+	1	1	+	2	1	2	1
Ajuga reptans	1	2	2	1	2	2	1	2	2
Bellis perennis	2	+	+	+	1	+	2	1	+
Trifolium pratense	1	+	+	2	1	2	1	1	3
Vicia cracca	2	2	1	1	2	+	1	+	2
Galium palustre	+	+	+	+					+
Vicia sepium	1			1		1	1	2	1
Anthoxanthum odoratum	1	2	+	2	1	+	1	1	2
Trifolium repens		+		+	+	+	2	1	2
Cardamine pratensis	1	1	1	2	1	1	+	+	+
Alchemilla vulgaris	+						1		1
Alopecurus pratensis				1	2	1	1	+	
Avena pubescens		+		+				+	
Veronica chamaedrys	+		+	1	+		+		
Rumex obtusifolius		+	1	2	1	2	1	1	1
Ranunculus repens	2	+		1			1	+	2
Glechoma hederacea	+		+	+	+		+	+	+
Lythrum salicaria	2	1	2		1				
Symphytum officinale	2		1	2	+	1	3	2	2
Potentilla erecta	1			+		+	+	+	+
Phragmites communis	1	+	2	+	1		+	+	+
Juncus effusus	2	1	2	1					
Senecio jacobaea				1			+	1	+
Achillea millefolium						2	1	+	1
Silaum silaus	1	1	+		1				
Knautia arvensis					1		1	2	1
Convolvulus arvensis					+		+	+	
Potentilla reptans					+		+		+
Molinia coerulea			1		+				
Hieracium pilosella				1		+		+	
Valeriana officinalis					1	1		1	1
Picris hieracioides					1		+	1	1
Euphorbia verrucosa							1	1	+
Geranium pratense						+	1	1	+
Carex hirta	1						1	2	2
Iris pseudacorus	1	2	2	+	1	2	1		
Lotus siliquosus		+	+	+	+	+	1	1	1
Artemisia campestris							+		+

Of rare occurrence : *Phleum pratense* (7), *Bromus erectus* (7). *Salix cinerea* juv. (5)

very much larger but now occupies only a fraction of its size in the 1700's (WALL, 1964). The meadows were all in the area which in 1731 was part of the lake basin. The soils are characterised by high water table throughout the year (for analyses see Table 14). The soils were truly organic. Peat is usually defined as soil with a content of organic material of more than 40% in the top 0–25 or 30 cm of the soil profile, but these soils have matured producing a good crumb

Table 13   Humidity (F) and nitrogen (N) values of experimental plots: Alsace

	Plot Nr.	F	N
Wet	F 1	3.87	3.45
	F 2	3.82	3.14
	F 3	3.98	2.99
	mean	*3.89*	*3.19*
Typical	F 4	3.60	3.40
	F 5	3.65	3.79
	F 6	3.64	3.66
	mean	*3.63*	*3.61*
Dry	F 7	3.11	3.53
	F 8	3.22	3.59
	F 9	3.34	3.30
	mean	*3.33*	*3.47*

structure. This is partly due to draining and ditching and partly due to amelioration by adding gravel. The humification of the peat is good down to the underlying sediments, and the humification has resulted in disintegration of the peat with subsequent decrease in porosity and increase in density.

The peat was *Carex* peat, and this is known to have high nitrogen content. HOLMEN (1964) showed that tall *Carex* peat contained 1–3% N and usually more than 2.5%. The nitrogen contents of the peat forming species is usually high, e.g. *Carex elata* 1.87 (GORHAM, 1953), *Eriophorum vaginatum* 1.15, *E. vaginatum* after fertilising 1.52 (TAMM, 1954). Peat of tall *Carex* spp. *(C. elata, C. appropinquata, C. lasiocarpa)* with some small carices, e.g. *C. panicea*, gave a nitrogen content of 2.72–3.44% N. The wet meadows investigated at the Federsee were on soils derived from this type of peat, although in the area there are also *Scheuchzeria-Sphagnum* peats. The vegetation has been well described by KUHN (1961). On the basis of floristic lists she distinguished the following subassociations and variants of *Cirsium oleraceum* association (A, B) and *Arrhenatheretum* (C):

(A)   Sedge subassociation (with *Carex panicea, C. fusca* and *Valeriana dioica* as differential species) with 5 variants:
1. Variant with *Carex davalliana, Molinia coerulea* and *Carex lepidocarpa,*
2. Typical variant,
3. Variant with *Carex gracilis,*
4. Variant with *Scirpus silvaticus,*
5. Variant with *Carex brizioides* and *C. disticha*

(B)   Typical subassociation

(C)   Arrhenatheretum subassociation with *Cirsium oleraceum*

The experimental sites selected corresponded to (C) (plots G 10, G 9 "*Arrhenatheretum*"), with all typical species of the *Arrhenatheretum* but with some

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Table 14 Soil characteristics of the experimental plots in Germany (surface soil)

Plot Nr.	Soil texture	sand	gravel	coarse sand 2–0.2 mm	fine sand 0.2–0.02 mm	silt 0.02–0.002 mm	clay 0.002 mm	% loss on ignition	Dry weight of 1 litre g	Volume of 100 g dry soil cm$_3$	CaCO$_3$ %	pH (mean 1963)
G 1	sedge	+	+	30.6	29.4	16.5	23.5	44.3 (42–51)	536.8	186.3	0	6.6
G 2	peat		+	27.5	32.2	18.9	22.4	54.2 (45–56)	430.3	232.4	10.8	6.7
G 3	fibrous		+	37.6	50.2	5.0	74.2	26.3 (20–33)	500.3	199.9	2.5	6.8
G 4			+	9.7	52.8	37.5	25.0	55.3 (52–54)	498.0	200.8	0.5	6.7
G 5	loam		+	11.2	33.5	29.3	27.0	44.0 (41–47)	510.4	195.9	0	6.7
G 6	Peat and	+	+	15.1	50.0	26.5	8.4	49.7 (46–59)	396.5	252.2	0	6.8
G 7	sand	+	+*	15.5	72.5	7.5	5.0	51.0 (47–53)	335.0	298.5	5.0	6.9
G 8	fibrous loam		+	25.2	25.2	27.2	22.4	52.8 (43–55)	440.0	227.3	7.6*	6.9
G 9	loam		+	6.4	28.2	46.4	19.0	38.7 (36–42)	663.8	155.6	0.8	6.9
G 10		+	+	29.0	26.0	25.0	20.0	35.0 (20–41)	652.8	153.2	12.5*	6.9

* small calcareous nodules

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Calthion species such as *Deschampsia caespitosa* and *Cirsium oleraceum;* to (B) a typical admixture of *Arrhenatheretum* and *Calthion* species but with dry indicators, e.g. *Poa pratensis* spp. *angustifolium, Leontodon hispidus, Daucus carota,* etc. (plots G3, G8, "dry"); to (B) but with no dry indicators, and wet indicators present in low amounts (plots G4, G5 "typical") and to (A)3, characterised by the presence of carices, especially *C. disticha* (plots G1, G2 "wet"). Plot G1 had *Senecio aquaticus* with a cover-abundance value of 3, and this site was similar to the *Bromus racemosus – Senecio aquaticus* Association described by Tüxen and Preising (1951). Plots G6, G7 ("*Scirpus*") corresponded to (A)4 with *Scirpus silvaticus* and *Carex fusca*, but also with high quantities of *Equisetum palustre* and *Angelica silvestris*. The stands of the experimental plots are described in Table 15.

Table 15 Stand descriptions of field plots in Southern Germany
(May–June 1963. Figures are cover values according to the Braun-Blanquet scale)

Current number	1	2	3	4	5	6	7	8	9	10
Plot number	G 10	9	3	8	4	5	1	2	6	7
Trisetum flavescens	3	3	1	2	1	2	+	+	+	
Arrhenatherum elatius	2	2	1	2	1	1	+			
Anthriscus silvestris	2	2	1	1	1	1			1	1
Heracleum sphondylium	2	2	2	2	2	1	+		2	1
Galium mollugo	1	2	1	1	2	1			+	+
Pimpinella major	+	+	1	1	1	1	1	+		
Daucus carota	1	1	1	1		+				
Phleum pratense	1	+								
Chrysanthemum leucanthemum	1	1	1	1						
Melandrium diurnum		+	1	+						
Poa pratensis	1	2	1	1						
Leontodon hispidus	1	1	+	+						
Lotus corniculatus	+		+	+						
Veronica arvensis		+	+	1						
Cirsium oleraceum	2	2	3	3	1	1	2	1	1	2
Deschampsia caespitosa	2	2	2	2	2	2	1	2	2	3
Polygonum bistorta			+		3				1	1
Geum rivale	1	+	1	2	1	1	2	5	2	2
Filipendula ulmaria	1	1	2	2	1	3	2	2	1	1
Galium uliginosum		+			1	1	1	+	+	+
Lychnis flos-cuculi			+		2	1	1	1	+	+
Crepis paludosa	+				2	+	1	2	+	+
Succisa pratensis			+		+		1	1		
Cirsium palustre		+			+		+	2	+	
Lotus uliginosus		1		+		1	1	+	1	+
Myosotis palustris	1	1				+	+	+	2	2
Agrostis alba				+	1	+	+	+		
Scirpus silvaticus									2	3
Angelica silvestris	2	+	1	+	2	2	1	1	3	3
Equisetum palustre	1	+	2	2	2	2	3	2	3	3

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Current number	1	2	3	4	5	6	7	8	9	10
Plot number	G 10	9	3	8	4	5	1	2	6	7
Cirsium rivulare					+			+	+	
Senecio aquaticus					+		3			
Caltha palustris					1	1	2	2	+	1
Lysimachia nummularia					+	1		+	1	2
Carex acutiformis	+		+	1	1	1	2	2	1	+
Carex gracilis					+		3	2	+	+
Carex fusca							+		3	3
Carex panicea				+	2	1	1	1	1	+
Carex disticha						1	+			2
Dactylis glomerata	2	2	1	2	1	1	+		+	+
Ranunculus acer	2	2	2	1	2	2	1	1	2	1
Rumex acetosa	+	1	+	+	2	2	+	2	1	+
Poa pratensis	1	1	1	1	1	1	1	+	+	1
Poa trivialis	+	1	+	+	1	1	+	+	+	+
Plantago lanceolata	2	2	2	2	1	2	+	+	1	1
Cerastium caespitosum		+	+	1	1	1		+	2	2
Holcus lanatus	1	1	1	2	2	2	1	1	1	1
Festuca pratensis	2	1	1	1	2	1	+			+
Lathyrus pratensis		+	1		1	1	+	+	1	1
Centaurea jacea	+	+	2	1	1	1		+	1	+
Taraxacum officinale	2	3	1	2	2	1	1	+	1	1
Ajuga reptans	+	+	1	1	1	2	1	1	2	1
Bellis perennis	1	1	1	+	+	+	+		+	
Trifolium pratense	2	2	2	2	1	2	1	+	1	1
Vicia cracca		+	1	1	1	1	+			
Galium palustre					+		1	1	1	+
Vicia sepium	+	1	+	1	+	1		+		1
Anthoxanthum odoratum	1	1	2	1	2	3	1	2	1	1
Primula elatior			+		1	1		+	1	+
Trifolium repens	1	2	1	1	+	1		+	+	+
Cardamine pratensis		+		+	1	1	2	2	1	+
Alchemilla vulgaris	+		2	+	1	+				
Alopecurus pratensis	1		1		1					+
Bromus mollis	+	1		+		1				
Avena pubescens	1			1	1	1	+			+
Veronica chamaedrys	+		+	+	+				+	1
Rumex crispus	1			1						
Ranunculus repens	1	1	1	1	1	+	+	+		+
Glechoma hederacea	+	+		+		+				
Agropyron repens	+	1	+							
Polygonum amphibium						1	1			
Mentha aquatica						+	1			
Lythrum salicaria				+		+	+			
Urtica dioica									+	+
Festuca rubra	+		+		+			+	1	1
Prunella vulgaris	+				+			+		

Of rare occurrence: *Molinia coerulea* (8), *Lamium album* (9), *Convolvulus arvensis* (2), *Achillea millefolium* (3), *Trifolium dubium* (1), *Hypericum perforatum* (9)

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The water table was high in all these plots and the better soil structure was found in the drier types (Plots G3, G8, G9, G10). pH varied little between the plots and the percent-$CaCO_3$ variations were more than likely due to calcareous particles among the gravel used for amelioration. Calcareous muds are present and have arisen by past sedimentation but if present are lower down in the soil profile (see GÖTTLICH, 1961). The soil texture of the *Scirpus* plots differed noticeably from the others in its high sand content. Possible this area has had a different history since the sand represents a band of sedimentation whereas in the others sedimentation was a mud (Table 14). Mean N and F values showed that the *Scirpus* plots approximated to the wet *Cirsium oleraceum* units (Table 16).

Table 16 Humidity (F) and nitrogen (N) values of experimental plots: Southern Germany

	Plot No.	F	N
Wet	G 1	4.20	2.73
	G 2	4.02	2.55
Typical	G 4	3.73	3.35
	G 5	3.77	3.05
Dry	G 3	3.50	3.21
	G 8	3.57	3.21
Wet	G 9	3.41	3.70
Arrhenatheretum*	G 10	3.26	4.33
Variant with	G 6	4.24	2.70
Scirpus	G 7	3.82	2.75

* *Arrhenatheretum* mean F < 3.3

The plots showed an increase in both N and F values from the wet vegetation sites to the *Arrhenatheretum*. All the meadows were well managed and the area was especially suitable for grassland studies due to the complexity of the land ownership and its multifarious divisions into strips, each managed by a different person or family. This is one reason why the floristic variants of the wet fertilised meadows in the Federsee region were so clear-cut.

4. Comparison of experimental sites

Despite the differences in soil texture and in calcium carbonate content, all the soils contained organic matter and had a favourable C/N ratio. In grassland litter decays rather quickly, and grasses tend to place organic matter in the soil because of the many short-lived fine roots, and they represent a store which by mineralisation gives CO_2, water and minerals. Despite the edaphic differences a similar vegetation was present in each region. The three regions also expe-

rienced climatic differences. Alsace has the driest climate with warmer winters and less precipitation and the climate tends to be more continental. S. Germany has colder winters and the heaviest precipitation (see Table 17). Climatic data for the three regions during the experimental periods are shown in figs. 2, 3 and 4. The plots in Switzerland, Alsace and Germany would support a mixed deciduous summer forest as a climax vegetation.

Table 17 Comparisons of the climates of the three experimental areas
(Data from UTTINGER, 1949; SCHUEPP, 1960, and L.KUHN, 1961)

	Month												
	J	F	M	A	M	J	J	A	S	O	N	D	
mm precipitation													Total
Zürich	49	45	63	78	111	139	136	127	100	72	53	57	1030
Buchau	55	45	58	74	85	110	112	102	86	67	55	65	914
Basel	44	43	54	65	80	92	91	85	79	67	57	53	810
Air temperature °C													Annual mean
Zürich	−0.8	0.2	4.0	7.8	12.7	15.7	17.2	16.5	13.3	8.3	3.3	0.1	8.2
Buchau	−1.8	−0.2	2.9	8.1	12.1	15.0	16.5	16.9	12.9	7.6	2.5	−0.6	7.7
Basel	0.4	1.2	4.8	8.5	13.3	16.5	18.3	17.6	14.3	9.3	4.3	1.3	8.8

The aim of the experiments was to obtain a picture of the nitrogen pattern of the association, and a large number of plots were sampled. This was to see whether there was any underlying similarity in nitrification in an association growing under different climatic and edaphic conditions, rather than to experiment closely in one area with many replications.

III. Water

1. Seasonal changes in soil water content

Moisture is the dominant factor of the soil for although other factors may be changed independently, change in moisture effects changes in the others. The amount of water held by a soil depends on the mechanical fractions, the soil structure and the content of organic matter. The parameter of agricultural importance is the concept of "field capacity", though only a normally drained soil has a field capacity according to the definition of VEILEMEYER. This is the percentage of moisture held in the soil after drainage has progressed so that further downward movement of water is slow. The field capacity expresses the maximum storage capacity. An imperfectly drained soil does not follow the water distribution as defined by VEILEMEYERS field capacity. In this case gravi-
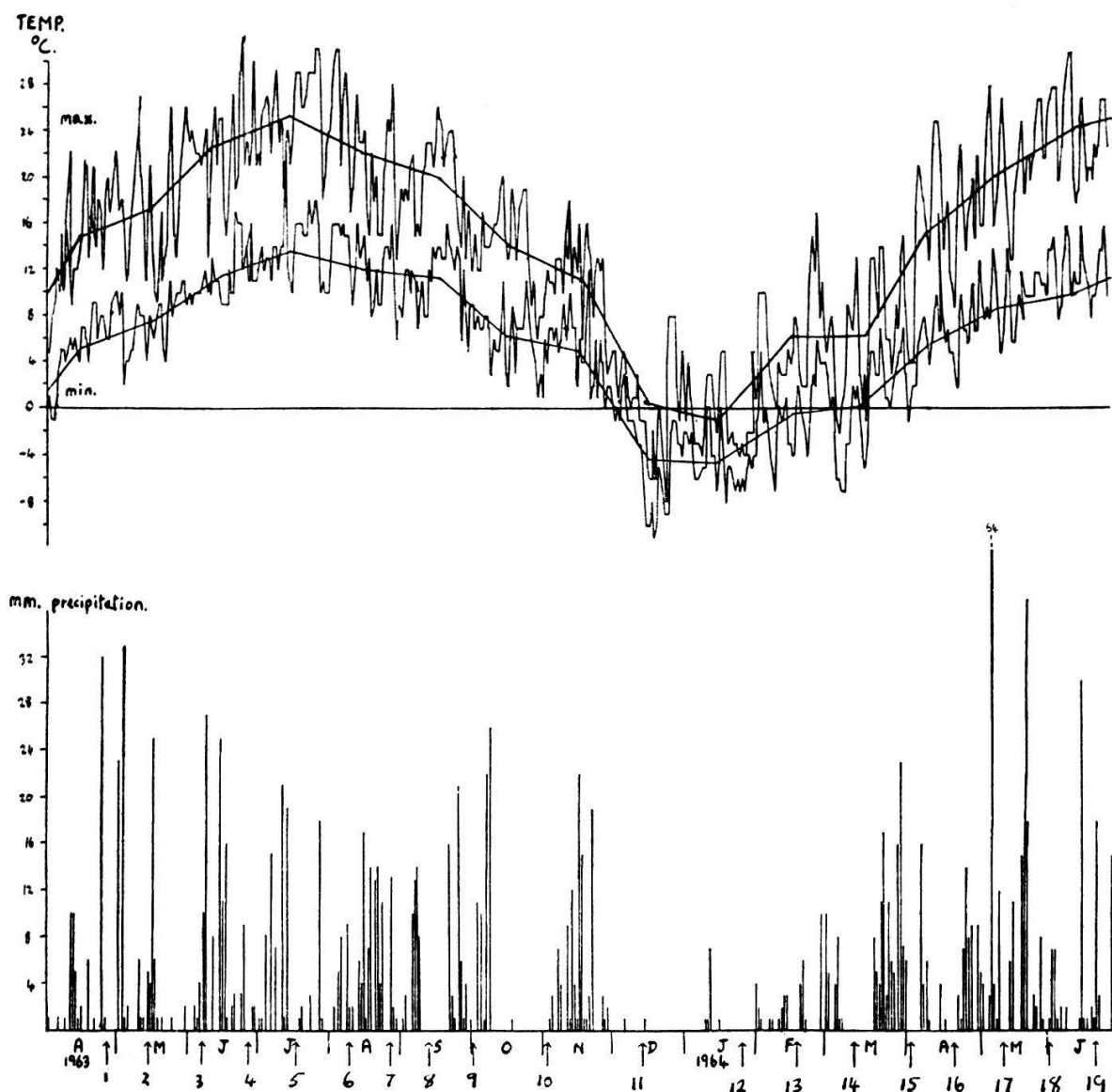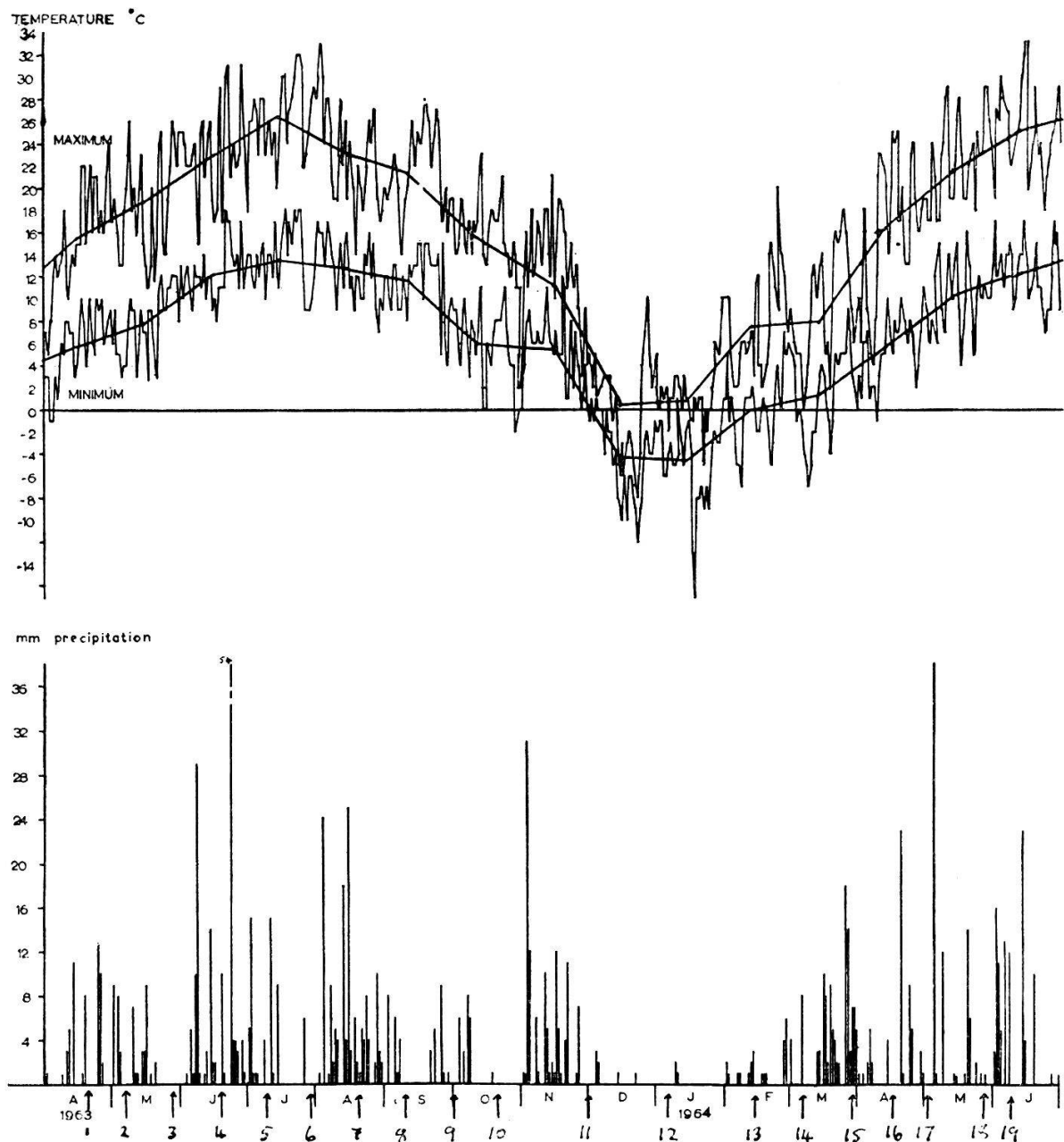
Fig. 2 Climatic data for the experimental sites in Switzerland.
(The arrows indicate data and current numbers of sampling)

tational water can not be removed 2–3 days after saturation. The soils of the wet fertilised meadows were nearly always moist at the surface and water content was usually in excess of the field capacity.

The water content fluctuated with the season; generally it was low in summer and high during winter. Many of the fluctuations are readily explicable, e.g. the small fluctuations during summer could be related to the precipitation and sampling soon after rain gave a higher soil water content. Probably also the observed values of soil water during the winter were too high, due to the fact that the soil was frozen and some free water as ice was included in the samples. The different variants of the *Cirsium oleraceum* meadows all showed the same seasonal trends although the wet types tended to show comparatively larger increases in relation to rainfall when the yearly means were considered. The sandy loams showed the most uniform variation in water content between the

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Fig. 3 Climatic data for the experimental sites in France.
(The arrows indicate data and current numbers of sampling)

vegetation types. The mineral soils were also parallel, but the organic soils displayed larger fluctuations between the variants.

The *Arrhenatheretum* behaved differently from the other vegetation types. High values of soil moisture were recorded for shorter periods than in the other types. In other wet meadows, similar seasonal trends in water content of the top 20 cm of the soil profile were pointed out by ANDERSSON and ERICSON (1963) in a *Filipenduletum* in Sweden and by ESKUCHE (1962) in three variants of wet *Arrhenatheretum* subass. with *Alopecurus pratensis* in Germany.

Ecologically the soil water content on a weight basis is not a very meaningful parameter. It is the amount of water that is available to the plants that is
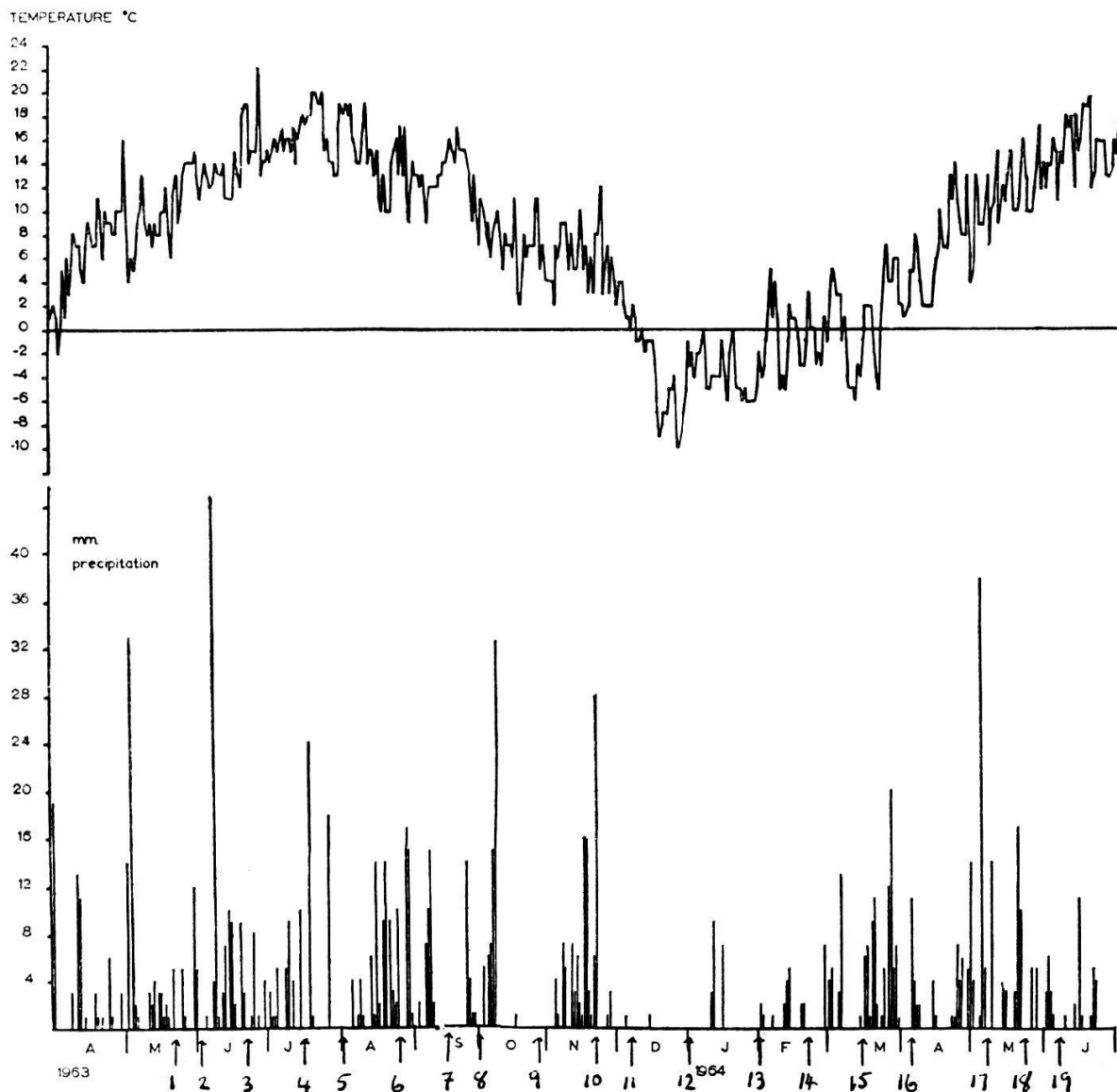
Fig. 4 Climatic data for the experimental sites in Germany.
(The arrows indicate data and current numbers of sampling)

important. This aspect is considered below (see section 3). On the other hand when the water content is too high, oxygen supply might become a minimum factor of decisive importance.

2. Water table

Changes in the level of the water table have been adequately recorded by several investigators (see for example KUHN, 1961; BAEUMER, 1962; ESKUCHE, 1962). Three tubes were inserted into three plots in the Swiss Lowlands. The tubes were provided with small seepage holes and the level of water in the tube fluctuated with the water table. The sites investigated were sample plots S 11: wet unit; S.6: typical unit, and S9: dry unit. The measurements are plotted in Fig. 5, and as was to be expected the water table decreased with the increasing occurrence of plant indicators for dryness. The curves for the typical and dry

variants were very similar. Most hygrophytes such as the large carices present in the wet variants are otherwise confined to stream margins. These species are dependent on the water which rises from the water table. When the water table is below ca. 80 cm from the soil surface the capillary conductivity of water may still be great enough to replace the water lost through transpiration. The plants depending on this capillary rise can grow downwards to reach the perched water table.

3. Soil water potential

In the soil water moves along hydraulic gradients. From there to root and from root to leaf. Plants take up water from the ground water or the capillary water and if the available water is exhausted the plants wilt. With increased soil suction the capillary conductivity of the soil decreases. As the soil dries large gradients of suction occur between the roots and the soil. The percentage water content of the soil when wilting occurs is the permanent wilting percentage and water in excess of this represents water which is available for growth. In the field, soil moisture content changes causing concomitant change in water potential or "suction", e.g. when water is provided from precipitation the suction is lowered. The soil moisture content at which fall off in transpiration occurs depends on the soil properties. The permanent wilting percentage falls with increased permeability.

Determinations of the water potential or "suction force" were made using the method of Ursprung and Blum (see ELLENBERG, 1939). Non hygroscopic glass capillary tubes about 1 cm long were filled two thirds full of prepared KNO_3 solutions of known osmotic pressures. These were fastened to a glass plate by means of a strip of plasticene and inverted over the soil in small glass jars. The place acted as the lid and the jars were sealed with vaseline. The tubes were filled quickly to prevent any losses by evaporation. When the jars were sealed the lengths of the liquid in the tubes were measured with a calibrated binocular microscope. The jars were left for two days and then the columns of liquid were measured again. The measurements were made in a controlled temperature room and the jars kept in a double insulated box. The length of the columns of liquid moved because evaporation took place from solutions with an osmotic pressure lower than the soil suction force and condensation occurred in those with higher osmotic pressures. The soil suction force lay between the osmotic pressures in the two capillaries which showed the smallest increase and decrease. The exact value of the suction could not be extrapolated because changes in the lengths of fluid were partially affected by the diameter of the tubes, the distance of the liquid from the end of the tubes and other factors.
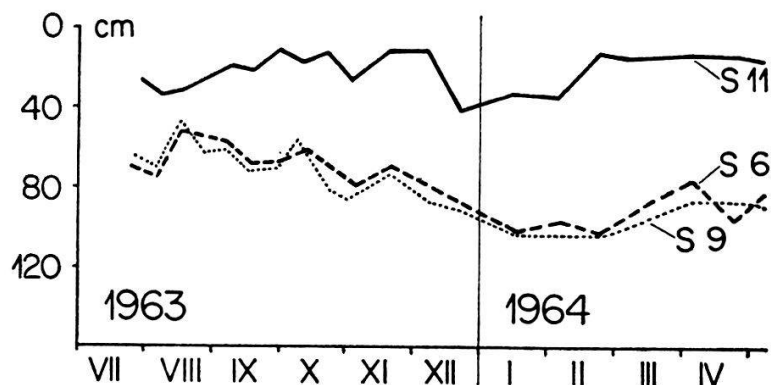

Fig. 5   Water-table measurements.

Temperature had to be maintained constant because a change of 1 °C can greatly alter the measurements, and the jars used must be small so that there is no gradient of temperature between the capillaries and the soil.

Although this method has a wide range it is only suitable to measure the suction force above 2 atm. Lower than that other methods have to be employed. The suction force also varies depending whether the fresh soil is dried, or a dry soil is wetted. Wetting tends to give lower values (SCOFIELD, 1963). The soils were collected after rain so that they were wet. Mixed samples were taken and these were spread out on pans and allowed to slowly dry at room temperature. Samples were taken at intervals and the water content and the suction force were determined. 9 mineral soils from Switzerland, 5 sandy soils from France and 5 organic soils from Germany were examined. The curves of suction force in relation to water content are not published here. It was apparent that the increase in suction force occurred at low water content in the sandy soils but at a much higher water content in the organic soils; and the mineral soils were intermediate. By converting the values of soil water content into their corresponding suction values curves of the seasonal variation in soil suction are produced.

In the "wet" variants the suction only rarely reached a value of ca. 5 atms. and for most of the experimental period the suctions remained low. The "dry" variants tended to reach higher values during dry periods, e.g. ca. 13 atms. in the organic loams and clays, though the sandy loams produced lower values. In general the fluctuations in suctions were more marked in the "dry" variants. The "typical" variants showed intermediate relations. These results suggest that the selection of these variants on floristic composition bore a close relation to the soil water relations. The *Arrhenatheretum* (G 10 and S 10) showed affinities with the "dry" variants though the fluctuations in suction was not so varied. The *Scirpus* variant showed a pattern differing from the other variants, and this may explain the peculiar nitrogen pattern to be described later.

When the suction force was compared to the water contents at different sampling times over the experimental period it was demonstrated that the soil suction force was nearly always less than 5 atms. and often less than 2 atms. Only under extreme conditions of drought does water become unavailable to the plants. This was seen in July 1964 after a long period of very low rainfall. Some plants began to wilt, e.g. *Cirsium oleraceum* and *Taraxacum officinale* which had regrown after mowing of the drier types in June (Fig. 6). The critical suction is ca. 10 atms. for many plants, though it may be less for some hygrophytes. ELLENBERG (1939) found that *Athyrium filix-femina* in deciduous woodland wilted at 3 atms.[1] though most herbaceous plants of woodlands survived 5 or more atms.[1] After 5 atms. suction the curve of suction against soil water content became very steep, illustrating that after the soil had reached 5 atms.[1] only a slight decrease in soil water content rendered the water unavailable. Species growing on soils, whose maximum suction curve never exceeds 3–5 atms. may be considered as wet indicators.

The suction force is dependent on the physical properties of the soils. KØIE (1951) showed a linear increase in water percentage with increase in percentage of silt-clay of soils from woodlands in Denmark; WILCOX and SPILSBURY (1941)

[1] These atms. represent mean tensions developed in the local soil volumes around the roots in the field. They do not indicate the exact value of wilting tensions.

Fig. 6 The wilting of *Cirsium oleraceum* in the wet meadows after a period of drought (Buchau July 1964).

demonstrated that the wilting coefficient increased with increase in clay content. There was no close correlation between mechanical analysis and water content in the meadow soils investigated although the loss on ignition was linearly related to the water content, as was expected. In Fig. 7 the water contents at 5 atms. are plotted against the percent-loss on ignition for the soils from France and Switzerland. It was concluded that the water content and suction force were related to the humus colloids.

Investigations of the water in the soil revealed that there were seasonal changes in the water content of the top soil and seasonal changes in the water table. Despite large seasonal fluctuations in water content, from measurements of the suctions, it appeared that water was nearly always available to the plants. It is, therefore, correct to term these grasslands "wet" meadows.

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IV. Nitrogen relations

1. Methods

At each experimental plot a large number of soil samples were taken at about 5 cm depth. Initially the turf was removed and care taken that no organic litter from the A_{00} horizon was mixed with the sample. The samples were sieved in their natural condition through a 4 mm wire mesh to remove any roots, stones or gravel and then thoroughly mixed. A sub-sample was left in a plastic container in a hole in the middle of the experimental plot at the depth from which the soil had been taken (see ELLENBERG, 1964). It was recovered by the turf. This sample provided a control and it was possible to determine the changes in soil nitrogen after the soil had experienced the normal changes in micro-climate. Other samples were transported to the laboratory and their water contents, pH, contents of NO_3, NH_4, and P determined immediately. A quantity of each soil was kept in glass jars in a humidity chamber at 20 °C with RH. 98–99% for varying periods of time for further determinations of the accumulated nitrogen fractions. The glass jars were covered with sheet cotton wool, and normally the water content of the soil was maintained at its initial level. Samples were taken at approximately 3-weekly intervals throughout the growing seasons but less frequently during the winter months.

Soil extractions were made using a 1-percent solution of Potassium aluminium sulphate. The initial weight extracted corresponded to 5 gm of dry matter. This was calculated after the percent humidity had been determined by drying weighed quantities in an oven at 105 °C and the moisture was converted to the percentage of the dry weight.

Soil was analysed for nitrate content by the 2.4 Xylenol Method. To 5 ml of soil extract was added 1 ml O-Xylenol (1% in 30% acetic acid) and 15 ml 85% H_2SO_4. This was incubated at 40 °C, cooled, diluted and distilled. The vapour was condensed and collected in 20 ml 2N NaOH made to 100 ml and the resulting yellow colour measured in a photo-electric colorimeter at 433 mu with a blue filter. The readings were compared to standards.
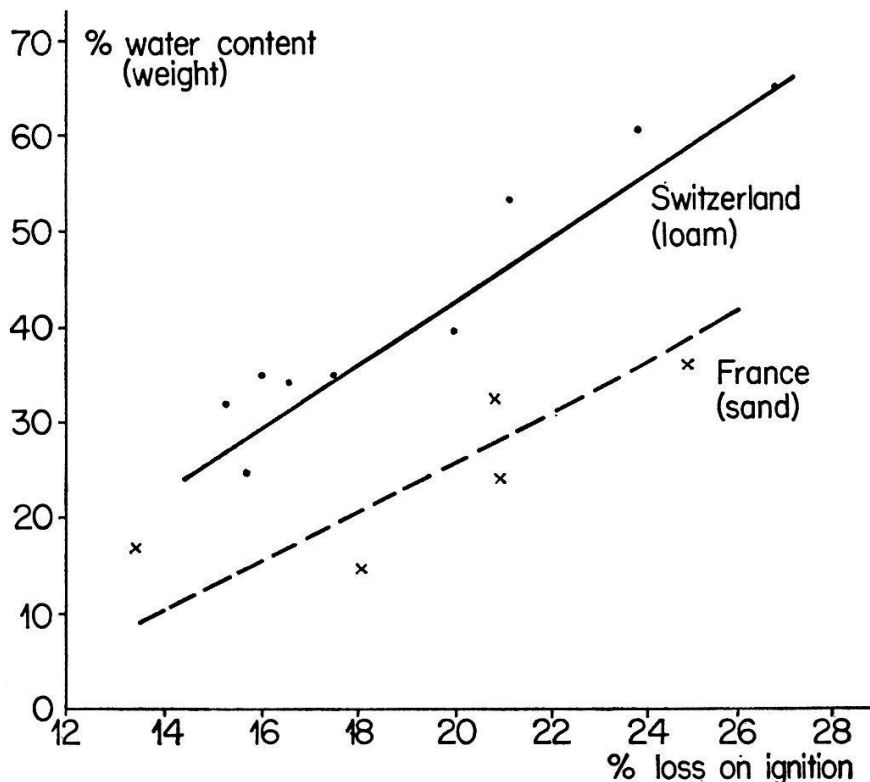

Fig. 7   The water content at 5 atm. and the % loss on ignition.

Ammonium content was determined by the Conway method using Conway dishes. In the centre compartment was placed 2 ml N/10 H_2SO_4, and in the outer 2 ml of soil extract was mixed with 2 ml of saturated K_2CO_3. The closed dishes were incubated at 40 °C and the H_2SO_4 was washed into a Nessler tube, Nessler's reagent added and diluted to a known volume. The resulting yellow brown colour was measured in a colorimeter at 431 mu with a blue filter and compared to standards.

Phosphorous content was measured by a modification of the ammonium-molybdate method, using 2.5-percent acetic acid for the soil extraction (see DENIGES, 1920, for original method). A blue colour developed after the addition of ammonium molybdate and stannous chloride reagents. The reaction relies on the molybdenum as ammonium phospho-molybdate in the presence of a suitable reducing agent giving a blue colouration. This was measured in an absorptiometer using a red filter at 650 mu.

pH was measured by means of a glass electrode. The soil was mixed with distilled water to a paste like consistency.

Sampling times are marked by vertical arrows on figures 2, 3, 4.

2. The seasonal course of nitrification

For simplicity the vegetation units were designated "wet", "typical" and "dry" since the floristic variations were closely related to the water relations. The nitrogen relations of the three experimental areas are discussed separately.

a. Swiss lowlands

(1) Soil water and pH

There were individual fluctuations in the curve for each plot and these did not always correspond between plots. The curves showed the same yearly trends, i.e. in spring the soil water was low, this rose in the summer, fell again August–September, and then remained high until the middle of January before falling again to the low spring values. In the spring of the second year the soils were noticeably drier than in the first period. All plots showed a great seasonal fluctuation, although plot S 6 and the *Arrhenatheretum* S 10 varied least. The slope meadows showed the same seasonal trends.

Only roughly could this pattern be related to the precipitation (Fig. 2). This was accounted for by the different soils with varying water holding capacities, degrees of porosity and run-off. The normal pattern of precipitations shows the period May–August to be the wettest with a maximum in June and July. During these months soil moisture was higher than in the drier months of early spring. In winter the mean precipitation per month was only circa one third of that of June, yet the soil moisture of the plots was maximum at this time. Much of the water was in the form of ice. It was concluded that the precipitation during the winter half of the year did not influence the soil moisture a great deal, but it had a dominant effect during the summer half of the year. The small differences between soils at any one sampling time must be related to the precipitation of several days previous to sampling and other factors such as the porosity of the soil, evaporation, degree of development of the vegetation, etc. This was demonstrated by the samples taken from plots S 3 and S 4 at the beginning of July. The

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soil of plot S 4 had a more compact structure, though the two plots supported a similar vegetation and they received a similar amount of rain. Plot S 3 had already been cut and the surface was more open to forces of evaporation, whereas plot S 4 had not been cut and the rain water was retained. Another example was shown by plots S 8 and S 12 with the second sample. At this time there was a sharp drop in soil moisture compared to the other plots.

pH also showed seasonal changes. Values were highest during the winter and were lowest during the late summer and autumn. This trend is caused by the influence of the ground water which in all plots had a high pH (see ELLENBERG, 1939 and 1958). Plot S 12 showed the greatest fluctuations but this was due to the lateral water movement on the slope.

(2) Nitrogen at sampling time

The inorganic nitrogen in the soil is present as ammonium and nitrate ions. These at any one time represent the balance of gains and losses and they cannot be used as a measure of the nitrification. Measurements of the quantities of these ions were necessary to obtain the increase or decrease in the nitrification experiments and to determine any apparent changes caused by fertilisation.

Nitrates were usually present in all plots but were in lower amounts during the winter (except in February). The quantity present was always less in the wet vegetation plots and reached zero values in the winter. The quantity of nitrates showed peaks during the April–May, July–August, a large one in September and the largest in February. Despite great differences the September maximum was present in all vegetation types, except plots S 6 and S 3. This may have been due to the sampling frequency. In the slope vegetation the seasonal variations were poorly marked and there were few differences between the *Arrhenatheretum* (plot S 12) and the dry vegetation plots.

Ammonium was present in less quantities than nitrate and although present in low quantities during the summer was always present during the winter. It was seen that in many cases when nitrate content was high ammonium content was low and when nitrate content was low that of ammonium was higher. In one of the wet vegetation types (plot S 3) ammonium reached high values during the winter. These seasonal variations in the proportions of NH_4 and NO_3 are well shown in Fig. 8. The sample taken during July possessed nitrate and ammonium present but not to the exclusion of one.

The seasonal variation in mineral nitrogen content appeared to be a property of the soil and was little influenced by fertilisation. Any nitrate present must be produced by nitrification or is artificially added as fertiliser. The proportion of nitrate to ammonium depends on (1) the rate of nitrification, (2) the uptake of nitrates by the plants and (3) loss of nitrates by leaching. The meadows are normally fertilised during the winter (December–February), spring (ca. April), then after cutting—in the dry types around later June and again in early October. It was noticed that when soil was analysed a few days after fertilising no excessive amounts of nitrogen were present. It was concluded that the nitrogen

added was rapidly used by the plants. It was difficult to relate the seasonal fluctuations of nitrate and ammonium content to the fertilisation. In some plots peaks of nitrate content corresponded to fertilisation, but the same peaks were present in other plots which were not fertilised until later. The amount of ammonium present during the winter may have been increased by winter fertilisation, but the ammonium level slowly rose from the onset of the colder weather and began to fall when fertilisation occurred.

The most important factor appears to be the amount of leaching of the nitrate ion. The nitrate is not leached when the soil is frozen and this emphasises that fertilisation during the winter may favour the natural denitrification. During periods of heavy rainfall nitrate, which is a labile ion, is washed downwards, although well-structured loams and clays can hold some of the nitrates against leaching due to their good crumb structure. In Fig. 8 the precipitation for 30 days preceding sampling is plotted. Rain is known to affect the mineral nitrogen since drying and then rewetting a soil tends to cause a flush of decomposition and mineralisation. There appeared to be some agreement during the summer in that with heavy rain nitrate was lost. The loss during winter when the rainfall was low and the nitrate content low may have been due to denitrification. The soils were very wet during this period and reduced aeration would favour denitrification and the accumulation of ammonia by ammonification. Freezing during the cold period kills many small roots and this results in ammonification of the proteins now available. The sharp increase in soil nitrate and fall in ammonium during February was probably an effect of short periods of favourable weather alternating with cold ones. JOHANSSON (1944) showed two maxima in the ammonium content of the soil, one in December and the other in July. In these wet meadow soils the maxima were in December and April–May, with small variations during the summer related to weather conditions. WAKSMAN (1931) suggested that "a slight freezing of the soil may have the same stimulating action as air drying, etc., in other words, shifting the soil equilibrium, so that a more rapid multiplication of bacteria may take place". This would explain the large increase of nitrates in February.

The fluctuations in mineral nitrogen are of importance to the plants. VAN DER PAAUW (1962) found correlations between the amount of rainfall during the winter months and the nitrogen response of crops and demonstrated that it was due to leaching of nitrogen. He quoted leaching as 0.25–1.25 kg N/ha/mm rain. FISHER (1924) found negative correlations between rainfall at different times of the year and cereal yields, the negative effect being maximum in December and January. This was attributed to unequal rates of nitrogen leaching. It must be expected that in the soils of the wet meadows, which are very wet in winter, there will be considerable migrations of nitrate under the influence of the water regime, as found in other soils by HARMSEN (1961). Ammonium is fixed by the humus substances and therefore it remains chiefly in the uppermost layers of the soil and only moves when converted to nitrate.

The general trends in nitrate content ran parallel in the different vegetation
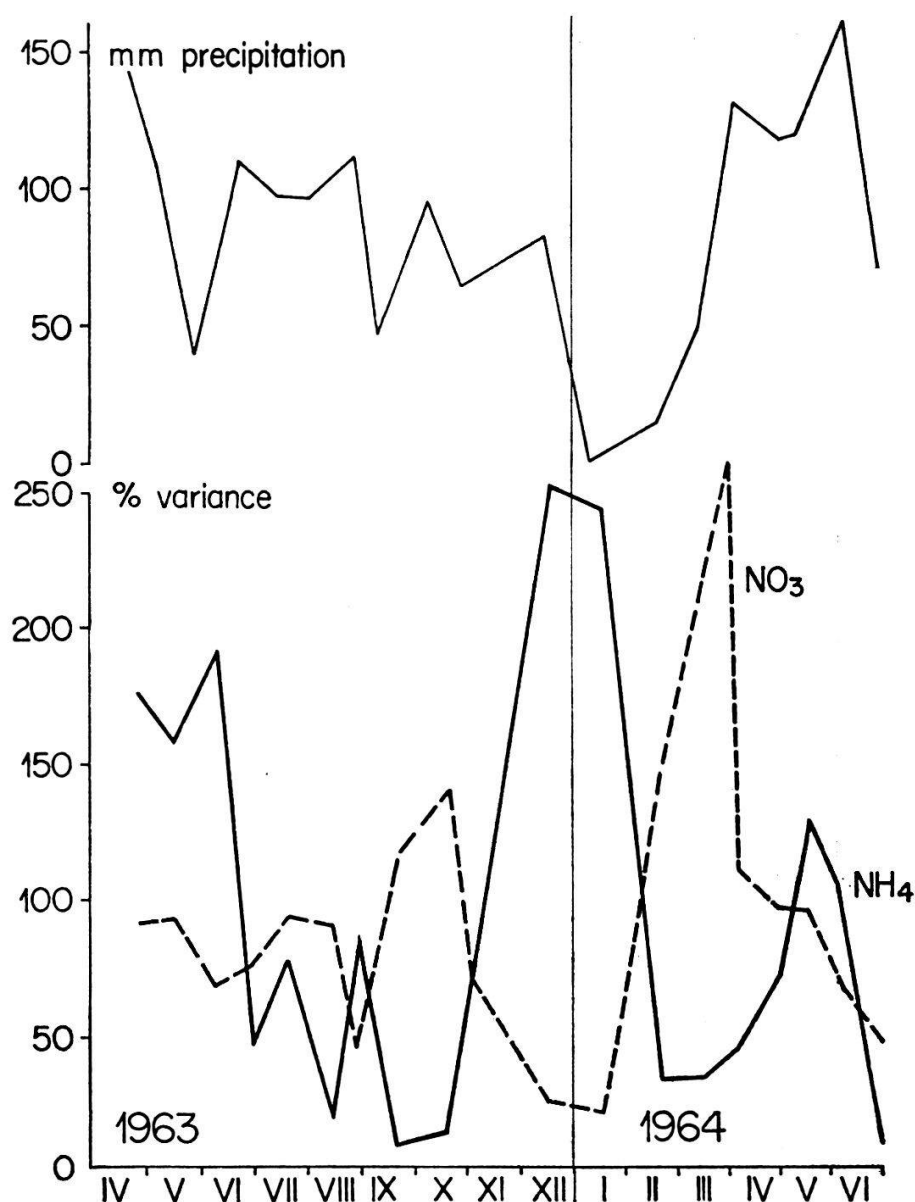
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Fig. 8 The nitrogen present at sampling in the field plots in Switzerland. (Curves represent the mean of all soils and are expressed as the % variance from the mean over the experimental period.) The upper curve shows the precipitation for 30 days prior to sampling.
Standard errors: $NO_3 = 37.5$ $NH_4 = 18.0$

types but with some time differences. Ammonium content fell when nitrate rose in most cases, although the samples S1 and S7 for the dry vegetation type showed high levels of both together. The fluctuations in actual amounts in the wet vegetation plots were small and these results were difficult to interpret owing to the great influence of soil water in these plots. In plot S3 there were large amounts of ammonium present throughout the winter, due to the fact that the meadow was not cut in autumn as usual, and there was consequently much litter present conducive to ammonification. Plot S2 which was shown to be a drier plot than S1 produced a larger quantity of nitrate in February. This could be accounted for by less leaching.

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Many of the observed differences must have been due to sampling. RUSSELL (1961) states that the nitrate content varies throughout the season and even from hour to hour. He quotes that values of nitrates present in a fallow soil and the general pattern was very close in the meadow soils of Switzerland. JENNY (1941) plotted the variability of total nitrogen at 0–21 cm depth in a virgin prairie. Samples were taken at intervals through the grassland and the variability showed a widespread Gaussian distribution. The variation was much less in adjoining arable land, where the value of "h" in the Gaussian distribution equation was 0.61 compared to 1.30. Despite the local variation the meadow soils showed a seasonal pattern in the nitrate and ammonium contents.
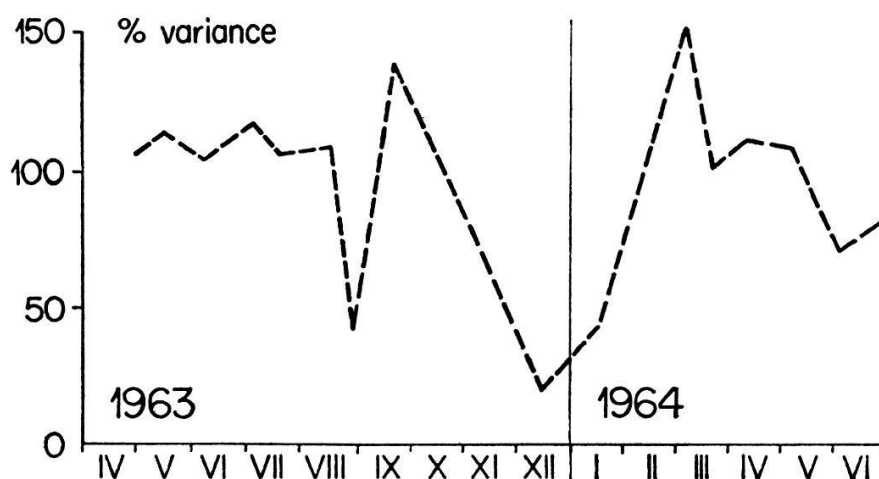

Fig. 9 The nitrification under controlled temperature conditions of the experimental areas in Switzerland.
S.E. = 7.6

Note: Figs. 9–23. The data are expressed as the % difference from the sample means.

(3) The capacity for nitrification

The pattern of nitrification under controlled conditions showed marked differences between the vegetation types. In all cases there was low nitrification in samples collected during the winter (Fig. 9). In the wet types activity was lowest for the longest period (October–January), of short duration in the typical (December–January) and only marked in December in the dry. This observation was consistent in all plots. It was concluded that the bacterial activity was limited by some factor operating especially in the wet types. This was probably water limiting aeration. The wet vegetation plots also showed a marked correlation with soil water content. When soil water content increased the nitrification decreased. This relationship was not close in the other vegetation types although present in some cases in plots S7 (typical) and S9 (dry). In a wet soil an inverse relationship between nitrification and water content would be expected since high soil water content lowers the aeration, and the microorganisms responsible for nitrification are strictly aerobes.

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Apart from the gradation between the vegetation types of the length of time during the year that the soil showed a capacity to nitrify there was a gradation in the amounts produced. Soils from the typical vegetation plots accumulated up to twice the amount of nitrate that soils from the wet plots produced and the dry plots produced up to six times that of the wet. Quantities were similar in the dry vegetation types and in those of the *Arrhenatheretum*. Soils of the same vegetation variant had similar seasonal variation in the nitrification under controlled conditions, except for the wet plots which showed large variations. For the two wet plots from the slope meadow the curves were parallel but the nitrification was reduced in the wetter one from the base of the slope. These represented the wet vegetation variant but the close correlation between the soil water content and nitrification was not so obvious as the four other wet plots (S1, S2, S3, S4). Nevertheless, these two plots demonstrated how important water was as a factor controlling nitrification. Plots S3 and S4 from the same site but possessing different water relations showed that the drier plot tended to produce more nitrate under controlled conditions.

The mean potential nitrate accumulations for the four vegetation variants are plotted in Fig. 10. The seasonal periodicity was well marked. In the most fertile soil, the *Arrhenatheretum* (Fig. 10d), there were large maxima in summer, autumn, winter and spring. It is probable that the two small maxima in March and May were conditioned by weather factors and represent one spring peak. The largest peaks were those in June–July and September–October. In the dry types the same peaks were present, but their main maximum was in September (Fig. 10c). Similarly, the typical variants showed the same four maxima though they were not so marked and they were all similar quantities (Fig. 10a). In the first part of 1964 there were some variations in one of the plots (S8) where the peaks in winter and spring were not so clearly distinguished, although in S6 and S7 these were well demarcated. During the early part of 1964 there were exceptional weather conditions in that the winter of 1963–64 was extremely dry. Although the wet meadow soils showed high water contents, the evaporation at the soil surface differed from the normal for that time of the year. The spring maximum tended to be slightly earlier in the dry types and this could be related to an interaction between the temperature and the water regime of the vegetation types. The winter maxima may result from sudden bursts of freezing affecting the bacterial population, and when the warmer weather starts there is a slight time lag before the spring maximum. This time lag was least in the more fertile plots and the longest in the poorer plots. The mean minimum temperature during February was only just below freezing point and this rose rapidly in March and April (Fig. 2). Soils of the wet types varied greatly between plots, e.g. plot S2 showed all four seasonal peaks, but the spring and sommer ones in 1963 were not so clear due to the lateness of the spring maximum, and there was a large winter peak, emphasising the lower water regime compared with plot S1 where this peak was suppressed. Variation in plot S1 in 1963 was conditioned solely by water which masked the seasonal effect. Plots S3 and S4 showed all four
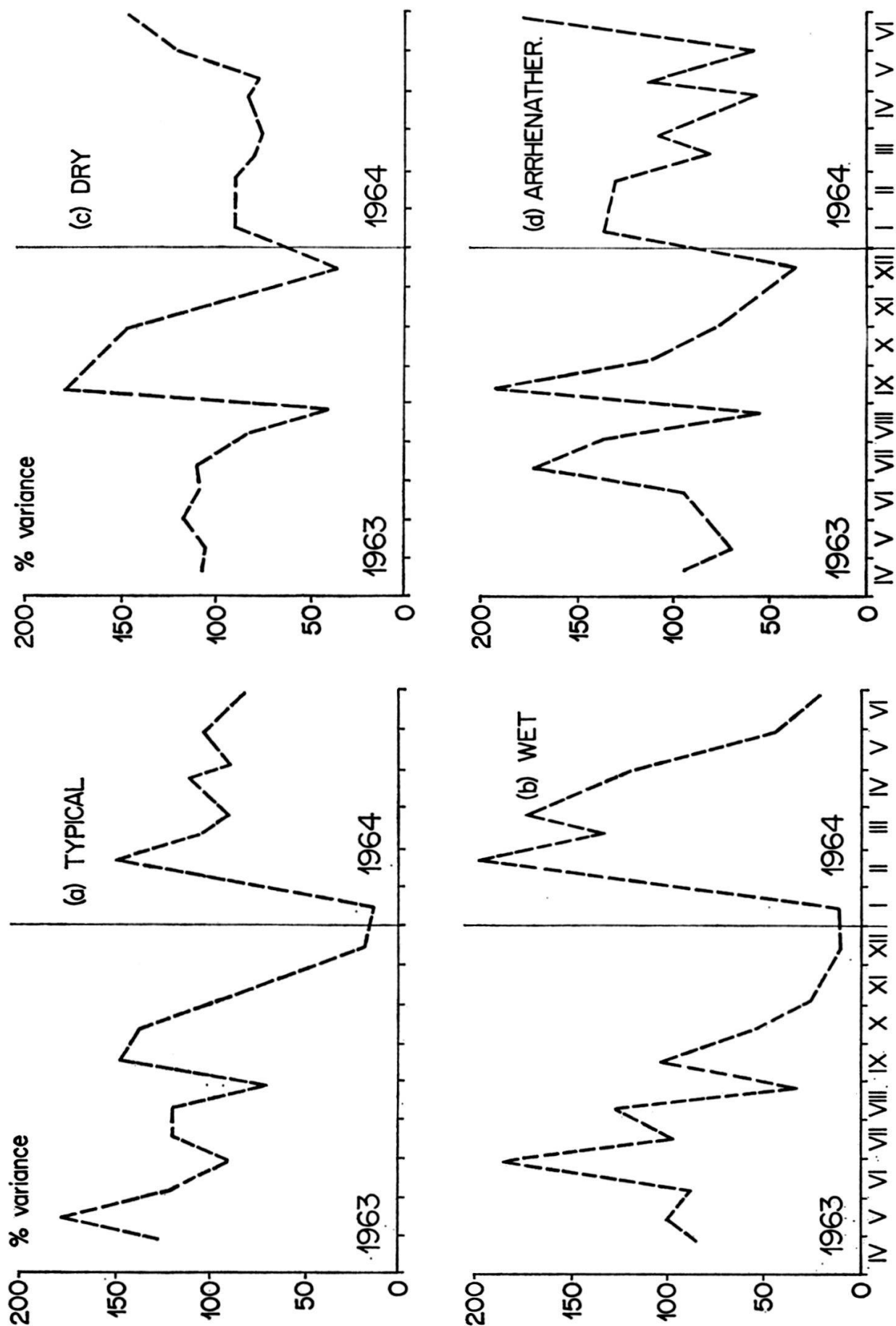
Fig. 10 The nitrification capacity (under controlled conditions) of the vegetation variants from Switzerland.
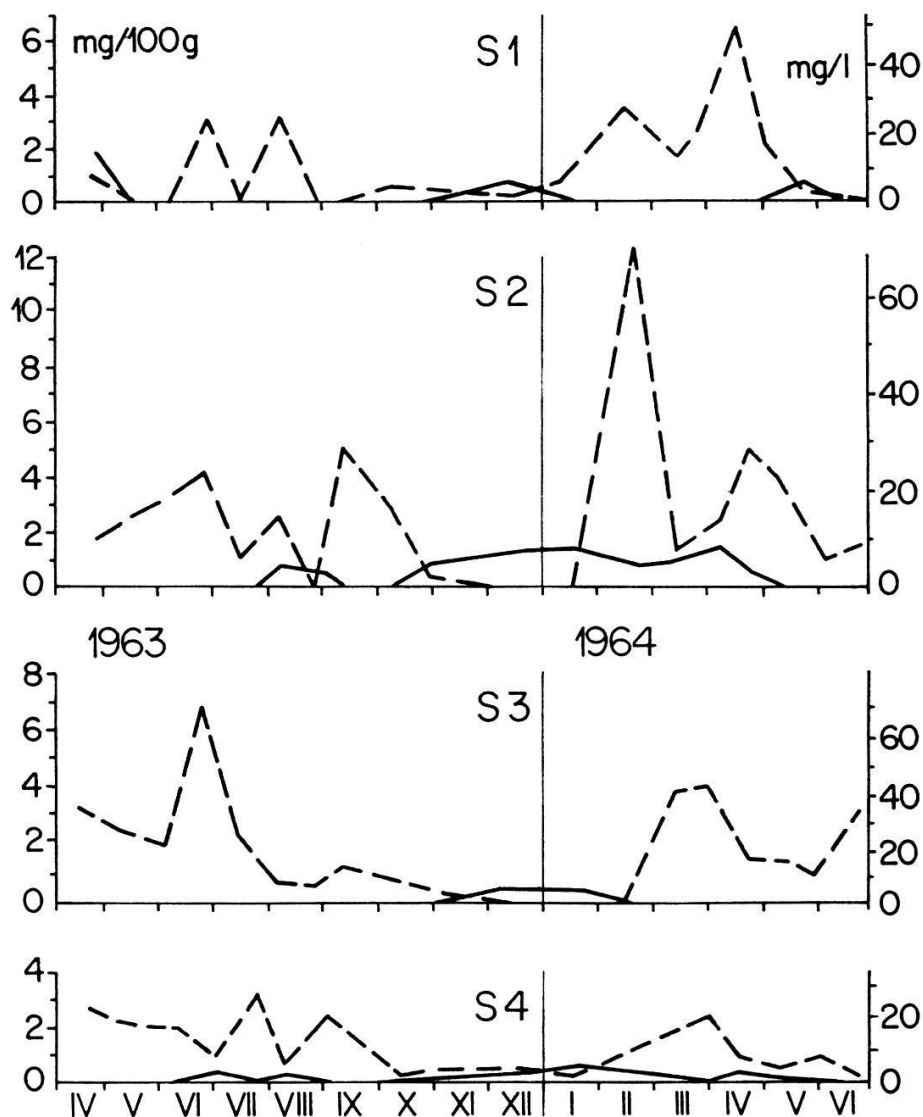S.E.: a) = 12.4   b) = 12.7   c) = 8.4   d) = 12.0

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Fig. 11   Nitrogen relations of soils from four plots after incubation (see text).
Values are plotted on the time scale for the date of sampling.

peaks (Fig. 11). In the wet soils, in general, the spring maximum was the most important. The two slope plots were also conditioned by the water factor.

Ammonium was not always present after incubation under controlled conditions. It was present in samples taken during the winter and in some cases when nitrification was low at other times of the year. There was non present in soils from the dry vegetation plots (although present in soil from the *Arrhenatheretum*). Soils from both the typical and dry vegetation variants showed that ammonium was unimportant in relation to nitrate, and probably its presence marked decomposition of organic matter during incubation. This may be catalysed by the presence of nitrates which appear rapidly under these conditions due to nitrification. In only one wet vegetation sample did ammonium appear to play an important role (plot S2).

The peaks of nitrate present in the field could be related to the peaks in the nitrification capacity, but in each case there was a time lag.

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(4) Nitrification in the field

The relationship between nitrification and moisture regime seen in the soils of the wet vegetation variants when incubated in the laboratory, was present in all plots when the nitrification was measured in the field. The water did not immediately affect the nitrification—in most cases there was a slight delay before increased water content influenced the nitrification. This was maybe a temperature effect. The rate of nitrification was slower than under controlled conditions where the samples were maintained at a constant temperature which favoured biochemical changes. Although the water regime modified the seasonal variations, it did not obscure them.

The pattern of nitrification in the field followed that in the laboratory, but the increases and decreases in nitrate accumulation were less (Fig. 12). The seasonal maxima of nitrate production were more marked because in the samples which possessed a low nitrification capacity, nitrification in the field was proportionately lower. When the seasonal nitrification in the field in the different vegetation variants was plotted, the seasonal peaks of nitrate production were made more obvious by the low values of production approaching zero.

Temperature played an important role as a factor controlling nitrification in the field. During the cold winter months nitrification in the field was depressed. This followed the observed temperature lower limit of 5 °C, below which nitrification is limited. This limit was observed by RUSSELL and APPLEYARD (1916; in arable soils) who concluded from the interrelations of the CO_2, bacterial numbers and NO_3 in the soil that temperatures lower than 5 °C limited biochemical processes. The same thing was demonstrated by ELLENBERG (1964) in *Aceri-Fraxinetum* and *Luzulo-Fagetum* and other Swiss woodland soils. Since they are biochemical oxidations that are restricted presumably there is an upper
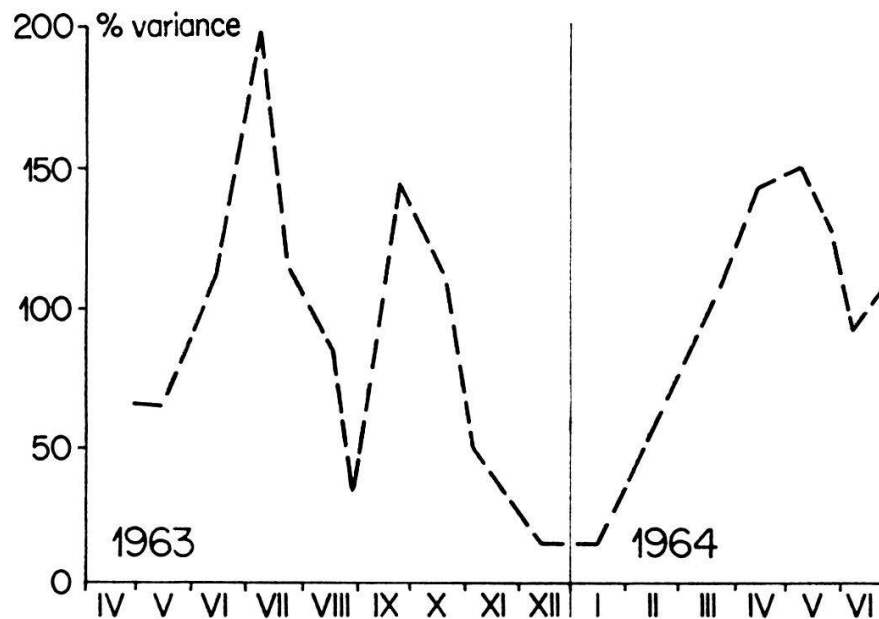

Fig. 12 The nitrification in the field of the experimental areas in Switzerland.
S.E. = 11.0
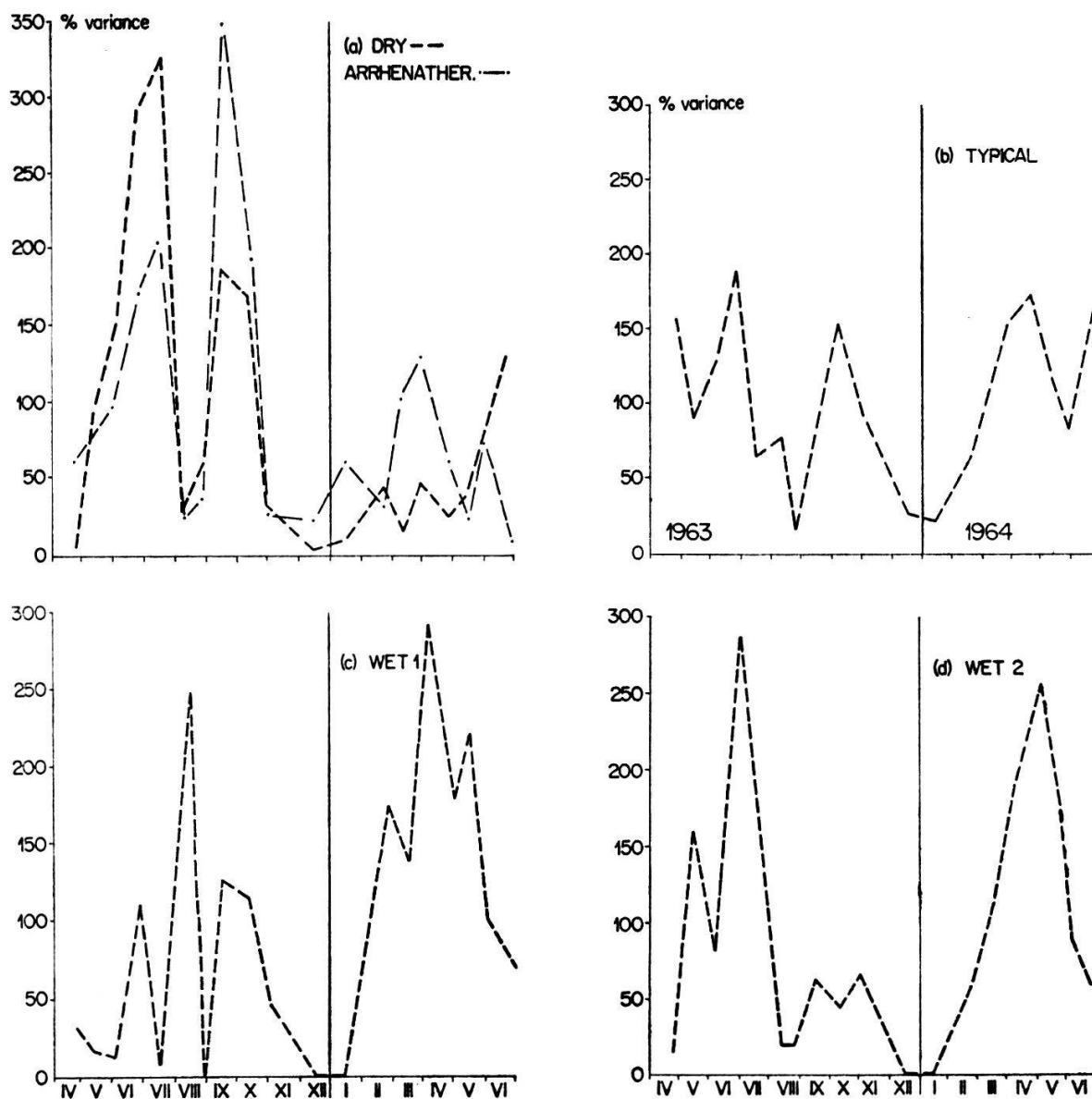
Fig. 13 Nitrification in the field of the vegetation units from Switzerland.
S.E.: a) dry = 18.2, Arrh. = 21.2   b) 12.0   c) 20.8   d) 18.7

temperature limit of ca. 35° though this hardly pertains to field conditions in Central Europe. Due to the low temperatures the seasonal maxima of potential nitrification were modified in that the winter peak was greatly reduced and more or less absent, and that nitrate accumulation there was merged into the spring peak. As under controlled conditions nitrification was greatest in the dry vegetation types, intermediate in the typical and lowest in the wet, and there was a similar gradation between the vegetation types in the time that the soils showed nitrifying activity.

There were two apparent patterns in soils from the wet plots. Some plots produced nitrate accumulation approaching that of soils from the typical plots (e.g. Fig. 13), but others only had peaks of nitrate production in spring and summer and the nitrification in autumn was low (Fig. 13 b).

Comparisons of nitrification in soils of the different vegetation variants pointed to differences not only in their potential nitrification but parallel differences in the actual nitrification in the field despite the modification of the basic pattern by both temperature and moisture.

When the nitrogen status of the vegetation variants was compared, the N value (calculated from the presence of plants in the stand with varying degrees of nitrogen requirements) was representative of the nitrogen relations in general. The plots with a higher N value were more fertile and accumulated the largest amounts of nitrate in the field and in the laboratory (Table 18), though this relation is obviously not very close. The mean value of nitrate-nitrogen present at sampling in all cases was ca. $\frac{1}{2}$ the mean value of nitrate produced experimentally by nitrification in the field.

Table 18   Comparison of the nitrogen status of the different types: Switzerland
(Values given as mg/litre of soil. They represent the mean of all the samples for the individual soil)

Vegetation type	Plot No	Nitrogen at sampling (mg/100 g soil)			Nitrification		N Value of vegetation[1]
		NO$_3$–N	NH$_3$–N	Total	lab. NO$_3$–N	field NO$_3$–N	
Wet	S 1	5.02	2.59		10.61	5.68	3.19
	S 2	2.60	2.90		16.00	4.04	3.80
	S 3	20.80	7.28		19.76	7.46	2.63
	S 4	4.10	1.64		11.14	6.98	2.37
	mean	*8.13*	*3.37*	*7.00*	*14.38*	*6.04*	*2.99*
Typical	S 5	6.28	2.18		31.26	16.40	3.21
	S 6	2.76	1.77		21.09	11.23	3.50
	S 7	12.17	3.00		46.09	18.48	3.00
	mean	*7.07*	*2.32*	*9.39*	*32.81*	*15.37*	*3.24*
Dry	S 8	6.72	2.67		66.93	14.12	3.13
	S 9	18.80	0.82		76.32	22.89	3.14
	mean	*12.76*	*1.75*	*14.51*	*71.63*	*18.50*	*3.13*
Arrhenatheretum	S 10	8.80	2.10	10.90	57.11	28.74	3.84
Slope	S 11	2.04	0.38		18.07	4.89	2.90
	S 12	2.09	0.37		22.58	5.26	2.64
	mean	*2.06*	*0.38*	*2.44*	*20.33*	*5.08*	*2.77*

b. Alsace, France

(1) Soil water and pH

The soils from Alsace differed from those of the experimental plots in Switzerland in their mechanical composition. Some of them were sandy and therefore

[1] See page 76

the rate of percolation was greater and their retention of water less if humus content remains the same as in others (Table 11). The water contents of the soils showed seasonal variations. They were wettest during the winter, October–February, and showed two periods of increased wetness in June–July and August–September of the first season and April of the second. The samples were started in April of 1963 and also at this period they showed a slightly wetter condition. These seasonal changes showed a marked correlation with the precipitation, the soil water content rising after heavy rainfall (see Fig. 3). It was striking that the soil water content (though not the available water) varied less than in the mineral soils from Switzerland. During the winter however, soil moisture content was unrelated to rainfall. This was due to the fact that the colder temperatures reduced evaporation and the lateral and downward movements of water were reduced. During periods of frost the water was immobilised as ice cementing the soil crumbs together. Frost normally extended well into the soil profile. Despite the lack of heavy precipitation during the winter of 1963–64 the minimum levels of soil water in late winter-spring were not extremely low and the values for April for both seasons were similar. In the mineral soils the low winter precipitation and the warmer spring temperatures had a drying effect on the soil which lasted through spring of the second season.

In all the soils pH was high due to their content of $CaCO_3$. The pH rose during the periods unfavourable to growth (October–February) and fell during periods of active vegetative growth. During the wet periods pH rose, and it fell when the soil water fell, like in the Swiss soils. This was due to the vertical movement of bases in the soil water. The causes of pH fluctuations are very complex and extremely difficult to interpret (see ELLENBERG, 1958). The soil water and pH values during late winter probably represented nearly maximal values. At this time there was some flooding in wet and typical plots. This was topographical and was related to the flatness of the old terrace of the Rhine which was low lying in relation to the surrounding country.

(2) Nitrogen at sampling time

The changes in the relative quantities of nitrate present on sampling showed similar trends in all plots. During late spring and summer, nitrate was nearly always present even if in low quantities. There was a large increase in September and October, but the nitrate was no longer present in December and remained at very low levels in the typical and dry vegetation plots, and at zero in the wet, until the following spring when there was an augmentation. The quantities of nitrate in soils from the typical and dry variants were greater than in soils from the wet. In the dry plots there were additional increases in July–August and in February. In the typical plots the augmentation of nitrate in February was present, but at a lower level. In the wet plots autumn and spring maxima were apparent, but for some reason there was a slight peak in July of 1963. In all plots the amount of nitrate present at any sampling time was not directly cor-
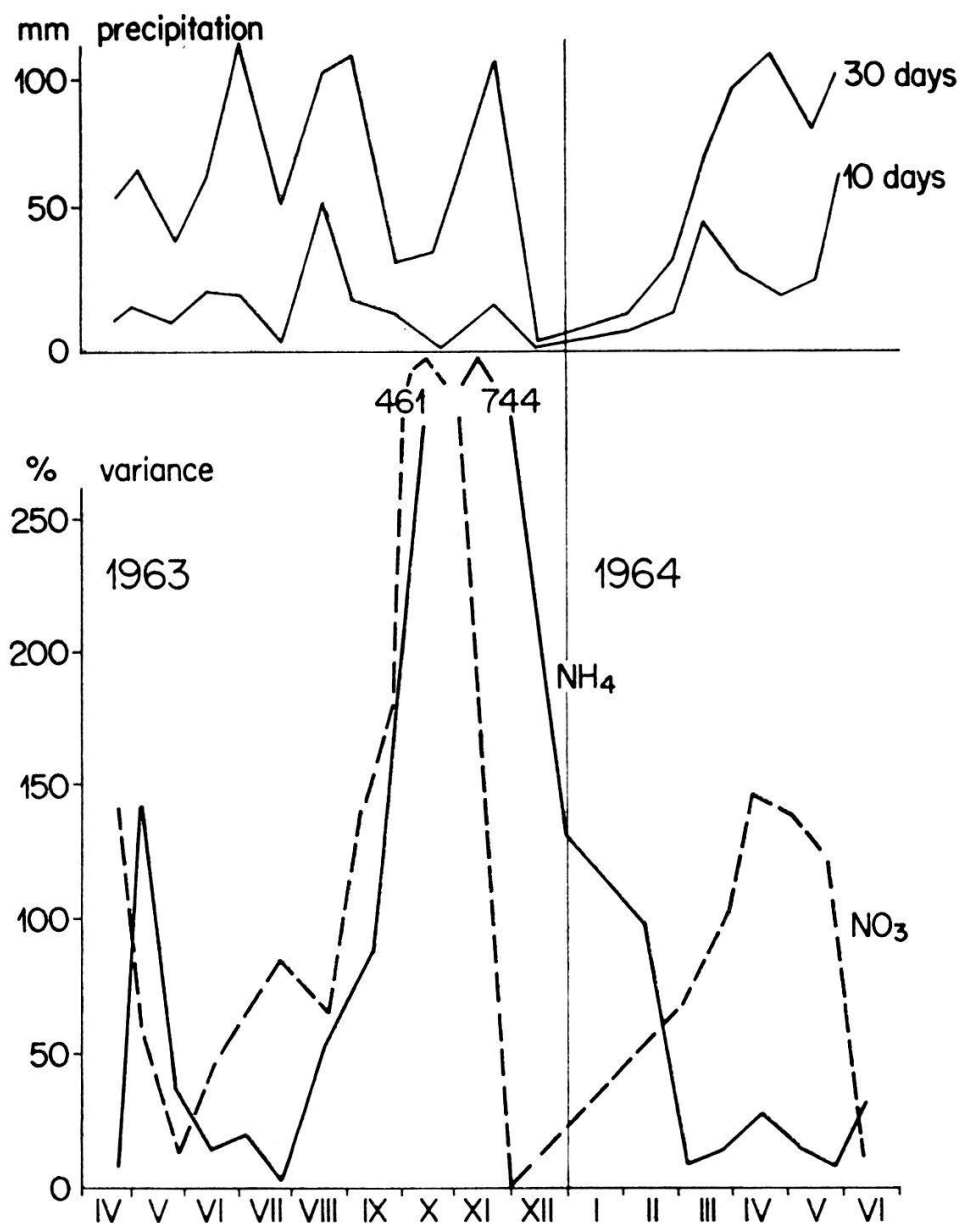
Fig. 14 The nitrogen present at sampling in the field plots in France, and the precipitation for 10 and 30 days prior to sampling.
S.E.: NO_3 = 22.3 NH_4 = 47.9

related to the fertilisation. It was obvious that the nitrogen added was rapidly used by the plants.

Ammonium was present in high amounts during the winter period. The occurrence of ammonia coincided with the fall of temperature which began in September (see Fig. 3). Ammonium did not persist at high levels throughout the cold period and in the more fertile plots (F4–F9) had fallen rapidly by January and persisted only as traces until March. Ammonium appeared earlier in the wet plots (F1–F3) and persisted at higher levels than in the more fertile. During the rest of the year ammonium occurred during the periods of heavy precipitation. Ammonium persists in the surface soil since it is not usually susceptible

to leaching although a little may occur in sandy soils. The concentration of ammonium was not always high when that of nitrate was low. During autumn they were both present in high quantities. The maxima of ammonium content during May and December occurred when the level of nitrate was low (Fig. 14). The smaller seasonal concentrations of ammonium in June–July and in April when nitrate concentrations were high were due to the water conditions at those times. It seemed that the importance of ammonium in the community during autumn was greater in sandy soils (cf. Switzerland). The ammonium in autumn probably represented mineralisation of litter.

The quantities of mineral nitrogen present as nitrate-nitrogen and as ammonium-nitrogen were greatly affected by the water regime of the soils. This was influenced by the precipitation except during the winter. In Fig. 14 the precipitation that the soils received in 10 and 30 days prior to sampling was plotted. The quantity of water reaching the soil only a few days prior to sampling appeared more important to the presence of mineral nitrogen, but this correlation was not so obvious as in the mineral soils. This was accounted for by the more rapid movements of the soil water in the sandy loams, with consequent vertical migrations of the nitrate ion. The low values of nitrate-nitrogen during the winter were probably due to flushing away of the nitrate when the soil moisture and water table were high. Ammonium which accumulated during this period remained due to its adsorption onto the humus colloids.

(3) The capacity for nitrification

The potential nitrification (measured after incubation for 6 weeks in the laboratory) changed throughout the year. As in the mineral soils from Switzerland the soils from wet vegetation plots showed the longest period of inactivity. In all plots nitrification was reduced in soil sampled during the winter (Fig. 15).

The wet plots produced maxima in nitrification capacity in July, September–October, a small one due to water in late winter, and another in May–June. The greatest potential activity was in summer and autumn. Similarly four maxima were present in soils sampled from the typical vegetation. These were in May, July, September, January, then April of the second season. The periods of maximum nitrification capacity mostly produced similar quantities of nitrates in any one plot in the different seasons, although the spring peaks were the lowest. The seasonal maxima of nitrification in the typical plots were similar to those in the dry, although the autumn peak appeared to predominate. In the dry plots, with the most fertile soils, the winter peak of potential nitrification was much larger than that in soils of the other vegetation variants (Fig. 16). These variants showed a gradation in the amount of nitrates accumulated; the quantity increased with increasing fertility, i.e. from the wet types, through the typical, to the dry types. The typical vegetation variants were intermediate between the two extremes. It was noticeable that the differences between the potential nitrification of the typical and dry variants were not so clearly separated as those found in the mineral soils. For the sandy loams the differentiation
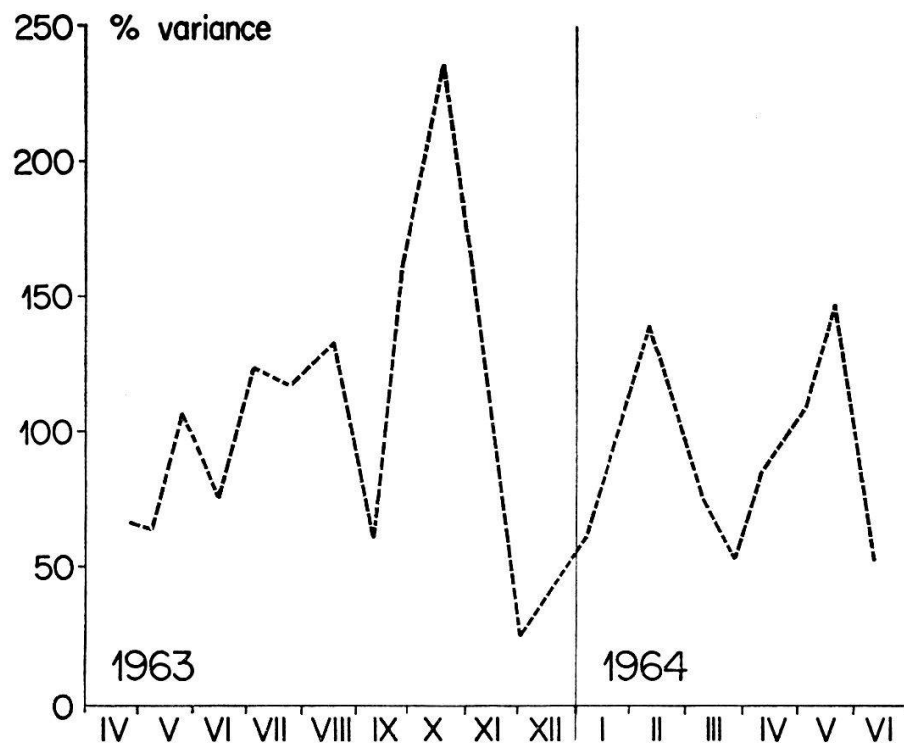
Fig. 15 The nitrification under controlled temperature conditions of the experimental areas in France.
S.E. = 10.8

in the pattern of nitrification capacity in the three vegetation variants was more clearly marked when the production of nitrates was considered as mg/l of soil.

Under controlled conditions ammonium was present after 6 weeks incubation during the periods of low nitrate production. This was obvious in soils samples during the winter. In soils from the dry plots ammonium was less important.

Unlike the mineral soils water contents and the nitrate production in the laboratory were not closely correlated.

(4) Nitrification in the field

The periodicity of nitrification in the field followed that in controlled conditions (especially in the more fertile plots), with the maxima and minima of production coinciding in all plots. As in the mineral soils, the capacity to nitrify which was present in late winter was restricted in the field, although some actual nitrification occurred in the field in the drier vegetation plots. The suppression of nitrification during the winter months was due to temperature limiting the bacterial activity (Fig. 4). Normally during this period of the year the capacity to nitrify was low but this was depressed even further by the cold temperatures (see Fig. 3). Consequent to this reduction of the winter peak of nitrification, the soils in the field only produced three periods of high actual nitrification—July, September and May. The periods of minimum nitrate production were most marked in the wet plots, but less so in the dry plots. The soils from the dry plots produced irregularities in the seasonal rhythm of nitrification, because there

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was a small peak of nitrate production in August between the normal peaks of production in early summer and autumn. The typical plots showed this also, but not the wet plots (Fig. 18). In this period soil water was high and the fall in the nitrification in September was probably a lag effect of frequent rainfall in August. This would mean that the peak in August represented the beginning of the large autumn peak which with the spring one of April–May was the most pronounced. This irregularity was also present in Fig. 15. The wet plots demonstrated that the autumn peak was the most pronounced in this vegetation variant. Of less importance was the peak in spring (in amount of nitrification). The summer peak also reached high levels of nitrate production.

Actual nitrification in the field showed that the two extreme vegetation variants (the wet and dry) were related by an intermediate type (the typical).

There appeared to be no clear inverse relationship between the water content and the nitrification. The highest concentration of nitrate present at sampling often tallied with the highest nitrate production by nitrification in the field. The peaks for nitrification represented values obtained after 6 weeks storage and a time lag would be expected. The data are plotted as net increase in nitrate, i.e. final amount minus initial nitrate content, and they brought out the point that
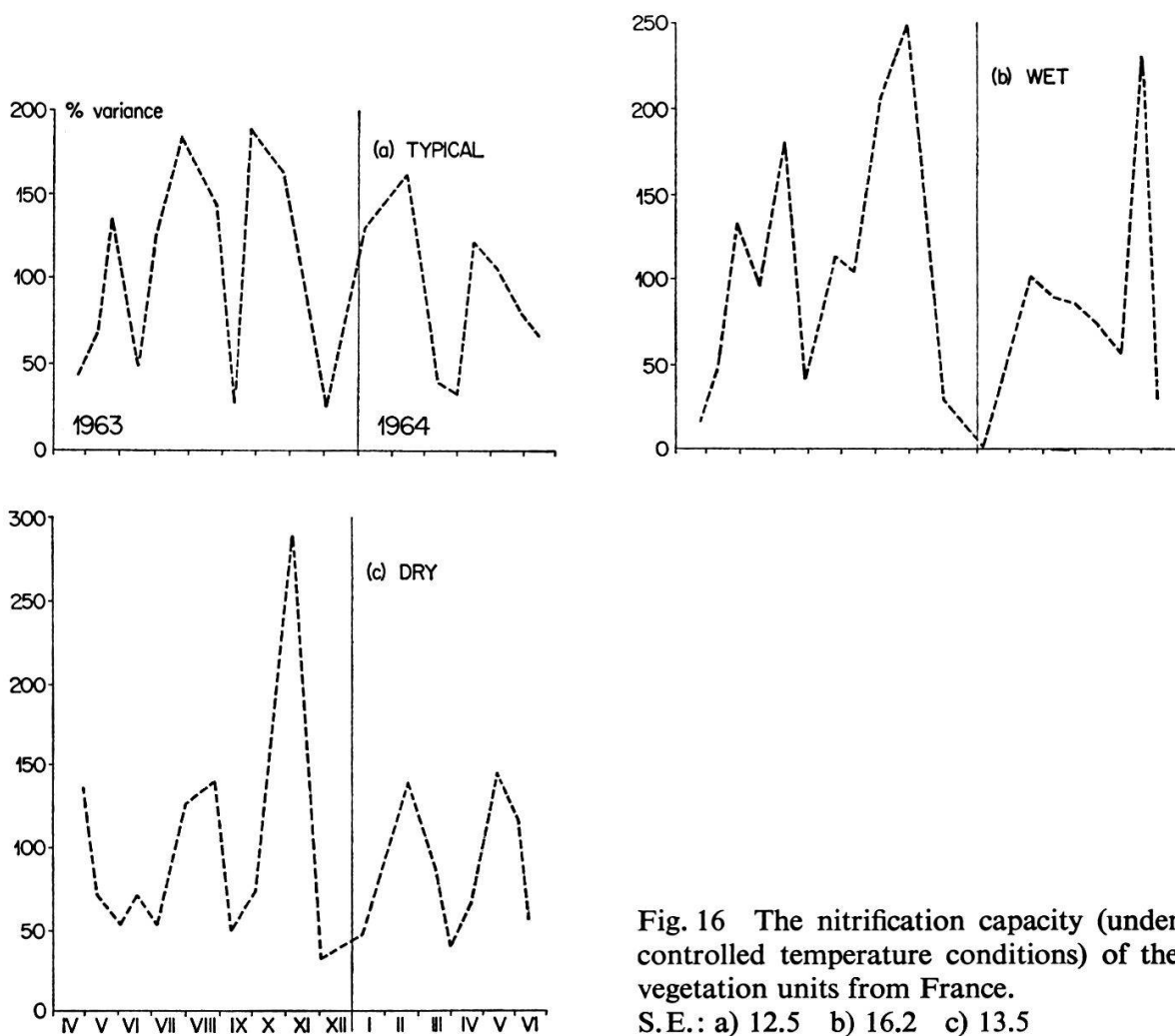

Fig. 16 The nitrification capacity (under controlled temperature conditions) of the vegetation units from France.
S.E.: a) 12.5 b) 16.2 c) 13.5
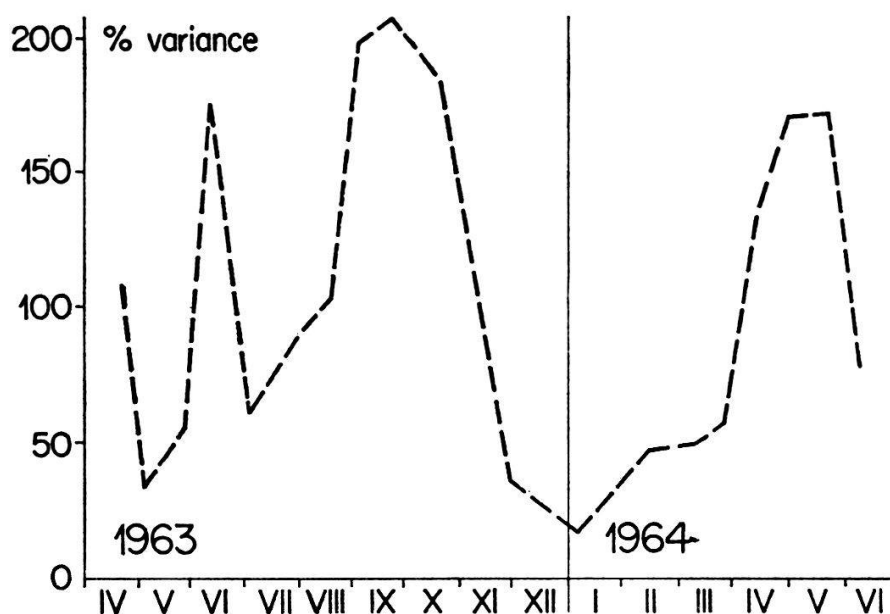
Fig. 17 The nitrification in the field of the experimental area in France.
S.E. = 13.8

in a sample showing high initial nitrate content nitrification was high and had probably been going on in the field prior to sampling.

The individual plots of the same vegetation variant varied in a similar way in the relations between potential and actual nitrification. Differences were to be expected since each plot in the field experienced its own individual microclimate.

A comparison of the nitrogen status of the vegetation plots produced increases in N at sampling and in potential and actual nitrification from the wet to the dry types. The correspondence with the N value of the plant communities was not good because this value was similar for the typical and dry plots. However, the capacity for nitrification in these two vegetation variants differed by ca. 50% and the actual nitrification by nearly the same amount (Table 19). The mean quantity of nitrate present at sampling approximated roughly to half of the mean nitrate produced by nitrification in the field. This relationship was noted also in the mineral soils.

c. Southern Germany

(1) Soil water and pH

The organic soils of the plots in Germany possessed the highest water contents (percent weight). This was due to their structure; the mass of fibrous decomposing material permeating the soil acted like a sponge and because of its colloidal properties, held water. That the water was not strongly held was seen from the fluctuations between sampling times. The water after heavy rainfall was temporarily held before it was able to percolate downwards. The soils were always wet to the touch.

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The soil moisture curves reached their lowest values in August–September, and in February after a slow fall from the high winter values. There was a smaller dry period in June–July and again later in October. The low values in February were increased by the increased spring precipitation and then fell again to the summer value. Correlation with the precipitation was not so obvious as that in the other two experimental areas, e.g. samples with high moisture content did not uniformly occur in all the plots. In this area the ground water is never very far below the surface, and to obtain an accurate picture of the moisture regime of the soil this should have been considered besides the precipitation. The high soil moisture at the end of October was due to the water table since the samples were taken after a period of low precipitation. The organic nature of the soil would favour capillary rise of water very much more than the more or less sandy loams. This fact was substantiated by the correlation between the fluctuations in pH and the water content of the soil.

A large increase in soil water was accompanied by an increase in pH; a fall in soil water, by a fall in pH. This occurred throughout the year even with the water fluctuations during the winter. An increase in pH is presumably due to the high calcium content of the water table, like in Switzerland and France. Superimposed upon this pattern was the seasonal tendency for pH to fall from spring to autumn. Then it rose again. KUHN (1961) measured the water table level in these wet meadow associations in the same area and found that the highest value was in July, but from November to March it was also high and within a few centimeters of the maximum. The maximum was ca. 20 cm below

Table 19   Comparison of the nitrogen status of the different types: Alsace
(Values given as mg/litre of soil. They represent the mean of all the samples for the individual soil)

Vegetation type	Plot No	Nitrogen at sampling (mg/100 g soil)			Nitrification		N value of vegetation
		NO$_3$-N	NH$_4$-N	Total	lab. NO$_3$-N	field NO$_3$-N	
Wet	F 1	3.83	1.56	5.39	18.29	7.60	3.45
	F 2	3.52	2.74	6.26	7.94	6.46	3.14
	F 3	3.35	3.91	7.26	9.23	6.57	2.99
	mean	*3.57*	*2.74*	*6.31*	*11.82*	*6.88*	*3.19*
Typical	F 4	4.87	7.04	11.91	14.97	12.01	3.40
	F 5	9.15	4.45	13.60	12.26	9.99	3.79
	F 6	5.25	8.90	14.15	17.09	10.94	3.60
	mean	*6.42*	*6.79*	*13.21*	*14.77*	*10.98*	*3.61*
Dry	F 7	7.48	4.92	13.40	31.56	20.28	3.53
	F 8	11.23	8.17	19.40	27.65	16.31	3.59
	F 9	9.98	4.51	14.49	31.92	16.80	3.30
	mean	*10.23*	*5.87*	*16.10*	*30.38*	*17.79*	*3.47*
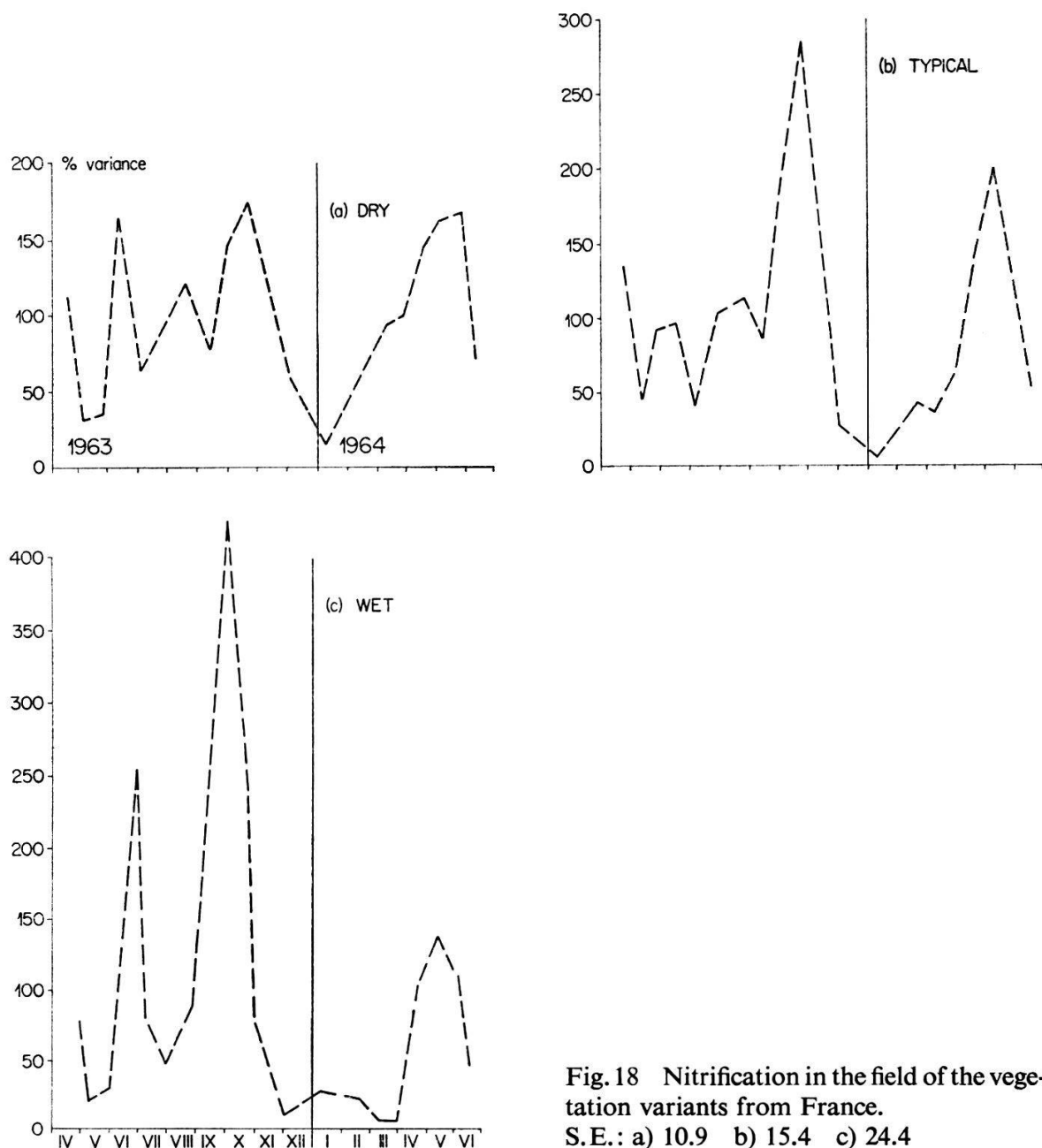
Fig. 18 Nitrification in the field of the vegetation variants from France.
S.E.: a) 10.9   b) 15.4   c) 24.4

the soil surface. The ground water contained Ca^{++}, ca. 17–25 mg/100 cm^3. Calcium carbonate contents of the surface soils of the plots were very low, and the vertical movement of the ground water with its basic ions affected the pH.

(2) Nitrogen at sampling time

Nitrate was present in all plots nearly the whole year. Nitrate levels fell to zero from December–March in the wet types. All the other plots were fertilised during the winter and the nitrate level did not fall when this occurred. After fertilisation the level tended to increase. Where there was no winter fertilisation the level of soil nitrate fell. During the rest of the year nitrate was present in the greatest amounts in the *Arrhenatheretum*, and the wet plots had the lowest

amounts. The other vegetation types showed intermediate nitrate levels. In this respect the *Scirpus* plots behaved more like the dry plots despite their wetter vegetation and less fertilisation. In the wet plots nitrate was present chiefly in spring and autumn, but in the typical plots nitrates were present for longer periods from midsummer to winter. The dry plots showed similar nitrate contents to the typical. There were high levels of nitrate in midsummer in the *Arrhenatheretum*, again in autumn and then in late winter and spring.

Apart from the levels of nitrate in winter, the amount present appeared to have no correlation with the fertilisation. Increase in the nitrate content occurred in soil of the same vegetation variants when one was fertilised and the other not.

The wet meadows contained the largest quantities of nitrates in the autumn and spring with some in midsummer (Fig. 19). These observations were comparable to the amounts present in the meadows in Switzerland and France, but in addition the soils from this region showed the winter peak of nitrate content. Presumably this was due to the fact that the soil temperature was colder in this site than in the others and the soil was frozen before and after the fertilisation. The low temperatures kept the nitrates at or near the soil surface. The fall in NO_3 in late September was attributable to the high soil water content at that sampling time. This caused a fluctuation in the main autumn peak. There was not always a close relation between the nitrate content and the water content of the soils, but during any one period when there were high nitrate levels in the soil small fluctuations were caused by the water regime.

The ammonium content of the soils reached its maximum during the winter, and although present at high levels in the *Arrhenatheretum* it was greatest in the *Scirpus* plots. Throughout the rest of the year ammonium was present in small amounts in May, July and September and occurred along with nitrate and not in place of it except in the plot supporting the poorest vegetation (the *Senecio aquaticus* meadow G 1). Whereas the nitrate content increased from the wet types to the dry vegetation types ammonium reached high winter values in all the vegetation variants. The seasonal pattern of ammonium content in the meadow soils corresponded very closely to that in the plots in Switzerland and France.

(3) The capacity for nitrification

The organic soils were characterised by their higher capacity for nitrification than the mineral and sandy soils. OLSEN (1921) also found that the nitrification was very active in organic peat soils. Soils of the vegetation variants increased their potential nitrification with decreased F values. The wet and typical variants possessed low nitrification capacities during winter and although the capacity fell in the dry types, it did not fall to such low levels. That of the *Senecio aquaticus* meadow and the second wet type fell to zero and less than 1 mg/100 g respectively; the dry to 2–4 and the *Arrhenatheretum* to 3–7. The potential nitrification in the *Scirpus* types during winter paralleled that in the typical. The low winter values of the wet types extended longer than in the other vegetation
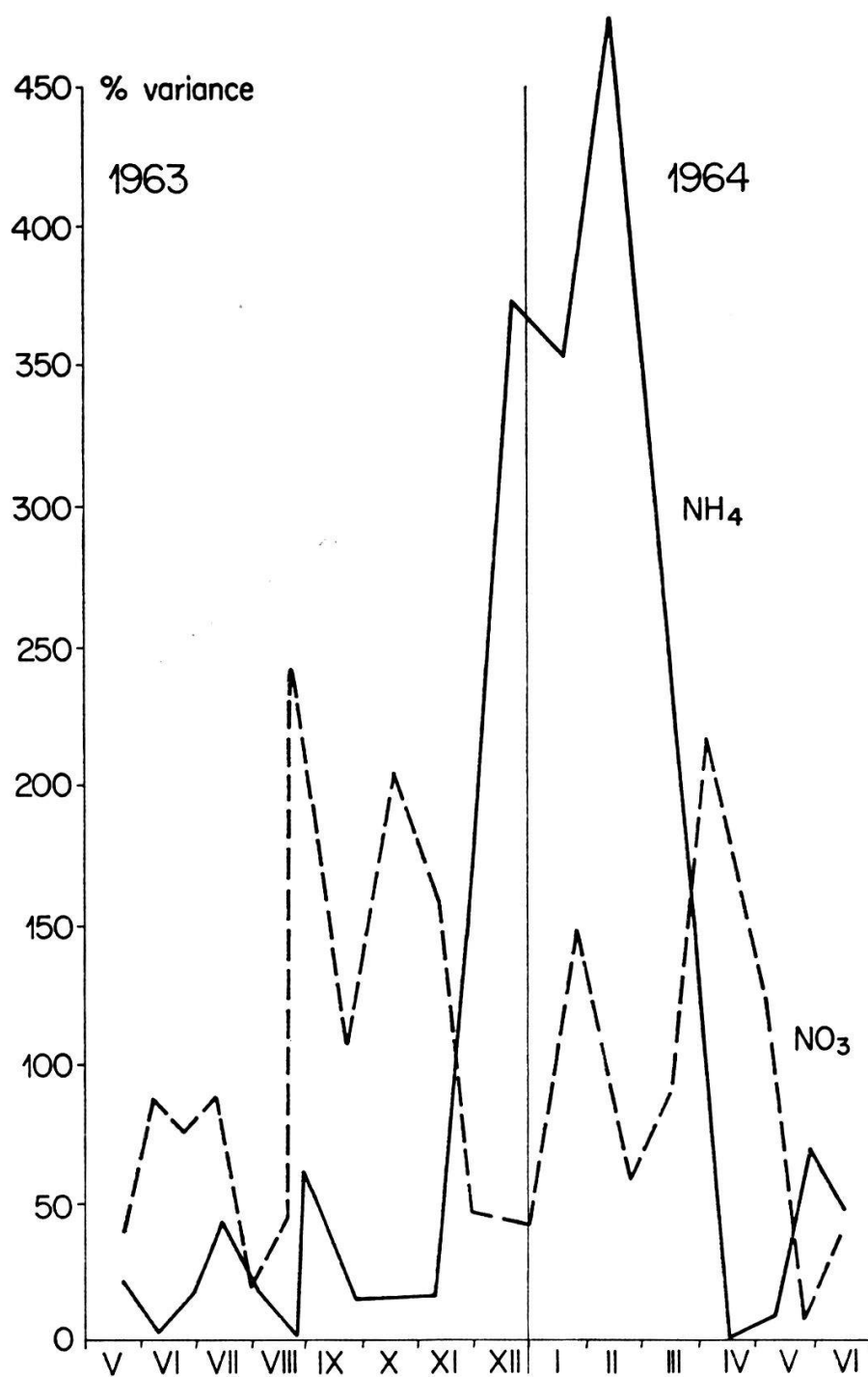
Fig. 19 The nitrogen present at sampling time in the field plots in Germany.
S.E.: $NO_3 = 15.7$ $NH_4 = 31.6$

variants. There was some relation to the water regime because the large fluctuations in water content definitely influenced the capacity for nitrification.

The four seasonal peaks were represented, i.e. July, autumn, February and May (Fig. 20). The peaks appeared later than those obtained from other experimental areas. The pattern in the soils from the plots in Germany was modified by the greater variations in water content. This was demonstrated by the *Arrhe-*

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natheretum. There was probably one large autumn maximum as in the mineral soils, but this was modified by high soil water causing a fall in September–October. Compared to the mineral soils the winter peak in the soils from Germany was exaggerated. The most important maximum for the dry plots was in summer (as in Switzerland), but again the winter maximum was large. The increased importance of these two peaks in the capacity for nitrification was seen in all the vegetation types (Fig. 21). Apart from the autumn peak being large in the three experimental areas, the relative importance of the other maxima was probably related to the differences in soil texture. The *Scirpus* variant showed its own pattern of potential nitrification. The nitrification tended to be similar to a much drier vegetation variant. This could have been caused by the excessive amelioration of the *Scirpus* plots by adding gravel, creating a different pattern of soil aeration. The *Senecio aquaticus* meadow differed in no great detail from the wet plot G2.

There was a correspondence between the potential nitrification and the nitrate present at any one time in the soil. This suggested that the nitrate in the soil was more a result of the soil activity than of artificial fertilisation.

Ammonium was present in the soils incubated under controlled conditions during the winter and occasionally during a time when the activity of the nitrifying bacteria was low.

(4) Nitrification in the field

Within limits nitrification in the field followed that under controlled conditions, but there were more departures from the parallelity, than in the mineral and sandy soils, e.g. in the *Arrhenatheretum* at plots G4 and G6 there were
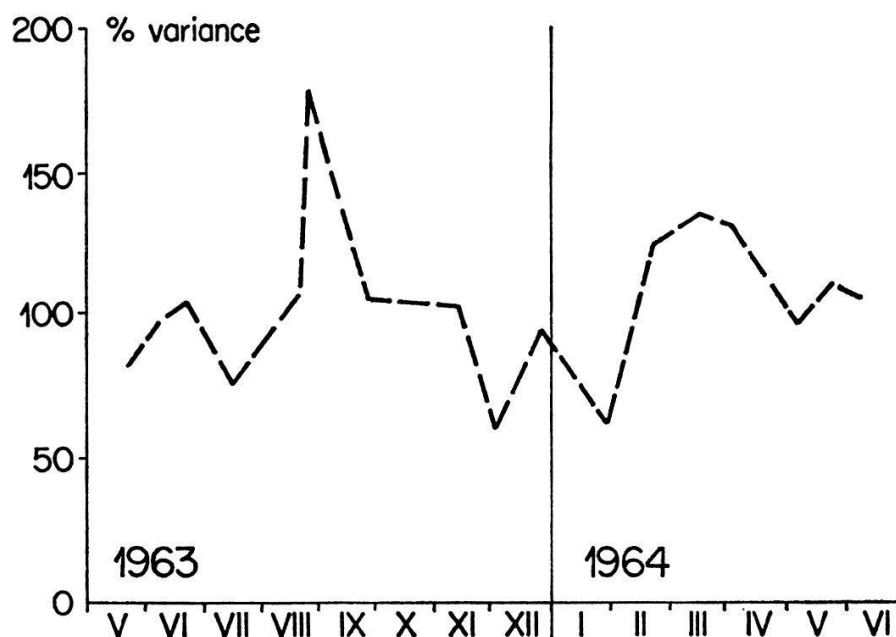
Fig. 20 The nitrification under controlled temperature conditions of soils from Germany. S.E. = 6.0
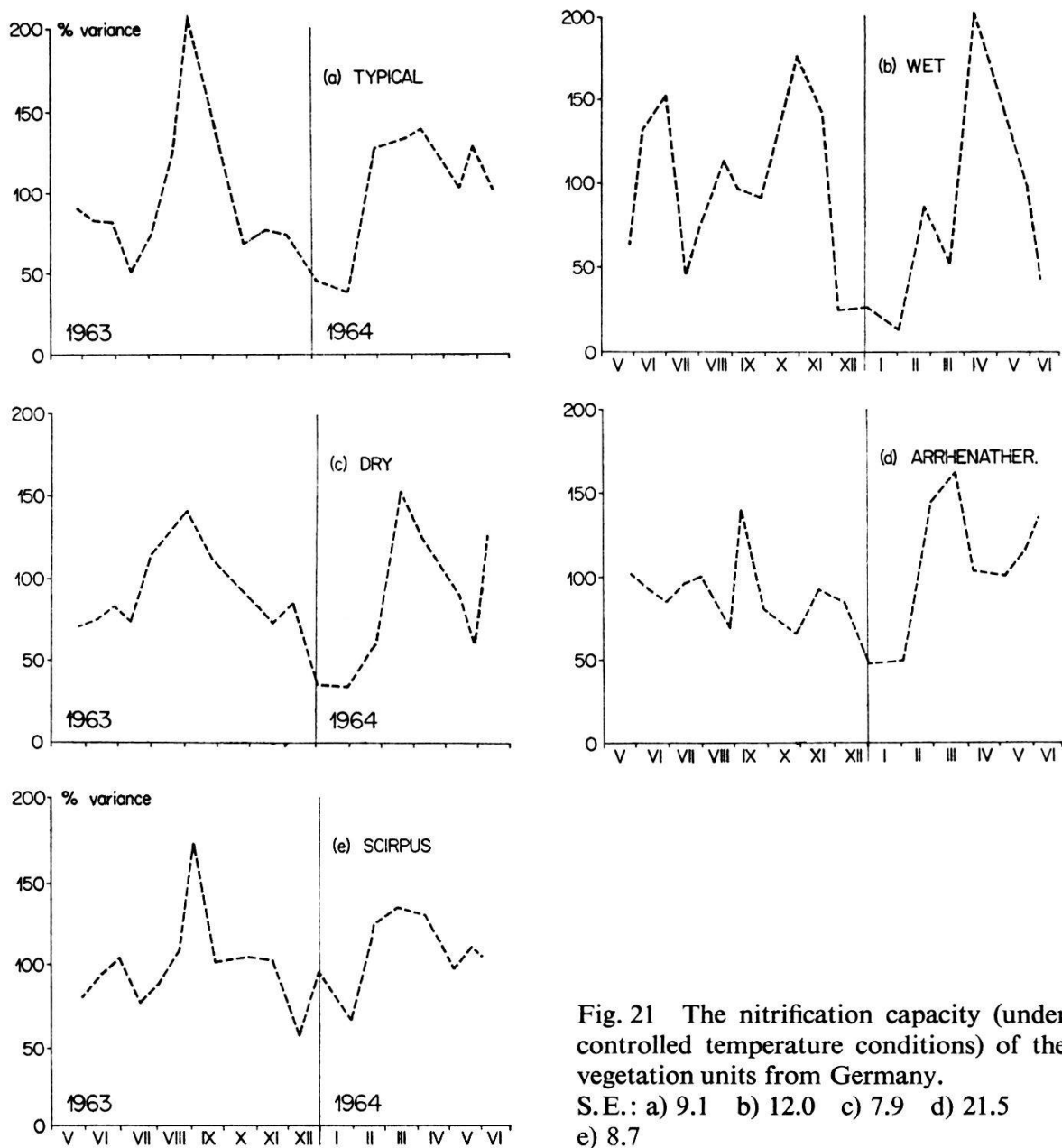
Fig. 21 The nitrification capacity (under controlled temperature conditions) of the vegetation units from Germany.
S.E.: a) 9.1 b) 12.0 c) 7.9 d) 21.5
e) 8.7

inverse relationships. However, in most soils the maxima in nitrification occurred about the same time. As the potential nitrification increased from wet to dry, so did the amount of actual nitrification. This reached low values in winter although in the drier and the *Scirpus* variants there was a low level of nitrification. There were 3 peaks as in the other areas in summer, autumn and spring (Fig. 22). The weather modified in the autumn peak. That this was caused by water is well illustrated in Fig. 23. The wet type (c) was greatly affected, the dry type and the *Arrhenatheretum* (a, d) less. The *Scirpus* variant showed some peculiarities in that the summer and autumn maxima tended to merge.

Ammonium was present during the winter in the samples left to nitrify in the field, and in some examples when conditions limited nitrification. In this respect all the samples behaved similarly.

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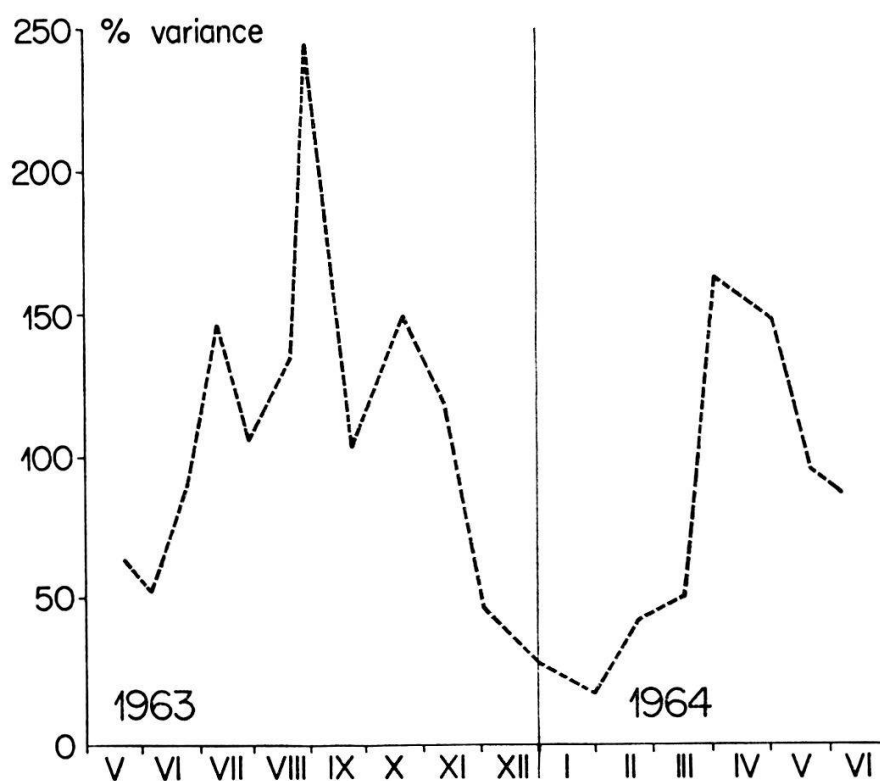
Fig. 22 The nitrification in the field of the experimental areas in Germany.
S.E. = 12.6

The different nitrogen status of the soils of the vegetation variants were similar to the other regions (Table 20). The N values and the potential nitrification were not well demarcated in the typical and the drier vegetation types. The nitrogen status of *Scirpus* variant approximated to the dry and not to the wet type. There were no obvious differences between the *Senecio aquaticus* meadow and the wet sedge *Cirsium oleraceum* meadow.

The three experimental areas showed a similar seasonal pattern in the nitrification, and the fluctuations between areas could be related to climatic differences, especially local precipitation. It appeared that the wet fertilised meadows possessed a characteristic pattern of nitrification which was evident in the different vegetation types. Those more fertilised, and consequently more fertile and with the highest mean N value and lowest mean F value showed a greater actual nitrification than the wet vegetation types.

3. Factors affecting the nitrogen budget

Something like 95% of the nitrogen present in the soil is bound in organic matter, and the "available N" represented by the remaining 5% exists as nitrate and ammonium. These ions result from mineralisation, i.e. ammonification and nitrification and the amount mineralised depends on:
(1) the water content of the soil,
(2) the profile relationships and the stratification of aeration,

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Table 20 Comparison of the nitrogen status of the different types: Germany
(Values given as mg/litre of soil. They represent the mean of all the samples for individual soil)

Vegetation type	Plot No	Nitrogen at sampling (mg/100 g soil)			Nitrification lab. field		N value of vegetation
		NO_3-N	NH_4-N	Total	NO_3-N	NO_3-N	
Wet	G 1	1.84	4.16	6.00	20.20	3.46	2.73
	G 2	1.59	1.85	3.44	17.89	2.84	2.55
	mean	*1.71*	*3.00*	*4.72*	*19.05*	*3.15*	*2.64*
Typical	G 4	4.45	2.05	6.50	49.69	5.80	3.35
	G 5	5.05	3.98	9.03	51.45	5.20	3.05
	mean	*4.75*	*3.01*	*7.76*	*50.57*	*5.50*	*3.20*
Scirpus	G 6	3.68	5.20	8.88	45.04	8.28	2.70
	G 7	10.13	4.45	10.58	25.30	8.09	2.75
	mean	*6.90*	*4.82*	*9.73*	*35.17*	*8.18*	*2.73*
Dry	G 3	3.40	2.45	5.85	42.10	9.15	3.21
	G 8	5.32	1.94	7.26	30.88	8.84	3.21
	mean	*4.36*	*2.19*	*6.55*	*36.49*	*8.99*	*3.21*
Arrhenatheretum	G 9	15.90	5.21	21.11	67.12	19.80	3.70
	G 10	19.44	3.25	22.69	81.06	14.87	4.33
	mean	*17.67*	*4.23*	*21.90*	*74.09*	*17.33*	*4.01*

(3) pH,

(4) temperature,

(5) supply of essential nutrients, the quantity of organic matter.

Experiments were conducted to investigate the effects on nitrogen relations of changing the water regime, of supplying ammonia and changing the pH with $CaCO_3$, and of supplying aerobic versus anaerobic conditions. The distribution of nitrification in the soil profile over a short distance was investigated and the bacterial populations responsible for the oxidative processes of nitrification were cultured.

a. The water factor

HELLER (personal communication) has clearly demonstrated that in soils of certain woodlands there is a close correlation between the water content of the soil and the capacity of the soils to nitrify. These soils however were sandy soils with a low organic content and the humidities were always low compared to the wetter hay meadows, e.g. *Molinietum*, and the wet fertilised hay meadows. ELLENBERG (1964) found the same thing with a clay-loam supporting *Aceri-Fraxinetum*. Normally nitrification proceeds actively within rather narrow limits of the water content of the soil. KOCH (1911) found that for a sandy soil 16% was optimum and activity was lower at 10% and 26%. The relation is not always clear without experimentation; for instance OLSEN (1921) cited a soil with an
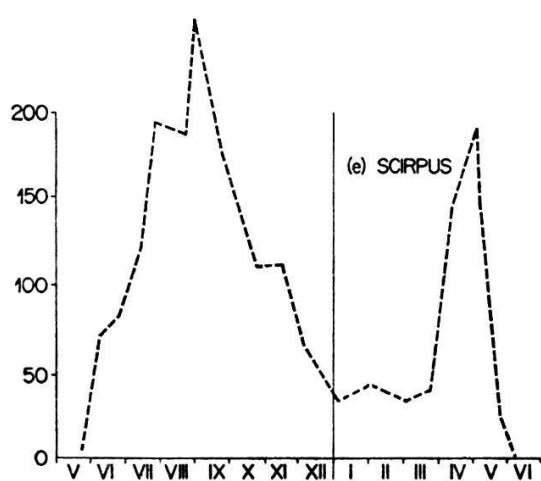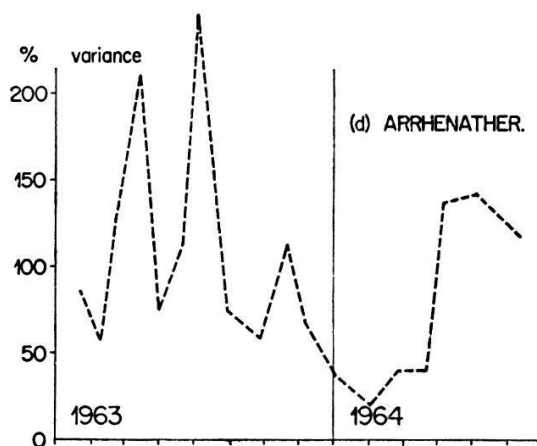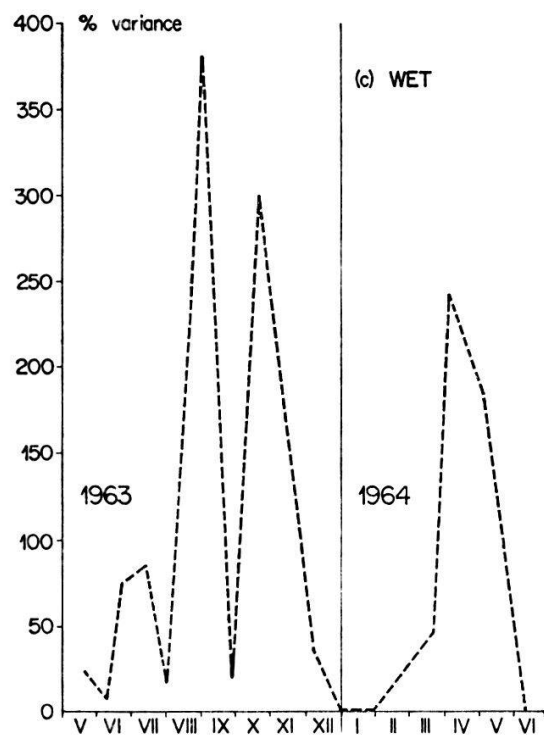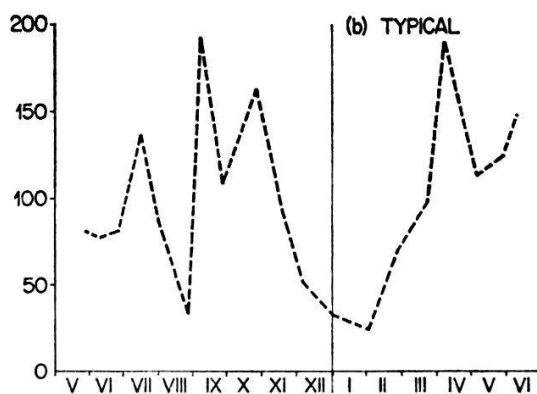
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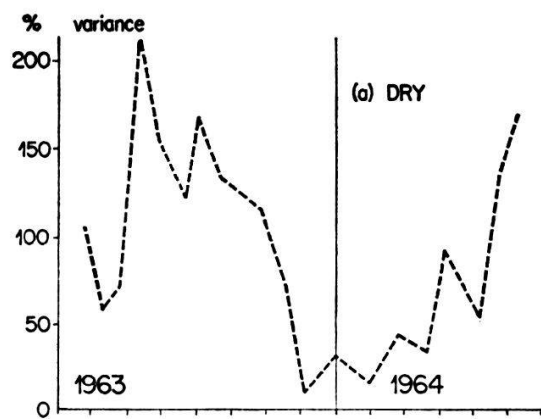
Fig. 23 Nitrification in the field of the vegetation units from Germany.
S.E.: a) 11.9   b) 11.0   c) 25.3   d) 13.1
e) 16.6

initial water content of 18.1% produced 48.27 mg NO_3/l, but the same soil with a water content of 26.3% produced an increase of 101.74 mg.

Unless the soil is extremely sandy, water is retained and with increasing water the soil atmosphere is decreased. In very wet soils conditions become anaerobic. The seasonal changes observed in the nitrification *in situ* and the nitrification capacity under controlled conditions fluctuated in the same way except during the winter months when climatic factors limited the nitrification in the field. In many samples it was observed that nitrification fell in accordance with high water content, and when the soil was relatively dry nitrification increased. There was no regular relation between water content and nitrification. For example in plot S4 the sample taken in late July had a water content of over 150% compared to the normal winter levels of 80–100%. Yet the nitrification was not greatly depressed. The moisture affects the bacterial activity. TRAAEN (1916) added ammonia as ammonium sulphate at seven moisture regimes and measured the percentage of the ammonia which was converted into nitrate after 26, 66, and 100 days. When the soil was very dry (3.5%) nitrification activity was limited and the best results were obtained at 17.5–20%. At 25% the amount converted was less.

For nitrates to be produced in the soil conditions must be aerobic and there must be a supply of suitable substrate. The soil organic matter holds not only the exchangeable cations (Ca, K, Na, Mg, Mn and Zn) but by mineralisation releases C, N, P and S by biological decompositions. These processes depend on temperature, humidity, aeration and pH. The soils of the wet meadows always contained sufficient humus to provide adequate initial material; provided the micro climate was suitable for its decomposition.

Two mineral soils were taken after rainfall by gathering many small samples, sieving and mixing from two mineral soils, one supporting the wet type of vegetation, the other the typical. The initial contents of water, nitrate and ammonium were determined. The soils were then spread out on flat pans in a laboratory and allowed to slowly dry. Eight subsamples were taken for each soil to give a graded series of soil water content. There were minute fluctuations in the N contents during drying and corrections were made to give the initial nitrate and ammonium contents. The soil moistures were:
Soil (1) wet vegetation: 65.2, 86.3, 100.1, 115.4, 125.6, 145.7, 166.0, 181.2 % weight
Soil (2) typical vegetation: 29.9, 35.7, 41.2, 45.7, 51.8, 62.0, 65.6, 75.5 % weight
The samples were put into glass jars and weighed and kept under controlled conditions. Every 3 days the weight was checked and any water loss was made good by a vaporiser. There were only small alterations. At 10, 20, 30, 50 and 60 days nitrate and ammonium contents were determined.

In the wettest samples nitrification was negligible. There was a gradual increase in the nitrification capacity with lower water content. Not only did the amount of nitrification increase but also the rate of nitrification. In soil (1) there was maximum nitrification with moisture contents of 125.6 and 145.7%. Samples drier than this showed less accumulation of nitrate (Fig. 24 A). In soil (2) the activity was similar over a range of the dry soils (29.9–45.7%), but between 45.7 and 75.5% activity was very different (Fig. 24 B). Ammonium was

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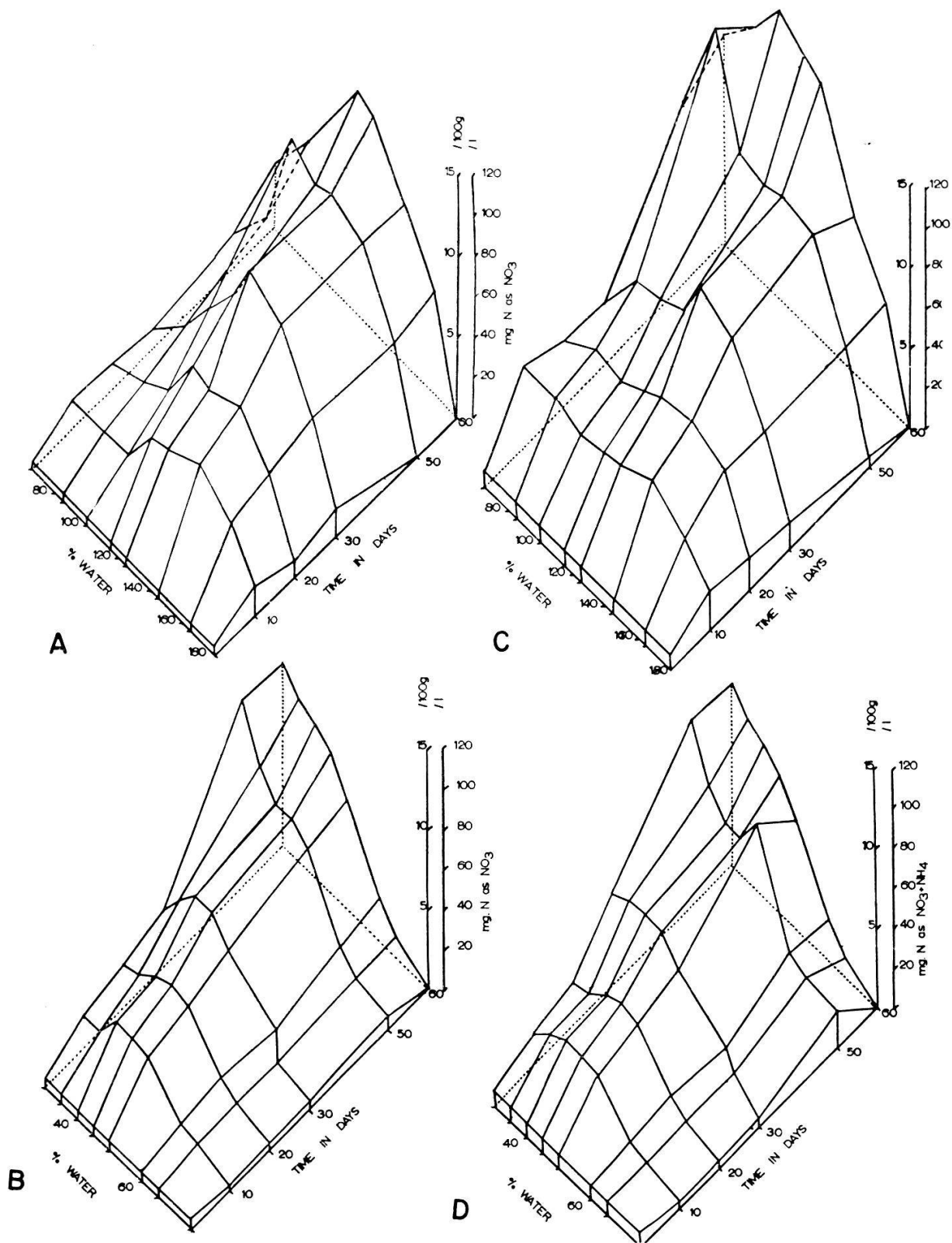
Fig. 24 The nitrogen in two soils kept under controlled conditions, with various soil-water contents. Soil (1): A C, soil (2): B D. A and B represent the nitrate content C and D represent the total nitrogen content.

Vertical axes show the N content in 100 g or 1 litre of soil.

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not present in any large amounts. In both soils there was some accumulation in the wettest samples, as a consequence of air deficiency. This ammonium was lost by 60 days. The accumulation of ammonium after 50 days may have been due to decomposition processes which normally reach a maximum about this time under controlled conditions, but if this was the case any nitrogen produced was lost and this may have been caused by denitrification. In soil (2) there were small quantities of ammonium present throughout the experiment, but these did not influence the pattern of nitrification. In the drier samples of soil (1), when nitrification was depressed ammonium content rapidly increased after 30 days. It appeared that this was not due to denitrification because the level of nitrate did not decrease greatly; the soil was too dry to favour maximum nitrification and limited the activity of the nitrifying bacteria.

For both soils there were humidity conditions favouring nitrification and conditions depressing it (the extremes of wetness and dryness). The actual quantities of water were characteristic for each soil though the range of humidities which produced the best nitrification was within the range normally found in the field during spring and summer.

It may be that the low capacity for nitrification during the winter months resulted from a combination of high water content, and the low temperature, limiting the activity of the bacteria by restricting aeration. When the temperatures were favourable water content (or lack of oxygen) was probably the biggest single factor affecting the bacterial activity.

Measurements of mineral nitrogen present at sampling times throughout the year showed that the nitrate content fluctuated; and the soil water regime and leaching due to precipitation appeared to be one of the major factors influencing the nitrogen balance. To test this the nitrate content of a more or less static drainage ditch bordering one of the plots in Switzerland (S 1) was measured at six different times. The results are shown below:

1963/64	June	August	October	December	February	April
mg NO_3-N/l	8.73	16.42	4.37	24.37	12.32	6.98
Soil NO_3 level	High	Low	High	Low	Medium	High

These times were chosen to avoid any sampling soon after fertilisation. When the soil nitrate was low the water contained a higher quantity of nitrate indicating that nitrate was leached from the surrounding soil. Obviously to provide a concrete example samples would be needed more frequently before and after rains, etc., but these six analyses do support the fact that soil nitrate is very susceptible to leaching. Nitrates are washed from the soil most rapidly in winter when precipitation is in excess of evaporation. BRIZZELL (1943) showed that in a culture of *Phleum,* loss of N from the soil (apart from the uptake by the crop and that lost by other factors), was due to considerable amounts in drainage,

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and this amount was 2.2 times greater on fertilised plots. Leaching of nitrates appeared to be an important factor in the wet meadows and the advantages of winter fertilisation seem questionable. The importance of this fertilisation must rest with the organic debris supplied which provides a store of nutrients which can become available when the bacterial activity is no longer limited by the temperature.

Water in the soil acts in two ways: (1) as a solvent and (2) by altering the aeration and permeability. In high quantities water may restrict nitrification due to the lack of oxygen and may remove N otherwise available for plant growth. It may well be that water is the major factor controlling the seasonal N rhythm.

b. The effect of added ammonium and calcium carbonate

Two sandy loams (F 3, F 8), two organic soils (G 1, G 4) and three loamy soils (S 1, S 7, S 8) were sampled to study the effect on nitrification of added ammonium and ammonium together with calcium carbonate. To samples containing 100 g of dry matter were added 30 mg of ammonium nitrogen as ammonium sulphate and 30 mg of NH_4-N as well as 200 mg of calcium carbonate. The samples and controls with no additions were maintained with their water content at sampling and incubated at 20 °C. After six weeks the nitrate content was determined in each sample, and samples were taken over a period of one year.

pH was measured initially and after the addition of ammonium and ammonium plus $CaCO_3$, since the amount of nitrate produced from ammonium sulphate depends on the initial and final reaction of the soil. By adding ammonium sulphate the ammonium ions enter the exchange complex and another base, usually Ca^{++} is displaced. There is a balance, because when the ammonium is nitrified, the nitrate ions are neutralised again by the Ca.

Differences in the nitrification can be attributed to the bacterial population and the availability of substrate, both limited by the physical factors of water, pH, temperature, etc. When large doses of ammonium were artificially supplied and the physical environment maintained constant, the differences observed were due to the bacterial activity.

In most instances the ammonium was converted into nitrate, and often the combined sum of 30 mg N supplied, and the control nitrification was less than the measured value. This indicated a slight catalysing of the decomposition processes by the presence of nitrogen substances. This was not so obvious in the heavy loams but more so in the sandy loams and marked in the organic soils (Table 21).

In all soils the results of the three treatments were parallel, and the samples with added ammonium showed the same fluctuations in nitrifying capacity between sampling times as the controls. The effect of $CaCO_3$ in the mineral and organic soils was to provide a higher pH, and the nitrification produced by the addition of the same amount of ammonium was greater. In the sandy loams this did not occur. The soils were calcareous and addition of $CaCO_3$ did not greatly increase the pH, and nitrification did not greatly differ from that produced by the addition of ammonium alone. In the sandy loams the pH 7.2–7.4 appeared to be an optimum for nitrification and in many samples during the year the addition of $CaCO_3$ depressed the nitrification.

Table 21 Summary of the nitrifying capacity of meadow soils and changes in pH value with the addition of ammonium and calcium carbonate (mean yearly values)

Vegetation type	Wet			Typical			Dry			Soil
Treatment	Control	$+NH_4$	$+NH_4+CaCO_3$	Control	$+NH_4$	$+NH_4+CaCO_3$	Control	$+NH_4$	$+NH_4+CaCO_3$	
pH	*5.9*	*−0.1*	*+0.7*	*6.3*	*−0.8*	*+0.6*	*6.3*	*−0.1*	*+0.7*	Heavy
mg NO₃/100 g[1]	1.4	33.1	42.0	5.9	36.0	53.7	10.3	44.9	56.1	loam
mg NO₃/litre	11.4	264.8	336.0	47.2	287.8	429.2	68.9	290.6	368.8	
pH	*7.4*	*−0.1*	*+0.2*				*7.3*	*−0.1*	*+0.3*	Sandy
mg NO₃/100 g[2]	1.5	57.1	52.6				2.5	47.6	54.2	loam
mg NO₃/litre	9.1	368.3					27.5	513.8	584.8	
pH	*6.7*	*−0.5*	*+0.5*	*6.8*	*−0.7*	*+0.5*				Organic
mg NO₃/100 g[3]	3.9	50.7	76.7	10.1	115.1	128.4				soil
mg NO₃/litre	21.2	274.0	413.9	50.3	575.5	642.0				

[1] see Table 9 (1, 7, 8)   [2] see Table 11 (3, 8)   [3] see Table 14 (1, 4)

In contrast the nitrification of a mineral soil from a *Molinietum* (which LEÓN proved to produce very low quantities of NO_3 or NH_4 in normal conditions) was compared after the same treatments. This soil produced 0.04 mg of NO_3-N after 6 weeks incubation; yet produced 28.7 mg after the addition of ammonium and 36.5 mg after the addition of ammonium and $CaCO_3$. The latter increase was caused by a rather large increase in pH (from 5.2 to 6.6). The experiment amphasised that the nitrifying bacteria were present in this soil, although normally inactive. The inactivity appeared to be due to the lack of available substrate.

In all soils, the adjustment of pH by $CaCO_3$ had the effect of emphasising the seasonal pattern of nitrification, e.g. in the wet mineral soil some of the large fluctuations were smoothed out. Normally the controls fluctuated greatly during the summer producing two peaks of nitrification in June and August. This was smoothed out by the addition of $CaCO_3$, and the true summer and autumn maxima of nitrification were clearly distinguished. RAPPE (1952) found the same thing with some arable soils. He concluded that the supply of easily nitrified nitrogen in organic compounds was sometimes too small to allow a full functioning of the microbial activity and the seasonal rhythms in nitrification observed after the addition of ammonium and ammonium plus $CaCO_3$, were only weakly marked in the controls. $CaCO_3$ exerts its effect by neutralising the acids formed during the nitrification process and it influences the nitrite accumulation. The following figures from FRAPS and STERGES (1930) illustrate this (Table 22):

Table 22   The effect of $CaCO_3$ on nitrite accumulation, data from FRAPS and STERGES (1950) (ppm NO_2-N)

Treatment	Soil 1	2	3	4
Control	0	0	0	4
500 ppm N as NH_4	3	3	0	0
$CaCO_3$ 1%	54	59	5	5
$CaCO_3 + NH_4$	255	218	260	310

FISCHER (1912) related the differences in nitrification between soil types to their lime contents. He found that the theoretical quantity of lime calculated as being necessary for the nitrification of a given quantity of ammonium did not in reality suffice for nitrification, the maximum rate of reaction being with three times the theoretical quantity. This was possibly due to the fact that *Nitrosomonas* and other nitrifying bacteria, especially in the zoogloeal form, adhere to particles of $CaCO_3$. Ca^{+++} is an essential requirement for the nitrifiers and in natural conditions organic matter seems to stimulate the organisms (BURGES, 1958).

c. The effect of aerobic and anaerobic conditions

Two soils with similar pH and $CaCO_3$ content from the plots in Germany (G4, G9) containing 242 and 261% water by weight respectively were subjected to 3 levels of aeration:
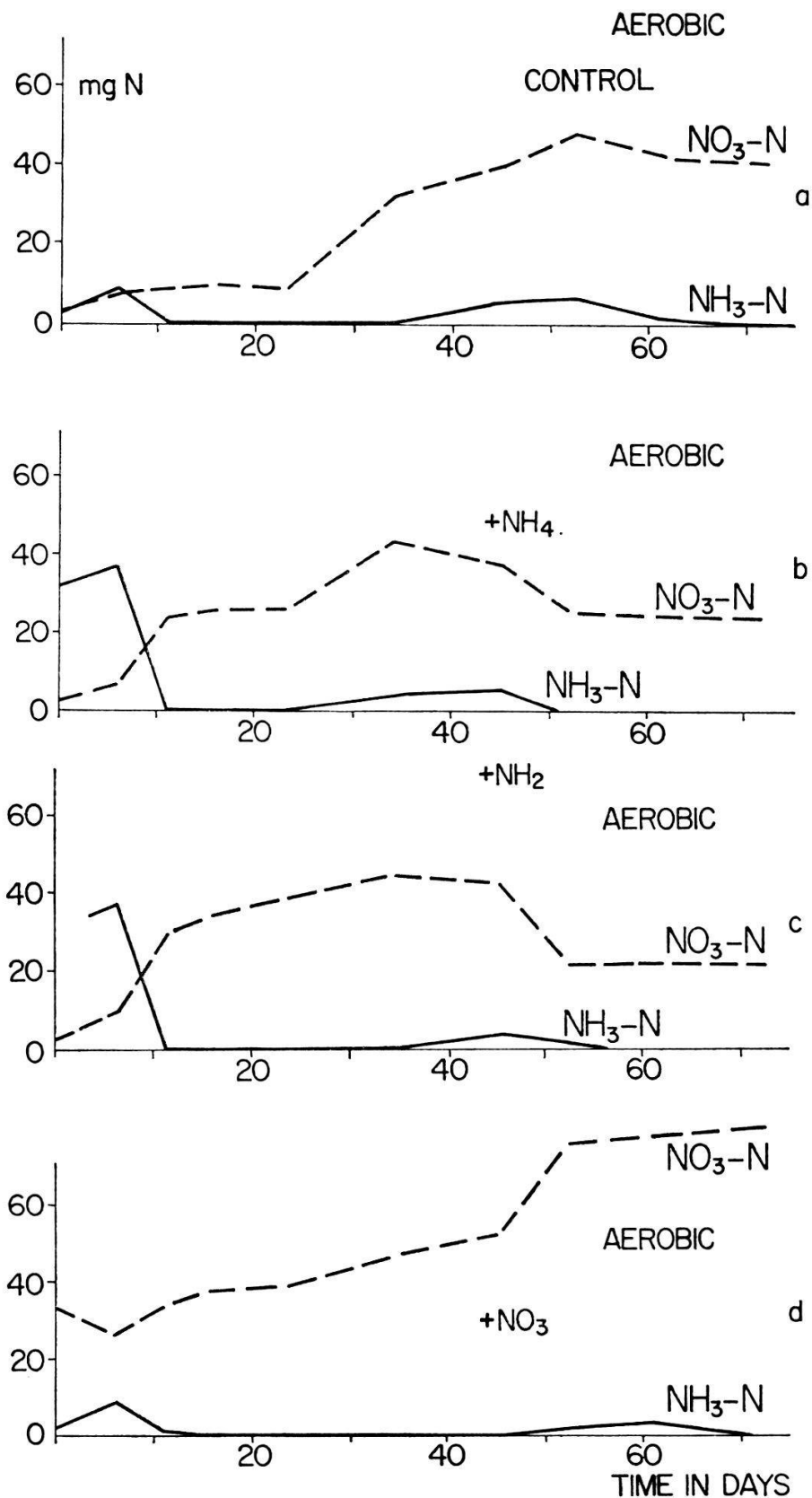
Fig. 25   The wet soil; nitrogen relations in aerobic conditions.

(1) controls: i.e. normal conditions (aerobic),
(2) anaerobic,
(3) inundated.

To provide anaerobic conditions 40 ml of pyrogallol was placed in a large tube and inserted into the jar containing the soil. The pyrogallol was made by mixing 5 parts of pyrogallic acid dissolved in three times its weight of water and 2 parts of potassium hydroxide dissolved in its own weight of water. The jars were provided with vaselined ground glass stoppers and were waxed after closing. An oxygen indicator was prepared by dampening filter paper strips with a mixture of 4.21 ml 1-percent glucose, 0.1 ml saturated solution of methylene blue and 0.1 ml N NaOH. The strips were inserted into the necks of the jars before closing. Bleaching of the indicator showed that the oxygen had been removed. To provide inundated conditions in each case a weighed quantity of soil was covered by the same amount of boiled water in jars which were subsequently sealed. The jars containing the control soils were left open and covered with cotton wool.

Superimposed upon this experimental design were four additional treatments. For each soil, under each condition of aeration nitrogen was artificially supplied:

(1) 0,
(2) 30 mg N as NH_4 (amm. sulphate) per 100 g dry soil,
(3) 30 mg N as NH_2 (asparagine) per 100 g dry soil,
(4) 30 mg N as NO_3 (KNO_3) per 100 g dry soil.

Each of the 24 treatments was replicated three times and all jars were placed into a humidity chamber and incubated at 20 °C. At periods up to 72 days the soils were analysed for their nitrate and ammonium contents and at each sampling time the pyrogallol was replaced in the anaerobic jars. There was close agreement between replicates although there were some replicate differences in ammonium content in the anaerobic series. The mean values are plotted in figures 25–30.

Controls. In both soils nitrate increased. In the wetter soil the increase was slow for 25 days, then more rapid. In the drier soil nitrate accumulation was more rapid at first. After 50–60 days the curves levelled out. Ammonium present initially was soon lost (by 10 days): presumably this was converted to nitrate. Ammonium appeared in the wetter soil after 35 days, reached a peak and then fell to zero. This occurred in the drier soil, though sooner. It was thought that this was due to decomposition of organic substances favoured by the near optimal conditions of the humidity chamber, because the nitrate level continued to rise. MEYER (1957) measured the relations between NH_3, NO_2 and NO_3 in an *Arrhenatheretum* soil by using Winogradsky's medium. Similarly NH_3 slowly fell and after 6 days NO_2 rose rapidly, reached a peak and fell whilst at the same time the level of nitrate began to rise.

When ammonium was given, the initial amount decreased as the nitrate increased. The ammonium was converted into nitrate since the curves of nitrate accumulation rose steeply at this time (cf. Fig. 25 a, b and Fig. 26 a, b). The nitrate continued to accumulate in both soils and there was the same small occurrence of ammonium due to decomposition. In the wetter soil, however, the nitrate level fell after 35 days (the control fell very slightly after ca. 52 days). This fall must have represented denitrification and loss of the nitrogen as N_2 gas because the nitrogen was not traceable as ammonium. This falling off was negligible in the drier soil. The addition of ammonium caused a twofold increase in the nitrate production of the drier soil. The amount of nitrate produced in

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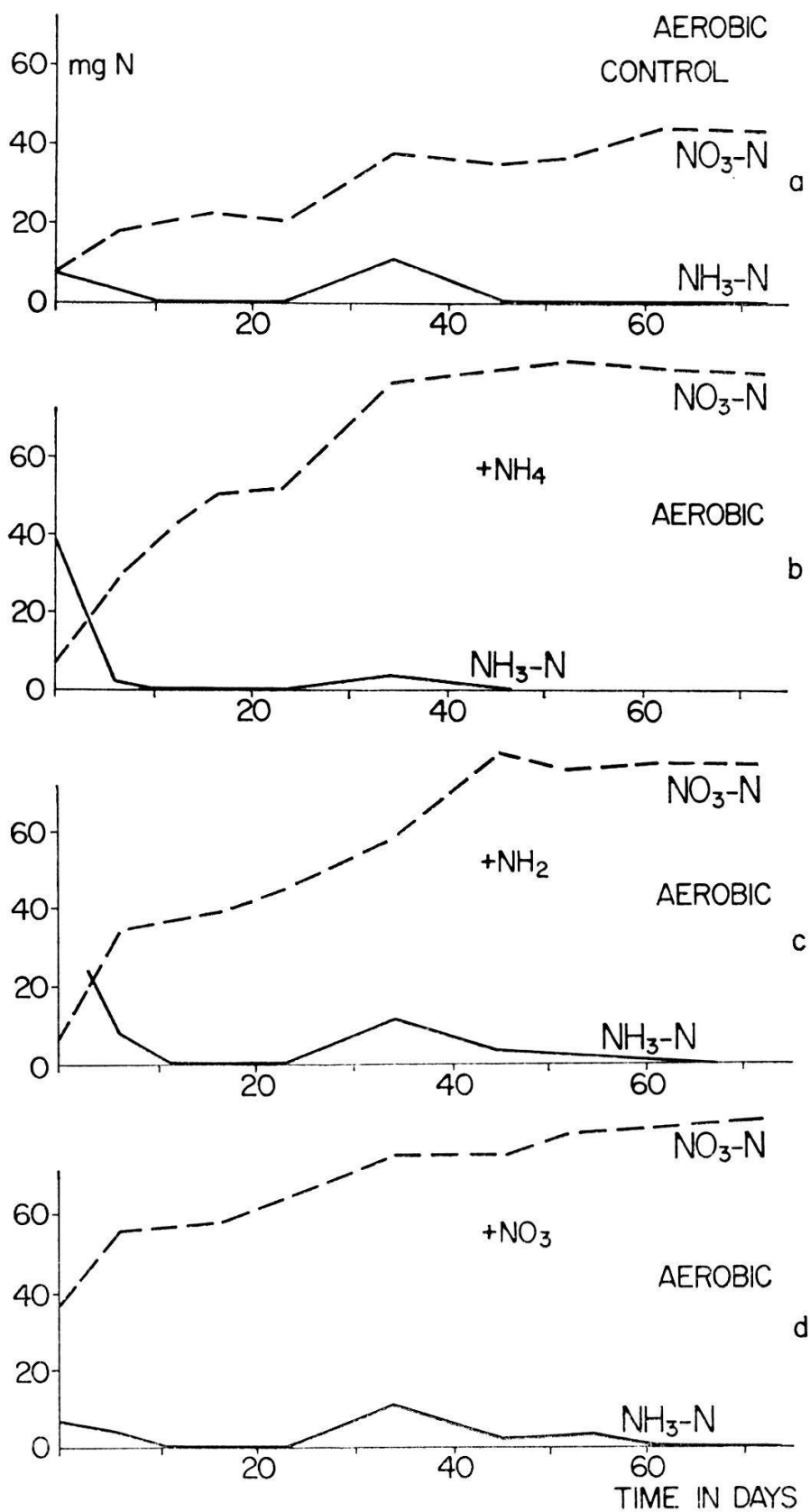
Fig. 26   The dry soil; nitrogen relations in aerobic conditions.

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the control plus the 30 mg N given was less than the amount produced after the addition of ammonium, and there was a net gain of ca. 5 mg. This may have been within the limits of error but probably represented a slight catalysing effect. In the wetter soil, the final nitrate accumulation after the addition of ammonium was considerably less than the control and this emphasised the denitrification that occurred in the control. In this case the denitrification commenced earlier (34 days cf. 52). Asparagine-N behaved similarly to ammonium-N, and the curves for the wet soil were more or less identical (Fig. 25b, c), though in the dry soil the nitrate level fluctuated after 45 days (Fig. 26b, c). It was noticeable that the ammonium-N and asparagine-N were utilised much more rapidly in the drier soil, and at 6 days the added levels had decreased considerably. In the wet soil they were utilised more slowly. As a substrate for the nitrifying bacteria asparagine seemed to be as effective as ammonium and the final nitrate accumulations were similar.

After the addition of nitrate the nitrification proceeded as in the controls but at a higher level. In the wetter soil the nitrate production equalled the control plus the added NO_3, and the presence of added nitrate seemed to reduce the slight denitrification after 52 days. Also the decomposition was retarded. In the drier soil the presence of nitrate slightly increased the rate of nitrification and acted as a catalyst because the final amount of nitrate produced totalled more than the control plus 30 mg.

Anaerobic. Anaerobic conditions greatly modified the nitrification. In the wet soil the nitrate level fell and reached zero at 45 days, and at the same time ammonium increased. The initial time lag in the loss of nitrate was probably due to the fact that there were still low O_2 tensions between the soil crumbs. The same occurred in the drier soil, but nitrification did proceed to a much higher level (23 mg cf. 7 mg, Figs. 27a, 28a). Decomposition in the aerobic controls was masked by the ammonium production.

The presence of ammonium greatly increased the production of ammonium. In the wet soil, ammonium reached high levels (125 mg) and this decreased, presumably by conversion to N_2 and N_2O. The high level of ammonium must have included that produced by decomposition and again the presence of an end product seemed to catalyse the bacterial change. In the dry soil there was some initial nitrification, probably due to some air still remaining between the soil crumbs. Thereafter decomposition was rapid resulting in the production of ammonia.

The addition of asparagine produced smaller effects than the addition of ammonium and denitrification. Only some was converted to ammonium (because some bacteria causing decomposition are anaerobes). This was in turn lost as N_2 (Figs. 27c, 28c).

Nitrate under anerobic conditions was lost due to conversion to ammonium, and it was lost much faster in the wetter soil. The fall in the curves of ammonium against time represented losses as N_2. Due to the anaerobic conditions, ammonium present initially in the soil was lost very quickly (Figs. 27a, 28c).
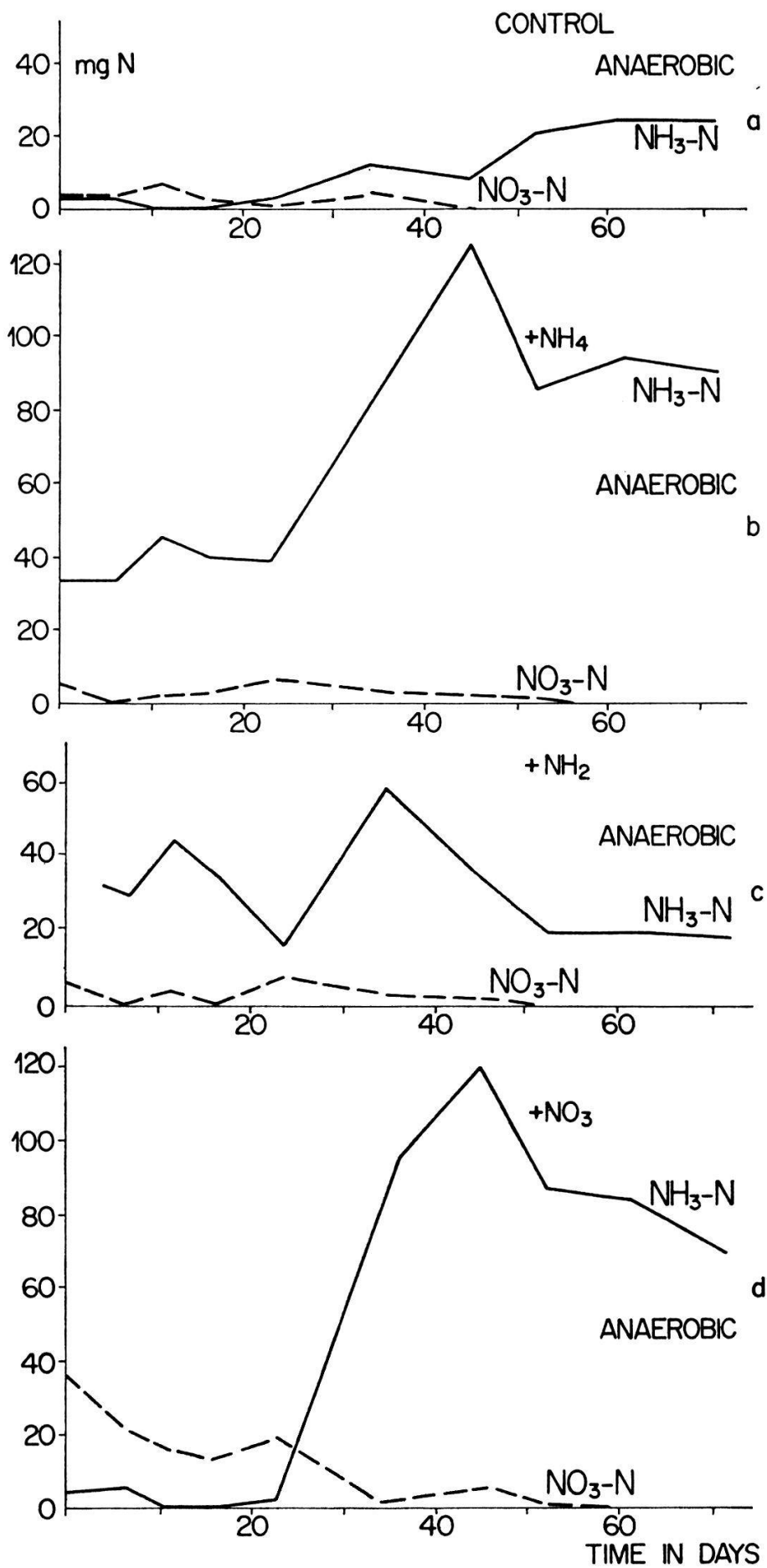
Fig. 27   The wet soil; nitrogen relations in anaerobic conditions.

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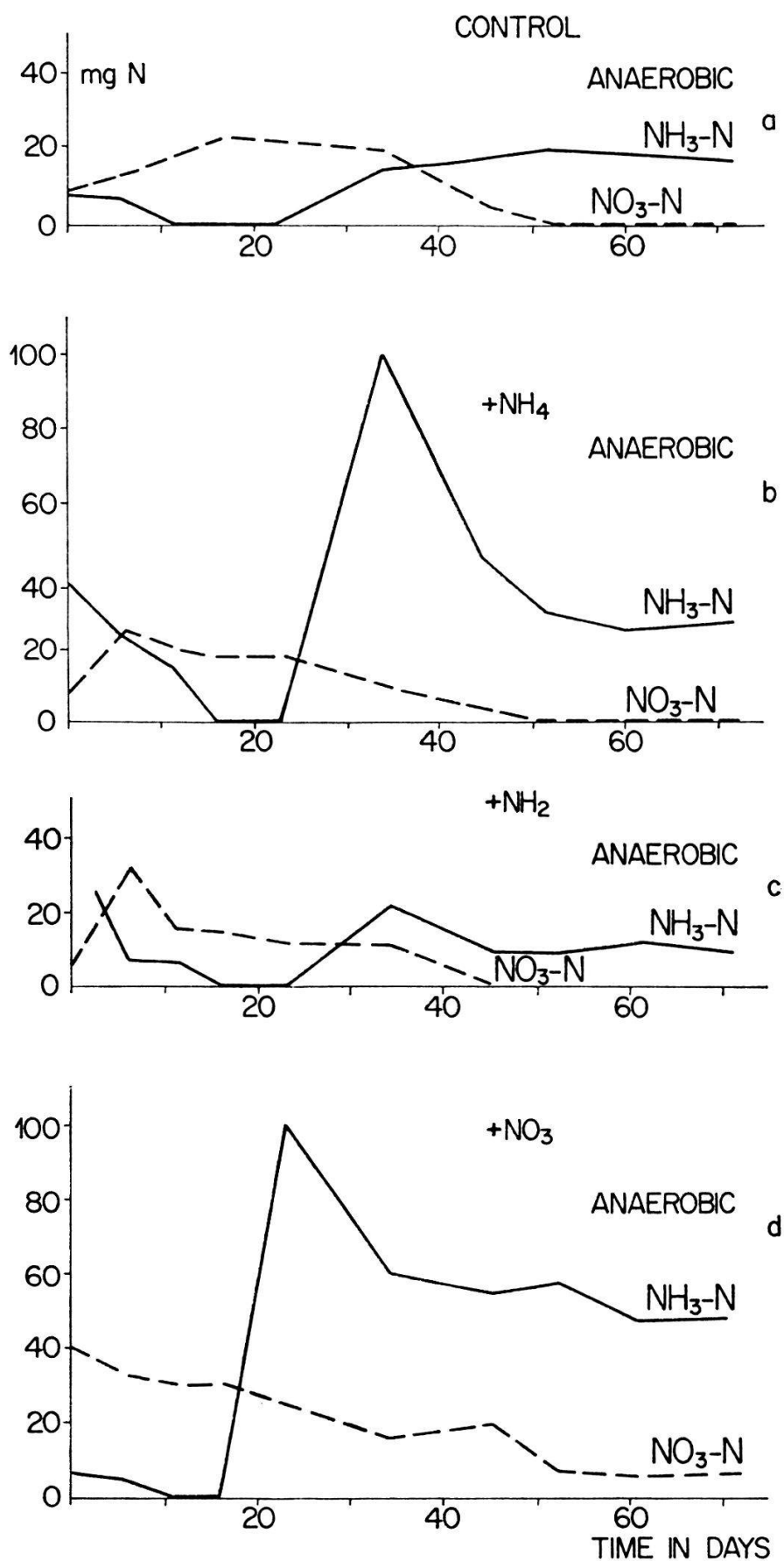
Fig. 28   The dry soil; nitrogen relations in anaerobic conditions.
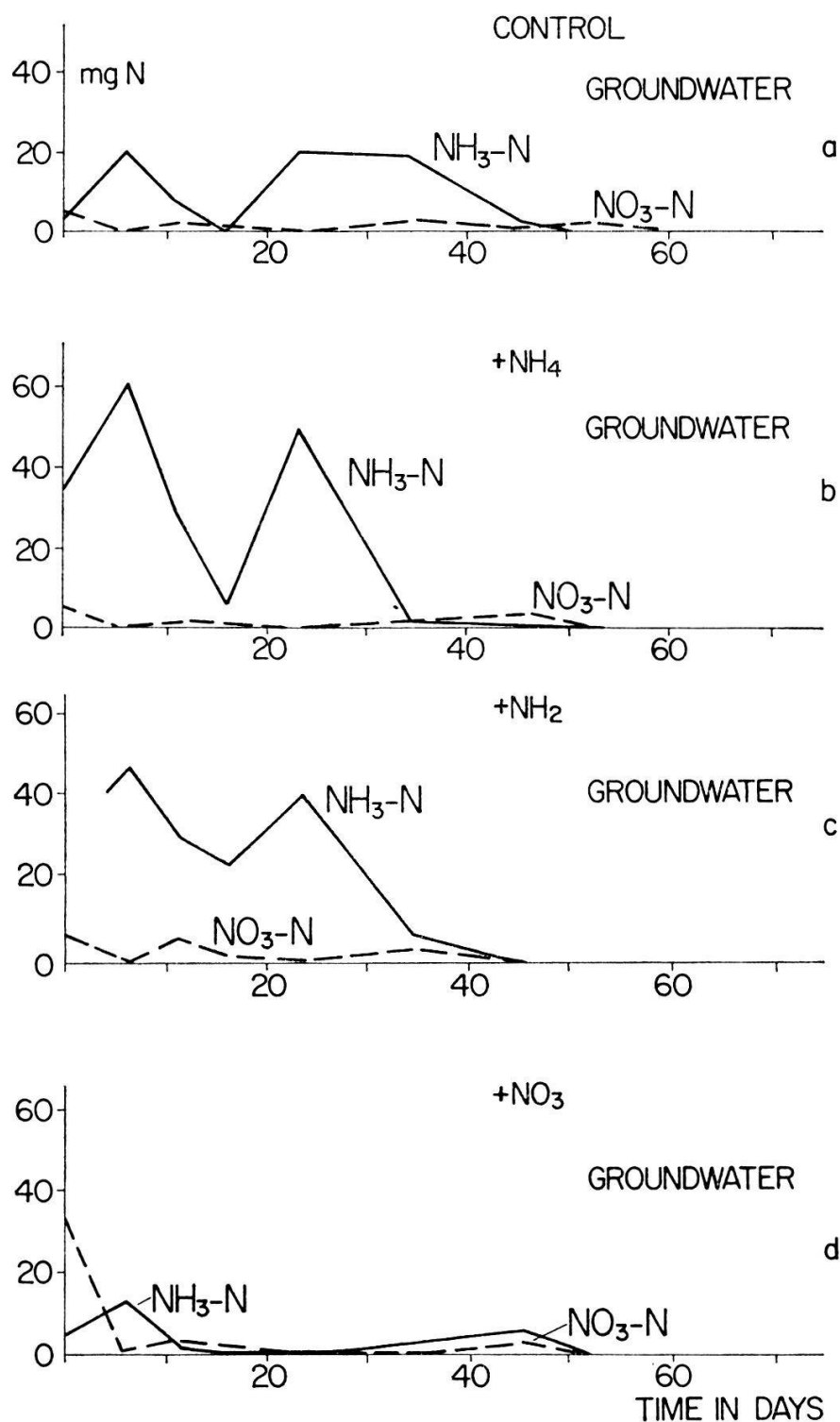
Fig. 29   The wet soil; nitrogen relations when flooded.

Inundated. The artificial ground water caused initial loss of nitrate and increase of ammonium in both soils. In the wetter one there was some accumulation of ammonium later and then a decrease, and in both soils there was some nitrification, even though the soil was completely inundated (Figs. 29a, 30a). The oxygen content of the ground water was measured by the method of Wink-
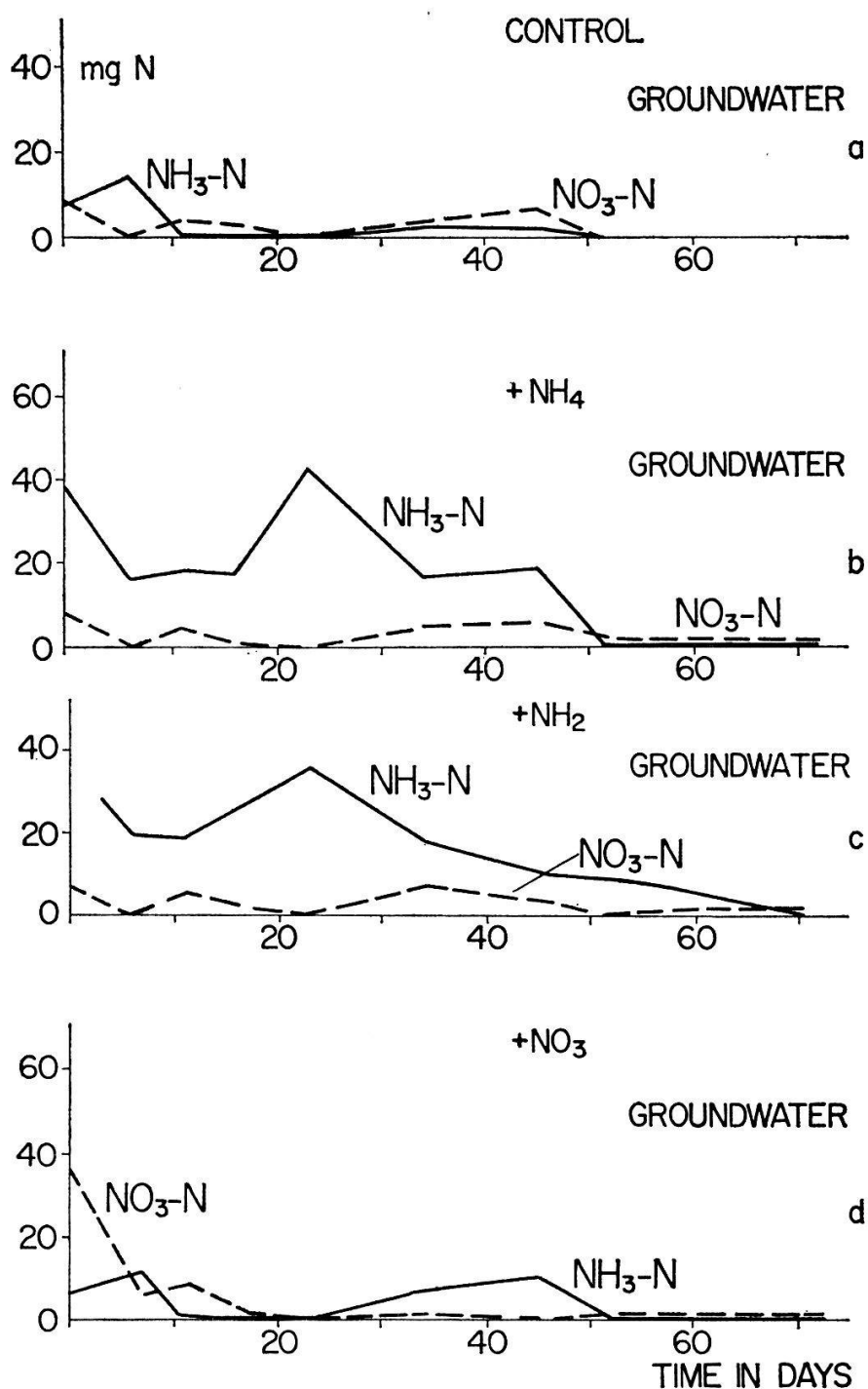
Fig. 30 The dry soil; nitrogen relations when flooded.

ler. Samples were taken near the surface of the water, at the level of the soil surface and below the soil surface. O_2 content showed a gradient of 7.17, 4.35, 4.17 ppm from above down. All N substances added were lost from the system. Here denitrification was active. Nitrate disappeared most rapidly, and the curves after the addition of NH_4 and NH_2 were similar (Figs. 29 b, c, d, 30 b, c, d). At the end of the experiment the artificial ground water was tested for the presence of nitrates and ammonium, and gave zero values for all jars.

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Soils of a *Senecio aquaticus* meadow and a *Magnocaricion* swamp were tested in the same way but analysed less frequently. Apart from their lower nitrification capacities the results differed in no degree from those for wet soil.

The ammonium is adsorbed on the lattices of the colloids of the organic particles and presumably they are the site of nitrate accumulation. QUASTEL (1946) found that the rate of nitrification was a function of the number of ammonium ions adsorbed onto or combined in the soil in the form of base-exchange complexes. When the soil atmosphere is changed this activity must be modified; a reduction in aeration results in a reduction in nitrification. Aeration may be reduced by local build up of high CO_2 concentrations or by excess of water. In the soil both act in combination. Normally the CO_2 in the soil fluctuates according to the activity of the plant roots and the micro-organisms. Nitrifying bacteria are aerobic and they possess small respiration, CO_2 being the waste product. HIBBARD (1919) showed that soil CO_2 increased proportionally to the amount of manure added and the total C showed a rapid decrease. This was due to bacterial activity. The soil structure in the experiments described above was modified according to the aeration. The normal fibrous structure of the controls was lost under anaerobic conditions presumably due to decomposition. This was probably conditioned by the relatively high constant temperature.

RUSSELL (1914) linked the CO_2 production and nitrate accumulation. He demonstrated that the NO_3 and CO_2 curves were similar and he termed them the main production curves. In an arable soil both curves closely followed the temperature during winter and the rest of the year followed the rainfall. Both rose in spring, fell in summer, rose in autumn and fell again in winter. That the NO_3 accumulation was conditioned by the rainfall was shown by the hot dry summers of 1911 and 1913 when the two maxima of spring and autumn merged and nitrification was high throughout the summers.

In the experiments no measures of nitrate oxide or N_2 gas were made. Restricted oxygen results in the production of some amides as well as ammonium but the effects of greatly lowering the O_2 tension (by pyrogallol) or flooding the soil (with an artificial ground water) demonstrated how sensitive the nitrification was to factors of aeration. In the wet meadow soils in the field denitrification must occur simultaneously with the nitrification process, the importance of one over the other being conditioned by aeration. Even in an arable soil with good aeration there is some denitrification present. ARNOLD (1954) examined the production of N_2O from both arable and pasture soils. They lost ca. one tenth of their mineral N a day as N_2O when the soils were wet, but this value was 100th less when the soils were dry. MEYER (1957) followed the N budget of same wet meadows in Winogradsky's medium. The relation to the air-volume percent was not always clear although the *Glycerietum* with an air volume of $< 1\%$ showed the highest denitrification. Some of these results are quoted since they represent the same types of meadows (Table 23).

With all the plots he examined he obtained a rectilinear increase in nitrification with increasing air volume. Probably it is the O_2 tension that is vital. In

Table 23 Relation of nitrification and denitrification to the air content of the soil (after MEYER, 1957)

Vegetation	Air volume %	Nitrification mg NO_2/l after 5 days	Denitrification mg NO_3 denitrified in 48 hours
Arrhenatheretum	39.1	4.1	3
	21.7	5.3	22
Cirsium oleraceum-Ass.	11.2	5.0	10
	8.4	8.3	6
Glycerietum	< 1	1.6	96

21 days with added ammonium and an O_2 content of 20%, 46% of the added N was converted to NO_3, but at 1% O_2, only 21% and only 2% at 0.4% O_2 (AMER and BARTHOLOMEW, 1951).

It seems that the O_2 tension has to reach extremely low levels to restrict nitrification. This would explain the nitrification observed under inundated conditions. Normally losses by denitrification are negligible at water levels less than two thirds of the soil water holding capacity. The wet meadows grow on soils with a high soil water holding capacity and the amount of denitrification in the field is correlated with the moisture regime. In the experiments following the seasonal fluctuations in nitrification only nitrate and ammonium were measured. Since denitrification results in the loss of N_2 or N_2O, denitrification was not easily detected; the ammonium arose by decomposition of organic compounds. The control soils in the experiments with varying aerations demonstrated that the traces of ammonium sometimes present when the potential nitrification was measured represent decomposition.

d. The distribution of nitrification activity in the field

The local variations in nitrogen supply were investigated over a small area by comparing the potential and actual nitrification at five plots on a transect. This was a wet meadow that was flooded once or twice each year, and bordering the stream were nitrophilous stands. By the side of the stream was (1) *Urtica dioica*, on the bank (2) *Festuca rubra* and *Galium mollugo*, and the plots (3), (4), (5) were in the meadow. Plot (3) was rich in carices *(C. acutiformis* and *C. panicea)*, plot (4) in *Filipendula ulmaria* and some carices, and plot (5) in *Cirsium oleraceum* and *Angelica silvestris*. The plots were examined during the summer. In the nitrophilous stand bordering the water the actual nitrification more or less equalled the potential; this was less marked in plot (2). Plots near the stream were presumably liberally supplied with nitrates from the water. The three stands in the meadow represented a gradient of humidity, and it was very noticeable that the proportion of nitrification increased from plot (3) to plot (5) (Fig. 31). These plots were separated by only 2.5 metres and the results empha-
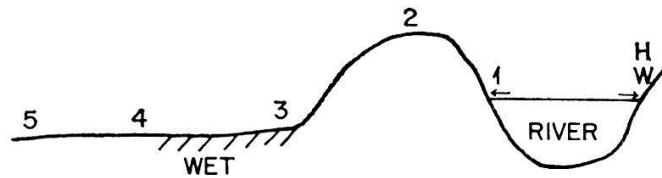
Sketch showing position of samples. H. W. represents high-water mark.
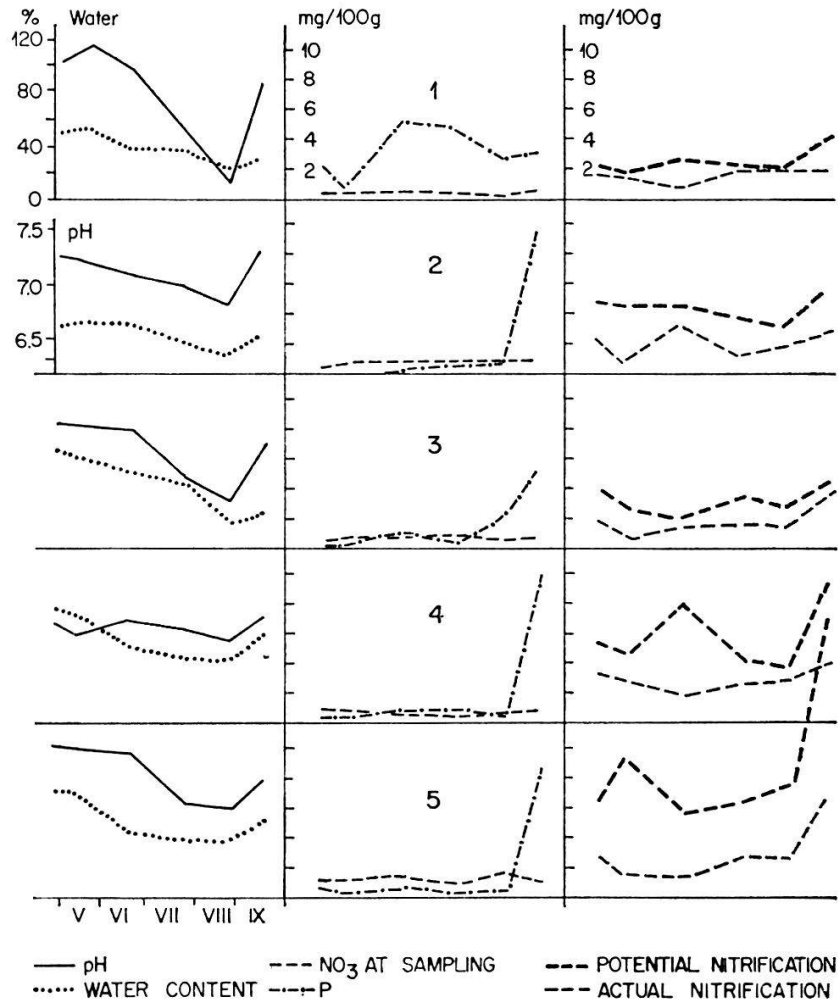
Fig. 31 Soil data from plots on a transect (sampling took place during the period May to September 1963).

sised the variation likely to occur in a meadow over a short distance. This was partly overcome in the sampling in the three experimental areas by taking a large mixed sample of many small samples. Here a large mixed sample was taken over a relatively small area.

The variations in nitrate content at sampling were not great, nor in soil P though the *Urtica dioica* stands showed high levels of P.

The five soils all had similar bulk densities and the results are given as mg per 100 g. Ammonium was rarely present and caused no variations in the overall picture.

The effect of soil depth on nitrification was studied by means of three profiles taken December 6, 1963:

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Soil 1. Organic soil from Germany: 0–3 cm organic material, 3–30 cm loam with humus. Below 30 cm grey clay. In the region 11–20 cm there were red iron flecks. Water table at sampling at 14 cm below the soil surface.

Soil 2. Organic soil from Germany: 0–1 cm organic material, 1–40 cm loam with humus, but with a better crumb structure and less peat-like than soil 1. Below 40 cm grey clay. Water table at sampling 19 cm below the soil surface. Iron flecks 15–20 cm.

Soil 3. Sandy soil from Alsace: 0–1 cm organic material, 1–18 cm silty-loam, 18–23 cm sand. Below 23 cm friable loam.

Soils 1 and 2 were gley soils. Under waterlogged conditions (prevalent in these soils) when the water table is high, iron and manganese become reduced to ferrous and manganous salts which are soluble and more mobile. When drying occurs these become re-oxidised and leave rusty concretions and small black manganese particles. The presence of brick particles was due to amelioration with gravel. There was slight evidence from the colour of the topsoil that the soils had been ploughed, probably about 50 years ago. The sandy soil was an alluvial soil.

In all cases four holes were dug and samples taken from sides of the holes at 1, 5, 10, 15, 20, 35 and 50 cm depth. Samples from the same layer were thoroughly mixed. On arrival in the laboratory the soils were analysed for N, P, CaCO$_3$ and pH.

Water content increased with depth although CaCO$_3$ and pH were similar throughout the profile. Phosphorus tended to be present only in the uppermost layers. Nitrate was only present in the top few cm although ammonium extended lower. The distribution patterns are presumably related to the oxygen contents. Samples of each horizon were incubated and the nitrification measured after 6 weeks. The highest nitrification was in the samples taken around 5 cm in the organic soils and 1–5 cm in the sandy soil (Table 24). The depth from which a sample is taken can considerably modify the nitrification.

It was noted that there was some nitrification in samples taken from below the water table. This may occur in the field provided there is sufficient oxygen available. In an experimental system using large cylinders and an artificial water table nitrate tended to accumulate in the top few cm of the water when nitrification was active in the soil above (e.g. after the addition of ammonium salts).

The activity of the nitrifying bacteria in the upper 20 cm of the soil was demonstrated in similar meadow soils from Czechoslovakia by VICHEREK (1962). He determined the N-percent in a *Deschampsietum caespitosae* (which is a poor meadow of the *Calthion*) and a wet *Arrhenatheretum*. The N was always higher in the uppermost layers. There is probably a temperature effect also, since below ca. 30 cm the soil temperature rarely rises above 10 °C.

e. The bacterial populations in relation to nitrification

Any change in the nitrification capacity of a given soil may be due to reduced population of the nitrifying bacteria or inactivation of the population caused by adverse physical conditions. Experiments were designed to culture the nitrifying bacteria and obtain counts as a measure of the population size. Counts were made at different sampling times and also from several horizons of the soil profiles.

From the large mixed sample from the field plot the equivalent of 1 g of dry soil was placed into a sterilised Erlenmeyer flask and 100 ml of 1-percent potassium aluminium sulphate was

Table 24 The nitrogen relations of soil profiles (mg/100 g). Soil phosphorus is also given

Depth in cm	Soil 1 (G 4)					Soil 2 (G 10)					Soil 3 (F 3)				
	NH_4—N		NO_3—N			NH_4—N		NO_3—N			NH_4—N		NO_3—N		
		After		After			After		After			After		After	
	Initial	6 weeks	Initial	6 weeks	P	Initial	6 weeks	Initial	6 weeks	P	Initial	6 weeks	Initial	6 weeks	P
1	1.3	0	3.3	12.0	0	0.1	0	0.3	9.3	0.1	0.3	0.1	0.2	6.5	0.2
5	1.7	0	2.7	13.5	0.1	0.1	0	1.7	14.2	1.6	0.3	0.1	0.8	6.0	0.6
10	1.0	0	0	11.7	1.6	0.3	0	0.3	7.7	0.5	1.1	0	0.8	5.5	0
15	1.3	0	0	12.2	0.3	1.8	0	0	1.7	0.1	0.7	0	0.9	4.8	0
20	1.3	0	0	7.7	0	2.0	0	0	6.2	0.9	0.5	0	0.9	1.0	0
35	0	0	0	6.7	0	0	0	0	3.5	0	0	0	0.8	0.4	0
50	0	0	0	3.5	0	0	0	0	0.4	0	0	0	0	0	0

added. This was violently shaken for 5 minutes. A dilution was prepared using sterile pipettes and sterile water. 1 ml of the extraction was diluted 100 times and 1 ml of this dilution further diluted 100 times. 1 ml replicates were plated.

The bacteria responsible for nitrification include several genera. *Nitroocystis, Nitrosogloea, Nitrosomonas, Nitrosococcus* and *Nitrospora* are responsible for the oxidation of ammonium, and *Nitrocystis* and *Nitrobacter* for the oxidation to nitrate. The stages of nitrification are not fully understood although nitrification appears to occur by a step-like oxidation, e.g. $NH_3 \rightarrow NH_2OH \rightarrow (NOH)_2 \rightarrow HNO_2 \rightarrow HNO_3$, and this is considered to be entirely a bacterial process. The bacteria of chief importance are *Nitrosomonas* and *Nitrobacter*. They are obligate chemoautotrophic and they flourish in inorganic media utilising energy derived from the oxidation to produce organic matter. A culture medium was prepared by the method of MILLBANK (1956)*.

Three solutions were prepared and mixed using 2 ml of solution 1, solution 2 and 12 ml of solution 3:
(1) 0.2 g NaCl, 0.05 g $MgSO_4.7H_2O$, 1.2 g Na_2HPO_4, 0.6 g KH_2PO_4, 0.1 g $NaHCO_3$, 1 mg $FeSO_4.7H_2O$, 1 g $MnSO_4.4H_2O$, tap water to 100 ml
(2) 0.8% w/v $(NH_4)_2SO_4$ in water
(3) 2.5% w/v Bacto-Agar
The solutions were mixed in a test tube, sterilised and then poured into a Petri dish whilst still warm. The Petri dishes used were sterile plastic disposable ones supplied by Oxoid. Immediately after pouring, the ml suspension was added. The plates were incubated at 25 °C for 25 days. 12 plates were prepared from each suspension, 6 were used to determine the nitrite producing bacteria, and 6 for the nitrate producing bacteria. The plates were tested for nitrite by adding several drops of sulphanilic acid solution (0.6% in 30% acetic acid) and immediately afterwards several drops of N-(1-naphthyl) ethylene diamine dihydrochloride (0.1% in 3% acetic acid). Nitrite stained bright red. The plates were tested for nitrate by adding several drops of acidic diphenylamine solution. Nitrate stained blue-black. It was apparent that nitrite was readily diffusible since on staining, the whole medium occasional took up a faint pink colour. The stain for nitrate tended also to stain for nitrite and the actual numbers were obtained by substraction.

Soils of the sandy loams and humus-rich loams were investigated, since it proved difficult to extract the nitrifying bacteria from the mineral clay loams. The results are given as mean number of colonies per plate. Comparisons of the numbers from two different soil types are not valid since there were different amounts of extraction.

Three experiments were designed:
(1) counts of nitrifying bacteria from different vegetation plots sampled at the same time,
(2) counts of nitrifying bacteria from the same plot sampled at different times,
(3) counts of nitrifying bacteria from different horizons of the profile sampled at the same time.

Experiment 1

Samples were taken from six plots from Germany (representing three vegetation variants), and four plots from France (representing two vegetation variants). The results are shown in Table 25.

* I am grateful to N. WALKER, of Rothamsted Experimental Station, England, who suggested this method.

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Table 25 Counts of nitrifying bacteria from several field plots (G sampled 13/9/63, F sampled 10/9/63)

Plot	Vegetation unit	Nitrification capacity mg/100 g	Bacteria staining for NO₂	NO₃		Total nitrifying bacteria/plate
			NO_2	NO_3		
			mean no./plate			
G 1	Wet	7.38	1.0	2.4		3.4
G 2		6.13	1.1	1.7		2.8
					mean	3.1
G 4	Typical	17.41	1.2	6.8		8.0
G 5		7.43	2.4	5.0		7.4
					mean	7.7
G 9		7.82	2.0	9.2		11.2
G 10	*Arrhenatheretum*	9.31	4.1	9.3		13.4
					mean	12.3
F 1	Wet	6.32	1.2	0.6		1.8
F 3		3.51	0.8	0.8		1.6
					mean	1.7
F 7	Dry	4.21	1.1	2.5		3.6
F 8		0.83	0.2	2.2		2.4
					mean	3.0

It was obvious that the more fertile plots contained a larger population of nitrifying bacteria and the plots of the same vegetation variant gave similar counts. The sandy soils gave lower counts of bacterial than did the organic. This was probably due to a lower extraction. There was some variation in the relationship between the numbers of NO_2 and NO_3 counts although the increase in the number of bacteria in the more fertile plots seemed to be caused by a larger increase in *Nitrobacter* in both soil types.

The soils were sampled around the autumn peak of nitrification. This peak had a slightly different spread in the various plots and this perhaps accounted for the differences in nitrate production. It was not possible to relate the bacterial counts to the nitrate production.

Experiment 2

Counts were made at four periods, October, December 1963, January, April (May for sandy soils) 1964 (Table 26).

Nitrification was high at times 1 and 4 and was low at times 2 and 3. The number of bacteria fell in all plots during the winter. This was due to a fall in the population of *Nitrobacter;* despite variations, that of *Nitrosomonas* remained similar. At time 4 there was a population burst resulting from an increase in both bacteria. This population burst corresponded to the spring

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Table 26   Counts of bacteria at different sampling times: Mean number per plate

	Sampling times	1			2			3			4		
	Date	28/10/63			6/12/63			2/1/64			6/4/64		
Plot	Vegetation	NO₂	NO₃	Total	NO₂	NO₃	Total	NO₂	NO₃	Total	NO₂	NO₃	Total
G 1	Wet	1.0	2.4	3.4	1.1	1.0	2.1	0.5	0.6	1.1	3.6	3.2	6.8
G 4	Typical	1.2	6.8	8.0	1.0	2.9	3.9	1.1	1.7	2.8	5.4	7.3	12.7
G 10	*Arrhen.*	4.1	9.3	13.4	4.2	4.6	8.8	3.5	2.9	6.4	11.8	11.4	23.2
	Date	21/10/63			2/12/63			6/1/64			2/5/64		
F 1	Wet	1.2	0.6	1.8	0.2	0.8	1.0	0.	0.8	0.8	2.5	6.1	8.6
F 8	Dry	0.2	2.2	2.4	0.4	1.9	2.3	0.3	1.8	2.1	7.3	11.4	18.7

flush of nitrates. The increase in *Nitrosomonas* suggested that there were many substances formed by mineralisation of dead roots, micro-organisms and soil animals, or of organic soil reserves is probably the prime factor causing the spring release of nitrates.

Experiment 3

Two of the organic soils were sampled at 1, 3, 5, 10 and 30 cm. The nitrate and water contents were determined and the nitrifying bacteria at different depths were counted (Table 27).

The nitrate content was inversely related to the water content in both profiles, i.e. with higher water content there was less nitrate. In the profile of G 4 the number of bacteria corresponded closely to the nitrate present. The number of bacteria and the nitrate content were not altogether parallel in plot G 10. In

Table 27   Nitrifying bacteria at different depths in the soil (6/12/63)

Plot	Depth cm	NO₃ mg/100 g	Bacteria staining for NO₂ mean no./plate	NO₃	Total nitrifying bacteria/plate	% water (weight)
G 4	1	0.8	2.2	8.9	11.1	202.3
	3	0.4	2.5	4.8	7.3	205.2
	5	0.7	1.6	4.0	5.6	204.1
	10	1.3	8.1	12.3	20.4	197.6
	30	0	1.2	1.7	2.9	220.1
G 10	1	0.3	1.0	3.1	4.1	151.2
	3	0.5	3.4	2.1	5.5	152.0
	5	0.5	2.0	9.0	11.0	141.2
	10	2.1	4.2	4.1	8.2	112.6
	30	0.1	1.1	2.8	3.9	171.7

both plots it seemed that the nitrate content, the bacterial population and the water content were related. Presumably increased water lowered the aeration and restricted the bacterial growth, thus limiting the amount of N oxidised. The individual numbers of *Nitrosomonas* and *Nitrobacter* varied according to the profile depth. The numbers of one seemed unrelated to the numbers of the other. This suggested that the aeration conditions in the profile were continually changing.

These three experiments showed that the actual population of nitrifiers fluctuated and during periods of low nitrate production the population was smaller. This occurred during adverse conditions and the high water and low aeration restricted not only the bacterial activity, but the generation time. Reproduction was inhibited and a smaller population was counted. These factors affecting the population size also acted differently in the vegetation variants. Aeration was poor in the wet types and good in the dry. It was significant that the bacterial population increased accordingly (experiment 1).

V. Phosphorus

Phosphorus content was measured to see whether there were any differences in phosphate relations between the vegetation types. The data are given as mean phosphorus content for the vegetation type.

Soil phosphorus content was determined in all plots throughout the growing season of 1963. The soil was extracted with 0.5 N acetic acid. Some of the phosphate which dissolves in the acid may be reabsorbed during extraction and to overcome this 1-percent hydroxy-quinoline was added to dilute acid (WILLIAMS, 1950). This reabsorption is of importance when iron hydroxides are present. These were noticeable as concretions in the organic soils from Germany and flooding of plots in Alsace caused the deposition of iron oxides (and maybe aluminium hydroxides, which also cause reabsorption during extraction).

1. Swiss Midlands

The amount of Phosphorus present varied greatly during the year and the fluctuations in all vegetation units were remarkably parallel (Table 28). Phosphorus was high in the periods April–May, July–August and during September.

Table 28 Phosphorus content of the mineral soils (mg/l) from Switzerland

Vegetation unit	1963 Spring			Sampling date Summer					Autumn		1964 Winter	
	27/4	14/5	6/6	26/6	16/7	6/8	27/8	13/9	2/10	2/11	10/12	21/1
Wet	2.1	13.5	16.1	3.2	*30.5*	13.2	0	27.9	7.5	0	0	0
Typical	11.2	*46.9*	11.6	3.0	39.3	12.6	0	29.0	7.3	3.0	0	0
Dry	15.4	63.0	1.0	8.3	20.9	*87.3*	0	34.8	8.0	7.8	0	0
Arrhen.	19.6	*187.5*	111.6	6.6	17.1	7.3	0	96.7	13.3	2.2	0.7	0

It fell to very low levels in early June, late August and during autumn. The two latter periods corresponded to the decrease in activity of the nitrifying bacteria and probably represented unfavourable soil conditions. There was no direct correlation with soil moisture content although the maxima of phosphorus content roughly corresponded to periods of high water content.

Phosphates in the soil are found in the soil solution as inorganic forms, and in the organic material. Normally the phosphorus in the organic material is "unavailable"; but it is mineralised slowly and thereby becomes "available". In arable soils phosphate movement in a vertical direction is extremely slow and nitrate ions would be leached before phosphorus. This is probably the case for most well-drained soils, but in soils which are subject to water logging phosphate may move much more easily down the profile, possible carried by ferrous ion (RUSSELL, 1961). Soils of the wet meadows always possessed a high moisture regime and it is likely that phosphorus was more labile in these grasslands.

Apart from the similar fluctuations in soil phosphorus during the year there were well marked differences in the quantity of phosphorus present in the vegetation types. When phosphorus was present in large amounts the actual quantities increased from the wet to the dry vegetation units, i.e. Wet < Typical < Dry < Arrhenatheretum.

2. Alsace, France

The soils from Alsace contrasted with those from Switzerland because there were only two large maxima of soils phosphorus content (Table 29): in April–May and early September. These did not closely correspond to the peaks in nitrification since there was no parallel to the summer maxima in nitrification, but the fluctuations of soil phosphorus were similar to those of NO_3. The lowest values were recorded in June–July and autumn, and it appeared that the soil water content was a controlling factor both for the nitrification and the phosphorus content. There was, however, a time lag. As in the mineral soils fluctuations in phosphorus content followed the same trends in the three vegetation units and there was more phosphorus present in the dry types.

3. Southern Germany

Phosphorus content was high during May–June and late October (Table 30). Low values were found August–September and in late autumn. The periods of

Table 29 Phosphorus content of the sandy soils (mg/l) from Alsace

Vegetation unit	1963 Spring				Sampling date Summer				Autumn		1964 Winter	
	20/4	7/5	28/5	19/6	9/7	30/7	20/8	10/9	1/10	21/10	2/12	6/1
Wet	8.2	12.4	4.2	0.5	1.7	5.0	16.8	*17.4*	0	0	0	0
Typical	10.3	11.6	7.0	2.0	6.8	4.3	*45.3*	26.8	7.0	0	0	0
Dry	*60.9*	23.0	16.0	1.9	0	13.9	38.9	45.8	8.1	0	0	0

Table 30 Phosphorus content of the organic soils (mg/l) from Germany

Vegetation unit	1963 Spring			Sampling date									1964 Winter	
				Summer					Autumn					
	20/5	3/6	24/6	18/7	1/8	24/8	16/9	1/10	28/10	20/11	6/12	2/1	31/1
Wet	6.4	*11.5*	6.3	2.6	7.3	2.7	2.0	11.0	7.2	*9.7*	0	0	0
Typical	8.4	10.3	11.8	5.7	9.9	0	1.0	0	6.0	*19.1*	0	0	0
Dry	11.8	16.7	10.0	2.3	4.1	3.6	0.5	6.3	7.0	*18.9*	0.8	0.2	0
Arrhen.	33.4	44.2	18.1	14.5	10.2	0	0	0	*46.3*	20.7	4.5	0	0
Scirpus	9.3	*10.4*	0.9	3.6	5.5	1.7	0.9	0.7	0	6.3	3.2	0	0

high phosphorus content did not correspond closely to those of high nitrification, although the two periods represented periods of soil activity and phosphorus was high when the nitrate content at the time of sampling was high. The low phosphorus values were recorded soon after the water table began to fall after reaching its highest levels. In the organic soils the water table appeared more important than the moisture content of the soils near the surface, although the two are related.

There was more variation between the vegetation units, though phosphorus content tended to increase from the wet variants to the dry variants. The *Arrhenatheretum* showed much higher levels of phosphorus than the other vegetation types. The *Scirpus silvaticus* rich variant showed slight differences from the other variants. Phosphorus was in low amounts for longer periods and the actual amounts were usually lower than in the wet unit. It might be that phosphorus is an important factor controlling the stability of the *Scirpus* variant.

Although the fluctuations in phosphorus content were not very similar in the three experimental areas, the actual relations between phosphorus and the vegetation units were the same. Phosphates are supplied by fertilisation, but these meadow soils contained adequate quantities of organic matter and phosphorus is slowly released from this. The mineralisation of phosphorus takes longer than that of nitrogen because after incubation at 20 °C for 6 weeks the content of phosphorus was more or less unchanged. Since both phosphorus and nitrogen are released by mineralisation there must be a relation between the two. HOLMAN (1964) found that an increase of phosphorus in organic soils was accompanied by an increased nitrogen content, and MALMER (1962) suggested that there was a curvilinear relation.

It is necessary for phosphorus to be added to agricultural land, due to the loss by harvesting and to the low level of available phosphorus (with its slow mineralisation in natural temperate vegetation). The continual fertilisation of the wet hay meadows and their relatively long age has meant that phosphorus is probably rarely deficient.

The phosphorus contents of the hay meadows could well be a factor determining their floristic composition and their subsequent yield and palatability. KUHNEN (1951) investigated species of grassland in relation to their ecological

indicator value for phosphorus. Not all of the characteristic species of the wet meadows were given phosphorus values, but the following may be correlated with the increase in phosphorus content from the wet to the dry vegetation variants.

Table 31   P indicator values, after KUHNEN (1951)
Increase in phosphorus indication from 1 to 5; 0 = indifferent. Species chiefly found on the wetter plots:

Lychnis flos-cuculi	2	*Colchicum autumnale*	2
Filipendula ulmaria	2	*Deschampsia caespitosa*	2
Cirsium palustre	2	*Carex fusca*	1
Cardamine pratensis	2	*Galium palustre*	0
Juncus effusus	2	*Holcus lanatus*	0

Species chiefly found on the drier and well fertilised plots:

Geranium pratense	4	*Tragopogon pratensis*	3
Heracleum sphondylium	3	*Carum carvi*	3
Crepis biennis	3	*Trisetum flavescens*	2
Avena pubescens	3	*Arrhenatherum elatius*	0
Bromus mollis	3	*Trifolium dubium*	0
Carex hirta	3	*Daucus carota*	0
Gallium mollugo	3	*Leontodon hispidus*	0

Species found on both (characteristic of the wet fertilised meadows):

Myosotis palustris	5	*Cirsium oleraceum*	4
Angelica silvestris	4	*Lysimachia nummularia*	4

That the floristic composition depends on the fertilisation is shown by the characteristic species which are indicators for good nitrogen status and good phosphorus status. Phosphorus is an essential plant nutrient, and from soil to soil the amount and availability of phosphorus varies. The similar differences between the relative amounts of phosphorus present in the vegetation units of the hay meadows in three contrasting regions emphasised the hypothesis that apart from water, both the availability of nitrogen and that of phosphorus determined the floristic variations.

VI. Acidity

Only large differences in the acidity of the soil result in changes in the floristic composition of grasslands depending on the tolerance of the species present. In the case of the wet fertilised meadows these differences proved to be small. Calculations of the mean R values of the stands in the original large table (see footnote on page 78) using ELLENBERG's scale of 0, 1–5, demonstrated a similarity between all columns of the table. The R value varied from ca. 3.6 to ca. 4.0. This represented mean pH of 6.3 ± 0.6. This emphasised that the *Cirsium oleraceum* grasslands and the wet *Arrhenatheretum* gave reactions close to the neutral

point; or on the average on the acid side of pH 7. Indeed, the three experimental areas gave a range of pH from 5.7 to 7.3. All meadows investigated therefore represented neutral grassland, and pH is not a factor controlling their floristic composition.

A comparison of the pH values of two or more plots gives little information unless the soils show extremes of acidity or alkalinity. A measure of the change in pH within the same plot was essential because of the sensitivity of nitrification to changes in pH, although SJÖRS (1954) suggested that for various types of meadows the pH dependence of nitrogen was more or less non existent. Normally nitrification in open field soils is limited by acidity and below pH 4.5 the rate of nitrification becomes negligible even though it has been recorded at lower pH values. Other microbiological processes, e.g. nitrogen fixation and decomposition of organic material, are also adversely affected by acidity.

Seasonal fluctuations in pH were recorded in each plot throughout the experimental period. Some of the normal variation in pH from point to point was eliminated by the mixed sampling, and several replicate measurements were made. Usually the pH in any one plot did not vary more than one unit of measurement. These small variations were unlikely to affect the nitrification to any great extent.

The sandy soils from France showed a fairly smooth variation in pH. This fell during spring and summer and rose again during autumn, and the highest values were during the winter. Soils from all three vegetation types behaved similarly. The seasonal movement of pH followed the same trend as that of soil water. The mineral soils were much more irregular although the same seasonal fall in summer and increase in winter was observed. Again there were no differences between the vegetation units. This was also the case for the organic soils, where again the seasonal change in pH followed those in water content.

VII. Discussion

Experimental investigations of the edaphic factors of the wet fertilised *Calthion* meadows and the wet forms of the *Arrhenatheretum* pointed to remarkable similarities in the habitats of these grasslands even on diverse soils and in different geographical regions. These results emphasised the overall stability of the community, and in the three experimental areas equilibrium was maintained in relation to the agricultural management.

The community was arbitrarily divided into vegetation units (and variants) representing stages in a hydrosere and distinguished by their floristic composition, the units containing species of ecological indicator value. These units were compared for each soil factor investigated.

The soil water content varied according to a seasonal pattern. pH varied similarly and this appeared to be related to the water regime. Water content (affecting aeration) seemed to be an important factor affecting nitrification, and water

along with nitrogen status acted as factors differentiating the vegetation units. Lack of water was rarely limiting to plant growth even in the drier units.

The overall nitrogen status of the community demonstrated that nitrogen was an important factor controlling the vegetation units. There was a regular pattern of nitrification which may be characteristic of the community. The sharp distinction between the *Cirsietum oleracei* and the *Arrhenatheretum* in the classification of the phytosociologists does not appear valid. Nor was the difference between the *Senecio aquaticus* meadows and the *Cirsium oleraceum* meadows clear. The nitrification pattern showed that the *Senecio aquaticus* meadow could be equated to the sedge rich wet types of the *Cirsium oleraceum* meadows and the latter graded both floristically and in the nitrogen relations into the *Arrhenatheretum*.

Insufficient work has been carried out on the nitrogen relations of different grassland communities, though it is clear that the hay meadows investigated possess a nitrogen budget very different from the *Molinietum* straw meadows (see LEÓN, page 3).

The two maxima in spring and autumn have been quoted by several authors. RAPPE (1952) however demonstrated four maxima. HALL (1924) has pointed out the periodicity in nitrate production in S. African soils. In the wet meadows, three maxima were apparent although there was a fourth potential maximum in winter which was suppressed by the adverse climatic conditions. Much of the periodicity in nitrification must be due to wetting and drying effects. If nitrification occurs in winter it can be explained in terms of freezing and thawing, and so the minima in nitrate production preceding and following it are presumably conditioned by the low temperatures and high water content with low aeration. Minima in nitrate production during the summer are more difficult to explain. Normally, however, there is high precipitation at this time, which though not having a long lasting effect may cause the decrease. It may also in part be due to a reduction in the mineralisation processes.

The maxima in nitrification observed in the field were intimately related to the growth pattern. In spring, nitrates were needed for the resumption of growth. Cutting in June and October, which is the usual agricultural practise, would mean that the peaks of nitrate production would be available for regrowth. Presumably the high autumn peak was related to litter deposition.

It is not possible to say exactly what causes the fluctuations in the pattern of nitrification. Several factors were investigated to test their effect on nitrification and since so many factors may cause modifications these probably act in cooperation. The relations between nitrogen and moisture, and between nitrogen and temperature are not only present in the vegetation types but there is a fundamental relationship over whole areas (see JENNY, 1941). There are other unknown factors affecting nitrification. RUSSELL (1961) cites observations that a crop depresses the rate of nitrification in a soil and there is direct evidence from N^{15} experiments that the micro-organisms in the rhizosphere can extract carbohydrates from roots and use soil nitrate which is converted to organic nitrogen.

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The amount of nitrogen available for the growth of the plants depends on ammonification and nitrification and on the NH_4 or NO_3 nitrogen stored in the subsoil (produced in previous seasons). In these wet meadows the latter is unimportant due to the fluctuations in the relatively high water table. The experiments have suggested that availability is related to the amount and nitrogen content of the humus in the soil, and on the rate of oxidation of the nitrogen compounds. The rate is directly related to the physical factors of the soil environment. The bacterial cultures demonstrated that the population of the nitrifiers changed in proportion to the nitrification. The population was high when nitrate production was high. The population size must be a prime factor influencing the seasonal course of nitrification. It can only be presumed that the population size was controlled by the physical factors. Both could influence nitrification independently although the seasonal trends suggested some relationship.

Soil phosphorus seemed to be an important factor controlling the vegetation units. This is of interest in light of the work of PIGOTT and TAYLOR (1964). They reassessed the claim that *Urtica dioica* was a nitrophyte. They showed that this species required high phosphorus as well as nitrogen. It may well be that many of the species of the wet fertilised meadows, which are considered to be more or less nitrophilous species, also require phosphorus. These meadows are examples of an extremely fertile community.

Section C—Productivity

I. Introduction

From the agricultural point of view yield is the important outcome of the grassland ecosystem. This producing system may be affected by climate, soil, plant (species and % cover), animal and man; and the annual production may be quite variable. KÖNIG (1950) showed the positive correlation between yield, precipitation and fertilisation over several years, and such factors must be taken into account when comparing yield from different areas.

The hay meadows of different floristic composition have different productivities, e.g. KLAPP (cited in SCHREIBER, 1954) found a dry *Arrhenatheretum* produced 37.9 dz/ha[1], *Alopecurus-Arrhenatheretum* 59.9 dz/ha and the wet fertilised *Cirsium oleraceum* meadows 45.9 dz/ha. The types of the wet fertilised meadows consist of different species combinations, each individual contributing to the yield. HUNDT (1958) gave the yields of the different sociological units (Table 32):

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Table 32 Yield of vegetation types of the wet fertilised meadows (after HUNDT, 1958)

		Yield dz/ha[1]
Cirsietum		
Wet		
Carex acutiformis	(1)	50
	(2)	30–50
Glyceria maxima		30–50
Carex fusca		30–50
Typical		40–50
Galium mollugo		50–60
Arrhenatheretum		60–80

The yields of the vegetation units were studied in the three experimental areas. The qualitative yield is as important as the quantitative yield. Grass may be of low palatability to the animal when its economic use is limited to straw, or in good hay used for fodder the palatability should be high. The relative fodder value has been investigated by various methods, e.g. by the formula of KLAPP *et al.* KLAPP (1956) demonstrated how the quality of the hay varied according to the vegetation type:

e.g. *Molinion*	2.5–4.5
Calthion	2.5–4.5
Arrhenatherion	5.0–6.5
Polygono-Trisetion	3.5–4.5

These values were computed from the fodder values given to the component species (0, 1 ... 8, —1 poisonous). The good fodder grasses have high values, e.g. *Festuca pratensis, Poa pratensis* (8), *Alopecurus pratensis, Dactylis glomerata, Poa trivialis, Trisetum flavescens* (7); and the sedges, e.g. *Carex acutiformis, C. gracilis, C. fusca,* and rushes, e.g. *Juncus effusus, J. conglomeratus* have low values. The legumes generally have high forage values (> 4). It is obvious that the wet vegetation units have a lower mean value than the dry. *Caltha palustris, Cardamine pratensis, Colchicum autumnale, Equisetum palustre, Ranunculus auricomnus,* etc., found in the wet forms are poisonous and thus reduce the fodder value. The yield data of HUNDT showed that some of the less fertile units produced a high yield, as high as the drier more fertile units, but the quality was poor and suitable only for use as litter. BARYLA (1963) evaluated feeding value and litter value of hay from the floristic composition of the hay (using ELLENBERG'S method, 1952) of various meadows in the Tyśmienica River valley of Poland. In the *Cirsio-Polygonetum* a higher yield, compared to the *Molinietum,* was not always associated with a higher feeding value.

The yield data of several field plots from the three experimental areas were partitioned into components in order to assess the quality of the hay, and protein content and fibre content investigated.

[1] 1 lb/acre = 1.12 kg/acre, 10 dz = 1000 kg

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The species present in the meadows are remarkably constant (see Section I), and many indicate high soil fertility. Several species from the meadows were cultures in sand to determine their growth reaction to different levels of nutrients. The nutrient balance is higher in the drier units, and it was thought that experiments of this kind might throw light on the species performance in the different vegetation types.

II. Yield

1. Quantity of hay

Yield was investigated by sample cuts. In each plot investigated three quadrats 50×50 cm were chosen at random and the herbage cut to within ca. 4 cm of the ground to simulate mowing. The sample harvests were dried in an oven at 80 °C. Experiments were conducted to assess the quantitative and qualitative properties of the hay.

The mean agricultural yields of the three main vegetation units are shown in Table 32. This table shows that amount of hay which the farmers obtained from 18 plots (six from Switzerland, six from France and six from Germany) during the year 1963. The sample cuts were made as the farmers were about to mow. In each experimental region the lowest yield was obtained from the wet variants and the highest from the dry. The figures represent the yield obtained at cutting. Some of the dry plots were cut twice and some three times. The overall production seemed to be determined by the vegetation since an extra cutting produced little increase in yield, although a plot cut only once produced a lower total yield than the same vegetation unit in the same area which was cut twice (S 19 and S 2, not in Table 33). The wet units contained sedges but

Table 33 The mean yield, obtained by the farmers, of some wet fertilised meadows. Data converted to air dry weight dz/ha. The mean is of three replicated cuts and the standard deviations are shown (S.D).

Vegetation unit	France			Switzerland			Germany		
	Yield	S.D.	Plot	Yield	S.D.	Plot	Yield	S.D.	Plot
Wet	17.0	1.6	F 3	13.8	2.2	S 19	27.5	2.5	G 1
	28.7	2.4	F 1	17.5	2.3	S 2	25.6	2.4	G 2
mean regional yield	*22.8*			*15.6*			*21.5*		
Typical	30.4	2.2	F 2	39.7	1.7	S 6	32.4	1.6	G 1
	31.2	2.6	F 4	29.5	1.8	S 5	36.1	1.7	G 5
mean regional yield	*30.8*			*34.6*			*34.3*		
Dry	35.7	1.7	F 8	42.2	0.9	S 9	38.3	1.8	G 3
	39.1	2.5	F 9	45.3	1.3	S 8	41.1	1.4	G 8
mean regional yield	*37.4*			*43.8*			*39.7*		
Least significant difference P = 0.05	8.2			6.5			7.3		

were distinct from the *Magnocaricion*. Reports in the literature of high yield from the wet types are almost certainly from units floristically close to the *Magnocaricion*, where the yield is dominated by the vigorous growth of species such as *Carex acutiformis*.

In Tables 34, 35 and 36 the results of other cuts through the growing period are shown apart from those taken by the farmer. (At this point only the lines indicated by "DW" need be considered.) Care must be taken in interpreting these results; for instance, it is only possible to compare values from one area and not the three regions. Also the values obtained from cutting such small quadrats tended to be too small. The samples were taken to see if there was any overall differences in the yield characteristics of the vegetation units. There was some variation between the replicates and this must be taken into account. The sort of variation is indicated for two of the cuts for each area.

Despite these drawbacks the data clearly showed that in all plots dry weight yield increased rapidly in the late spring or early summer. This represents the second phase in the typical growth curve. Growth is slow in the early spring and then becomes rapid and more or less linear. After cutting regrowth was also rapid but greater in the dry units. In the autumn there was some decrease in the dry weight yield in some plots. This only occurred in the wet and typical units in Germany and Switzerland although it occurred in the dry units from France. This fall off in yield was due to dropping off of plant parts and seed production. In most dry plots investigated the dry weight continued to increase until the autumn. This was related to the time that the plot was mown. The earlier it was mown the greater was the tendency for the yield in autumn to fall, because the plants had a longer period in which to mature.

The distribution of growth throughout the period is shown by the relative growth rate (RGR) calculated from the formula of FISHER (1921).

$$\text{RGR} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

where $t_2 - t_1$ is the length of the growing period in weeks and W is the mean dry weight at harvest (Table 37). Early in the growing period of the stand RGR was high; this decreased as the growing season progressed. This was interrupted by the mowing and immediately afterwards RGR was high due to regrowth. Late in the growing season RGR reached negative values in many plots. RGR after cutting was higher in the dry units than in the wet (e.g. G2 wet 1.54, G3 dry 2.16 and 1.47).

The growth of stands of the vegetation units differed both in the amount and rate of production.

2. Quality of hay

Each sample after cutting was partitioned into 3 fractions—grasses, legumes and herbs. All grass like species, e.g. Carices, *Scirpus silvaticus*, *Luzula campestris*, were included in the grasses; such species as *Equisetum arvense* were included in the herbs. Each fraction was dried

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and weighed separately and the percent contribution to the yield of each fraction was calculated (Tables 34, 35, 36.)

Legumes in a hay contribute greatly to its palatability. The percentage of these was highest in the dry units. Some examples are shown in Fig. 32. The grasses tended to increase in early summer and the herbs increased in the autumn. The percentage yield of legumes in the dry units approximated to that in an *Arrhenatheretum* (grasses 60%, legumes 10%, herbs 30%; SCHNEIDER, 1954). The amount of grasses in the *Cirsietum* was lower than these values for an *Arrhenatheretum*. The legumes in each cut varies from year to year. KLAPP and STÄHLIN (1936) gave the percent of grasses, legumes and herbs in two yearly cuts for 7 years. The second cut always contained a lower quantity of grasses than the first, and the herbs increased in the second cut. The legumes varied. These relationships are also shown by the data in Tables 34–36. The yield of clovers in

Vegetation unit:
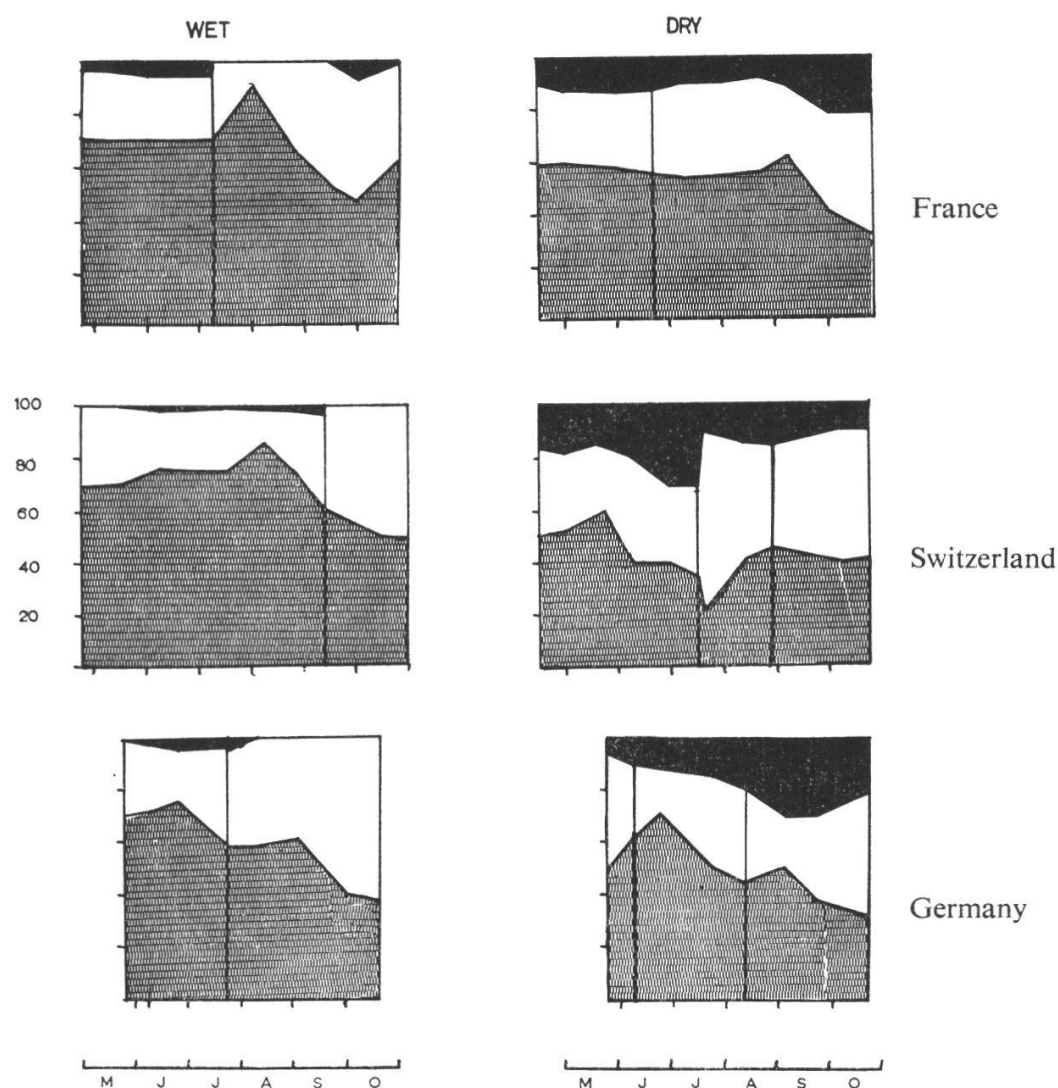
Fig. 32   The % of grasses (dotted), legumes (black), and herbs (unshaded) in the hay (1963). Data represent individual plots (mean of 3 replicate cuts).

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Table 34 Yield characteristics of field plots in Switzerland (means of 3 replicates). For each plot DW represents the mean dry weight converted to g/m²; L and H represent the percent contribution to the yield by legumes and herbs. The remaining percent equals the grasses, i.e. (100−L+H) = G%

Vegetation		Days 1963 (1 = January 1st)												
		106	126	153	172	177	188	197	207	220	237	254	258	278
S 3 Wet	DW	28.3	65.9	82.9		137.2	150.4	165.1		150.9	149.2		143.9	141.5
	L	*0.2*	*0.2*	*2.1*		*2.0*	*2.1*	*2.7*		*2.9*	*1.6*		*0.6*	*1.0*
	H	31.2	35.4	33.1		30.2	31.0	31.4		34.7	39.8		51.2	54.2
S 6 Typical	DW	132.3	182.2	247.5		264.0	270.9	26.1		57.8	104.9		119.1	125.9
	L	*6.4*	*9.0*	*12.4*		*17.2*	*17.1*	*5.4*		*6.7*	*6.6*		*7.1*	*8.3*
	H	33.4	30.1	30.2		29.3	31.1	31.1		26.6	32.3		47.0	48.3
S 5 Typical	DW	70.6	111.2	176.8		192.8	205.5	8.5		10.6	29.1		109.9	125.8
	L	*8.3*	*16.1*	*17.2*		*18.4*	*18.1*	*12.4*		*11.8*	*14.6*		*16.2*	*16.7*
	H	26.4	31.4	37.9		33.4	31.1	39.4		41.2	40.7		45.8	50.1
S 9 Dry	DW	40.3	117.2	195.5		328.7	33.6	63.9		61.3	132.9			
	L	*17.3*	*17.4*	*26.9*		*30.1*	*13.5*	*12.6*		*13.6*	*15.0*			
	H	29.7	24.3	21.0		22.2	33.6	38.3		43.2	45.3			
S 8 Dry	DW	40.3	100.6	167.5	183.5		117.6	143.0	148.5	29.6	77.3	93.2		
	L	*18.3*	*19.2*	*29.2*	*32.3*		*10.3*	*15.5*	*16.0*	*8.2*	*11.5*	*11.4*		
	H	33.4	20.2	35.6	37.2		59.8	49.3	41.2	53.1	45.4	49.3		

| = mowing

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Table 34(a)   The variations in the data and standard deviations at 126 and 220 days

Vegetation			Days 1963			
			126		220	
			Variation	S.D.	Variation	S.D.
S 3	Wet	DW	60.7– 69.9	4.00	141.1–162.0	8.58
		L	0 – 0.4	0.17	0.8– 3.2	1.61
		H	28.8– 38.0	4.70	34.3– 36.1	1.05
S 6	Typical	DW	177.2–190.1	5.65	55.5– 59.6	1.71
		L	3.3– 11.0	4.09	2.4– 8.9	3.04
		H	26.3– 37.0	4.86	20.7– 30.0	4.10
S 5	Typical	DW	98.8–119.2	8.89	7.6– 14.2	2.82
		L	14.5– 17.0	1.13	9.1– 11.9	2.17
		H	25.6– 37.1	4.70	36.8– 44.8	3.31
S 9	Dry	DW	115.4–118.1	1.32	60.1– 61.7	0.87
		L	17.3– 18.0	0.58	12.2– 15.0	1.14
		H	23.5– 26.1	1.28	41.1– 44.3	1.14
S 8	Dry	DW	93.5–107.4	5.68	26.5– 33.8	3.08
		L	14.8– 24.2	3.86	6.8– 9.4	1.07
		H	16.5– 23.6	2.89	50.3– 56.2	2.42

Table 35   Yield characteristics of field plots in Alsace (means of 3 replicates). For each plot DW represents the mean dry weight converted to g/m²; L and H represent the percent contribution to the yield by legumes and herbs

Vegetation			Days 1963 (1 = January 1st)									
			107	120	134	153	178	197	232	254	272	298
F 1	Wet	DW	24.8	53.8	86.8	121.4	133.0	17.2	33.3	40.3	55.5	37.2
		L	3.8	3.8	5.6	5.6	6.0	0	0	0	0.7	2.3
		H	26.2	26.5	24.1	23.7	24.3	28.8	9.1	48.3	44.3	38.2
F 8	Dry	DW	73.6	116.5	208.5	217.5	249.8	37.6	117.2	143.5	159.2	89.3
		L	11.3	12.3	14.1	14.1	13.2	9.2	9.3	13.1	22.4	22.3
		H	28.7	27.1	27.7	28.5	31.4	36.3	34.3	27.3	37.2	40.2

❙ = mowing

meadows fluctuates from year to year. Self-seeding normally occurs when late-cut hay is made. An early cutting, or intense cutting may reduce the self-seeding. This is not so important in the drier units where *Trifolium repens* contributes to the regrowth after the first cut, since it spreads vegetatively. Overseeding, e.g. with *Medicago* species, would greatly improve the hay value, but probably only for one year.

Table 35(a)   The variation in the data and standard deviations at 120 and 232 days

Vegetation			Days 1963 120 Variation	120 S.D.	232 Variation	232 S.D.
F 1	Wet	DW	45.6– 55.0	1.97	32.4– 34.0	0.67
		L	*2.9– 4.0*	*0.63*	*0*	*0*
		H	24.8– 26.7	1.45	7.3– 9.9	1.25
F 8	Dry	DW	112.9–118.1	2.55	114.5–120.3	2.39
		L	*11.4– 12.7*	*0.20*	*8.8– 9.7*	*0.34*
		H	25.8–280	0.89	33.7– 34.9	0.53

Table 36   Yield characteristics of field plots in Germany (means of 3 replicates). For each plot DW represents the mean dry weight to g/m²; L and H represent the percent contribution to the yield by legumes and herbs

Vegetation			145	151	176	198	219	239	262	278	290
G 1	Wet[1]	DW	95.6	111.5	163.5	183.5	34.0	108.6	87.6	92.2	93.9
		L	*0.5*	*1.7*	*4.2*	*6.6*	*1.4*	*1.0*	*0*	*0*	*0*
		H	31.3	35.5	31.5	37.0	39.1	43.2	48.6	51.5	54.4
G 2	Wet	DW	83.9	117.4	130.9	141.5	20.3	82.9	116.9	120.6	116.6
		L	*0.2*	*3.1*	*6.2*	*5.0*	*0*	*0*	*0*	*0*	*0*
		H	29.3	29.1	19.7	36.2	41.2	39.6	53.6	59.8	62.1
G 5	Typical	DW	183.8		247.8		78.6	104.6	118.9		116.6
		L	*4.4*		*10.2*		*8.2*	*10.3*	*14.4*		*17.3*
		H	31.3		33.5		37.1	38.3	45.6		47.0
G 3	Dry	DW	176.8	199.8	33.6	65.2	91.6	111.6	63.9	74.7	102.9
		L	*7.2*	*12.5*	*13.0*	*13.7*	*15.6*	*21.2*	*30.3*	*29.8*	*22.4*
		H	44.3	26.3	20.4	33.8	34.4	33.6	18.7	32.2	47.2

[1] *Senecio aquaticus*

The quality of the hay as fodder increased from the wet to the dry units. Some of the wet meadows with many sedges in the hay are suitable only for litter.

Measurements of the protein content of cuts from the vegetation units from Switzerland showed clear cut differences (Table 38). Hay from the dry types had a higher protein content than hay from the wet types, at all four sample cuts. The typical plots gave values slightly lower than the dry ones, except for cut 2, which was higher. Protein content increased from cut 1 to cut 2, then showed a decrease.

Table 36(a) The variation in the data and standard deviations at 145 and 219 days

| Vegetation | | | Days | | | |
| | | | 145 | | 219 | |
			Variation	S.D	Variation	S.D.
G 1	Wet	DW	90.2– 98.8	3.85	33.1–36.2	1.57
		L	0.1– 0.9	0.33	0.9– 2.0	0.46
		H	26.6– 34.0	3.33	36.7–43.2	2.91
G 2	Wet	DW	81.1– 85.3	1.98	17.5–22.9	2.01
		L	0 – 0.5	0.23	0	—
		H	26.4– 32.5	2.42	36.8–43.5	2.69
G 5	Typical	DW	173.0–190.2	7.74	77.1–79.4	1.06
		L	2.7– 5.0	1.16	7.0– 8.3	2.98
		H	27.2– 36.1	3.67	34.4–42.3	2.68
G 3	Dry	DW	172.2–178.9	3.26	91.1–91.8	0.39
		L	7.0– 7.4	0.02	15.2–16.3	0.50
		H	41.4– 47.0	2.29	30.8–38.2	3.02

The percent fibre in the hay also showed differences between the units. The wet plots gave the highest fibre contents which remained at similar values at all four cuts. Apart from cut 1 hay from the typical plots had a lower fibre content and the dry plots gave the lowest values. There were some anomalies in the results for the fibre content. This was probably because the number of samples was too small.

In Table 38 the values for fibre contents of the grasses, legumes and herbs have not been separated. At each sample cut the 3 samples were taken (see p. 170), then 3 subsamples of each were analysed. The values of protein and fibre were computed from the separate analyses of the grasses, legumes and herbs, separated at each sample cut and the results were then converted into the percent contribution to the hay from the percent dry weight analysis.

The changes in protein content during the growing season appeared characteristic of grasslands (see P. G. ARCHIBALD, 1930; OLOFESSON, 1962). The normal pattern was complicated by the regrowth after the farmer's harvests.

III. Mineral nutrition

Many of the species of the wet fertilised meadows are not restricted to the particular associations but occur in other communities. The association was characterised by a particular species composition even though some of these species have wide edaphic tolerances. This tolerance might be due to a broad physiological homeostasis (*sensu* WADDINGTON, 1957) in the individual plants

Table 37 Relative growth rates of field plots (RGR)

Days 1963 (1 = January 1st)

Switzerland

Area and vegetation		Spring			Summer										Autumn	
		106–126	126–153	153–172	153–177	172–188	177–188	177–197	188–197	197–207	197–220	207–220	220–237	220–254	237–258	258–279
S 3	W	1.10	0.06		0.15			0.06			−0.03		−0.04		−0.01	−0.01
S 6	T	0.11	0.08				0.02		1.64		0.94		0.23		0.04	0.01
S 5	T	0.16	0.12		0.01		0.04		1.70		0.77		0.39		0.04	0.03
S 9	D	0.37	0.14		2.94		0.52		−0.05		0.30					
S 8	D	0.32	0.13	0.04		2.06			0.16	1.18		1.27		0.08		

Alsace

Area and vegetation					Days 1963				Autumn	
		107–120	120–134	134–153	153–178	178–197	197–232	232–254	254–272	272–298
F 1	W	1.54	0.24	0.13	0.03	0.61	0.58	0.06	0.09	0.10
F 8	D	0.23	0.29	0.02	0.04	1.74	0.22	0.06	0.03	−0.16

Germany

Area and vegetation				Days 1963				Autumn		
		145–151	145–176	151–176	176–198	176–219	198–219	219–239	239–262	262–278 262–290	278–290
G 2	W		0.18		0.04		1.54	0.45	−0.06	0.02	0.01
G 1	W		0.15		0.02		0.60	1.44	0.10	0.01	−0.02
G 5	T		1.00			0.87		1.11	0.31	−0.01	
G 3	D	0.14		2.15		0.15		0.10	1.47	0.16	

W = wet units, T = typical unit, D = dry unit

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Table 38 Mean values of protein and fibre content of hay at 4 sample cuts (see Table 34, plots S3, S6 and S9). Means of 3 samples and 3 subsamples analysed[1]

		Sample	1	2	3	4
		days 1963	153	188	220	237
Vegetation			Protein percent			
Wet	Gramin.		6.2	*8.7*	5.0	3.8
	Legumes		0.2	*4.1*	0.3	0.0
	Herbs		*4.2*	1.3	2.2	3.8
	G + L + H		10.6	*14.1*	7.5	7.6
Typical	Gramin.		4.0	*14.8*	7.6	4.4
	Legumes		2.0	*3.0*	1.0	1.6
	Herbs		1.9	*7.1*	5.2	5.6
	G + L + H		7.9	*24.9*	13.8	11.6
Dry	Gramin.		4.9	2.6	*5.6*	5.4
	Legumes		4.3	*5.5*	2.3	2.0
	Herbs		4.8	7.1	*7.7*	6.0
	G + L + H		14.0	15.2	*15.6*	13.4
			Fibre percent			
Wet	G + L + H		26.6	*28.3*	27.6	26.7
Typical	G + L + H		*28.8*	18.2	21.8	21.9
Dry	G + L + H		*21.8*	18.8	20.4	20.9

[1] The analyses were kindly carried out by the staff at the Agricultural Research Station at Oerlikon (Zürich)

or to edaphic ecotypes within the species, though this is rarely the case. BRADSHAW *et al.* (1960) suggested that from an ecological point of view any small differences in mineral nutrition may be important. Plant communities are highly competitive systems and a change in conditions favouring one species or ecotype may be important. They described the response of 8 species of grasses to different levels of P in nutrient culture. Some species grew similarly at all concentrations, but for others growth was poor at all levels. These results were related to the natural distribution of the species in relation to soil P. The nutritional status of the environment might determine the distribution of the plants. Nutritional adaptations of plant populations within a plant species have been pointed out (e.g. by BRADSHAW and SNAYDON, 1959, in *Agrostis tenuis* and *Festuca ovina* —and by SNAYDON and BRADSHAW, 1962, in *Trifolium repens*). These varietal differences may complicate the interpretation of nutritional investigations, but from an ecological standpoint are important.

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Several species of the wet fertilised grasslands were examined for their response to varying levels of some macronutrients. It was possible to compare the response of species which cohabit naturally in the field and it was hoped that any data would throw light on the changes in the floristic assemblage between the vegetation units.

1. Methods

Thirteen species were chosen for growth in sand culture. Plants were obtained from a typical wet fertilised meadow and clones obtained by cutting up individuals used in the experiments to ensure genetic uniformity. The typical sociological amplitude of the species is shown in Table 39 (after OBERDORFER, 1962). The plants were grown in 20 cm clay pots lined with polythene bags. A hole in the bag corresponded to the drainage hole and this was plugged with glass wool to allow free drainage. White sand had been washed in 2-percent hydrochloric acid and distilled water prior to use. The plants were planted as small unrooted cuttings with about two leaves. Three plants were planted per pot and the pots were arranged in three randomised blocks in a cool greenhouse. 16 hours lighting was provided by mercury-vapour lamps. The culture solution was the Bangor modification of that recommended by HEWITT 1952 (Table 40). The stock solution was used in a 1:10 dilution with distilled water and 200 ml were given per pot on alternate days. The pots were leached weekly with just over a litre of distilled water.

Three experiments were designed to test the response of the species to different levels of N, P, Ca.

Table 39　The sociological amplitude of the 13 species grown in seed culture (N = N-value of ELLENBERG, 1952)

Species	N	Characteristic of	Also in
Dactylis glomerata	4	Molinio-Arrhenatheretea	Mesobromion, Fagetalia Ruderal
Arrhenatherum elatius	4	Arrhenatherion Arrhenatheretum	Ruderal
Holcus lanatus	3	Molinio-Arrhenatheretea	
Trifolium repens	3	Cynosurion	Plantaginetalia majoris Often sown in grassland
Ranunculus acer	3	Molinio-Arrhenatheretea (optimum in Arrhenatherion, Polygono-Trisetion, Calthion)	Molinion Mesobromion Ruderal
Cirsium oleraceum	3	Cirsio-Polygonetum and other Calthion associations	Filipendulo-Petasition Alno-Padion
Filipendula ulmaria	3	Molinietalia (especially Filip.-Petasition)	Alno-Padion Carpinion
Taraxacum officinale	4	Arrhenatheretalia	Ruderal
Chrysanthemum leucanth.	2	Arrhenatheretalia	Mesobromion
Angelica silvestris	3	Molinietalia (especially Calthion and Filipendulo-Petasition	Ruderal Alno-Padion Senecion fluviatilis
Medicago lupulina	2	Mesobromion	Arrhenatheretalia Ruderal
Ajuga reptans	0	Arrhenatheretalia	Fagetalia
Galium mollugo	0	Arrhenatherion	Alno-Padion

Table 40 The basic culture medium used in sand culture experiments (This gives 100 ppm N and 48 ppm S.)

	ppm[1]	g/l	ml used in 5 l of stock solution
Macronutrients			
$Ca(NO_3)_2 \cdot 4H_2O$	Ca 100	295	100
$NaH_2PO_4 \cdot 2H_2O$	P 42	108	100
KNO_3	K 78	101	100
$MgSO_4 \cdot 7H_2O$	Mg 37	184	100
FeEdta	Fe 5	17.5	100
Micronutrients			
$CuSO_4 \cdot 5H_2O$	Cu 0.064	1.0	⎫
$MnSO_4 \cdot 4H_2O$	Mn 0.55	11.15	⎬ 10
$ZnSO_4 \cdot 7H_2O$	Zn 0.065	1.45	⎭
H_3Bo_3	B 0.37	4.65	⎱ 20
$NH_4MoO_4 \cdot 4H_2O$	Mo 0.019	0.088	⎰

[1] The ppm are those in the watering solution

2. Experimental results

a. Response to nitrogen

The thirteen species were grown at 4 levels of nitrogen, 1, 50, 100, 250 ppm. The nitrogen level was varied by changing the amount of sodium nitrate added. At the low levels of nitrogen, potassium was replaced by potassium chloride and the calcium nitrate by calcium chloride. The sand was tested for pH after watering with the solutions. It was not necessary to make any adjustments. The plants were harvested after 100 days growth (Oct. 1963–Jan. 1964). The shoot and root portions were dried separately (80 °C), and leaf area determined by using Ozalid paper developed with ammonia.

An analysis of variance of the untransformed data showed the effect of species and nitrogen levels were highly significant:

Analysis of variance (Experiment 1), *** $P < 1\%$ (see also Table 41)

	df	ms	F	
Error	94	0.5239		
Blocks	2	0.0045	0.0086	ns.
Nitrogen	3	9.4420	18.0225	***
Species	11	3.7848	7.2243	***
Species and nitrogen	33	2.3160	4.4207	***
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Due to lack of available space in the greenhouse the three blocks were laid out with only 12 species in each. The pots containing *Arrhenatherum elatius* were placed in any available space and were moved. This species was not included in the analysis of variance.

Table 41   Variations in dry weight (g) per plant at four levels of N. The N level at which maximum growth was recorded is printed in italics for each species

| | Parts per million N. | | | |
	1	50	100	250
Dactylis glomerata	0.65–0.87	0.74–1.50	1.13–1.31	*1.27–1.59*
Arrhenatherum elatius	0.15–0.43	0.45–0.90	1.39–2.29	*1.65–2.93*
Holcus lanatus	0.71–1.01	1.26–1.69	1.93–2.66	*3.44–4.67*
Trifolium repens	0.69–0.72	0.71–0.87	*0.84–1.03*	0.87–0.95
Ranunculus acer	0.57–0.66	*1.07–1.23*	0.59–0.85	0.95–1.17
Cirsium oleraceum	0.12–0.20	0.22–0.25	*4.87–6.74*	0.81–1.11
Filipendula ulmaria	0.14–0.24	0.31–0.39	*0.82–0.91*	0.22–0.24
Taraxacum officinale	0.33–0.35	0.62–0.67	0.21–0.54	*1.19–1.29*
Chrysanthemum leucanth.	0.10–0.13	*0.40–0.52*	0.38–0.47	0.18–0.23
Angelica silvestris	0.36–0.57	0.37–0.64	*2.00–2.11*	1.30–1.96
Medicago lupulina	0.04–0.06	0.15–0.21	0.93–1.00	*1.10–1.21*
Ajuga reptans	0.03–0.04	0.19–0.24	*1.08–1.41*	1.21–1.30
Galium mollugo	0.10–0.49	0.54–0.66	0.81–1.23	*1.07–1.70*

The nature of the response to increased concentrations of nitrogen was different. This was indicated by the highly significant interaction species × nitrogen (P = 0.001). Growth of all species increased from 1 to 10 ppm. Table 41 showes that some species responded in the same way to N, e.g. *C. oleraceum*, *A. reptans*, *F. ulmaria* and *A. elatius* showed a reduced yield at high N levels. *Chrysanthemum* grew better at lower N. *Ranunculus* and *Angelica* showed a slight decrease in growth at increased N. There was a discrepancy in the results for *Taraxacum officinale* in that the yield at 100 ppm N was lower than at 50 or 250 ppm N. This could have been due to variation in the size of the cuttings planted. (The same uncertainty may of course be true for other values.) The growth forms at different levels of nitrogen varied. Normally most plants respond to nitrogen fertilisation by increased growth although the clovers do not reach such large increases. This was shown by *Trifolium repens* in this experiments and by *T. repens* and *T. pratense* by REMY and VASTERS (1931).

Very little work has been recorded on the anatomical response of plants on different nitrogen supply. Preliminary investigations of the stomatal frequencies were carried out on the material from Experiment 1. These plants were grown under ± constant conditions of illumination and watering and provided excellent material for these studies. Studies of field material are complicated by the possible presence of ecotypes, but the plants cultured were from the same clones. At high nitrogen it has been supposed that the number of stomata/mm², the number of vessels/mm² and the number of cells of the epidermis/mm² are less. This has been shown in some xeromorphs, e.g. *Andromeda polifolia* (SIMONIS, 1948), *Vaccinium vitis-idaea*, *V. uliginosum* and *Eriophorum vaginatum* (MÜLLER-STOLL, 1947). Stomatal frequency may be very sensitive to extremes of environment and this was demonstrated in a mesophyte, *Cerastium tetrandum*, in re-

sponse to light and wind (WHITEHEAD, 1956). SALISBURY (1927) has pointed out the variations in stomatal frequency in relation to (a) the leaf area, (b) the position on the plant, and (c) the habitat.

With these position effects in mind leaves of similar age were selected from parts of the plants. Leaves were taken from three plants from each treatment and 25 random microscope fields were counted. The mean stomatal frequencies for the underside of the leaves are shown in Table 42.

Table 42   Number of stomata per mm². Counts made on the underside of the leaves

| | Parts per million N | | | |
	1	50	100	250
Dactylis glomerata	*7.68*	5.80	5.28	4.52
Arrhenatherum elatius	6.48	*6.52*	5.88	5.72
Holcus lanatus	4.08	*4.12*	3.28	3.32
Trifolium repens	17.68	*19.40*	17.60	17.80
Ranunculus acer	10.40	20.60	9.32	9.52
Filipendula ulmaria	11.60	11.40	*23.00*	7.60
Taraxacum officinale	*38.60*	36.48	36.20	21.20
Chrysanthemum leucanthemum	5.80	8.00	*8.88*	6.00
Angelica silvestris	*17.88*	17.60	17.59	16.92
Ajuga reptans	*33.60*	31.40	23.20	12.00
Galium mollugo	*16.52*	12.68	11.48	11.12

There appeared to be real differences in some species in relation to the nitrogen supply although it was noticed that the grasses gave a lower response than some of the other species, and the large differences in *Ranunculus acer* and *Filipendula ulmaria* were not readily explicable. *R. acer* with some other species of *Ranunculus* are being further investigated and will form the subject of a future paper.

At 1 ppm N growth was usually poor and the differences on stomatal frequencies between 1 and 50 ppm were irregular. This work is being continued and will be the subject of a further paper. Apart from stomatal frequency the shape of the epidermal cells changed with the nitrogen supply. The cell walls were tessalated at low nitrogen but smoother at high nitrogen.

b. Response to phosphorus

Four phosphorus levels of 1, 5, 15, 50 ppm were obtained by variations in the sodium dihydrogen phosphate in the culture solution without any compensating changes in other substances. The same species were grown as in Experiment 1 with the exception of *Medicago lupulina*. The experiment was laid out in a cool greenhouse in Feb. 1964 and harvested after 92 days. At harvest dry weight yield was measured.

The analysis of variance of the data indicated that the species significantly differed in their response to increasing phosphorus concentration:

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Analysis of variance (Experiment 2), ******* $P < 1\%$ (see also Table 43)

	df	ms	F	
Error	94	0.0501		
Blocks	2	0.0247	0.4930	ns.
Phosphorus	3	1.7369	34.6687	***
Species	11	1.8604	37.1337	***
Species and phosphorus	33	0.9090	18.1437	***
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Apart from *Angelica silvestris* all the species showed a marked response to increase in phosphate from 1 to 5 ppm. At 15 and 50 ppm *Ajuga reptans, Holcus lanatus, Dactylis glomerata* and *Trifolium repens* all showed reduced yield. Only *Filipendula ulmaria* and *Arrhenatherum elatius* increased in growth even at the high levels. All the other species showed a fall off at the highest level of phosphate.

Table 43 Dry weight (g) per plant at 4 levels of P. The level of P at which most growth occurred is printed in italics for each species

| | Parts per million P. | | | |
	1	5	15	50
Dactylis glomerata	0.32–1.18	*0.70–0.90*	0.40–0.55	0.33–0.39
Arrhenatherum elatius	0.16–0.28	0.42–0.43	0.56–0.63	*0.61–0.79*
Holcus lanatus	0.30–0.49	*0.68–1.02*	0.60–0.69	0.27–0.35
Trifolium repens	0.15–0.24	*0.62–1.00*	0.35–0.50	0.13–0.16
Ranunculus acer	0.21–0.34	0.55–0.68	*0.92–1.05*	0.65–0.94
Cirsium oleraceum	0.15–0.26	0.61–0.83	*3.29–3.42*	2.34–2.41
Filipendula ulmaria	0.48–0.54	0.50–0.62	0.49–0.82	*1.62–3.97*
Taraxacum officinale	0.09–0.15	1.12–1.29	*1.42–1.98*	0.44–0.55
Chrysanthemum leucanth.	0.07–0.08	0.15–0.17	*0.17–0.18*	0.10–0.14
Angelica silvestris	*2.80–3.10*	0.40–0.46	0.46–0.55	0.58–0.65
Ajuga reptans	0.32–0.57	*0.62–1.16*	0.50–0.81	0.19–0.27
Galium mollugo	0.23–0.27	0.30–0.32	*0.56–0.73*	0.45–0.57

c. *Response to calcium*

Nine species were grown at three levels of calcium (5, 100, and 200 ppm). Calcium was varied by using calcium chloride and the nitrogen of the calcium nitrate was compensated by sodium nitrate. The experiment was planted in April 1964 and harvested after 85 days. The species showed significant differences between growth at different levels of calcium.

The analysis indicated that the calcium treatments were significant at P = 0.05. The data showed small differences in yield between certain calcium levels (Table 44). *Dactylis, Arrhenatherum, Cirsium* showed similar growth at 100 and

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Analysis of variance (Ca). Dry weight yield, $*P = 5\%$, $***P < 1\%$

	df	ms	F	
Error	58	0.0202		
Blocks	2	0.0515	2.550	ns.
Species	9	2.0222	100.109	***
Calcium	2	1.0722	53.079	*
Species and Calcium	18	0.8261	40.896	***
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Table 44 Dry weight yield per plant at three levels of Ca (g). Mean of three replicates (variation given in brackets). The mean is given in this table and not presented as a figure. The level of Ca at which highest growth was observed is printed in italics for each species

	Parts per million Ca		
	5	100	200
Dactylis glomerata	0.28 (0.20–0.31)	*1.23* (1.19–1.31)	1.05 (0.98–1.07)
Arrhenatherum elatius	0.16 (0.10–0.21)	*1.78* (1.73–1.84)	1.59 (1.55–1.65)
Holcus lanatus	0.84 (0.61–0.97)	*1.44* (1.34–1.58)	0.60 (0.53–0.83)
Ranunculus acer	*0.56* (0.51–0.60)	0.30 (0.24–0.35)	0.30 (0.26–0.34)
Cirsium oleraceum	0.19 (0.18–0.21)	0.48 (0.43–0.45)	*0.49* (0.48–0.51)
Filipendula ulmaria	1.62 (1.43–1.82)	*1.69* (1.63–1.74)	0.74 (0.54–1.00)
Taraxacum officinale	*1.48* (1.34–1.62)	0.24 (0.22–0.26)	0.20 (0.17–0.24)
Ajuga reptans	0.21 (0.18–0.23)	0.52 (0.50–0.54)	*0.88* (0.81–0.94)
Galium mollugo	0.33 (0.32–0.34)	*0.91* (0.79–0.98)	0.75 (0.69–0.84)

200 ppm calcium and *Filipendula* at 5 and 100 ppm. *Ranunculus* and *Taraxacum* grew better at low calcium levels and *Ajuga* and *Cirsium* at high levels, though on the whole the species investigated tolerate a wide range of pH in the field and many grow on calcareous soils. They are species of neutral grassland and this experiment emphasised their edaphic tolerance to calcium.

IV. Discussion

It was observed that the yield of the vegetation units differed. Differences between units must also be related to the component species. Several species are not very productive, e.g. *Cerastium caespitosum*, and species such as *Ranunculus auricomnus* and *R. ficaria* flower early and contribute little to the hay. They survive because of their early seeding properties. Other species present in low amounts in the wet fertilised meadows are species which tend to die out with intense manuring or cutting, e.g. *Avena pubescens*, *Bromus mollis*, *Briza media*.

The species differ in their response to cutting. The good agricultural grasses grow quickly after cutting (*Arrhenatherum, Alopecurus, Dactylis, Festuca pratensis, Lolium, Poa pratensis, Trisetum*). Others, e.g. *Festuca rubra*, do not grow well after the first cutting. Development of the grasses may be modified by the manuring. On unmanured plots, *Festuca rubra, Filipendula ulmaria* and *Vicia cracca* develop late in the summer. On the heavily manured plots other species develop earlier. The vegetation units with the lowest fertility ("wet") showed a slower growth than those with higher fertility ("dry"). Nitrogen favours the growth of grasses and in the wet variants the grasses tend do show a greater seasonal variation. Phosphate favours the legumes and the more intense fertilising of the dry variants was reflected in the higher contribution of the legumes to the hay. The quality of the hay was indicated by the percent-legume content and the protein and fibre contents. Protein quantity decreased towards the end of the season but appeared to be higher on the plots that were fertilised the most. Crude fibre content remained high throughout growth on the low yielding plots but showed a decrease in midsummer on the higher yielding plots. This was caused by the low fibre content of the regrowth.

There is a close relationship between the transpiration and a meadow hay yield, though this does not imply direct cause and effect; when temperature and soil moisture are not limiting, the growth of the grass is a function of the available energy (SMITH, 1962). Data on the relative growth rate (RGR) of the community may be related to the radiation. Two periods may be recognised: (1) the period with high RGR resulting in a closed green surface, (2) a period of decreasing growth rate when a large portion of the leaves receive a light intensity below the compensation point. At this time there was dropping off of parts. This pattern was modified by the mowing regime. Frequent mowing meant that there was no stage of senescence.

Differential response to N, P and Ca in sand culture of some typical species of the wet fertilised meadows emphasised that on contrasting soils exhibiting differences in nutrient availability (either as a result of mineralisation or of fertilisation) the species composition of te population may change. It appeared that the behaviour of the species in the field could be determined by their response to N as measured in culture. Species typical of the *Calthion*, e.g. *Filipendula ulmaria, Cirsium oleraceum* and *Angelica silvestris* are found less abundantly in the wet *Arrhenatheretum*. These findings along with the very clear reaction of species like *Arrhenatheretum elatius* suggest that the higher fertilisation of these grasslands controls the species composition. The interference between species in a population must be considered as well as nitrogen. *Holcus lanatus* in culture exhibited an increase in growth with increased nitrogen supply, yet in the fertile *Arrhenatheretum, Holcus lanatus* tends to indicate poor conditions. It is presumably excluded by the interference from other species (see ELLENBERG, 1963).

The data of soil phosphorus available throughout the growing season (see Section B) indicated that more phosphorus was available for growth in the dry

variants. In sand culture the species showed very different responses. *Filipendula ulmaria* and *Cirsium oleraceum* to a lesser extent grew rapidly with increased phosphorus and showed a greater response to increased phosphorus than some of the species more typically associated with the more fertile vegetation units.

The higher levels of soil phosphorus in the *Arrhenatheretum* would, therefore, seem to favour the growth of most of the species of the wet fertilised meadows. However, these species reacted very differently to nitrogen in culture. Ecologically, providing there was adequate moisture, these species would grow in the dry units if there was no fall off in growth at high nitrogen. Considered together the results of the sand cultures help to explain the distribution of the species in the vegetation variants. That the behaviour of the species in sand culture to varied phosphorus level did not always agree with their tolerance in the field is reflected by the P values tentatively given by KUHNEN (1951). Although with regard to nitrogen the occurrence of the species in their natural environment (their ecological optimum) agreed with their physiological optimum with regard to phosphorus the species do not always grow on sites offering optimal conditions. The interspecific interference in the population may be a cause of this and this has been demonstrated by ELLENBERG (1959, 1963).

The growth response in culture to three levels of calcium showed that most species grew better with a medium calcium supply. This is in agreement with the distribution of the wet fertilised meadows with regard to pH. Calcium did not appear to be as important as nitrogen or phosphorus in determining the species distribution within the vegetation units. Many of the species present in the wet fertilised meadows are tolerant of a wide range of soil pH and a wide range of soil $CaCO_3$ content.

Nitrogen appeared to be the most important factor controlling the distribution and growth of the species and also the yield of the vegetation units. Nitrogen in the soil differed between the vegetation units in accordance with the intensity of nitrification, but also the fertilisation (including both N and P) differed (see Section B). These differences resulted in corresponding variations in yield and it is suggested that nitrogen is the major stabilising factor of the community.

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E. Acknowledgments

F. Summary

The nitrogen relations and other ecological investigations on wet fertilised meadows

Section A—*Systematics*

The present sociological nomenclature was examined. The wet fertilised meadows investigated are described as the associations *Polygono-Cirsietum oleracei* (TÜXEN and PREISING, 1951) and *Bromo-Senecionetum*. There appears to be an edaphic difference between the two associations. Both are subdivided by some authors. For experimental purposes it was considered more meaningful to regard the wet fertilised meadows as a single group: the *Cirsietum oleracei medioeuropaeum*.

An ordination of vegetation tables revealed that the *Cirsietum* was not clearly distinct from the wetter forms of the *Arrhenatheretum*. There were also montane varieties of the community, but it is probably better to regard these simply as variants of the community. The subdivision of the *Molinio-Arrhenatheretea* is clearly too artificial. Probably in nature a multidimensional continuum exists, the named associations are representing parts of the continuum which are distinguishable floristically.

The distribution of the *Cirsietum oleracei medioeuropaeum* was considered. It seemed to be of subatlantic origin, and the present distribution must be correlated with management practices. Various facets of the physiognomy of the community were described.

Section B—*Soil factors*

Three experimental areas were selected, i.e. (a) Swiss Midlands, (b) Alsace, (c) Baden-Württemberg. These offered contrasting soil conditions.

The two major controlling factors were water and nitrogen. Ground water and soil moisture content were examined, and the latter was correlated with the soil water tension. Studies of the "available water" by determining the yearly variations in suction force showed that water was rarely a limiting factor.

The nitrogen relations were studied by measuring the seasonal pattern of nitrate- and ammonium-contents in the field and by measuring the seasonal pattern of potential and actual nitrification. There were similarities in the patterns of both potential and actual nitrification in the three areas, although they were modified locally in response to climate.

Various factors affecting the nitrogen budget were investigated in the laboratory, e.g. aeration, water content, calcium carbonate content, ammonium supply and the distribution of nitrifying activity horizontally and vertically in the soil. Populations of the nitrifying bacteria (nitrite and nitrate producers) were cultured and the fluctuations in the population size was related to the pattern of nitrification. These experiments were discussed in relation to the nitrogen budget of the community, and it appeared that along with water, nitrogen was a major factor controlling the stability of the community.

Soil phosphorus was also determined and the content showed a characteristic seasonal pattern as did pH and water content. Phosphorus may be a factor likely to cause the differentiation into some vegetation variants.

Section C—*Productivity*

The productivity of the wet fertilised meadows was measured both quantitatively and qualitatively. From sample cuts the hay yield was estimated and the hay was fractionated into three portions important from the agricultural point of view: grasses, legumes and herbs. Protein and fibre contents were measured.

Since mineral nutrition was found to be important (Section B), the growth of several species, typical and constant of the community, was measured in sand culture. Their responses to varying levels of nitrogen, phosphorus and calcium were tested. The results were discussed in relation to the role played by these macronutrients in the light of the results in Section B.

Zusammenfassung

Die Stickstoffversorgung und andere ökologische Faktoren in gedüngten Feuchtwiesen

Abschnitt A *Pflanzensoziologische Systematik*

Die in der Literatur gegebene systematische Einteilung und Nomenklatur der gedüngten Mähwiesen auf bodenfeuchten Standorten wird kritisch referiert. Die untersuchten Bestände gehören grossenteils zum *Polygono-Cirsietum oleracei* (TÜXEN und PREISING, 1951), während das *Bromo-Senecionetum* vorwiegend in Nordwestdeutschland und angrenzenden Gebieten vertreten ist. Manche Autoren unterteilen beide Assoziationen mehr oder weniger weitgehend. Für die vorliegenden Untersuchungen erschien es zweckmässig, sämtliche gedüngten Feucht-wiesen als eine einzige Gesellschaftsgruppe aufzufassen *(Cirsietum oleracei medioeuropaeum)* und diese in drei Untergruppen einzuteilen: «trockene», «typische» und «feuchte» Kohl-distelwiesen.

Eine Zusammenstellung zahlreicher Vegetationsaufnahmen aus Südwestdeutschland und der Schweiz ergab ausserdem, dass sich das *Cirsietum oleracei* nicht scharf abtrennen lässt von relativ feuchten Ausbildungen der Glatthaferwiesen *(Arrhenatheretum)*. Es gibt auch montane Ausprägungen der gedüngten Feuchtwiesen, die in der Literatur in verschiedener Weise als Assoziationen gefasst werden. Es ist aber wohl besser, die meisten von diesen einfach als Höhenvarianten der im Tiefland recht ähnlich ausgebildeten Gesellschaften aufzufassen. Die Unterteilung der *Molinio-Arrhenatheretea* ist offensichtlich zu künstlich. In der Natur bilden die zu dieser Klasse gehörenden Kulturwiesen ein vieldimensionales Kontinuum. Die genann-ten Assoziationen und ihre Untereinheiten sind Bereiche in diesem Kontinuum, die sich floristisch hervorheben lassen.

Die geographische Verbreitung der Kohldistelwiesen wird anhand der Literatur untersucht. Sie haben ihr Schwergewicht im subatlantischen Bereich, ähnlich wie die Rotbuchenwälder. Als anthropogene Gesellschaften fehlen sie aber in Gebieten, in denen die feuchten Grasländer nicht gedüngt oder nur beweidet, aber nicht mehrmals im Jahr gemäht werden. Der teilweise von der Bewirtschaftung abhängige Aspektwandel der untersuchten Feuchtwiesen wird eben-falls beschrieben.

Abschnitt B *Bodenfaktoren*

Drei Untersuchungsgebiete wurden ausgewählt, weil sie sich in den Bodenverhältnissen stark unterscheiden, aber gleiche Gesellschaften tragen: das Schweizer Mittelland westlich von Zürich (vorwiegend lehmige Böden), das südliche Elsass (Böden mit Sanduntergrund) und das Federseegebiet in Baden-Württemberg (mehr oder minder entwässerte Flachmoorböden).

Als für die Artenzusammensetzung wahrscheinlich wichtigste Faktoren wurden vor allem der Wasser- und der Stickstoffhaushalt der Böden untersucht. Insbesondere wurden die Grund-wasserstände und die Bodenfeuchtigkeit im Laufe zweier Jahre gemessen und mit den Saug-spannungen (dem Wasserpotential) der Böden in Beziehung gebracht. Aus den Jahresschwan-kungen des pflanzenverfügbaren Wassergehaltes geht hervor, dass die Gesellschaften des *Cir-sietum oleracei* (mit Ausnahme der relativ trockeneren, dem *Arrhenatheretum* nahestehenden Untereinheiten) nur selten unter Wassermangel leiden. Die deutsche Bezeichnung «Feucht-wiesen» ist also berechtigt.

Um das Stickstoffangebot der Böden zu beurteilen, wurden die jahreszeitlichen Schwankun-gen des Gehaltes an Nitrat und Ammoniak sowie die jahreszeitlichen Schwankungen der Nitrat- und Ammoniak-Akkumulation in inkubierten Mischproben untersucht. Letztere blieben jeweils 6 Wochen lang teils unter konstanter Temperatur (20 °C) und hoher Luftfeuchtigkeit im Laboratorium, teils unter Feldbedingungen in dem Bodenhorizont, aus dem sie entnommen worden waren. Labor- und Feldwerte laufen im grossen und ganzen parallel, doch sind letztere wegen der niedrigeren Temperaturen meist geringer. Die jahreszeitlichen Schwankungen sind beträchtlich und lassen sich nur teilweise aus dem Temperaturgang und den Schwankungen des

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Wassergehaltes der Böden erklären. Immerhin zeigte sich aber deutlich, dass die gedüngten Kohldistelwiesen zu allen Jahreszeiten reicher an pflanzenverfügbarem Stickstoff waren als die (in den gleichen Jahren von LEÓN untersuchten) nicht gedüngten Pfeifengraswiesen *(Molinietum)*, und zwar auch dort, wo sie seit Monaten nicht mehr gedüngt wurden. Ausserdem erwies sich, dass die «trockenen» Untereinheiten in der Regel mehr mit Stickstoff, insbesondere mit Nitraten, versorgt werden als die «typischen» und diese wieder mehr als die «nassen».

Zur Ergänzung wurden im Laboratorium verschiedene Faktoren untersucht, die das Nitrat- und Ammoniakangebot der Böden beeinflussen, z.B. Durchlüftung, Wassergehalt, Kalkgehalt und Düngung mit Ammonium oder Nitrat. Die Populationsdichte der Nitrat- und Nitritbakterien schwankt parallel zum Nitratangebot der Böden. Mit zunehmender Bodentiefe nimmt das Stickstoffangebot nicht so rasch ab wie in Waldböden, was teilweise damit zusammenhängen dürfte, dass infolge der wiederholten Mahd kein Streumaterial anfällt. Insgesamt zeigt sich, dass der Stickstoff neben dem Wasser tatsächlich einer der das Gesellschaftsgefüge beherrschenden Faktoren ist.

Der Gehalt des Bodens an pflanzenaufnehmbarem Phosphor (nach einer in Bangor üblichen Methode gemessen) schwankt im Laufe des Jahres ebenfalls erheblich. Er ist bei den gedüngten Feuchtwiesen verhältnismässig hoch und hat möglicherweise mit entscheidende Bedeutung für ihr Artengefüge.

Abschnitt C *Produktivität*

Um die Produktivität der gedüngten Feuchtwiesen quantitativ und qualitativ beurteilen zu können, wurde der Ertrag an Grünmasse und Heu in mehreren Ernteproben bestimmt. Repräsentative Teilproben wurden in Gräser, Leguminosen und Kräuter gesondert, um den Protein- und Rohfasergehalt dieser landwirtschaftlich wichtigen Gruppen getrennt bestimmen zu können. Im grossen und ganzen gehen die Erträge und Heuqualitäten parallel zur Stickstoffversorgung der Bestände; doch ist die Zahl der Stichproben noch zu klein, um endgültige Aussagen machen zu können.

Der Einfluss des Stickstoffs und des Phosphors sowie des Kalium- und Kalziumkarbonats auf die Produktivität einzelner für die Gesellschaft wichtiger Pflanzenarten wurde mit Hilfe von Sand-Nährlösungskulturen im Gewächshaus geprüft. Hierbei erwies sich der Stickstoff wiederum als wichtigster kontrollierender Faktor, wenn auch manche Unregelmässigkeiten auftraten, die durch umfangreichere Experimente geklärt werden müssten.

Stand descriptions of field plots in Switzerland.

	WET	TYPICAL	DRY
Number	1–24	25–37	38–53

Experimental Site Number: 1, 2, 4, 12 | 11, 8, 7, 5, 3 | 9, 6, 10

WET TYPES — INTERMEDIATE — DRY TYPES

Note: the numerical cover-abundance values filling the 53-column × ~150-species data grid are too dense and low-resolution to transcribe reliably and are therefore not reproduced here. The species row labels are given below.

Species of Calthion (CO)
- Filipendula ulmaria
- Cirsium oleraceum
- Lychnis flos-cuculi
- Myosotis palustris

Wet Indicators
- Carex acutiformis
- CU Angelica silvestris
- CU Equisetum palustre
- Carex panicea
- Crepis paludosa
- Molinia coerulea
- Carex tomentosa
- CU Caltha palustris
- Carex hostiana
- Carex elata
- Carex fusca
- Carex gracilis
- CU Polygonum bistorta
- Galium palustre
- Inula salicina

Dry Indicators
- AO Arrhenatherum elatius
- Poa pratensis ssp. angustifolia
- Festuca pratensis
- AO Tragopogon pratensis
- Picris hieracioides
- Veronica chamaedrys
- AO Crepis biennis
- Achillea millefolium
- AO Daucus carota
- AO Leontodon hispidus
- Plantago media

Species of Arrhenatherion (AO)
- Galium mollugo
- Heracleum sphondylium
- Anthriscus silvestris
- Trisetum flavescens

Species of Molinio-Arrhenatheretea (MA)
- Ranunculus acer
- Rumex acetosa
- Trifolium pratense
- Cerastium caespitosum
- Lathyrus pratensis
- Poa trivialis
- Vicia cracca
- Colchicum autumnale

Other Species
- Holcus lanatus
- Dactylis glomerata
- Taraxacum officinale
- Ajuga reptans
- Plantago lanceolata
- Cardamine pratensis
- Anthoxanthum odoratum
- Festuca rubra
- Bellis perennis
- Trifolium repens
- Ranunculus repens
- Rumex obtusifolius
- Chrysanthemum leucanthemum
- Lotus corniculatus
- Lotus uliginosus
- MA Centaurea jacea
- Phragmites communis
- Myosotis palustris
- Deschampsia caespitosa
- Symphytum officinale
- Potentilla reptans
- AU Triticium dubium
- Poa pratensis ssp. latifolia
- Festuca arundinacea
- Valeriana officinalis
- Vicia sepium
- Primula vulgaris
- Succisa pratensis
- Alchemilla vulgaris
- Iris pseudacorus
- AU Avena pubescens
- Lysimachia vulgaris
- Lysimachia nummularia

- Geum rivale
- AO Bromus mollis
- CO Lythrum salicaria
- Potentilla erecta
- Agrostis alba
- MA Pimpinella major
- Primula elatior
- Carex flacca
- Crepis mollis
- Anemone nemorosa
- Sanguisorba officinalis
- Selinum carvifolia
- Lolium multiflorum
- Primula veris
- Stachys officinalis
- Galium verum
- Valeriana dioica
- Medicago lupulina
- Mentha aquatica
- Carex davalliana
- Juncus inflexus
- Convolvulus sepium
- Briza media
- Equisetum maximum
- CO Orchis latifolia
- Phleum pratense
- Luzula campestre
- Linum catharticum
- Hypericum maculatum
- Carex montana
- Juncus effusus
- Cirsium arvense
- Viola hirta
- Silaum silaus
- Salvia pratensis
- Ranunculus ficaria
- Veronica serpyllifolia
- CO Scirpus sylvaticus
- Galium boreale
- Hypericum perforatum
- Urtica dioica
- Brachypodium pinnata
- Veronica arvensis
- Trollius europaeus
- CO Cirsium palustre

Plantago major + (5, 25, 27), Calagrostis epigeios 2(26), t(57), + (37). Phalaris arundinacea 1 (37), + (20, 25). Serratula tinctoria 2 (24), 1 (33, 40). Rhinanthus major 1 (18, 35), + (1). Myosotis arvensis → (22, 23, 49). Cirsium pal. × ol. 1 (5) + (4, 8). Potentilla sterilis 2 (53), + (6, 23). Iris sibirica 2 (24), 1 (48), + (55). Juncus subnodulosus 2 (40), 1 (14), + (22). Carex umbrosa 1 (7, 26, 53) + (12). Picea juv. + (1, 4, 5). Rumex crispus 1 (52), + (12, 38). Fraxinus juv. + (4, 5). Succisa asper + (7, 10). Melandrium diurnum 1 (11, 41), + (7). Ranunculus auricomus 2 (23) + (32). Lamium album + (21, 52). Ranunculus flammula 1 (19), + (23). Orchis incarnata + (17, 25). Lamium purpureum + (20, 38). Chaerophyllum hirsutum 1 (12) + (25). Primula veris 1 (41) + (3). Molinia littoralis + (20, 22). Carex pallescens 1 (35), + (22, 48). Carex caryophyllea 1 (8, 26). Pulicaria dysenterica 1 (4, 22). Mentha longifolia 2 (14), + (38). Taraxacum palustre 1 (17), + (14). Aegopodium podagraria 2 (22, 25). Salix nig. juv. + (24). Rubus caes. 1 (24). Quercus rob. juv. + (8). Prunus spin. juv. + (5). Ononis repens + (4). Ranunculus bulbosus + (30). Polygonum amphibium 1 (7, 11).

Tussilago farfara 1 (7). Geranium pratense 2 (11). Capsella b.-pastoris + (12). Solidago virgaurea + (12). Galium silvaticum + (52). Equisetum arvense + (2). Poa palustris + (23). Bromus erectus 1 (6). Allium oleraceum 1 (51). Koeleria cristata 1 (5). Orchis morio 1 (35). Scabiosa columbaria 1 (38). Hieracium auricula + (41). Cerastium arvense + (23). Allium spp. 2 (35). Vicia angustifolia + (23). Glyceria maxima + (23). Knautia arvensis + (51). Carum carvi + (40). Polygala vulgaris + (39). Leontodon autumnale + (21). Potentilla anserina + (36). Listera ovata 1 (25). Eriophorum angust. + (40). Carex brizoides + (49). Cynosurus cristatus 1 (36). Calamagrostis canescens 3 (3). Festuca ovina 1 (26). Carex flava + (5). Carex lepidocarpa + (8). Sanguisorba minor 1 (5). Campanula patula + (6). Laserpitium spp. + (12). Saturaja acinos + (12). Agrimonia eupatoria + (6). Campanula rapunculoides + (6). Campanula glomerata 1 (5). Hypochoeris radicata + (22). Stachys palustris + (1). Euphorbia verrucosa + (14). Geranium molle + (14). Scrophularia nodosa 1 (48). Polygonum aviculare + (48). Eupatorium cannabinum + (8). Aquilegia vulgaris 1 (4).