Pattern and process in Norwegian upland grasslands:
a functional analysis

Vandvik, Vigdis[1]* & Birks, H. John B.[1,2]

[1]*Botanical Institute, University of Bergen, Allégaten 41, N-5007 Bergen, Norway;* [2]*Environmental Change Research Centre, University College London, 26 Bedford Way, London WC1 OAP, UK;*
Corresponding author: Fax +4755589667; E-mail vigdis.vandvik@bot.uib.no

Abstract. Four classes of functional and morphological plant traits – established strategies (the CSR scheme *sensu* Grime 1979), life-forms (*sensu* Raunkiaer 1934), morphology, and regenerative strategies – are used as tools for explaining vegetation gradients at summer farms in the mountains of western Norway. These farms are assembly points for free-ranging domestic grazers, and differ floristically and ecologically from the surrounding heath or woodland vegetation. DCA and TWINSPAN are used to relate major gradients in a floristic data set from 12 summer farms to two sets of explanatory variables: (1) environmental variables representing physical factors, plot position, soils, and land use, and (2) the 4 classification schemes. The main floristic gradient parallels a spatial gradient from the centres of the farms to the surrounding vegetation. A functional interpretation based on the concurrent use of the 2 sets of explanatory variables suggests that the gradient is one of decreasing disturbance and increasing environmental stress caused by decreasing grazing and manure effects away from farms. Partial CCA is used to investigate the relationships between the 4 functional/morphological plant trait classes. The 4 classification schemes are partially redundant, and do not represent different trends of specialization within the landscape. There is no strong evidence for decoupling of the traits of the vegetative and regenerative phases within the data. The combination of general process-based theories and specific plant attribute responses enhances the generality and interpretability of the study.

Keywords: Disturbance; Ecological strategy; Grazing; Life form; Monte Carlo permutation test; Ordination; Plant trait; Regeneration; Stress.

Plant nomenclature: Lid & Lid (1994).

Abbreviations: C = competitor; CEC = Cation Exchange Capacity; LOI = loss-on-ignition; PFT = plant funtional type; R = ruderal; S = stress-tolerator.

Introduction

The tradition of classifying plants and vegetation into major types on the basis of plant form has a long history (e.g. von Humboldt & Bonpland 1807; Raunkiaer 1934). This tradition is based on the observation that the capacity to survive under different geographic, climatic, and ecological conditions is often linked to plant architecture and physiognomy. Sparked by the interest in global climate change (Woodward & Cramer 1996; Díaz & Cabido 1997) and the effect of disturbance (McIntyre et al. 1999a; Weiher et al. 1999; Díaz et al. 2001) on vegetation, research on plant functional types (PFT) have received renewed attention. One approach to identify PFT has been screening programmes for measuring traits of large numbers of species (e.g. Grime et al. 1997), and to use the resulting species-by-trait matrices to derive data-defined PFT (Leishman & Westoby 1992; Thompson et al. 1996; Díaz et al. 1998). An alternative approach to the functional analysis of plants and vegetation is to start from general ecological processes and to construct conceptual models about how these processes affect specific plant attributes. Process-based models focusing on the vegetative or established phase (Grime 1974; Tilman 1988; Keddy 1990), on regeneration (Grubb 1977; Noble & Slatyer 1980; van der Maarel & Sykes 1993), and on dispersal (Taylor et al. 1990) have been suggested, and the number and nature of relevant traits, as well as the degree of coupling expected between traits of different life-history phases, have been debated (e.g. Wilson 1990; Zobel 1992; Mabry et al. 2000). The different models are not mutually exclusive, however, and if environments are ordered along two axes, representing the frequency of disturbance and the 'harshness' of the environment, then several models predict similar functional responses, at least for adult plant traits such as growth rate, investment in defence, seed production, longevity, and tolerance to suboptimal conditions (Southwood 1988). An important aspect of process-based models is that they

open up the possibility of using plant strategies as explanatory tools to identify processes influencing observed vegetation patterns (e.g. del Moral 1983; Smith & Rushton 1994; Cottrell 1996; Vetaas 1997). An advantage of the C-S-R model (Grime 1974) in this context is that data on relevant traits and strategies of many species are available (e.g. Grime et al. 1988; Heikkinen & Kalliola 1990).

Since prehistoric times the mountainous regions of Norway have been utilized for extensive summer grazing and hay-making (Kvamme 1988). Domestic animals (sheep, cattle, goats, horses) are allowed to range freely in the mountains during daytime, but are gathered in barns or small enclosures during nights. The assembly points, or 'summer farms', are semi-natural grasslands that differ in species composition and appearance from the surrounding low-alpine heath or sub-alpine woodland vegetation (Nordhagen 1943; Austrheim et al. 1999; Vandvik & Birks in press). There are many potentially important ecological gradients in the summer-farm landscape. Climate is a major growth-limiting factor in the sub- and low-alpine zone (Woodward 1988; Austrheim et al. 1999). Locally, climate varies with altitude, slope, and insolation. Precipitation is plentiful in our study area (Odland 1981), but both aridity and waterlogging may be important locally. The naturally infertile soils, especially the low amounts of available nitrogen and phosphate, are regarded as major limiting factors in montane heaths and grasslands in Norway (Baadshaug 1983) and elsewhere (Ellenberg 1988; Grime et al. 1988). Soil erosion may occur, especially on steep slopes. Finally, grazing animals are important ecological factors in semi-natural vegetation. Most obviously, grazers may act as disturbance agents through defoliation (Huntly 1991; Hulme 1996) and gap creation (Grubb 1977). Additionally, they may alter grassland vegetation through fertilization from faeces (Baadshaug 1983) and urine (Steinauer & Collins 1995), and by acting as dispersal agents (Fischer et al. 1996).

Following a functional approach, the expected response to the major ecological and land-use gradients in the summer-farm landscape in terms of plant functional traits and strategies may be predicted. Plant strategy theory (e.g. Grime 1979; Southwood 1988) predicts that if disturbance factors such as soil erosion, grazing, or trampling are important determinants of vegetation patterns, then trends in adaptions to disturbances should be recognized along the gradients. Similarly, if growth-limiting factors such as climate, moisture, or soil fertility are important, then the floristic gradients should be paralleled by trends in adaptions to 'harsh environments' or stress. In this way, variation in species traits and strategies may be utilized to assess the relative importance of different environmental factors and processes for patterns in summer-farm vegetation.

The first part of the work presented here aims to detect and interpret patterns in the study system: 1. What are the main floristic gradients in summer-farm vegetation? 2. What ecological gradients (as measured by environmental variables) can account for the gradients? 3. What ecological processes (as indicated by trends of specialization in the vegetation) underlie these gradients? The second part uses summer farms as a model system to explore and test predictions from plant strategy theory: 4. How much of the vegetation patterns can 4 different trait classification schemes (CSR strategies (*sensu* Grime 1979), life forms (*sensu* Raunkiaer 1934), simple morphological descriptions, and regenerative traits and strategies) account for? 5. Are the different classification schemes for established plant traits complementary, representing different trends of specialization within the landscape, or are they redundant? 6. Are traits of the vegetative and regenerative phases coupled or decoupled?

Methods

Study area and sampling design

Summer farms in Røldal ($n = 12$), western Norway, were selected for study. The farms are situated within an area of ca. $10 \text{km} \times 20 \text{km}$, at $650 - 850$ m above sea level (a.s.l.), and are surrounded by mountains reaching $1600 - 1700$ m a.s.l. The climate is sub-oceanic, with high autumn precipitation, heavy winter snowfall, and relatively small differences between mean January (ca. $-6 \,^{\circ}\text{C}$) and July (ca. $12 \,^{\circ}\text{C}$) temperatures (Aune 1993). Annual precipitation is ca. 1350 mm (Førland 1993). Sub-alpine birch forest is the dominant vegetation in the study area. The climatic forest limit is 800-900 m a.s.l., depending on aspect. Vegetation above the forest limit consists mainly of low-alpine dwarf-shrub heath (Odland 1981).

In July and August 1992 $2 \text{m} \times 2 \text{m}$ plots were placed subjectively in order to sample the major floristic variation at each farm, including heavily grazed, trampled, and manured vegetation, less intensively utilized grasslands, and surrounding heaths and woodlands. The cover-abundance of all vascular plants was recorded using the Domin scale (Dahl 1957), giving a total of 144 taxa in 130 plots (Fig. 1, below).

Environmental explanatory variables

Environmental variables ($n=22$) were measured and compiled for each plot or farm (Table 2). Farm size was measured in the field as the average distance from the farm centre (barn, milking shed, or other assembly point

for animals) to the border between the semi-natural grassland and the surrounding heath or woodland. As the spatial gradient extending from the farm centres to the surrounding vegetation was considered – *a priori* – to parallel a gradient of decreasing animal influence on the vegetation, distance from each plot to the farm centre was measured. In order to standardise this variable between farms, distance was divided by farm size. The resulting variable, *relative distance,* varies between 0 and 3. Aspect and slope of each plot were measured, and a simple radiation index, a potential measure of plot-scale local climate, was calculated (Oke 1987). Soil samples were collected from each plot, air-dried, and sieved through a 2 mm sieve prior to chemical analyses. Metal cation and phosphate concentrations, pH, total nitrogen (Kjeldahl method), and loss-on-ignition (LOI) were measured and base saturation and cation exchange capacity (CEC) were calculated using standard procedures (Røsberg 1984). Cation and phosphate concentrations were log-transformed, and total N was expressed as $N : LOI$, which was considered to be a simple but useful index of the ecologically relevant *available nitrogen* in the soil (Schroeder 1984).

Species traits

Species traits representing 4 different functional or morphological classification schemes were compiled for each species (Table 2). First the species were classified with respect to their established strategies *sensu* Grime (1979). Each species was assigned to a primary class, stress-tolerator (S), competitive (C), or ruderal (R), or into intermediate strategies (Fig. 1). The second classification scheme was Raunkiaer (1934) life forms. Third, a set of simple morphological descriptions of the mature plants was compiled. These included the longevity (annual or perennial), leaf position (rosette, semi-rosette, leafy stem), plant height (divided into 4 classes), and capacity for lateral spread (no, some, vigorous). Fourth, species were classified with respect to traits of regeneration, phenology, and dispersal. These included regeneration strategies (vegetative, widely dispersed, seed bank, seasonal), flowering phenology (flowering starts in spring, early summer or late summer) and duration (1, 2, 3, or ≥ 4 months), and adaptations for dispersal. The different attributes were expressed as 29 dummy (+/−) or class variables, representing a total of 62 different specific attribute states (Table 2, Fig. 1). Data were obtained from the standard Norwegian flora (Lid & Lid 1994) and the literature (Grime et al. 1988; Heikkinen & Kalliola 1990).

Data analyses

The data were compiled into 3 matrices: *floristic data* (130 observations × 144 species), *environmental data* (130 observations × 22 environmental variables), and *trait data* (144 species × 29 trait variables). The data were analysed using the computer program CANOCO 3.12a (ter Braak 1987; 1990) with default settings, downweighting of rare taxa, and strict convergence criteria for ordinations, and TWINSPAN version 2.2a (Hill 1979, modified by C.J.F. ter Braak & H.J.B. Birks) with strict convergence criteria for classifications. Ordination plots were drawn by CANODRAW 3.0 (Šmilauer 1993). Detrended Correspondence Analysis (DCA) (Hill & Gauch 1980) of the floristic data with detrending-by-segments and non-linear rescaling showed that the first DCA axis was 4.85 standard deviations (SD), and unimodal-based ordination methods were thus appropriate for these data (ter Braak & Prentice 1988).

The questions in the first part (identifying within-system patterns in plant-environment and gradient-attribute relationships) were addressed using an indirect (correlative) multivariate approach (see Økland 1996; McCune 1997; Ejrnæs & Bruun 2000). The environmental variables were related to the floristic gradients using standard unconstrained ordination techniques. The relationships of explanatory variables to the floristic gradients were interpreted through the inter-set and multiple correlation coefficients, provided within CANOCO, of the environmental variables and groups of variables with the DCA axes. A TWINSPAN classification of the samples was performed to delimit vegetation types within the data. These are here called Q-mode analyses. As CANOCO cannot handle external (explanatory) variables for 'objects' (ter Braak 1987; 1990), relating species traits to the species-by-sample ordination axes was done in the following way (see Díaz et al. 1992; Vetaas 1997): First, a DCA was run on a transposed matrix of the floristic data (144 species × 130 samples). In this analysis rare species were downweighted manually. As the species are now 'objects' and the samples 'variables' in this analysis, the trait data (144 species × 29 traits) could be used as 'explanatory' variables. As above, the results were interpreted through the inter-set correlations and multiple correlation coefficients of explanatory variables (attributes) with the DCA axes. A TWINSPAN classification of the transposed floristic data was performed to distinguish species groups with similar distributional patterns within the data, and the attribute spectra of these groups were investigated. These are here called R-mode analyses.

The questions in the second part (testing the relative explanatory power of the different attribute classes)

were addressed, and the questions in the first part elabo-
rated, using a direct (hypothesis-testing) multivariate
approach (Økland 1996). In order to quantify the frac-
tion of variance that different groups of environmental
(physical characteristics, soil chemistry, plot position,
land use) and plant trait (CSR strategies, morphology,
life forms, regenerative traits) predictors could poten-
tially account for, the following analyses were run both
in the Q-mode and R-mode context. First, CCAs were
run with each predictor group individually. Within
groups, the forward selection option in CANOCO with
statistical testing by unrestricted Monte Carlo permu-
tation tests for each added variable (ter Braak 1990; ter
Braak & Verdonschot 1995) was used to exclude vari-
ables that did not contribute significantly ($p > 0.01$) to
the explained variance. This was done to avoid over-
estimation of the explained variance in the data (Borcard
et al. 1992; Økland & Eilertsen 1994). Partial CCAs
with each predictor group as constraining variables and
all other groups as covariables were run to quantify the
unique contribution of each group – or the amount of
variance they explain when the effect of all other pre-
dictors groups are allowed for statistically. The statisti-
cal significance of this unique contribution was tested
using Monte Carlo permutation tests within CANOCO,
with 499 unrestricted permutations, and significance
judged by the overall (trace) statistic. In order to answer
questions 5 and 6, additional CCAs and partial CCAs
were run for different combinations of plant trait groups
to quantify shared and unique variances – or the degree of
overlap between different classification schemes (Borcard
et al. 1992). The statistical significance of each unique
contribution was evaluated as described above.

Results

The very high correlations between the Q-mode and
R-mode DCA axis 1 ($r = -0.99$) and axis 2 ($r = -0.98$)
sample scores (Table 1) and the very similar eigenvalues
for the Q- and R-mode ordinations (0.55 vs. 0.58, 0.23
vs. 0.26) confirm that the solutions are essentially the
same, and that we are justified in comparing the rela-
tionships of environmental variables and species traits
to these axes. As the Q- and R-mode axes 1 and 2 are
negatively correlated, the R-mode axes were reversed
(multiplied by -1) in the figures and tables for ease of
interpretation.

Floristic gradients and environment

Many environmental variables are strongly corre-
lated to the first floristic gradients, and species-environ-
ment correlations are high, suggesting that the relevant

Table 1. Ordination summary of the Q- and R-mode DCAs.
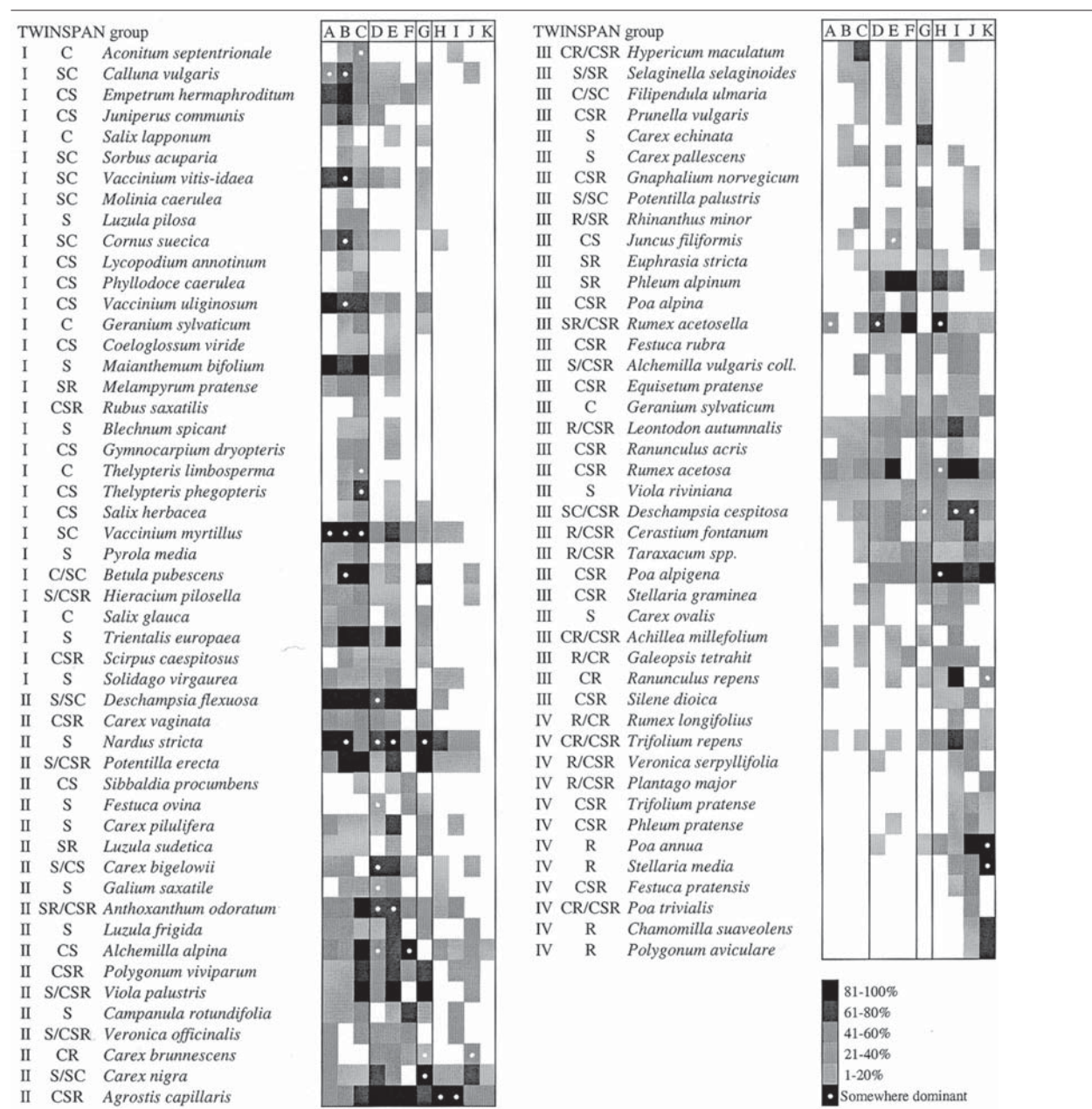SD = standard deviation.

Axes	1	2	3	4	Total inertia
Q-mode DCA					
Eigenvalues	0.55	0.23	0.15	0.11	4.23
Lengths of gradient (SD units)	4.85	2.65	2.53	2.05	
Species-environment correlation	0.92	0.81	0.81	0.71	
% variance of species data	12.9	18.3	21.9	24.6	
R-mode DCA					
Eigenvalues	0.58	0.26	0.21	0.14	5.33
Correlations with Q-mode axes	0.99	0.97	0.73	–0.06	
Sample-attribute correlation	0.84	0.41	0.45	0.35	
% variance of species data	10.9	15.8	19.8	22.4	

environmental variables are included in the analyses
(Tables 1 and 2, Fig. 2b). On the basis of its environ-
mental correlations, the first gradient can be interpreted
as one of decreasing soil nitrogen, phosphate, and pH
and increasing slope along the spatial gradient from
farm centres to the surrounding heath or woodland.
Once the environmental variables are accounted for, the
spatial gradient has a low unique contribution to the
explained variance (Table 3), suggesting that the meas-
ured environmental variables capture important aspects
of the farms-to-surroundings gradient. Slope is strongly
correlated to the gradient (Fig. 2b), and potential effects
may be through effects on soil erosion (high on steep
slopes), microclimate (resulting from differential insola-
tion), or soil moisture (high only on flat ground). The
strong correlations of nitrogen and phosphate to the gra-
dient suggest that it can also be interpreted as a gradient of
decreasing manure-related effects from the farm centres
towards the nutrient-poor grasslands and heaths (Table 2,
Fig. 2b).

The second floristic gradient can be described as a
complex of (1) altitude and (2) a gradient from mineral
to organic soils, which is interpreted as a gradient of
increasing soil moisture. As humic colloids have very
high adsorptive capacities (Schroeder 1984), soil or-
ganic content is strongly correlated to CEC and pH
(Table 2, Fig. 2b).

The 11 TWINSPAN vegetation types occupy dis-
tinct positions along DCA axes 1 and 2 (Figs. 1, 2a).
Groups A, B, and C, heathland plots situated on steep
slopes away from farm centres, are concentrated on the
positive side of DCA axis 1. Wet (group G) and drier
nutrient-poor grasslands (groups D, E, F) have interme-
diate axis 1 scores, but are separated to some extent
along DCA axis 2. The central grasslands (groups H, I,
J, K) have the lowest DCA axis 1 scores, and occupy
fertile soils near farm centres. Groups H, I, and J are
separated along DCA axis 2, while group K occupies an
extreme DCA axis 1 position.

Fig. 1. Two-way table of TWINSPAN groups A – K, with the percentage occurrences of the species in each sample group (see legend), the TWINSPAN species group I – IV to which the species belong, and their classification according to the C-S-R scheme. All species present with three or more occurrences in the data are shown.

Floristic gradients and plant traits

The high number of significant correlations between plant traits and DCA axis 1 (Tables 1 and 2, Fig. 2c) show that this was a gradient, not only floristically and environmentally, but also in CSR strategies, predominant life forms, morphologies, and modes of regeneration and dispersal. Summer farms are characterized by R, C-S-R, and S-R strategies, while S, C, and C-S species occur predominantly in the heathlands. A CSR triangular ordination (Grime 1979) of samples (Fig. 3) highlight the trend in established strategies, and suggests that decreasing disturbance (Triangular ordination R-axis and DCA 1: Spearman rank correlation $r = -0.73$) is by far the most important structuring process along the gradient, but that increasing stress (S-axis and DCA 1: $r = 0.39$) may also be important. Competitiveness also increases along the gradient, but the correlation is
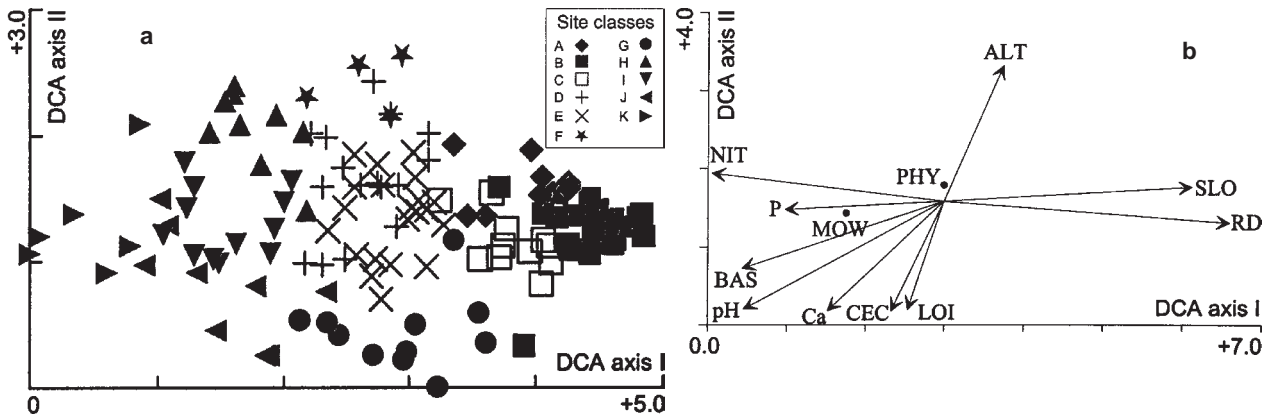
Fig. 2. a. Ordination of samples on DCA axes 1 and 2. TWINSPAN vegetation types are shown as different symbols. Groups A, B, and C represent heath and woodlands, D, E, and F are nutrient-poor grasslands, G is grassland on humid soils, and H, I, J, and K represent nutrient-rich grasslands. **b.** Ordination of environmental variables that are significantly correlated with DCA axes 1 and 2 in Q-mode DCA space. Axes are scaled in standard deviations. For each variable, data scale, range, correlation coefficients with the DCA axes, and abbreviations are given in Table 2 and Fig. 1. **c.** Ordination of species traits that are significantly correlated with DCA axes 1 and 2 in R-mode DCA space. Axes are scaled in standard deviations. For each variable, data scale, correlation coefficients with the DCA axes; for abbreviations see Table 2.

relatively weak (C axis and DCA 1: $r = 0.28$), suggesting that this trend of specialization is of minor importance along the gradient. Hemicryptophytes and therophytes decrease from farm centres to heathlands, while chamaeophytes and phanerophytes increase. This pattern is also evident in the morphological traits, as annuals and semi-rosettes decrease, while tall plants and plants with leafy stems increase along the gradient. In regenerative traits, plants with seeds showing no specialization for dispersal and flowering throughout the growing season are characteristic of farm centres, while dispersal by ingested seeds is characteristic of heathlands (Fig. 2c).

DCA axis 2 is positively correlated with S-R strategists, and negatively correlated with plant height, C strategists, and aquatic dispersal (Table 2, Fig. 2c), but the weak correlations and the low multiple correlation coefficients of plant trait groups with DCA axis 2 suggest that species distributions along this floristic axis can not be fully accounted for by the compiled plant traits.

The 4 R-mode TWINSPAN species groups differ in their distribution along the farm-to-surroundings gradient and between vegetation types (Fig. 1). These distributional groups differ considerably in C-S-R strategies, life forms, and phenology, but less clearly in regenerative
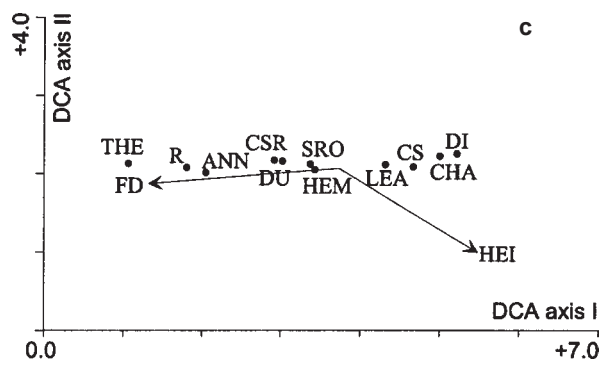

Fig. 3. C-S-R triangular ordination of samples. For clarity, only centroids of the TWINSPAN vegetation types are shown. The positions of the group centroids are calculated on the basis of the strategies of all species present in the plots, weighted by abundance. Spearman's rank correlation coefficients between samples scores on DCA axis 1 and the C-S-R axes are: C = 0.28 ($p < 0.01$), S = 0.39 ($p < 0.001$), R = − 0.73 ($p < 0.001$).

Table 2. Correlations of environmental variables and species traits with DCA axes 1 and 2. Abbreviations and scales of all variables and traits are given. Multiple R is the multiple correlation coefficient for each subset of variables with the DCA axes after forward selection within groups (see text).

Environmental variables		Scale	Data range	Axis 1	Axis 2
Plot position					
Distance to centre	RD	continuous	0-3	**0.70**	–0.10
Physical characteristics					
Altitude	ALT	m	620-844	0.13	**0.38**
Slope	SLO	°	0-35	**0.60**	0.01
Incoming radiation	RI	continuous	0.41-0.90	0.17	0.07
Metabasalt bedrock	MET	+/–	0-1	0.01	–0.08
Phyllitic bedrock	PHY	+/–	0-1	0.10	**0.32**
Amfibolitic bedrock	AMF	+/–	0-1	0.10	0.20
Multiple R:				0.61	0.41
Soil chemistry					
Loss–on–ignition	LOI	%	8.6-92.4	–0.08	**–0.39**
Relative Nitrogen	NIT	% of LOI	0.05-0.44	**–0.49**	0.10
Extractable Phosphate	P	log(mg/100g)	0.2-6.0	**–0.39**	0.00
Soil pH	pH		3.9-6.5	**–0.48**	**–0.35**
Extractable Calcium	Ca	log(mg/100g)	2.5-6.7	–0.28	**–0.40**
Extractable Magnesium	Mg	log(mg/100g)	1.3-5.1	–0.17	–0.27
Extractable Sodium	Na	log(mg/100g)	0.1-4.1	–0.27	–0.27
Extractable Potassium	K	log(mg/100g)	2.7-5.6	–0.05	–0.30
Cation exchange capacity	CEC	meq/100g	4.8-83.0	–0.12	**–0.42**
Base saturation	BAS	% of cations	15.1-98.4	**–0.49**	–0.16
Multiple R:				*0.70*	*0.63*
Land use					
Farm size	SIZ	m	40-150	0.00	–0.22
Mowing	MOW	+/–	0-1	**–0.44**	–0.10
Sheep grazing	SHE	+/–	0-1	0.25	0.06
Goat grazing	GOA	+/–	0-1	0.06	–0.03
Years since abandonment	YRS	yr	0-42	0.14	0.21
Multiple R:				0.46	0.29

Species attributes		Scale	Axis 1	Axis 2
Strategies (CSR)				
Competitive	C	+/–	0.23	–0.19
Stress-tolerant	S	+/–	0.17	–0.12
Ruderal	R	+/–	**–0.43**	0.00
Stress/competitive	CS	+/–	**0.44**	0.03
Competitive/ruderal	CR	+/–	–0.22	0.07
Stress/ruderal	SR	+/–	–0.08	0.24
C-S-R strategists	CSR	+/–	**–0.34**	0.08
Multiple R:			0.72	0.26
Life form				
Phanerophyte	PHA	+/–	0.27	–0.10
Chamaeophyte	CHA	+/–	**0.47**	0.12
Hemichryptophyte	HEM	+/–	**–0.42**	–0.06
Geophyte	GEO	+/–	0.18	0.01
Therophyte	THE	+/–	**–0.42**	0.02
Multiple R:			0.70	0.07
Morphology				
Annual	ANN	+/–	**–0.32**	–0.02
Semi-rosette	SRO	+/–	**–0.33**	0.08
Leafy stem	LEA	+/–	**0.41**	0.06
Rosette	ROS	+/–	0.04	–0.01
Plant height	HEI	classes	**0.35**	–0.23
Lateral spread	LAT	classes	0.19	–0.08
Multiple R:			0.60	0.28
Regeneration, phenology and dispersal				
Vegetative regeneration	RV	+/–	–0.19	–0.02
Widely dispersed propagules	RW	+/–	0.09	–0.14
Buried seed bank	RB	+/–	–0.15	0.05
Seasonal regeneration	RS	+/–	0.00	0.05
Flowering time	FT	month	–0.04	0.06
Flowering duration	FD	months	**–0.49**	–0.05
Wind dispersal	DW	+/–	0.14	–0.12
Unspecialised dispersal	DU	+/–	**–0.39**	0.10
Ingested dispersal	DI	+/–	**0.47**	0.12
Adhesive dispersal	DA	+/–	–0.12	–0.04
Aquatic dispersal	DQ	+/–	–0.15	–0.19
Multiple R:			0.66	0.22

strategies and modes of dispersal. The *outside* species (44 spp.) mainly occur in the heathlands. They are C-S, S, and C strategists, the group is morphologically diverse, and dispersal is by wind or ingested seeds. The *widespread* species (26 spp.) grow both on and off farms. They are S, C-S-R, or C-S strategists, and the majority are hemicryptophytes. Many species show no specialization for dispersal, whereas others are dispersed by adherence to animals. The *farm* species (54 spp.) are only occasionally encountered outside summer farms. C-S-R strategists and hemicryptophytes predominate, and regenerative strategies and dispersal are more diverse than in the preceding group. Finally, the species of the *central* grasslands (20 spp.) have C-S-R, R, or C-R strategies, and are hemicryptophytes or therophytes. These species are either dispersed by adherence to animals, or they have no specialization for dispersal.

Trait classification schemes

The results of the (partial) CCA analyses (Table 3) showed that all trait classification schemes captured a substantial fraction (8.0 - 10.8%) of the floristic variation in the data. When all groups were included as explanatory variables the trait data accounted for a total of 23.2%, indicating that there was considerable redundancy between classification schemes. Established strategies (C-S-R scheme) and Raunkiaer life forms both had significant unique variances (Table 3), indicating that these 2 schemes related to distinct trait syndromes and sorted along different ecological gradients in the data. The simple morphological descriptions had no significant unique variance (Table 3), and more detailed partial CCA's (Fig. 5a) showed that a large fraction of the variance accounted for by morphol-
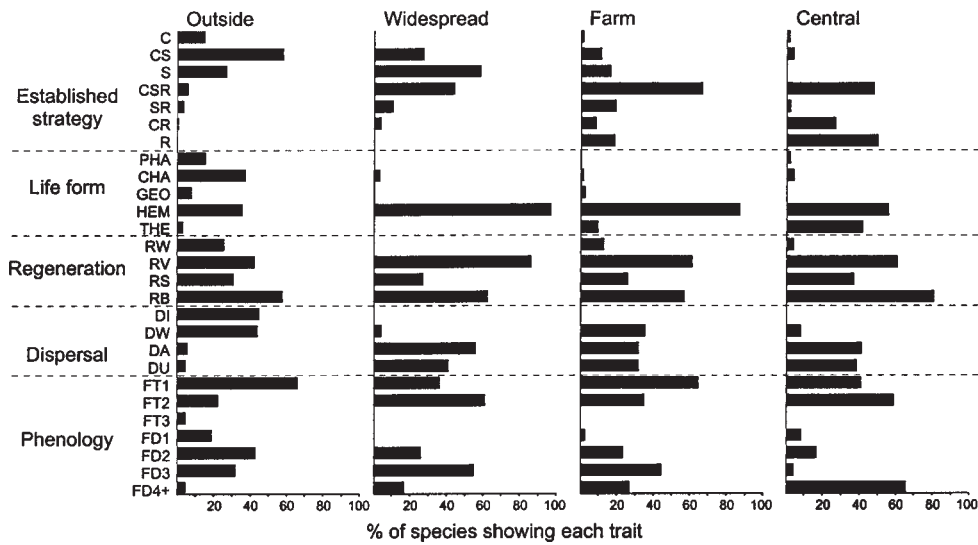
Fig. 4. Functional trait spectra of the TWINSPAN species groups. Morphological traits are not shown. Horizontal bars represent the percentage of all species in the group, weighted by occurrence, having a particular trait. The quantitative phenological variables, flowering time and flowering duration, are divided into classes: FT1, FT2, and FT3 represent spring, early summer, and late summer flowering, respectively. FD1 - FD4+ represent duration of flowering in number of months per year. Otherwise, functional trait abbreviations follow Table 2.

ogy was shared with C-S-R- strategies and life forms. Statistically, the morphological traits could be uncoupled from the C-S-R strategies but did not have a significant unique contribution once the Raunkiaer life forms had been allowed for. The regenerative characteristics could account for a relatively large fraction of floristic variance, but this fraction was to a large extent shared with the C-S-R- strategies and life forms. The regenerative characteristics were only marginally significant once C-S-R strategies had been accounted for, and they could not be uncoupled from the Raunkiaer life forms (Table 3, Fig. 5b).

Discussion

This study investigates the potential importance of different environmental factors for floristic patterns in an upland semi-natural landscape, using different functional classification schemes. Such pattern-seeking studies are necessarily based on observational field data, and, as a result, the different explanatory variables are inextricably confounded. Although the data and methods used here cannot determine causality, the potential value of the approach is that it can evaluate the relative importance of different ecological factors and processes and indicate the existence of superfluous or missing explanatory variables.

Table 3. The explanatory power of the different groups of environmental and plant trait variables. Significant variables are the variables included in each group after forward selection. Variance explained is the percent of total inertia accounted for when the group is used as constraining variables in CCA, and the unique contribution is the percent of total inertia accounted for when the effect of all other groups are removed in partial CCA. *P*-values refer to the unique contribution (see text).

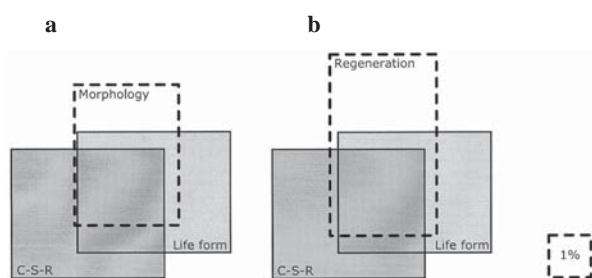| Variable group	Significant variables	Variance explained	Unique contribution	*P*-value
Groups of environmental explanatory variables				
Relative distance	RD	5.7	1.1	0.03
Physical factors	SLO, ALT, RI, MET	8.9	3.2	0.01
Soil factors:	LOI, NIT, pH, Ca, Mg, K, BAS	16.4	10	0.01
Land-use factors:	MOW, SHE, YRS	5.2	2.4	0.01
Groups of plant attribute explanatory variables				
EÉtablished strategy (CSR)	C, S, R, CS	10.8	5.3	0.01
Growth form (Raunkiær)	HEM, THE	10.1	3.0	0.01
Morphology	ANN, SRO, LEA, HEI	8.0	2.9	0.39
Regenerative characteristics	FD, DI, DQ, DW, DU	10.5	4.6	0.57

Fig. 5. Graphical representation of the unique and shared (overlapping squares) variances explained by **(a)** the morphological traits, and **(b)** the regenerative traits with the C-S-R strategies and Raunkiaer life forms (R-mode analyses). Areas reflect the percentage variance explained by each fraction of variance. The statistical significance of the variance uniquely attributable to the focus group when the C-S-R strategies and life-forms are partialled out (|) is tested using Monte Carlo permutation tests within CANOCO, with 499 unrestricted permutations, and significance judged by the overall (trace) statistic. Results: Morphology | C-S-R: $p < 0.002$, Morphology | Life form: $p = 0.59$, Regeneration | C-S-R: $p = 0.027$, Regeneration | Life form: $p = 0.72$.

Pattern and processes along the farms-to-surroundings gradient

The overriding floristic gradient in the data correlates with distance to farm. Within the data, floristic composition is more strongly affected by this gradient than by gradients such as soil moisture, microclimate (as measured by radiation index), altitude, bedrock, or land-use history. However, a complex of environmental factors and biological processes may account for the gradient, and an evaluation based on the concurrent use of Q- and R-mode analyses is as follows. The established (C-S-R) strategies confirm the importance of decreasing soil fertility from the farms to the surroundings (Fig. 2b), as the gradient is paralleled by the increasing importance of stress-tolerance (Figs. 2c, 3). The sharply decreasing importance of disturbance-tolerant species (Figs. 2c, 3), however, suggests that decreasing disturbance may be a major process underlying the gradient. Slope is also strongly correlated to the gradient, so that disturbance-tolerance is high in flat areas and low on steep slopes at summer farms (Figs. 2c, 3). This contradicts the expected effects of soil erosion, suggesting that this factor is not important within our data. Relationships within the environmental data show that the effect of slope is also independent of microclimate (as measured by RI, Table 2) and soil moisture (as reflected by LOI and CEC, Table 2, and TWINSPAN groups, Fig. 1). Grazing and trampling thus remain as the most probable causal factors for the disturbance gradient, as summer farms are assembly points for free-ranging grazing ani-

mals. The high explanatory power of slope for patterns in the data may be a result of differential land-use in a rugged landscape, summer farms being located on relatively level ground surrounded by steep hillsides.

This interpretation is further validated by the responses of plant morphology and life form, showing that tall plants with erect shoots, leafy stems, and long life-cycles increase, while low-growing or prostrate plants with short life cycles decrease away from farms. This agrees with the recurrent sets of plant traits commonly reported to be associated with grazing (Harper 1969; Noy Meir et al. 1989; Díaz et al. 1994; McIntyre et al. 1995; Milchunas & Lauenroth 1993; Díaz et al. 2001). Although the overall responses to livestock and the suite of morphological traits associated with this response are well documented (Milchunas & Lauenroth 1993), several causal mechanisms have been suggested. The classical model focuses on top-down defoliation, which reduces the competitive advantage of tall plants and increases the relative advantage of grazing-tolerant species (Harper 1969). Alternative explanations focus on herbivore selectivity (Anderson & Briske 1995), the effects of droppings and urine patches (Steinauer & Collins 1995; Day & Detling 1990), or the effects of animals on regeneration (Grubb 1977; Noy Meir et al. 1989; van der Maarel & Sykes 1993) and dispersal (Fischer et al. 1996; Poschlod et al. 1998). In this study we did not attempt to test these mechanisms specifically, but rather to use the plant-strategy approach to evaluate their potential importance within a grazed system. Our analysis suggested that (1) grazing animals are important ecological factors within these grasslands, (2) animal effects create strong local floristic and functional gradients at summer farms, and (3) these gradients reflect strong local variation in disturbance effects, but also fertilization effects.

Pattern and processes along the moisture/altitudinal gradient

On the basis of the available environmental variables the second floristic gradient is interpreted as a complex of (1) increasing altitude and (2) decreasing soil moisture. Both gradients should be related to increasing environmental stress and decreasing competitiveness within upland grasslands (Grime 1979). Two species groups (C and S-R strategists, Fig. 2c) respond as expected along the gradient, but there is no overall trend in the data, as there are no significant correlations between the second DCA axis and the C, S, or R axes in the triangular ordination (Fig. 3). Within the other plant trait groups there are only a few weak correlations with DCA axis 2. This suggests that (1) relevant traits were not measured or (2) the important ecological processes

may be independent of plant traits. For example, grazers are important dispersal vectors in pastoral landscapes (Poschlod et al. 1998). We might therefore expect high frequencies of zoochory in the *central*, *farm*, and *widespread* species groups. The high frequency of unspecialized dispersal and the scarcity of wind-dispersal in these groups are more difficult to explain, especially as this contrasts with observations from similar systems (e.g. McIntyre et al. 1995). However, in an experimental study of dispersal in grasslands, Fischer et al. (1996) show that the probability of ectozoochory is generally high and, importantly, it is independent of seed or fruit morphology. Clearly, if the realized dispersal mode is trait-independent, then trends in dispersal attributes do not merit interpretation.

Complementary or redundant classification schemes

Species attributes representing all established trait classifications are related to the first floristic gradient in the data, and variance decomposition shows that all classification schemes account for considerable, but partly overlapping, fractions of the variance. This result is to a large extent expected, as the life form classification (Raunkiaer 1934) is based on morphology, and as C-S-R theory predicts that functional strategies should differ in recurring sets of morphological traits (Grime 1979; Grime et al. 1997). We might thus conclude that the classification schemes are at least partially redundant in this system (Fig. 5a). But in addition to the shared variance, two of the classification schemes, the C-S-R strategies and life forms (Raunkiaer 1934), also have significant unique variances (Table 3, Fig. 5), indicating that they relate to partially independent vegetation patterns within the data. Many authors have argued that process-based models oversimplify the complex patterns in nature, and that functional studies should focus on the responses of specific plant attributes (e.g. Belsky 1992; McIntyre et al. 1995). This is not supported in our study, as the process-based C-S-R model (Grime 1974) is the classification scheme that relates most strongly to the overall floristic variation (Table 3) and also to the major gradient (Table 2). A strong point of process-based models is that they focus on general processes rather than specific attributes and therefore enable meaningful comparisons between very different ecological systems and geographical regions. At such scales the responses of specific traits may be context-sensitive (McIntyre 1999b; Mabry et al. 2000; Díaz 2001). Contrasting views on process-based models may largely reflect different research strategies and aims (Grubb 1985; Grime 1989; Mabry et al. 2000): is the focus on detailed responses to specific environmental conditions, or on the recognition of recurring patterns in the relationships between plant traits and habitat characteristics? Clearly, these approaches are complementary, rather than mutually exclusive. In our study, the C-S-R model provides a useful framework within which vegetation patterns, specific attribute responses, and environmental gradients can be summarized and interpreted.

Coupling of established and regenerative traits

Plant strategy theory (e.g. Grime 1979; Southwood 1988) argues that there is not necessarily a relationship between the vegetative and reproductive attributes of plants, so that the two sets of traits may be independent, or decoupled. Decoupling has mainly been studied through relationships within the trait × species data, for example by comparing correlations within and between trait classes and performing trait-based classifications. In support of the theory, a number of studies have found weak relationships between the two sets of traits (e.g. Leishman & Westoby 1992; Thompson et al. 1996; Díaz & Cabido 1997), but strong correspondence has also been reported (e.g. Mabry et al. 2000). As seedlings are small, less competitive, less protected against predators, and more vulnerable to adverse environmental conditions such as freezing or deficiency of water or nutrients than mature plants, they are often more restricted in their ecological tolerances (Grubb 1977; van der Maarel & Sykes 1993). If the traits of the vegetative and reproductive phases are decoupled, and if the two life stages are affected differentially by ecological factors, then vegetative and reproductive traits should relate to different ecological gradients within landscapes. A strong (but not necessary) evidence for decoupling is then that the regenerative and established traits account for unique fractions of the distributional data within a landscape. We test this for summer farms by quantifying and testing the unique and shared variances of the reproductive traits with Raunkiaer life forms and C-S-R strategies (Table 3, Fig. 5b). Our results show that there is considerable overlap in the variance accounted for by the different classification schemes, and that reproductive traits have no statistically significant unique variance once the life forms and strategies of the mature plants are accounted for. Thus we find no strong evidence for decoupling in our data.

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