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Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland

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Summary

1 The cover of plant species was recorded annually from 1988 to 2000 in nine spatially replicated plots in a species-rich, semi-natural meadow at Negrentino (southern Alps). This period showed large climatic variation and included the centennial maximum and minimum frequency of days with ≥ 10 mm of rain.

2 Changes in species composition were compared between three 4-year intervals characterized by increasingly dry weather (1988–91), a preceding extreme drought (1992–95), and increasingly wet weather (1997–2000). Redundancy analysis and ANOVA with repeated spatial replicates were used to find trends in vegetation data across time.

3 Recruitment capacity, the potential for fast clonal growth and seasonal expansion rate were determined for abundant taxa and tested in general linear models (GLM) as predictors for rates of change in relative cover of species across the climatically defined 4-year intervals.

4 Relative cover of the major growth forms present, graminoids and forbs, changed more in the period following extreme drought than at other times. Recruitment capacity was the only predictor of species' rates of change.

5 Following perturbation, re-colonization was the primary driver of vegetation dynamics. The dominant grasses, which lacked high recruitment from seed, therefore decreased in relative abundance. This effect persisted until the end of the study and may represent a lasting response to an extreme climatic event.

Key-words: colonization, community stability, competition, disturbance, invasibility, permanent plot, plant succession, plant-weather relations, regeneration by seed, time series

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Introduction

As the global climate changes, ecologists expect that extreme climatic events will be followed by radical or irreversible vegetation changes with local colonizations and extinctions (Grime *et al*. 1994). In perennial grasslands severe droughts may open gaps for regeneration by causing the mortality of established plants. Differences between plant species in regenerative characteristics, such as persistence of the seed bank or capacity for clonal growth, may influence vegetation responses (Grime 1981; Klimeš *et al*. 1997; Thompson *et al*. 1997). Regenerative success depends both on the rate of vegetative growth and the tolerance of shoots, roots and other storage organs to drought, and on the output of seeds and the ability of the resulting offspring to exploit post-drought conditions (Grime 2001). A recently formulated theory explaining the intermittent nature of invasibility of plant communities (Davis *et al*. 2000) proposes that susceptibility to invasion increases with resource availability (i.e. the difference between resource supply and resource uptake). However, the extent to which regeneration and stability in species composition are coupled with disturbances such as droughts is not well established (Grubb 1988) and long-term data are needed (Collins 1995).

A few observational or experimental studies, with continuous records over 4–40 years have, by chance, included an extreme drought (Brenchley & Warington 1958; Albertson & Tomanek 1965; Hopkins 1978; Lepš *et al*. 1982; Willems 1985; Grime *et al*. 1994; Rosén 1995; Tilman 1996). However, most of these studies either confounded drought effects with other explicit sources of variation, or lacked temporal continuity and/or spatial resolution in their sampling. So far therefore there is no conclusive evidence for an extreme drought causing changes in the composition and structure of a species-rich meadow that persist for more than a few years.

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We predicted that a radical change in species composition might be more likely to occur after an extreme drought than at other times. The idea that re-colonization patterns can re-shape the composition of vegetation after disturbance follows from the theory of invasibility (Davis *et al.* 2000), but other mechanisms are possible. Competition, for example, could be relatively more important in periods without water shortage (thus favouring dominants), or the reduction in vigour of dominants could favour tolerant species during droughts (Buckland *et al.* 1997; Dunnett *et al.* 1998). The scenarios give rise to different predictions about the timing of changes. If change is caused by a resource pulse after disturbance (Davis *et al.* 2000) then the greatest rate of response will occur during the period of high light availability that follows high mortality, i.e. just after the drought. If, however, competitive exclusion drives change, the greatest response will be during periods of relatively high water supply and, if the reduction in vigour of dominants is responsible, change will be fastest during periods of relatively low water supply, i.e. during the drought.

Methods and materials

STUDY SITE

The grasslands at Negrentino (46°27′40″ N, 8°55′30″ E, 720–860 m a.s.l.) include *c.* 5 ha of species rich meadows. These represent one of the few remnants on valley slopes in Ticino (southern Alps of Switzerland), where mowing for hay production at traditional dates (June and September) has been maintained by farmers. Two regular harvests yield *c.* 300 g m^{-2} dry wt of hay in years with average humidity. The long-term data presented here are based, as in Stampfli (1995), on the central 1.1 × 1.6 m areas of nine permanently marked 2 × 2.2 m 'control' plots in a *c.* 250-m^2 study site. The plots were originally established in 1988 as part of an experimental study of changes in the composition of herbaceous species due to abandoned mowing (Stampfli 1992; Stampfli & Zeiter 2001). The vegetation can be characterized as *Mesobromion* grassland (Ellenberg 1996) and most of its component species are stress-tolerators, stress-tolerant ruderals, stress-tolerant competitors, C-S-R strategists or intermediate between these four types (Hodgson *et al.* 1995). The soil is moderately acid (pH = 5.4, top soil sample measured 1989 in water) and deeply weathered (depth mostly > 1 m) with high silt and low nutrient content. There is no indication of inflow of soil water below ground. Located on a southerly, exposed slope, plots show an average inclination of 14.8°.

Successional processes were not important as the twice yearly mowing was maintained in the sample plots and in areas surrounding the study site. No major disturbances or environmental perturbations, other than those due to mowing and climatic droughts, were apparent. No effects due to pests or small mammals known to show periodic mass activity in other areas were observed and trampling by visitors or grazers was prevented by fencing.

The climate is temperate-humid according to the classification by Walter & Lieth (1964). Ticino is in the wettest region of the Alps in terms of total precipitation but, based on the number of rainy days, it is remarkably dry compared with the rest of the Alps (Frei & Schär 1998). Comprovasco, located *c.* 250 m lower and *c.* 1 km away from the study site, has an annual mean precipitation of 1321 mm (1901–2000, MeteoSwiss, Locarno-Monti) with much falling between March and November. NW to NE winds may occur at any time of the year, causing very dry atmospheric conditions in the lee of the main mountain range.

Daily precipitation records from Comprovasco (annual reports 1893–1958, electronic database 1959–2000, MeteoSwiss, Zürich) show that several warm-seasonal droughts have occurred across the past century (Fig. 1). An exceptional drought was recorded in the three consecutive years 1989–91, an unusual period characterized by more northerly winds (Stampfli 2001).

Yield of the June harvest was positively related to spring means of relative humidity and sums of precipitation days and negatively related to means of radiation and sums of sunshine hours (automatic measurements at Comprovasco for 1988–2000, hourly data, MeteoSwiss, Zürich, data not shown). Climatic drought therefore appears to limit plant growth at the study site.

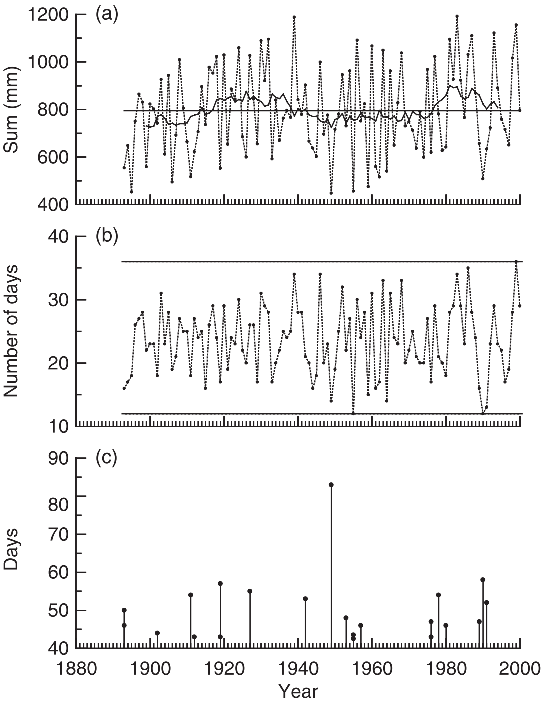

Fig. 1 Aspects of warm-seasonal precipitation (1 April to 30 September) at Comprovasco in 108-year series (1893–2000, daily records at 07.00): (a) precipitation sums (mean, moving average using a 13-year window); (b) number of days with precipitation ≥ 10 mm, ranges between extremes (horizontal lines); (c) dry periods of ≥ 42 consecutive days with precipitation < 10 mm (closed circles with spikes).

COLLECTION OF WEATHER DATA

The wetness or humidity of a growing season was characterized by climatic measures that are based either on precipitation (i.e. physically related to the input of water to the soil) or on vapour pressure deficit (VPD, i.e. physically related to the loss of water from the vegetation and the soil). VPD was calculated from hourly data of temperature and relative humidity measured at Comprovasco (MeteoSwiss, Zürich) with a constant value of 0.085 MPa for air pressure.

Measurements from a rain gauge (ARG100) and six soil moisture sensors (EQ2 equitensiometer) recorded hourly at the study site since April 1999 with a data logger (DL2e, Delta-T, Cambridge, UK) helped to define the drought threshold. Intermittent showers resulting in < 10 mm of daily rain usually did not affect soil moisture at 10 cm below ground (data not shown). Drought length was therefore considered as the duration of a period with < 10 mm of daily rain.

The humid daylight period was defined as the number of daylight hours that are not limited by water stress, i.e. hours with a radiation sum > 10 Wm^{-2} and a VPD < 1 kPa. This definition assumes that there is a threshold of plant water potential below which plants close their stomata and thus reduce their photosynthesis. Studies on woody plants suggest that stomata close when the vapour pressure deficit exceeds *c.* 1 kPa (Bond & Kavanagh 1999; Hogg *et al.* 2000; Zweifel *et al.* 2002) and this value was used in the absence of separate data for grassland herbs.

VEGETATION RECORDS

Vegetation was sampled at points using a pin. In the central areas of all plots 176 points were exactly relocated each year during a sampling period of 11–21 days, between 30 May and 26 June, centred around 16 June, in a rectangular 11 × 16 grid at 10-cm spacing (Stampfli 1992). One leading person was involved and the same equipment (see Stampfli 1991) was used across time. Species density is the average number of herbaceous vascular species per point. Species cover is the number of points at which the species is present divided by the number of points sampled. Relative cover is species cover divided by the sum of cover over all herbaceous vascular species in the community and relative cover of graminoids the summed cover of graminoids (*Poaceae*, *Carex* and *Luzula*) divided by the summed cover of graminoids and forbs (non-gramineous herbs and woody dwarf shrubs). Nomenclature follows Lauber & Wagner (1996).

CLASSIFICATION OF PLANT CHARACTERISTICS

Growth potential

Species were classified as having the capacity for rapid colonization of gaps (splitting and non-splitting clonally spreading herbs; types 3, 5, 11, 13 *sensu* Klimeš *et al.* 1997) if shoots or roots showed horizontal spread > 5 cm $year^{-1}$. For species suspected of having underground connections, up to five individuals were excavated in areas adjacent to the plots. The horizontal length of branchless sections of shoots or roots was measured and the species was included if at least one section exceeded 5 cm.

Recruitment capacity

New recruits, which germinated from seed over 3 years (1 April 1998 to 31 December 2000) in 108 permanently marked 50-cm^2 circles in the nine plots, were recorded on 20 occasions. Circles were randomly positioned, one in each 30-cm section of two 180-cm lines running north–south, 10 cm to the east and west of the central area. Recruits were therefore representatively sampled over all plots without disturbing the central areas. The effect of relative abundance of species on the number of seedlings was eliminated by calculating residuals from a linear regression of number of seedlings on relative cover (mean over all plots and years 1997–2000) that had been forced through the origin. These residuals were used as our measure of recruitment capacity, and all species recorded at more than three points in at least one plot, in at least one of these 4 years, were analysed.

Expansion rate

Fast growing species may be expected to be more competitive under humid and less tolerant under dry conditions compared with slow growing species (Grime 2001). Expansion rate was determined in a humid season (2001) as the increase in species cover between spring (12 April) and the average of species covers in summer (9–20 June) and autumn (17–18 September) divided by species cover in spring. Averaging summer and autumn data aimed at balancing seasonal differences among species. Species cover on each occasion was based on 216 points (points 1, 3, 5, 7, 9 and 11 in rows 1, 3, 14 and 16 of the permanent grid in each of the nine plots, i.e. a 20-cm grid of easily accessible points). Expansion rates were calculated for species that were recorded at more than seven out of 216 points on at least one sampling date.

ANALYSES OF VEGETATION DATA

The data were divided into three 4-year series characterized by increasingly dry conditions (1988–91), a preceding extreme drought (1992–95) and increasingly wet conditions (1997–2000). All the plots in which a species was present on at least five out of 176 points in at least one of the 4 years were included in repeated-measures ANOVAS. This effectively excluded species with many zeros and reduced the effects due to sampling error, which is higher with species with low abundances.

One rare species was excluded because it was absent from all plots in one year. Relative cover was *arcsine* transformed to improve the normality of the residuals. The ANOVA was done as a split-plot design with time as the within-subject factor and space as the random between-subject factor, with plots as subjects, in SYSTAT (version 10, Systat Software Inc., Richmond, USA). As these data are not independent across time the Huynh-Feldt's adjustment was used to decrease the degrees of freedom when the F statistic was inflated by severe violation of the sphericity assumption (Crowder & Hand 1990; von Ende 2001). Subsequently, a linear contrast was constructed to determine the percentage of variance accounted for by a linear trend across the 4 years and to allow this trend to be tested in an ANOVA with 1 d.f. in the numerator and $n - 1$ d.f. in the denominator (Winer *et al.* 1991; n = number of plots).

A multivariate approach used data for all species and plots to determine the general unidirectional trends of species composition over all plots for the three 4-year series. In a redundancy analysis with plot as a nominal covariable, the percentage of total variance explained by the first axis, which was constrained by the ordinal variable year, was calculated in CANOCO (version 4.5, Centre for Biometry, Wageningen, the Netherlands). Data were standardized by sample norm (Lepš & Šmilauer 2003) because change in relative rather than absolute abundance of species was of interest. The significance of the constrained axis was tested in Monte Carlo permutation tests, which take the split-plot structure of the repeated measures analysis across time into account.

Recruitment capacity and expansion rate were tested as quantitative predictors and clonal growth as a categorical predictor in general linear models (GLM in SYSTAT). Rates of change in relative cover across 4-year intervals were calculated for each species as the slope of relative cover over all plots against year, standardized by dividing by 4-year means of relative cover over all plots, thus removing the effect of relative abundance. Complete models and stepwise backward selection procedures were used to find the best predictors for each of the intervals 1988–91, 1992–95 and 1997–2000. Models were constructed for all species and for those with significant rates of change.

Community stability was assessed across 13 years, 1988–2000. The relationship between species density and weather was determined in a linear regression on proportion of humid daylight hours in spring (1 April to 16 June). Change in relative cover of graminoids was tested as effect of time with plots as subjects using repeated-measures ANOVA.

Results

CLIMATIC VARIATION

Humid conditions prevailed in the 7-year period preceding the start of the vegetation records in 1988 (Fig. 1). Across the 13 years of the study, growing seasons showed considerable variation in humidity when assessed by climatic variables reflecting either water loss or water gain (Fig. 2). The study period included the long-term maximum and minimum for number of days with ≥ 10 mm of rain (Fig. 1b), with exceptionally long dry periods in July–September 1989, 1990 and 1991 (Fig. 1c). A 113-day period in 1989 (from 11 July) only showed 2 days with ≥ 10 mm of rain, and a 91-day period in 1990 (from 4 July) only one such day. In 1991 the study site saw the hottest and driest summer of the 13-year period, with only 7 days of ≥ 10 mm of rain between mid-April and mid-September and a persistently reduced humid daylight period between mid-May and mid-October In humid summers (1988, 1999, 2000), days with ≥ 10 mm rain were separated by a maximum of 25 days.

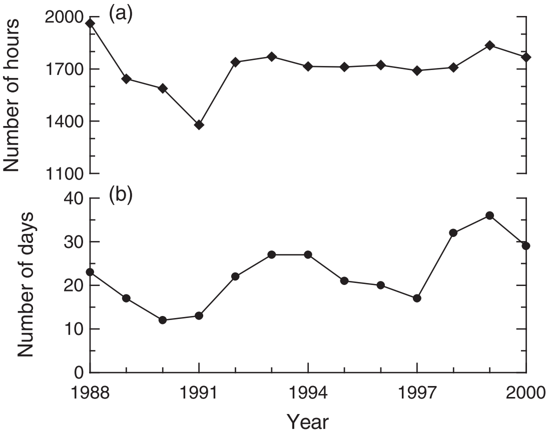

Fig. 2 Variation of warm-seasonal humidity (1 April to 30 September) across years, expressed as (a) length of humid daylight period, and (b) number of days with ≥ 10 mm of rain at Comprovasco (based on hourly data, MeteoSwiss, Zürich).

The length of humid daylight period and number of days with ≥ 10 mm of rain (Fig. 2) led to the classification of 1988–91 as increasingly dry, 1992–95 as intermediately humid, and 1997–2000 as increasingly humid.

TRENDS IN SPECIES COMPOSITION ACROSS 4-YEAR INTERVALS

During dry and humid intervals, change in cover was not dependent on the relative abundance of species but, in the period following the extreme drought (i.e. with intermediate humidity), the most abundant species decreased and species with low cover increased (Fig. 3).

Repeated measures ANOVA of relatively abundant species showed similar numbers of increasing and decreasing species in both the dry and the humid periods (Table 1). Four species (*Brachypodium pinnatum*, *Carex caryophyllea*, *Lotus corniculatus*, *Luzula campestris*) showed negative and five (*Helianthemum nummularium*, *Festuca rubra*, *Agrostis capillaris*, *Anthyllis vulneraria*, *Scabiosa columbaria*) showed positive trends from 1988 to 1991. Four species (*Bromus erectus*, *Festuca tenuifolia*, *Helianthemum nummularium*, *Trifolium montanum*) showed negative and five (*Prunella vulgaris*, *Agrostis capillaris*, *Trifolium*

Table 1 Repeated-measures ANOVA and linear contrast of relative cover across intervals with increasingly dry (1988–91), intermediately humid (1992–95), and increasingly humid (1997–2000) summers. Number of plots (n), F-statistic with ε-adjusted probability level, percentage of variance accounted for by linear contrast and probability level of positive (+) or negative (–) trend (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$). Due to multiple testing, one or two species per interval are expected to show significance at the probability level $P < 0.05$.

	Interval 1988–91					Interval 1992–95					Interval 1997–2000				
	ANOVA			Linear contrast		ANOVA			Linear contrast		ANOVA			Linear contrast	
Species	n	F	$P\varepsilon$	Var.	P	n	F	$P\varepsilon$	Var.	P	n	F	$P\varepsilon$	Var.	P
Achillea millefolium	2	.		.		2	.		.		4	3.0		89	
Agrostis capillaris	9	6.7	**	51	+*	9	3.0		52		9	11.1	***	86	+**
Anthoxanthum odoratum	8	11.6	***	8		5	19.5	****	94	+***	9	36.7	****	70	+****
Anthyllis vulneraria	9	14.9	****	83	+***	7	2.3		74		8	2.9		73	
Arabis ciliata	2	.		.		5	1.2		36		4	3.2		72	−*
Brachypodium pinnatum	9	9.9	***	53	−*	9	8.7	**	97	−**	9	3.9	*	38	
Briza media	9	1.5		1		9	3.0		76	−*	9	1.4		13	
Bromus erectus	9	1.4		83	−*	9	122.0	****	94	−****	9	11.8	***	89	−**
Campanula rotundifolia	5	1.5		97		3	1.2		35		2	.		.	
Carex caryophyllea	9	9.6	***	96	−**	9	0.4		5		9	3.7		42	
Carlina acaulis	4	0.4		5		3	0.3		80		1	.		.	
Clinopodium vulgare	0	.		.		1	.		.		3	1.5		8	
Dactylis glomerata	5	2.0		16		0	.		.		0	.		.	
Danthonia decumbens	9	4.3	*	24		8	2.3		1		9	0.8		16	
Dianthus carthusianorum	1	.		.		4	0.3		100		4	1.0		57	
Festuca rubra	8	6.9	**	73	+*	8	10.2	***	1		8	1.6		45	
Festuca tenuifolia	9	7.4	**	8		9	0.2		3		9	9.4	***	91	−**
Helianthemum nummularium	6	8.0	**	94	+*	7	0.2		1		7	7.6	*	72	−*
Hypochaeris radicata	5	3.2		4		6	2.3		93		7	1.8		0	
Koeleria macrantha	4	0.9		26		4	5.9	*	96		3	0.2		83	
Leontodon hispidus	5	1.6		81		0	.		.		5	6.5	*	68	
Lotus corniculatus	9	15.3	****	67	−**	6	0.5		4		8	2.4		85	
Luzula campestris	9	9.1	**	94	−**	9	5.5	*	76	+*	7	8.3	**	82	+*
Pimpinella saxifraga	4	7.6	*	71		7	12.6	***	100	+**	9	3.2		99	+*
Plantago lanceolata	9	14.0	***	7		9	57.6	****	86	+****	9	0.9		17	
Potentilla pusilla	7	4.8	*	17		8	1.8		63		8	3.3	*	36	
Prunella vulgaris	2	.		.		7	13.4	****	98	+***	9	21.1	****	99	+***
Ranunculus bulbosus	4	2.5		35		5	2.0		73		4	1.3		72	
Salvia pratensis	5	0.1		19		5	2.7		63		8	0.5		5	
Sanguisorba minor	4	1.3		2		3	3.3		97		2	.		.	
Scabiosa columbaria	7	7.0	**	94	+*	7	17.9	***	100	+**	8	2.5		88	
Silene nutans	7	0.5		2		7	1.4		82		5	0.6		0	
Thalictrum minus	3	4.3		91	+*	3	0.6		1		3	1.1		94	
Thymus pulegioides	7	3.6		89		9	4.8	*	66		9	8.8	***	33	
Trifolium montanum	9	1.1		10		7	1.0		82		9	7.0	**	78	−**
Trifolium pratense	3	3.0		50		0	.		.		3	1.0		78	
Trifolium repens	2	.		.		1	.		.		8	21.2	****	81	+***

repens, *Anthoxanthum odouratum*, *Luzula campestris*) showed positive trends from 1997 to 2000.

In contrast, the number of increasing species clearly exceeded the number of decreasing species in the period following the extreme drought (Table 1). Two species (*Bromus erectus*, *Brachypodium pinnatum*) showed negative and six (*Plantago lanceolata*, *Scabiosa columbaria*, *Prunella vulgaris*, *Pimpinella saxifraga*, *Luzula campestris*, *Anthoxanthum odoratum*) showed positive trends.

In the redundancy analyses, there was a more marked overall trend in relative abundances of species in 1992–95: the first constrained axis explained a higher fraction (9.7%) of the total variation in the species data than in 1988–91 (4.6%) or 1997–2000 (5.1%). In Monte Carlo permutation tests, independence of the species data on time was rejected in all intervals at the highest possible probability level ($P < 0.083$).

PLANT CHARACTERISTICS

Fifteen out of 60 species showed an ability to spread horizontally at > 5 cm year^{-1} and a total of 2182 new seedlings were recorded over 3 years, 2083 of which could be identified to 46 taxa of established herbs (Appendix S1 in Supplementary Material). Among the 30 most abundant species, 25 showed recruitment from seed, seven rapid spread by shoots or roots and four both characteristics. Despite much variation between plots, seedling emergence showed a distinct pattern, with grasses having relatively low recruitment

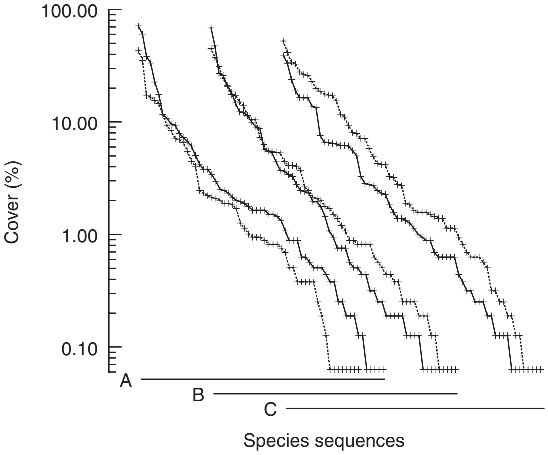

Fig. 3 Rank-cover graphs with mean species cover over all plots for first (solid line) and last (dashed line) year of intervals, A (1988–91), B (1992–95) and C (1997–2000).

capacities. Only one grass, *Anthoxanthum odouratum*, was among the 10 best recruiters and the grasses *Bromus erectus*, *Brachypodium pinnatum* and *Festuca rubra*, and the sedge *Carex caryophyllea*, showed very poor recruitment, despite their high cover.

Thirty species exceeded the threshold of abundance that allowed calculation of their expansion rate.

PREDICTORS FOR VEGETATION CHANGE

In general linear models that included the 30 most common species neither recruitment capacity, expansion rate or clonal growth predicted change in cover across 1988–91 or 1997–2000. None of these variables was retained in the model after stepwise backward selection (with alpha-to-remove $P = 0.15$). Recruitment capacity was, however, a significant predictor for 1992–95 and was the only variable retained in the model after stepwise backward selection (Fig. 4). Similar results were also obtained when all 50 species with known recruitment capacity were included in the model ($P < 0.01$), or when only those species with significant rates of change (Table 1), were considered ($P < 0.05$). All data used in analyses with GLM are given in Appendix S1.

COMMUNITY STABILITY

Over the 13 years of this study no new species from outside the study site invaded the plots and, apart from a few rare species with proportions < 0.05%, all taxa were present during each 4-year interval. The mean cover of vascular plants exceeded 98% in all years, except in 1991, when it decreased to 96%. The variation of species density averaged over all plots (Fig. 5a) was correlated with the proportion of humid daylight hours in spring (d.f. = 11, $r^2 = 0.31$, $P < 0.05$). Relative cover of graminoids (Fig. 5b) was constant from 1988 to 1991 and from 1994 to 2000, but decreased significantly across 1991–94 (d.f. = 3,24, $P\varepsilon < 0.00001$, Huynh-Feldt adjusted probability).

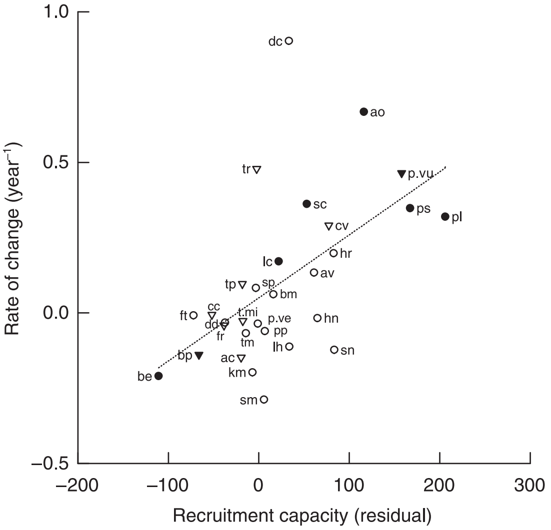

Fig. 4 Rate of change predicted by recruitment capacity for 30 most abundant taxa (initials represent species, see Table 1 and Appendix S1 in Supplementary Material; d.f. = 1,28, $F = 12.8$, $P < 0.01$ for linear regression). Species are classified as showing potential for fast clonal growth (triangles), or not (circles), and having significant rates of change across 1992–95 (closed symbols), or not (open symbols).

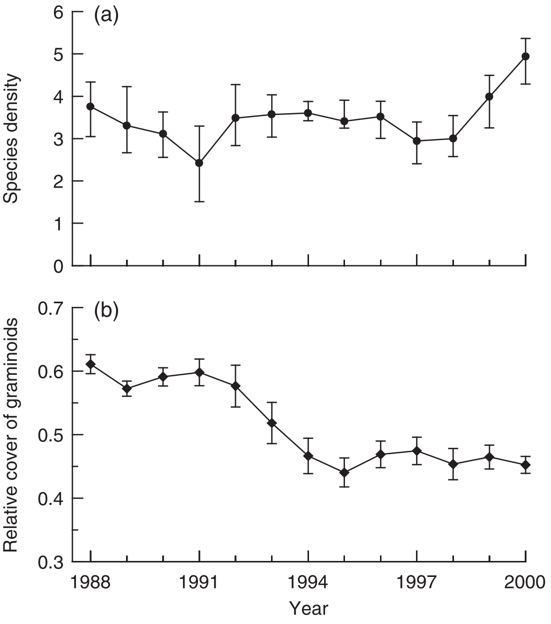

Fig. 5 Community variables (a) species density (mean, range) and (b) relative cover of graminoids (mean, SE) across nine plots.

Discussion

VEGETATION CHANGE

Warm season humidity in the southern Alps differed between years. Some years had persistent dry northern winds, which desiccated soils, and long periods without substantial rain, whereas others had frequent south-west winds and prevailing humid weather. This was an important natural factor conditioning semi-natural meadows. Rainfall also limited biomass production in the Park Grass Experiment (Silvertown *et al.* 1994), but temperature was critical in other correlative studies (Herben *et al.* 1995; Dunnett *et al.* 1998), showing that different grasslands are sensitive to different climatic factors.

There was no evidence during the humid interval (1997–2000) for the operation of competitive exclusion (as proposed for such conditions by Buckland *et al.* 1997). The relatively high proportion of dominant grasses (*Bromus erectus*, *Brachypodium pinnatum*, *Dactylis glomerata*) and a relatively low species density in 1988, compared with other wet years, 1999 and 2000, suggests, however, that such a process may have operated over the 7-year period with six humid summers that preceded this study. Nor was the related idea that the vigour of dominant grasses is reduced during droughts supported by data from the dry period (1988–91), with graminoids and forbs suffering similarly. Community composition started to shift once the drought was over because the relatively large number of graminoid individuals that had died was replaced by individuals of a relatively large number of forb species.

The greatest change in community composition, as reflected in relative cover, occurred shortly after the drought ended, supporting the hypothesis that change is caused by a resource pulse after disturbance. The fact that recruitment capacity explains changes in relative cover of species after extreme drought, but not in other periods, suggests that the changes were driven by regeneration from seed. Despite obvious spreading of *Thymus pulegioides* and *Rumex acetosella* in some patches, horizontal growth was generally less successful than gradual seeding. The failure of abundant grasses to re-colonize may be due to them having fewer and shorter-lived seeds than the more successful forbs (Hodgson *et al.* 1995; Thompson *et al.* 1997). Moreover, these forbs which, unlike *Bromus erectus*, germinate in spring may have been favoured by better conditions in spring. Although no new species invaded, the success of species with high regenerative capacity shows that the community was more open to colonization after the drought.

Expansion rate was determined in a wet season and a positive effect on rate of change might therefore be expected in humid conditions, but it did not drive changes in species composition under any conditions. Competitive exclusion or tolerance of drought may still operate but, under the particular conditions of this study, regeneration had a much stronger effect.

PERSISTENT EFFECT OF DROUGHT

Replicated permanent plots, and the absence of confounding treatments, allowed us to show direct, albeit delayed, responses of species composition to drought. As the weather gets drier, plant growth decreases, but the community components remain stable. Regeneration directs changes in community components after the drought is over: plant growth shows little variation, as the weather is now relatively stable. Once a new stable state has been established, plant growth increases as the weather gets wetter, but the effect of extreme drought on relative abundance persists.

Other studies have reported similar reductions in variables related to plant growth due to severe drought, but not persistent change in major vegetation components (Hopkins 1978; Tilman & El Haddi 1992; Grime *et al.* 1994; Willis *et al.* 1995). In the Park Grass Experiment (Silvertown 1980, 1987; Silvertown *et al.* 1994), species increased or decreased following the 1921 drought but, for 27 years with continuous data, the proportions of grasses, forbs and legumes did not change significantly from pre-drought values (van den Bergh 1979; Silvertown 1987). Tilman (1993, 1996) found that biomass in a prairie grassland returned to pre-drought values within a year, and decreases in C3 vs. C4 grasses and species richness were reversed within 5 years.

Other studies suggest compositional changes after drought but are not clear about how much, how long, or why functional components shifted (e.g. Willems 1985; Grime *et al.* 1994).

In more arid environments, extreme droughts have been demonstrated to drive cyclic changes in grasslands (Albertson & Tomanek 1965; van der Maarel 1981; Rosén 1995). At our site, however, a return of the major community components to a pre-drought state is unlikely.

It is not clear whether regeneration after drought would direct vegetation changes in a similar way in other grasslands. Extreme events are, by definition, rare and long-term, high-resolution sampling in species-rich herbaceous vegetation would be needed to demonstrate their effects. Responses may differ if dominant species differ in their response to stress (Lepš *et al.* 1982). Moreover, the superiority of a particular regenerative strategy depends on many, possibly unknown, factors that vary with location.

Our results suggest that, with an increasing probability of extreme droughts (Tsonis 1996; IPCC 2001), successions and species invasions become more likely, particularly in mountain areas with highly variable precipitation.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC900/JEC900sm.htm

Appendix S1 Species list: graminoids and forbs recorded in nine plots at Negrentino, Switzerland, with characteristics and relative cover across 4-year intervals 1988–1991, 1992–1995 and 1997–2000.

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