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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):

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

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).

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

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 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

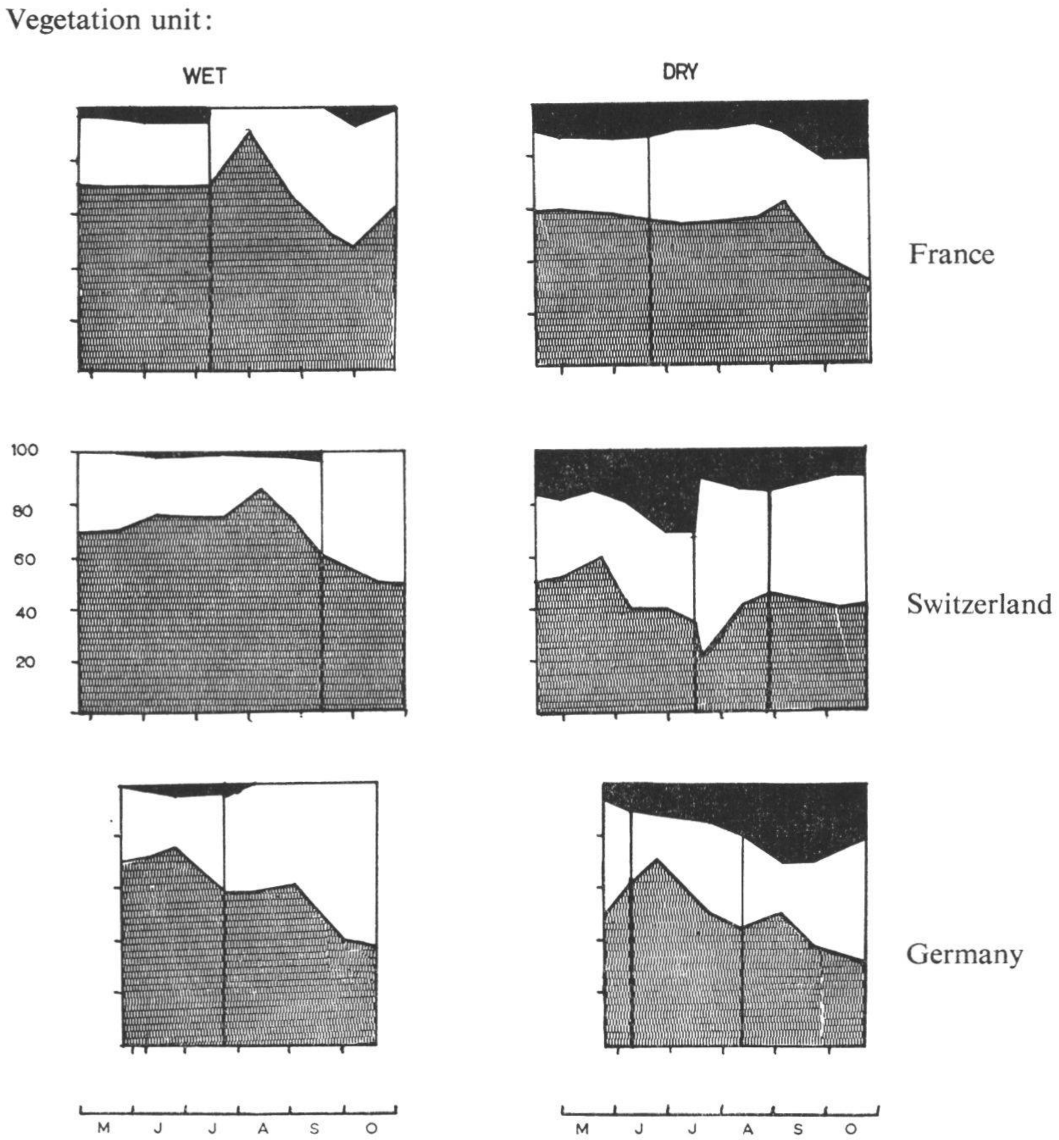

Fig. 32 The % of grasses (dotted), legumes (black), and herbs (unshaded) in the hay (1963). Data represent individual plots (mean of 3 replicate cuts).

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

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

Vegetation			Days 1963 126 Variation	S.D.	220 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		Days 1963 232	
			Variation	S.D.	Variation	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/m^2; L and H represent the percent contribution to the yield by legumes and herbs

Vegetation			Days 1963 (1 = January 1st) 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)

Area and vegetation		Spring 106–126	126–153	153–172	Summer 153–177	172–188	177–188	177–197	188–197	197–207	197–220	207–220	220–237	220–254	Autumn 237–258	258–279
Switzerland																
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		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		

Days 1963

Alsace		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

Days 1963

Germany		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

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 days 1963	1 153	2 188	3 220	4 237
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.

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	} 10
$MnSO_4 \cdot 4H_2O$	Mn 0.55	11.15	
$ZnSO_4 \cdot 7H_2O$	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	***
	143			

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/mm^2, the number of vessels/mm^2 and the number of cells of the epidermis/mm^2 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 response 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:

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	***
	143			

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

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	***
	89			

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.

D. References

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