Folia Geobot. Phytotax., Praha, 30: 117-130, 1995

Species Composition and Standing Crop Variation in an Unfertilized Meadow and Its Relationship to Climatic Variability During Six Years

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Keywords: Evaporation, Fluctuation, Plant populations, Time-lags of response, Relative moisture, Weather

Abstract: Year-to-year variability of species composition and hay yield were investigated during a six-year period (1988-1993) in a traditionally mown meadow of great species richness at Negrentino in southern Switzerland. Climatic parameters (temperature, duration of sunshine, global radiation, precipitation, evaporation, relative moisture) measured at a nearby weather station were calculated for ten-day units and compared to quantitative vegetation data. Yields of the first and second harvest were positively correlated with the mean relative moisture during the first and second growth period.

Distinct variation patterns were recognized among the 48 species and interpreted as direct or indirect responses of interacting species to climatic conditions during three periods of the year. The first variation pattern including abundant graminoids reflects a strong direct effect by weather conditions in the first growth period. Species of the other variation patterns responded differently to extreme summer droughts with apparent time-lags. Some species reflect warm and humid conditions in early spring followed by dry conditions in a particular year; others combine features of different variation patterns.

INTRODUCTION

Regularly mown unfertilized meadows are rapidly disappearing and the maintenance of their great species richness has become a high priority topic in nature conservation. Variability in external conditions plays an important role in maintaining species diversity (GRUBB et al. 1982). According to the competitive equilibrium hypothesis (HUSTON 1979), high diversity occurs when low to intermediate growth rates are combined with low to intermediate frequencies of population reduction - in meadows of temperate zones high growth rates are permanently or periodically prevented by a shortage of water and nutrients and cold winter temperatures, and plant populations are periodically reduced by mowing. This provides sufficient time for various factors to be effective that tend to prevent competitive exclusion, such as fluctuating environmental conditions. The weather fluctuates notoriously and is generally accepted to have a considerable effect on harvest (KLAPP 1971) and botanical composition (WATT 1960, 1962, 1971, RABOTNOV 1966, 1974), but other external and endogenic cyclic processes are also believed to cause fluctuations of the species abundance in grasslands (RABOTNOV 1974, NEWMAN & ROVIRA 1975). The understanding of the factors controlling floristic composition in grasslands is still limited (GRUBB et al. 1982) and the relationship between species fluctuations and weather is usually obscure (VAN DEN BERGH 1979). A further investigation of the effects of fluctuating environmental conditions on species composition of various meadows is attractive because of its great importance for grassland management (RABOTNOV 1974, BAKKER 1989).

In Switzerland, the management of an increasing number of meadows is regulated today by management contracts between farmers and nature conservation administrations. Assessing the success of such management efforts is difficult because undesired management effects may be hidden by climatically induced short-term fluctuations among others. In the short term, plant-population monitoring programs may be inadequate, unless we know more about the varying nature of the plant species involved. A better understanding of the relative importance of different climatic factors and their combinations for the plants in grasslands will help to improve designs of programs for success assessment.

In a few unfertilized meadows at relatively dry sites at lower montane elevations in southern Switzerland the floristic composition has been maintained by regular mowing for at least the past 50 years. If mowing is stopped, a process of competitive displacement well known from studies in several European countries (GREEN 1980, SCHREIBER & SCHIEFER 1985, BOBBINK & WILLEMS 1987) is induced: *Brachypodium pinnatum* vigorously increases and achieves strong dominance in a few years (STAMPFLI 1992). One of the goals of a long-term experiment at Negrentino is to find out how long different plant species survive when mowing is stopped and which ones can be preserved when mowing is resumed after different periods of abandonment. The present paper deals with results from the control plots of this experiment where traditional mowing was continued. The variability of standing crop, abundances of single species and climatic factors are described, and relations between climatic variables referring to the growing period and vegetation data are investigated.

MATERIAL AND METHODS

Study site and vegetation data

The vegetation data were collected in six successive years (1988-1993) on nine mown plots of the study site at Negrentino (a-plots, see STAMPFLI 1992). The study site, embedded in a south-facing slope at an elevation of 820 m, has been regularly mown by local farmers who cut the grass twice a year, around the end of June and in September. Formerly, the use of manure was normally restricted to adjacent meadows of north-eastern and eastern exposure. Since 1988, the study site has been fenced in and nine plots have been mown at traditional dates by scythe by a skilled farmer. The soils are moderately acid, pH = 5.4 (top of soil sample, measured in water), deeply weathered (thickness of A and B horizons measured 105 cm in a profile a few meters east of plot 3a) and of a relatively high silt and rather low nutrient content. Large rocks are scattered in the soil.

The nine mown plots, 2 × 2.2 m in size, are located in a rectangular grid of three columns of three mown plots alternating with three columns of three abandoned plots; distances between the mown plots are 3.8 m horizontally and 1.1 m vertically. The slope angle varies from a few degrees in the upper plots to about 20° in the lower plots. Species frequency was measured in a "central area" of 1.1 × 1.6 m in each plot by the point-quadrat method at regularly spaced points (STAMPFLI 1991, 1992). The nomenclature of vascular plants follows BINZ & HEITZ (1990).

The species composition of the study site reflects features of *Mesobromion* communities. Species density is very high: 10.9 species per 0.01 m^2 (average of 48 quadrats in three blocks of 4 × 4 located in the upper left corner of the "central area" of plots 1a, 2a, 3a), 38.6 species per 1.76 m^2 (average of the "central areas" of the nine a-plots), and a total of 67 species (nine a-plots) were found in 1993. Most species appeared to be quite evenly distributed.

The same 9 × 176 points were sampled in six successive years. Sampling was done as late as possible but before the first harvest which traditionally varies depending on phenological, as well as other, conditions. The sampling period, which lasted two to three weeks, was initiated according to phenological observations whenever possible. At that moment *Bromus erectus* was in flower and the flowering optima of most of the other species had passed over. The sampling sequence of points remained the same each year in order to minimize eventual fluctuations due to sampling time. Variation patterns of species were calculated by the following procedure: a correlation matrix of the 48 species recorded every year was computed using standardized frequency values; species not displaying at least one correlation coefficient of at least 0.9 in the matrix were considered "singles" and excluded. The remaining species were classified according to their trends during the six years 1988-1993. Trends were computed as linear regression coefficients and standardized frequency value on year. Increasing (regression coefficient > 0.1) and declining species (regression coefficient < -0.35) represent patterns B and C respectively. Species displaying intermediate trends and declining species which distinctly increased since 1991 represent pattern A. Within main groups species were separated by correlation coefficients (pattern A), regression coefficient (pattern B) and by correlation coefficients (pattern C2) and regression coefficients (patterns C1, C3).

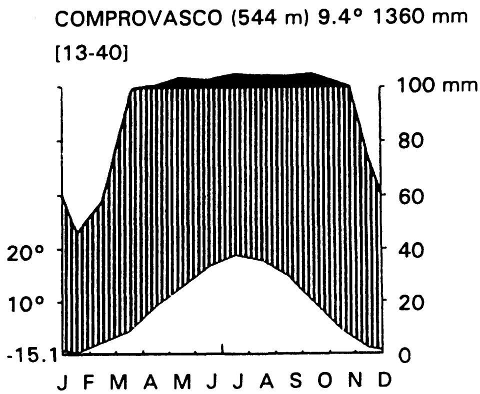


Fig. 1. Climate of Comprovasco. Diagram after WALTER & LIETH (1964) indicating mean monthly values of precipition (upper curve) and temperature from January (left) to December (right): 20 mm correspond to 10 °C (unit on vertical axis), reduced scale for mean values of monthly precipitation exceeding 100 mm. Figures following the station name: elevation above sea level, mean annual temperature (13 years), and mean annual precipitation (40 years); in the lower corner: absolute minimum of temperature.

Standing crop was determined based on nine samples cut a few centimeters above the ground with a small lawn-mower (STAMPFLI 1992) in the last week of June and again in the middle of September, each year. The harvest was separated in gramineous species and forbs; samples were desiccated at 100 °C for 24 hours.

Climatic data

The climate of the study site is temperate-humid with a pronounced but not very long cold season (Fig. 1). Dry northern winds may blow at any time of the year, but are more frequent in the first half. Prominent climatic features of the southern valleys of the Swiss Alps in comparison with the North are: a higher duration of sunshine, a lower relative moisture, and a greater variability of precipitation (AMBROSETTI 1971).

The climatic data used in this paper are based on measurements at the meteorological station of Comprovasco situated at an elevation of 575 m, 245 m lower and about one kilometer away from the study site. Climatic parameters have been automatically measured since January 1988 at intervals of ten minutes; hourly averages/sums of these parameters were provided by a data-base of the Swiss Meteorological Institute (SMA Zürich). Six parameters presumably affecting species composition (precipitation, evaporation, relative moisture, temperature, duration of sunshine, and global radiation) were selected. Ten-day unit values (averages or sums as appropriate), were calculated for the period from 31 January 1988 to 27 October 1993. Time units are numbered within each year from one to 36 (Tab. 1). Before vegetation data measured at yearly intervals can be compared with continuously measured climatic data some computations are indispensible. As the weather in different seasonal periods of the year may be of different relevance for the vegetation, three main yearly intervals were distinguished: a first growth period, generally from April to June (time units 10-18), a second growth period from July to mid September (units 19-26), and a third period of slow growth from mid September to March (units 27-36, 1-9). The limits between intervals I-II and II-III are clearly defined by mowing, the limit between III-I is poorly defined as it corresponds to the beginning of spring which is variable from year to year (DEFILA 1991).

RESULTS

Variability of standing crop

Yields differed considerably between years (Fig. 2). In 1988 the harvest of hay exceeded the amount expected by the farmers, and in 1990 it was less than 40% of the 1988 amount. First and second cut roughly show the same fluctuations. The second cut yielded more than half of the first one in 1988 (57%), 1992 (54%) and 1993 (56%), but was below 40% in 1989 and 1990.

Variability of species through time

In all nine plots combined, 48 out of 70 species were recorded every year from 1988 to 1993 (Tab. 2). Among the top ten (ranked by average point frequency values), there are 8 out of a total of 13 gramineous herbs. Most frequent were relatively tall (*Bromus erectus*, *Festuca tenuifolia*, *Brachypodium pinnatum*) and short perennial grasses (*Danthonia decumbens*), a sedge (*Carex caryophyllea*) and a chamaephyte (*Helianthemum nummularium*). The most strongly fluctuating species, as indicated by their variation coefficients, were *Trifolium repens* and *Anthoxanthum odoratum* (Tab. 2). Among the abundant species, *Plantago lanceolata*, *Thymus pulegioides*, and *Potentilla pusilla* show the greatest variability. Least variability was found among the most abundant grasses (*Bromus erectus*, *Festuca tenuifolia*, *Danthonia decumbens*), among abundant grasses and forbs (*Briza media*, *Agrostis tenuis*, *Trifolium montanum*, *Thalictrum minus*) but also among less abundant forbs (*Carlina acaulis*, *Salvia pratensis*).

Out of the 48 species, 31 were assembled to eight groups representing three main types of variation patterns A, B and C (Tab. 2, Fig. 3): Species of variation pattern A, including

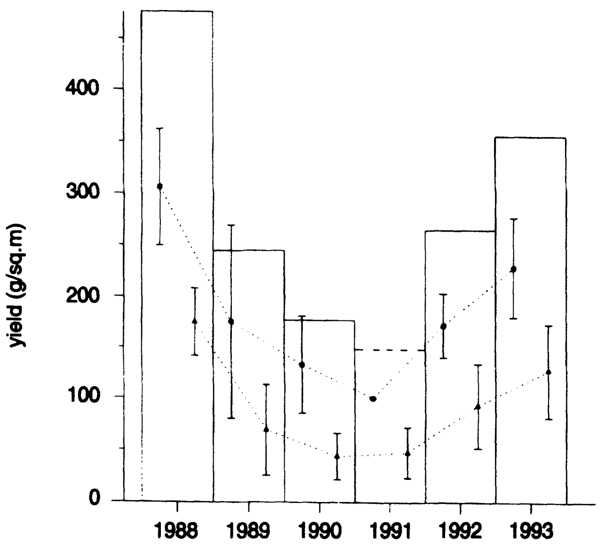


Fig. 2. Variability of standing crop, specifically total annual yield (bar), and yield of first (left) and second (right) harvest. Mean and standard deviation of n = 9 samples (n = 8 samples in 1988). Data of first harvest 1991 missing; displayed 1991 value is based on a rough estimation (carried out in the field in comparison with results of preceding years).

abundant, competitive grasses, decrease continuously from high values in 1988 to an absolute minimum in 1991 and subsequently rise in abundance to a distinct relative maximum in 1992 (A1) or show a steady increase (A2). Species of variation pattern B, including forbs of low stature, exhibit different forms of upward trends, most clearly between 1991 and 1992. Species of variation pattern C show declining trends, their values are low in 1991 and the following years. Some of the 17 "single" species combine distinct features of different variation patterns, e.g. *Plantago lanceolata*, which shows a peak in 1989 (pattern C2) and strongly increases since 1990 (pattern B1).

The correlated species behaviour among the nine plots was explored by ordination using correspondence analysis (Fig. 4). Year-to-year changes are small and differently directed on most plots, but large and continuous on plot 6a between 1989 and 1993. On this plot ranks among abundant species changed strongly, two species (*Holcus lanatus*, *Viola hirta*) vanished, gaps of bare soil increased, *Thymus pulegioides* expanded massively and four species appeared for the first time at the study site: *Veronica arvensis* and *Rumex acetosella* (displayed in extreme positions, Fig. 4), and *Linum catharticum* and *Conyza canadensis*, which appeared as single individuals (not recorded by the point-quadrat sampling technique).

Variability of climatic parameters

Time units (ten-day units) distinguished by prominent high or low values of climatic parameters happened to occur in prolonged time series, indicating longer periods of outstanding weather conditions (Tab. 1a,b). A remarkably humid period lasted from May to September 1988 and a dry period occurred from April to September 1991. The humid period mentioned above included six units (60 days) of high precipitation, nine units of low evaporation, and eight units of high relative moisture; the dry period was characterized by eleven units of low relative moisture, eight units of high evaporation, and five units of low (interrupted by one unit of high) precipitation.

Table 1a. Extraordinary humid (+) and dry (–) periods at Comprovasco between 1988 and 1993 on the basis of time units (ten days). Positive or negative deviations of at least one standard deviation from the six-year mean (five-year mean for time units 1-3, 31-36) are indicated for precipitation (p), negative evaporation (e), and relative moisture (m). Missing values are indicated by dots (.); asterisks (*) indicate period of the plant data collection.

Month	Ten-day unit	1988			88/89			89/90			90/91			91/92			92/93			1993		
		p	e	m	p	e	m	p	e	m	p	e	m	p	e	m	p	e	m	p	e	m
April	10					.		+	.			.			.	–		.	+		.	
	11							+	+	+								–	–			
	12							+								–		–			+	+
	13				+	+	+		–	–												
	14				+	+	+							–	–	–	–	–			+	
	15														–	–				+		
	* 16										+			–	–	–	+	+	+			
	* 17					+	+		–	–				+								
	* 18								–	–	+		+	–				+	+			
July	19				+	+	+							–	–	–						
	20								–	–	–	–								+	+	+
	21				+	+	+					–			–	–						
	22					+	+				–				–	–	+					
	23				+	+	+							–	–	–						
	24				+	+										–				+	+	+
	25					+	+		–						–	–	+					
	26											–	–							+	+	+
September	27												–					+	+	+	+	+
	28					.		–	.	–		.		+	.			.		+	.	
	29					.		–	.	–		.			.			.		+	.	
	30				+	.		–	.	–		.	+	–	.	–	+	.			.	
	31					.		+	.			.	–		.	+		.			end	
	32					.			.	–		.		+	.			.				
	33					.	–		.		+	.	+		.			.				
	34					.	+		.			.			.		+	.	+			
	35					.	–		.		+	.			.			.				
	36					.	–	+	.			.		+	.			.				
January	1					.			.	–			.	+	+	.			.			
	2					.			.	–	+	.	+		.			.				
	3		begin			.	–	+	.	+		.			.			.				
	4	+	.			.	–		.			.			.	+		.				
	5		.			.		+	.	+		.			.			.				
	6		.	–	+	.	+		.			.			.			.				
	7		.			.			.	–		.		+	.	+		.				
	8		.		+	.	+		.			.			.			.	–			
	9		.			.			.	–		.		+	.	+		.				

Between corresponding intervals considerable differences were found from year to year (Tab. 1a,b). These differences can be expressed by means or sums of climatic data computed for both growth periods (Tab. 3). A strong interdependence (correlation coefficient $|r| > 0.83$ in both periods) was found between relative moisture and evaporation (–), and between radiation and relative moisture (–), evaporation (+), and duration of sunshine (+). Climatic explanatory variables can be defined for various periods of time. However, because of the small size of samples through time, only variables of the growth period that is presumed to be most significant were included for a statistical analysis here.

Correlations between climatic variables and vegetation data

Relative moisture was the only factor significantly correlated with yield in both the first and second growth periods (Fig. 5). Correlations with the other water factor climatic variables (evaporation and sum of precipitation), were significant only in the second growth period (evaporation: $r = 0.920$, $P < 0.01$; precipitation: $r = 0.971$, $P < 0.01$). Standing crop was not correlated with energy climatic variables, except for duration of sunshine with which yield was negatively correlated in the first growth period ($r = -0.817$, $P < 0.05$).

Table 1b. Climato-energetically extraordinary periods at Comprovasco between 1988 and 1993 on the basis of time units (ten days). Positive or negative deviations of at least one standard deviation from the six-year mean (five-year mean for time units 1-3, 31-36) are indicated for temperature (t), duration of sunshine (d), and global radiation (r). Missing values are indicated by dots (.); asterisks (*) indicate period of the data collection.

Month	Ten-day unit	1988			88/89			89/90			90/91			91/92			92/93			1993		
		t	d	r	t	d	r	t	d	r	t	d	r	t	d	r	t	d	r	t	d	r
April	10.													+	+	+	-		-			
	11				+				-	-	-							+	+			
	12							-				+	+	-			+	+			-	-
	13					-	-		+	+	+			-								
	14					-	-							-		+	+	+	+			-
	15													+	+	+	-	-	-	+		
	* 16							-										-	-	+	+	+
	* 17							+	+	+	-					-						
	* 18							+	+	+			-		+		-	-	-			
July	19				-	-	-							+	+	+	-					
	20											+	+	+						-	-	-
	21								-	-		+			-	-	+			-		+
	22							-	-	-							+					
	23								-	-				+				+	+			
	24				-	-	-										+	+			-	-
	25											-	-	+	+	+				-		
	26						+					+	+	+						-	-	-
September	27					+	+							+				-			-	-
	28				+				+	+										-		
	29								+	+	+											-
	30				+			+	+	+		-	-				-					
	31					+	+	+						-							end	
	32													-	-	-	+	-	-			
	33				-	+	+		-	-			-				+					
	34							-	+								+	-	-			
	35				+		+			-	-				+							
	36					+	+	+		-	-				-							
January	1				+		+	-					-	-								
	2				+				+	+	-	-	-				+					
	3		begin				+		-	-	-	+	+				+					
	4		-	-		+	+				-											
	5				+				-	-	-							+				
	6		+	+		-	-	+									-					
	7	-										-	-	+								
	8	-		+	-		-	+				-	-			+		+				
	9				+	+	+						-	-								

Relative moisture in the first period showed largest correlation coefficients with abundance values of species of variation pattern A (Fig. 3) including the four most abundant graminoids: *Bromus erectus* ($r = 0.889$), *Carex caryophyllea* ($r = 0.837$), *Salvia pratensis* ($r = 0.826$), *Brachypodium pinnatum* ($r = 0.823$), *Trifolium montanum* ($r = 0.821$), *Achillea millefolium* s.l. ($r = 0.795$) and *Festuca tenuifolia* ($r = 0.775$). The correlations between relative moisture and the first five of these species (ten percent of the 48 species recorded every year) are significant at the level $P < 0.05$ for a single comparison. With Bonferroni-adjusted significance levels for 48 comparisons no significant correlations were detected between climatic parameters and single species.

The sum of evaporation in the first period which is strongly interdepending with relative moisture, also showed relatively large but negative correlation coefficients ($r < -0.71$) with the four most abundant graminoids.

DISCUSSION

Changes of meteorological conditions are the most probable primary cause of fluctuations in the meadow of the study site since year-to-year variability in human activity and hydrological

Table 2. Species recorded in the years 1988-1993, on mown plots at Negrentino, and calculated for variation pattern, mean and standard deviation (SD) of frequency (percentage of 1584 points where species was present) and variation coefficient (CV).

Species	Pattern	Mean	SD	CV
Bromus erectus	A1	59.9	9.13	0.15
Festuca tenuifolia	A1	45.0	8.06	0.18
Brachypodium pinnatum	A1	25.6	6.38	0.25
Carex caryophyllea	A2	23.7	5.77	0.24
Helianthemum nummularium	B2	20.1	4.41	0.22
Danthonia decumbens	C3	17.5	3.10	0.18
Festuca rubra		12.6	3.47	0.28
Plantago lanceolata		11.6	4.72	0.41
Briza media		10.7	1.55	0.14
Agrostis tenuis		10.4	1.54	0.15
Trifolium montanum	A2	9.3	1.31	0.14
Thymus pulegioides	B1	8.6	5.10	0.59
Potentilla pusilla	B2	7.2	3.48	0.48
Thalictrum minus	B1	4.8	1.03	0.21
Luzula campestris	A2	4.4	2.04	0.47
Lotus corniculatus	C1	4.2	2.29	0.55
Koeleria cristata	A1	3.9	1.09	0.28
Silene nutans	B3	3.8	1.17	0.31
Anthyllis vulneraria		3.5	1.77	0.50
Scabiosa columbaria	B1	3.1	1.41	0.45
Sanguisorba minor	B3	3.1	0.73	0.23
Hypochoeris radicata		2.9	0.64	0.22
Salvia pratensis	A1	2.7	0.53	0.20
Dianthus carthusianorum	B2	2.4	0.86	0.36
Arabis ciliata		1.8	0.76	0.41
Pimpinella saxifraga		1.8	0.50	0.28
Anthoxanthum odoratum	C2	1.8	1.76	1.00
Campanula rotundifolia		1.7	0.57	0.33
Ranunculus bulbosus		1.7	0.45	0.27
Carlina acaulis		1.6	0.22	0.14
Leontodon hispidus s.l.	C1	1.4	0.93	0.66
Prunella vulgaris	B1	1.4	0.82	0.60
Primula veris s.l.	C3	1.3	0.49	0.38
Trifolium repens	C2	1.3	1.57	1.23
Hippocrepis comosa		1.2	0.34	0.29
Dactylis glomerata	C2	1.1	0.66	0.62
Achillea millefolium s.l.	A2	1.1	0.35	0.33
Leucanthemum vulgare		1.1	0.35	0.32
Potentilla erecta		0.6	0.22	0.36
Trifolium pratense	C3	0.6	0.51	0.92
Rumex acetosa	A2	0.5	0.34	0.73
Sedum sexangulare		0.4	0.27	0.61
Centaurea nigrescens	B1	0.4	0.17	0.40
Ajuga reptans	C1	0.4	0.13	0.34
Veronica spicata		0.3	0.12	0.38
Trisetum flavescens	C3	0.2	0.13	0.53
Clinopodium vulgare	B3	0.2	0.12	0.57
Galium verum		0.2	0.12	0.59

Table 3. Climatic variables computed from values of the first (time units 10-18) and second (time units 19-26) growth period at Comprovasco. The sum of evaporation is computed for time units 11-18 due to missing values in early April.

Year	Mean Temperature (°C)	Mean Moisture (%)	Sum Evaporation (mm)	Sum Sunshine (h)	Sum Radiation (Wh/dm^2)	Sum Precipitation (mm)
Period I						
1988	12.84	72.90	1896	273.5	3538	307.2
1989	12.68	67.22	2743	389.3	3985	453.1
1990	13.16	68.38	2352	333.2	3601	348.6
1991	12.49	56.79	3118	433.2	4058	217.9
1992	13.12	68.50	2413	349.8	3748	359.3
1993	13.72	69.91	2040	344.1	3624	447.5
Period II						
1988	17.59	74.04	2094	428.5	3522	528.0
1989	18.20	67.44	2849	384.8	3563	180.5
1990	18.63	63.99	3192	501.5	3900	151.9
1991	20.38	62.19	3397	480.0	3836	102.4
1992	18.65	71.26	2424	433.8	3580	352.9
1993	17.04	71.55	2162	404.5	3500	400.1

conditions can be excluded and environmental variability caused by zoogenic or phytoparasitical factors (Rabotnov 1974) were not observed during the six years.

The year-to-year variability of standing crop described in this study is best explained by the mean of relative moisture during the growing period: The fact that precipitation is not the best explaining variable is not surprising (see also Watt 1960, Heady 1977); rainfall is often irregular and excessive, and incisive droughts may be hidden by a single thunderstorm. Nevertheless, the value of precipitation data to explain standing crop is improved when the number of days with a certain minimum of rain is considered. The fact that relative moisture, and not global radiation or temperature, was correlated with yield, reflects the predominance of the water supply as the limiting factor determining standing crop in meadows at relatively dry sites.

Droughts affecting the standing crop of a meadow implicitly affect the abundance of its vegetation components. Whereas water supply in April, May and June is the primary factor determining the abundance of the species of variation pattern A, variation patterns B and C are not correlated with climatic variables of the growth period in the corresponding year. These species are interpreted as primarily dependent from competitively superior neighbours, their reponses to climatic variables are indirect and complicated by time-lags.

Species of fluctuation pattern B (Fig. 3) increased after the severe summer droughts of 1989, 1990 and 1991 during which predominant species had continuously been reduced and gaps of bare soil had reached a maximum extension. Depending on how long indirect effects of drought are sustained different forms can be distinguished: there are temporary effects only visible one year after a drought (pattern B3) and persisting effects still visible two years after a drought (pattern B2) and probably even longer (pattern B1).

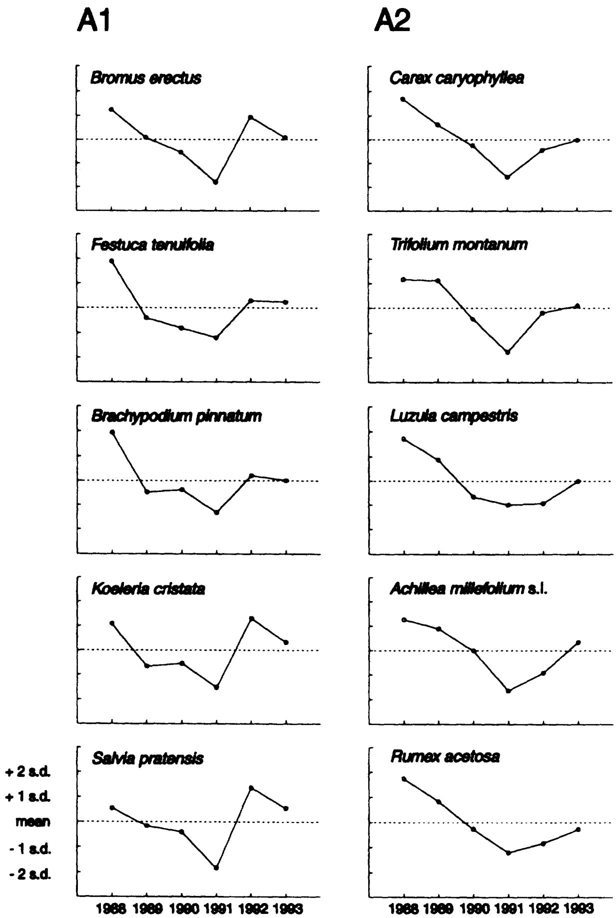
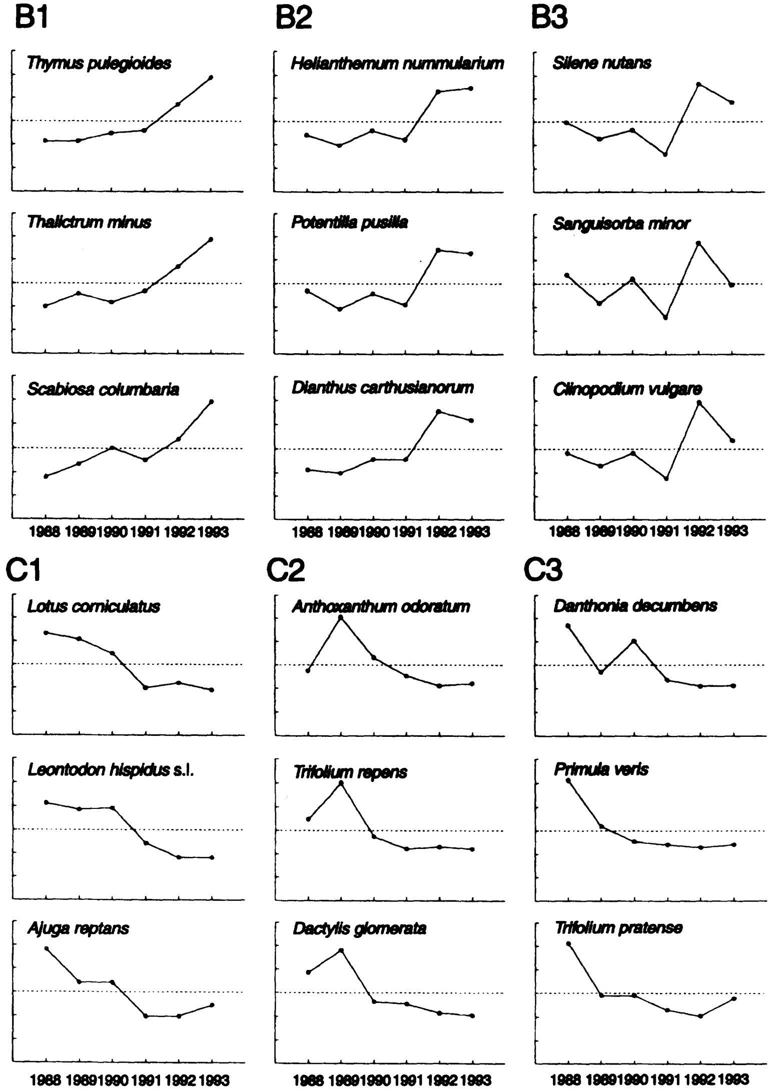


Fig. 3. Eight groups of species representing three main variation patterns A, B, C, mown plots Negrentino. For single species standardized yearly deviations from the six-year mean of frequency (percentage of presence at 1584 points) are displayed. One unit on the vertical axis corresponds to one standard deviation (Tab. 2).

The species of fluctuation pattern C (Fig. 3) are similar in that they are vulnerable to drought conditions. Despite "favourable" climatic conditions in the two years following a severe drought, these species do not recover immediately. Two forms of variation patterns, C2 and C3, deviate from C1, as species responses differed with regard to particular weather conditions in early spring 1989 and during the first growth period. Species with an early vegetative growth rhythm, *Anthoxanthum odoratum* and *Plantago lanceolata*, strongly responded to extraordinarily warm weather in winter and humid conditions in March and April; these unusually favourable conditions gave them an advantage over most of the other species which suffered from relatively dry conditions during their main vegetative growth period in May. The 1989 maximum of *Trifolium repens* cannot be interpreted by weather conditions alone, as it was due to a mass development on a single plot - presumably the plot richest in nutrients (STAMPFLI 1992).



Repeated extreme climatic conditions can induce persisting changes of patches of species (patch dynamics in the sense of VAN DER MAAREL 1988). In our case the three consecutive summer droughts 1989, 1990, 1991 resulted in a decrease of floristic similarity among the plots: the mean of all between-plot similarity values, using VAN DER MAAREL's coefficient (VAN DER MAAREL et al. 1978), decreased from 0.728 in 1988 to 0.599 in 1993. Plot 6a was not apparently different from the other plots in 1988, the mean of its floristic similarity with the other eight plots decreased from 0.784 (1988) to 0.443 (1993). A reduced water retaining capacity due to a rock within the soil (proved with an iron bar on plot 6a) is most evidently the combined environmental factor explaining differences in patch dynamics in dry years; it does not seem to be limiting in years of "normal" climatic conditions. The two competitive

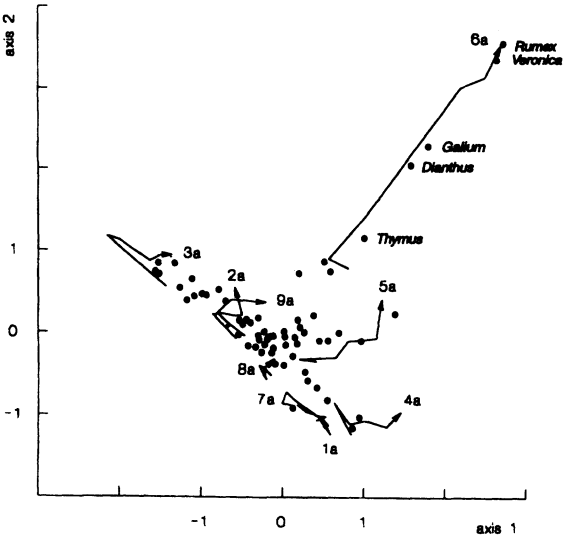


Fig. 4. Time series 1988-1993 of mown plots 1a-9a (arrows) and positions of 70 species (dots) on biplot of ordination by correspondence analysis using CANOCO (TER BRAAK 1990). 54 samples (nine plots, six years) were ordinated by species frequency values based on 176 points per plot. The first two axes account for 44.5% of the variance. Indicated species increase along with changes on plot 6a.

grasses *Bromus erectus* and *Brachypodium pinnatum* show a very similar fluctuation pattern at the spatial level of this study. To a very limited extent in 1990, dominance reversals were visible between these two species at the scale of patches. Observations in permanent plots near Göttingen (BORNKAMM 1961, ELLENBERG 1978: 654), referring to a relative increase of *Brachypodium pinnatum* vs. *Bromus erectus* in relatively dry springs (especially in May), were not confirmed. BORNKAMM (1961) argues based on the positive relationship between the ratio of climatic variables in May "precipitation (mm)/mean temperature (°C)" and the cover-value ratio "*Bromus/Brachypodium*". The corresponding climatic variable (based on values measured in May, time units 13-15) does not coincide with the frequency ratio of the two grasses in our study at Negrentino (r = -0.733, $P >$ 0.05). Differences in species assemblages, soil factors and regional climate may cause differences in variation patterns between sites, however it is rather pointless to discuss contradictory results unless sampling techniques and designs are comparable. Cover charts used by BORNKAMM do not allow a quantitative determination of overlapping grasses, and particular patch dynamics cannot be excluded at the small spatial scale (2 m^2) of his observations.

Recently an increase of *Brachypodium pinnatum* due to increased atmospheric nitrogen input was reported from Dutch chalk grasslands (BOBBINK & WILLEMS 1987, BOBBINK et al. 1989, BOBBINK 1991). No indications of such a trend were visible during the six-year observation of this study. True long-term studies, more than ten years of observation, are required to detect probable trends due to increased atmospheric deposition or climatic change.

CONCLUSIONS

The considerable temporal variability found in this study largely confirms the notion that grasslands are highly dynamic in time, as described in recent papers (HERBEN et al. 1993a, b, VAN DER MAAREL & SYKES 1993). Our results support the idea that year-to-year changes of standing crop and abundance of predominant grasses are largely determined by climatic variables while year-to-year changes of most of the other species are primarily dependent on competitively superior neighbours. Apart from the management regime, the water supply is

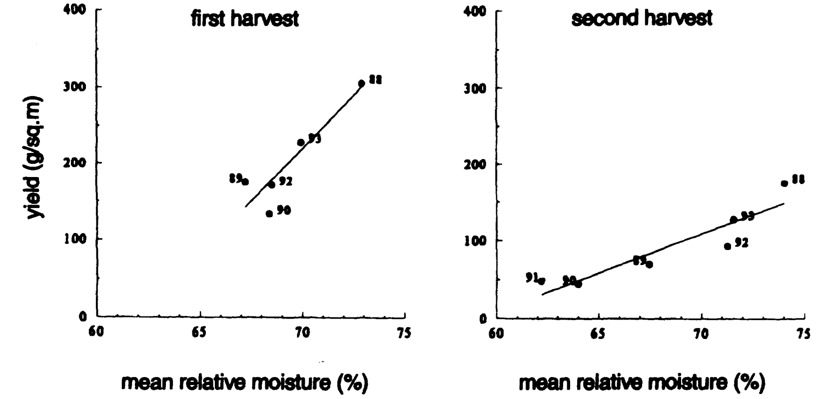


Fig. 5. Relationship between mean relative moisture (first and second growth period) and yield of standing crop (first and second harvest) in the period 1988-1993; both correlations are significant (first period: $r = 0.913$; second period: $r = 0.919$, $P < 0.05$). First harvest value of 1991 accidentally missing; the correlation is not significant with an estimated 1991 value (100 g/m^2, $r = 0.802$, $P = 0.055$).

obviously the most important factor determining the species composition in dry grasslands. Fluctuations of the weather regulate the competitive species and therefore contribute to the coexistence of many species in dry grasslands as was put forward by the competitive equilibrium hypotheses (HUSTON 1979).

Successive observation during at least ten years appear to be inevitable for a more general confirmation of the causal relationships between vegetation and weather found in this study. Time-lags of species responses to climatic variables will be recognized more completely and the possibilities for a statistical analysis of the relevant climatic explanatory variables will be improved. The relative importance of temporal climatic and spatial environmental factors for the dynamic behaviour of species can be further elucidated; various spatial scales, soil types, species assemblages and local climate types have to be considered.

Acknowledgment: I would like to thank Gregor Nyffeler for his preparation of the climatic data, and all persons engaged in field work, especially Robert Brügger, Beat Fischer, Fredi Guggisberg, Sonja Häfelfinger, Catherine Kost, Jonas Lüthy, Gregor Nyffeler, Hansueli Pestalozzi, and Astrid Vassella. I would also like to thank Werner Dähler and Klaus Zimmermann for their computer consultations, and Pim van der Knaap, Natalie Stadelmann and Astrid Vassella for reviewing the manuscript. This study is part of a research project on meadows in Ticino carried out at the Systematic-Geobotanical Institute of the University of Berne under the supervision of Prof. Dr. Otto Hegg, and supported by the Swiss National Science Foundation (grant numbers 31-9096.87, 31-30055.90, 3100-039431.93), the national and cantonal governments (BUWAL, Museo Cantonale di Storia Naturale, UPN) and the Swiss League for Nature Conservation (sezione Ticino).

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