

Mechanisms of structural change derived from patterns of seedling emergence and mortality in a semi-natural meadow

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Abstract

Questions: Is seedling emergence limited by the set of viable seeds, by incompatibility between the phenology of seed shedding and timing of mowing, or by dry weather in germination periods?

Does seedling mortality fluctuate with season and weather?

Location: Negrentino, southern Alps, Switzerland.

Methods: Fecundity estimates of the dominant grass *Bromus erectus*; highly frequent counts of spontaneous seedlings by species and calculation of a community-level average mortality rate across 5 years; species-level records of seed shedding date and measurements of seed mass; measurement of soil moisture.

Results: *B. erectus* produced 143.9 viable seeds/m²/year while the density of its seedlings was a 55 times smaller fraction. Grasses had fewer seedlings than forbs and their phenology of seed shedding was less compatible with mowing date. Soil moisture was a strong determinant of seedling emergence in spring and less so in autumn. Average seedling mortality declined with age of the populations and reached a maximum in an extremely dry summer. In relatively wet summers establishment success was positively related to seed mass.

Conclusion: Community structure is susceptible to drought through mechanisms that selectively reduce recruits of coexisting plant functional groups. We propose that (1) more frequent intense droughts tend to reduce species that depend on frequent recruitment from seed, hence favour long-lived clonally spreading species, (2) drought timing selects between species with different germination phenology and drought resistance, and (3) drought impacts can be mitigated by changing management regimes that affect seed shedding.

Keywords: *Bromus erectus*; Extreme drought; Haymaking date; Regenerative strategy; Resilience; Seed mass; Seed production; Seedling recruitment; Seasonal precipitation; Soil moisture.

Nomenclature: Lauber & Wagner (1996).

Abbreviation: ADMR = average daily mortality rate.

Introduction

Growing-season droughts that cause important reductions of plant productivity have occurred in the past, even in European areas with a temperate humid climate. Regional climate models predict increased frequency of summer drought in Central and Southern Europe, with expected important economic and ecological consequences for productive and semi-natural grasslands (Fuhrer et al. 2006). In one case, frequently occurring intense droughts have indeed resulted in a persistent change of grassland community structure (Stampfli & Zeiter 2004). However, other long-term field studies reported a temporary shift in plant populations that returned to a pre-drought state within up to 5 years after a severe event (van der Maarel 1981; Grime et al. 1994; Dunnett et al. 1998; Rosén 1995; Tilman 1993, 1996; Tilman & El Haddi 1992; Morecroft et al. 2004) and thus rather support a ‘dynamic-equilibrium’ view with constant proportions of graminoids and forbs as long as land use and nutrient levels are held constant (Silvertown 1980a).

Various mechanisms are involved in grassland responses to extreme drought. When a water-input deficit builds up, soil moisture becomes scarce and plants desiccate, traits that grant drought-tolerance such as root type and rooting depth may select among species (Buckland et al. 1997; Dunnett et al. 1998). Structural shifts occur when dominant species die during long and very harsh droughts (Albertson & Tomanek 1965), or when dominants have a relatively lower drought tolerance than competitively inferior plants (Morecroft et al. 2004). Grasses with shallow, fibrous roots may be vulnerable to soil-moisture deficits in some communities (Morecroft et al. 2004) but adapted to regular drought stress in other grasslands (Cerletti 1997). Drought resistance generally is not lower for grasses than for forbs; rather grasses exhibit a spectrum of more or less drought-tolerant species (Tilman 1996; Stampfli & Zeiter 2004).

Most species in European grasslands are long-lived perennials and have the capacity for recruitment from seed and vegetative spread (Klimeš et al. 1997) and

both strategies are involved in vegetation recovery after drought. Dominant grass turf may slowly decay and be colonized by a co-dominant with creeping rhizomes (Lepš et al. 1982); however, in temporarily open vegetation after frequent intense droughts, recruitment from seed may play a more important role than vegetative spread (Stampfli & Zeiter 2004). Recruitment from seed may result in more radical vegetation changes in dry grasslands than vegetative spread due to varied seed traits, such as abundance, dimensions, mass and persistence in the soil, and germination requirements that contrast with the relatively uniform growth rates (Thompson et al. 1996; Grime 2006).

Seedling emergence after a drought depends on the presence of viable seeds and the factors affecting germination. Seed production in local populations of species-rich grasslands varies considerably across years depending on weather, temperature and rainfall, but has rarely been studied (Herben et al. 1995; Zobel et al. 1998). The chances of light-induced germination may rise when the vegetation is thinned out (Silvertown 1980b; Baskin & Baskin 1998). Still, for species, seedling emergence may follow distinct, often seasonally predictable patterns (Grime 2001). Moisture supply is the principal determinant of germination for species that normally emerge after a relatively dry season; increased diurnal fluctuations in temperature could further enhance germination (Thompson et al. 1977; Thompson & Grime 1983; Probert 2000). Species with a requirement for chilling to break seed dormancy are activated after a cold season (Grime et al. 1981). In their early stage, new seedlings may yet benefit from a thin vegetation, later on however, they will receive a relatively short supply of carbon, due to periodic shading from recovering established neighbours or herbivory. Thus, successful establishment may critically depend on the amount of resources in reserve, reflected by seed mass (Leishman et al. 2000; Jensen & Gutkunst 2003; Fenner & Thompson 2005; Louault et al. 2005).

We explore the structural and seasonal patterns of seedling emergence and mortality for a constantly managed meadow, a plant community of mostly perennial herbs with graminoids and forbs as major life forms. The aim of this study is to search for recruitment-related mechanisms by which changes in vegetation structure could result from changes in seasonal climate. Focussing on four aspects we investigate the following hypotheses:

1. Poor seedling emergence of *Bromus erectus* results from low fecundity. This dominant perennial grass relies on recruitment from seed (Grime et al. 1988), however, poor seedling emergence and recovery compared to many forb species with the same strategy was a major reason of change in vegetation structure after an extreme summer drought (Stampfli & Zeiter 2004).

2.a. Species with seeds reaching maturity and being shed from standing plants in any of the phenological periods delimited by haymaking dates have higher numbers of emerging seedlings than other species. b. The phenology of seed maturation is associated with life form. We expect that graminoids have later phenologies of seed maturation than forbs (Smith et al. 1996).

3. Dry weather in germination seasons reduces the number of emerging seedlings. We expect a positive causal relationship between soil moisture and the number of emerged seedlings because seeds need to absorb water over many days before they can germinate (Baskin & Baskin 1998).

4.a. Summers involve a higher risk of mortality because of desiccation in dry, or starvation in wet periods. b. Under conditions of early summer drought seedlings of graminoids and forbs differ in mortality if these life forms differ in seasonal emergence and hence age stages of seedlings. We expect that older seedlings are more resistant than younger ones. c. In wet periods large seeded species show less mortality than small seeded species.

Methods

Study site

Vegetation data come from nine southerly exposed, regularly spaced 2 m × 2.2 m permanent plots in an ancient species-rich meadow ('a-plots' in Stampfli 1992, 1995; 'control' plots in Stampfli & Zeiter 2001, 2004), located at Negrentino, southern Switzerland (820 m a.s.l.; 46°27'40" N, 8°55'30" E). In close proximity farmers have maintained mowing for hay production at traditional dates, end of June and mid September. At these dates, we have regularly mowed the nine plots since 1988, using traditional haymaking tools such as scythe for cutting, hayfork for turning over, and wooden rake for collecting; mowing was temporarily interrupted in a relatively small area nearby ('b-plots' in Stampfli 1992; Zeiter et al. 2006). Annual harvests have yielded ca. 300 g.m⁻².a⁻¹ dry weight of hay on average, in years without extreme summer droughts (Stampfli 2001). The average slope inclination is 14.8° and single plot inclinations vary in the range of 8–23.5°. 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. The climate is temperate-humid according to the classification by Walter & Lieth (1964). Mean annual precipitation is 1320 mm and varies in the range of 779–1951 mm (Comprovasco 1901–2000, MeteoSwiss Locarno-Monti). Many and sometimes very intense rain falls between March and November, but also very dry atmospheric conditions caused by NW to NE winds in

the lee of the main mountain range, occur often during many times of the year.

Measurement of soil moisture and precipitation

We measured drought intensity across the growing season (March-October) in terms of soil water potential (Ψ_{soil}) in 2000-2003 and simulated Ψ_{soil} for 1997-1999. We measured Ψ_{soil} at intervals of 10 minutes by means of a soil moisture sensor (EQ2 equitensiometer, Delta-T, Cambridge, UK) installed at an inclination of 20° , between two plots, at 5 cm below ground and hourly data were recorded with a data logger (DL2e, Delta-T, Cambridge, UK). The simulation applied a recursive model structure that couples Ψ_{soil} with two key processes of the soil water balance, the wetting of the soil by rain and the drying of the soil by evapotranspiration (R. Zweifel unpubl.; App. 1). The model parameters precipitation, radiation, relative humidity, wind velocity, and air temperature were based on hourly data from the weather station at Comprovasco (MeteoSwiss Zürich) located ca. 250 m further down the valley slope and ca. 1 km away from the study site. Dry soil was defined as $\Psi_{\text{soil}} < -80$ kPa, a value that is reached in spring or autumn after ca. 1-2 weeks without rain starting from a water-saturated soil. With this threshold, duration of dry soil differentiated well between wet and dry germination periods in our years of observation.

Employing daily precipitation records at Comprovasco, distributions of monthly or seasonal precipitation are totaled over 111 years (1893-2003) and serve as reference for the characterization of our period of observation; missing values (1977-1987) were reconstructed from nearest stations (data of MeteoSwiss Zürich).

Determination of seedling emergence and mortality

New seedlings were recorded during three visits in 1997 (4 May, 2 June, 22 June) within the nine permanent plots, in 54 randomly positioned and permanently marked 50-cm² circles, in an attempt to estimate density of seedlings by species along the edges of a central area (Fig. 1) used for annual records of species cover (Stampfli & Zeiter 2004). In a next step, new seedlings were recorded over 5 years (01.04.1998 - 05.11.2002) during 29 visits, in totally 108 randomly positioned and permanently marked 50-cm² circles (Fig. 1). The frequency of visits was 10 per year in the first, and 4-5 per year in the following years and the interval length between visits varied across time. Regular annual visits in mid/late April, late June, and mid September delimited the periods, P₂ (from mid spring to first mowing) and P₃ (from first to second mowing). Visits in November/December or February delimited between period P₄ (from second mowing to early

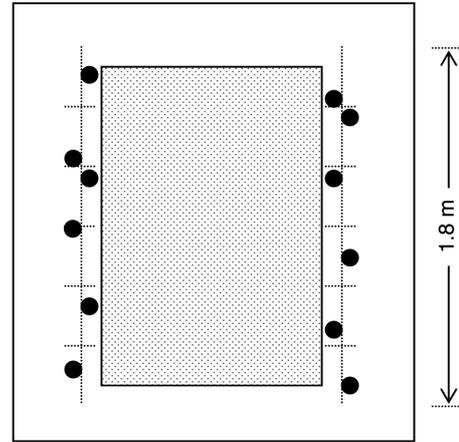


Fig. 1. Single plot with 12 circular areas (black dots) in stratified-random positions used for seedling records along edges of the central area (1.1 m × 1.6 m, shaded rectangle) in 1998-2003. In 1997 six circles represented two adjoining strata.

winter) and P₁ (from late winter to mid spring) whereby earlier visits ideally delimited P₄ (years 1998 and 2002) and allocated rare seedlings emerging in winter to period P₁ and later visits ideally delimited P₁ (years 1999-2001) and allocated rare seedlings emerging in winter to period P₄. Seedlings were marked with coloured ringlets so that annual age groups could be distinguished. For each species with > 4 seedlings in the years 1998-2002, we examined if emergence shows a seasonal pattern, i.e. > 75 % of the seedlings emerge either in spring (P₁, P₂), autumn (P₃, P₄), or in both seasons but prefer the cool periods (P₄, P₁), or not. We measured the consistency by the number of single years showing > 75 % seedlings within a particular seasonal pattern.

Survival or mortality was determined for 27 census intervals from 1 April 1998 - 15 September 2002 and two intervals delimited by dates of additional censuses on 24 April and 21 June 2003. A community-level mortality rate was determined for each of five annual age groups of seedlings, i.e. between spring 1998, 1999, 2000 or 2001 and September of the next year, and between spring 2002 and June 2003. For each species, daily mortality rates were calculated over all plots as:

$$m_d(t) = 100 \times (1 - [1 - (n_d/n_o)]^{1/t}) \quad (1)$$

with n_d = individuals which died in an original population (n_o) over a census interval of t days (Sheil & May 1996). This formula underestimates mortality for long census intervals in communities with mixed species, each with a different mortality rate (Sheil & May 1996). Therefore, we followed their suggestion to calculate an overall average mortality rate as:

$$m_{all}(t^*) = 1 - \left[\frac{\sum_{i=1}^S n_{i0}(1 - m_i)^{t^*}}{\sum_{i=1}^S n_{i0}} \right]^{1/t^*} \quad (2)$$

with S = number of species, n_{i0} = number of individuals of species i at time = 0, m_i = daily mortality rate of species i , and t^* = time. This formula relies on the assumption that mortalities are homogeneous for individuals of the same species and constant over time. It is sensitive to the unreliable and often extreme mortality rates of rare species (Newbery & Lingenfelder 2004). Mortality rates were thus made conditional on the minimum number of individuals per species, n_{min} . For all census intervals, we calculated m_{all} including all species with $n_{min} = 21, 19, 17, \dots, 1$. Correlation coefficients between the m_{all} with different n_{min} across the time series of the annual age groups of 5 years were calculated to optimise n_{min} over many census intervals. The matrix of correlation coefficients showed close correspondence between m_{all} with $n_{min} > 6$ ($r^2 > 0.94$), differences appeared between m_{all} with $n_{min} > 6$ and $n_{min} < 6$ ($r^2 < 0.76$). Thus, an average daily mortality rate (ADMR) was most reliably calculated for species with a minimum of seven individuals in each census interval. Considering a possible effect of seedling age on ADMR across seasons due to seedling emergence time, we compared ADMR calculated for all species and ADMR calculated for species emerging in autumn only, i.e. a selection of younger individuals on average.

Seed production and seedling emergence of Bromus erectus

Culms of *Bromus erectus* were counted in a permanent central 0.33-m² area in each of the nine plots (Stampfli 1992) in June across 15 yr (1988-2002). Spikelets containing 'normal'-looking seeds were counted for all culms but maximal in a sample of 10 culms per plot. Fecundity in 2000 was estimated based on the proportion of viable seeds per spikelet that was determined in a representative sample of three randomly selected culms per plot ($n = 27$), collected on 25 June 2000. Spikelets consist of 4-14 flowers (Hegi 1997). Our sample included totally 365 spikelets with 586 'normal'-looking seeds, 634 undeveloped ovaries with awns, a few predated seeds, and an unknown number of undeveloped flowers. We checked the viability of 'normal'-looking seeds in a germination test over 58 days in the laboratory. Assuming a constant number of viable seeds per spikelet, we estimated the fecundity of *Bromus erectus* by a multiplication of spikelet density in the years 1998-2002 by viable seeds per spikelet in 2000 for a comparison with seedling density in the same 5-year interval.

Phenology of seed maturation and seedling emergence

Date of first seed shedding, i.e. the day when a mature fruit opens or seeds are detached from the mother plant, was recorded for all species rooted in the nine plots during regular visits (June-July, September-October) in the years 1999, 2000, and 2004. A classification of compatibility of seed maturation with haymaking dates used two categories according to whether (a) first seed shedding falls in one of three periods in the growing season delimited by the two haymaking dates (30 June, 15 September), or whether (b) no mature seeds are shed from standing plants, either because no seeds are produced or seeds are not detached before haymaking. For the analysis of the hypothesis that seed-shedding species have higher numbers of seedlings than other species we selected all abundant species with known category of seed shedding and used log-transformed number of seedlings in a t -test (SYSTAT version 10; SPSS Inc. 2000). For the analysis of association between life form and compatibility of seed maturation with timing of haymaking we selected all species with seedling records and known begin of seed shedding and used a Yates' corrected χ^2 -test.

Year-to-year variation of soil moisture and seedling emergence

In linear regressions (SYSTAT version 10; SPSS Inc. 2000), we selected the variable log duration of soil dryness ($\Psi_{soil} < -80$ kPa) for the period March-May or August-October as our predictor of weather effect on seedling emergence in spring or autumn. For emergence in spring or autumn, we calculated the density of newly emerged seedlings in our records in March-June (1997-2002) or September-November (1998-2002). In years without records in November, we included later records (December 1998 or February 2001, 2002).

Seedling mortality: seasonal variability and weather influence

We approximated the seasonal trend in ADMR from the five annual age groups of seedlings that emerged, survived or died under weather conditions without long or intense drought (April 1998-April 2003) and estimated the influence of a subsequent severe drought in May/June 2003 on ADMR. The resistance ($R = P-1$) of graminoids and forbs to this drought was based on seedlings emerged between 1998-2002 and alive on 22 April 2003 (100 %) and the proportion (P) of recruits surviving until 21 June 2003. P was determined for two cohorts, those emerging in 2002 and those emerging earlier.

For a period of relatively wet weather (September 1998-2002), survival across 1 year after emergence was

determined by species for three annual cohorts whereby the proportion of individuals surviving until April (species emerging in spring), September (species emerging in autumn), or June (other species) of the next year was calculated. The cohorts 1999-2001 were selected for species emerging in spring and the cohorts 1998-2000 for other species, so that seedlings of autumn and spring emerging species had experienced the same summer conditions. We collated seed-mass data of 27 species from measurements of populations at Negrentino and those of eight species from measurements of populations at other grassland sites (Pree, San Michele) in the southern Alps based on Zeiter et al. 2006, Kupferschmid et al. 2000, and own unpublished work (App. 2). Missing data of four species were supplemented from a database of Sheffield (Grime et al. 1981). Life form as categorical and log seed mass as numerical predictor for survival were tested with GLM (SYSTAT version 10; SPSS Inc. 2000) for species with at least ten germinated individuals.

Results

Seed production and seedling emergence of Bromus erectus

Spikelet density of *Bromus erectus* normally varied between ca. 100-200 m⁻².a⁻¹, two years showed exceptionally low densities (Fig. 2). The germination test found a viability of 80.0 % of the 'normal'-looking seeds ($n = 586$), 17.4 ± 2.5 (mean, SE) viable seeds per culm, or 1.27 ± 0.15 (mean, SE) viable seeds per spikelet. The period 1998-2002 showed an estimated density of 143.9 m⁻².a⁻¹ viable seeds and a mean annual density of 2.6 m⁻².a⁻¹ seedlings (Table 1). All seedlings emerged in autumn.

Phenology of seed maturation and seedling emergence

In the 5-year period 1998-2002, 625 seedlings of graminoids and 3230 seedlings of forbs emerged in the sampled circles and 98.9 % could be assigned to one of 49 species (Table 1). The mean annual density of emerged seedlings was 1429 m⁻².a⁻¹, densities varied in the range of 854 m⁻².a⁻¹ (in 1998) and 1961 m⁻².a⁻¹ (in 2000). Six out of the 50 most abundant species in the central rectangle did not recruit in the circles sampled (Table 1). Graminoids had obviously fewer seedlings than forbs and this difference was most remarkable among the eleven most abundant species that include five grasses with a late phenology of seed shedding (Fig. 3). Species that do not normally shed mature seeds from standing plants (Table 1, Ss = 0) had fewer seedlings than species with other phenologies of seed maturation ($t_{44} = -2.81$; $p < 0.01$). The former were more frequent

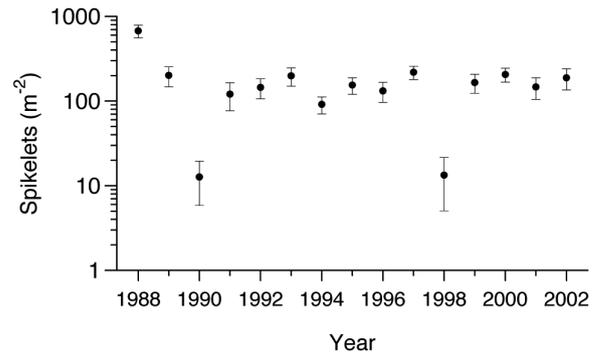


Fig. 2. Spikelet density (mean, SE) of *Bromus erectus* in the years 1988-2002.

among graminoids than among forbs (Table 1; $N = 45$; $\chi^2 = 18.5$; $p < 0.001$).

Seasonal emergence culminated in spring and showed a second maximum in autumn. Maximal emergence (22.0 seedlings.m⁻².d⁻¹) was recorded between late February and mid April 2001 and minimal emergence (0.2 seedlings.m⁻².d⁻¹) between late November 1999 and early February 2000, the single census interval in winter. A majority ($n = 35$) of the species showed a seasonal preference of emergence, either in spring ($n = 14$), in autumn ($n = 13$), or in both seasons but preferring cool periods between second mowing and mid April ($n = 8$).

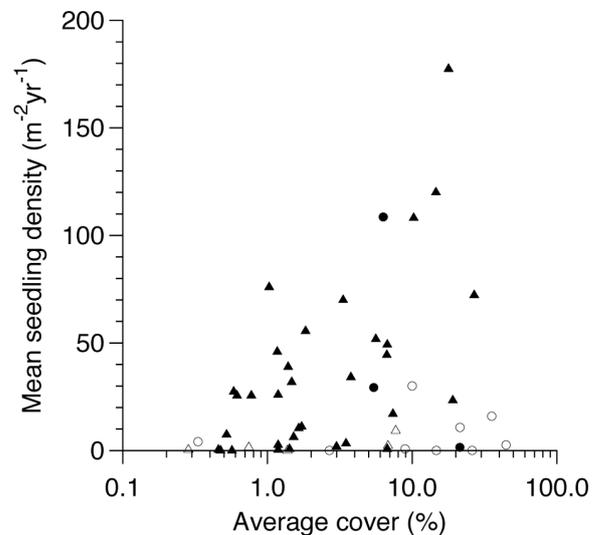


Fig. 3. Mean annual seedling density and average cover of 50 most abundant species (1998-2002). Graminoids (dots), forbs (triangles), species showing exclusive seed set in first crop and late phenology of seed shedding (open symbols), other species (closed symbols).

Table 1. Recruitment in nine plots at Negrentino; species with seedlings in circular areas or without seedlings but then being abundant in central rectangle (Fig. 1); life form (Lf): forb (f), graminoid (g); start of seed shedding (Ss): hampered (0), before end of June (1), before mid September but not before June cut (2), after mid September (3); seed mass (Ms), superscripts indicate data from other sites, Pree [a], San Michele [b], Sheffield [c], italics indicate that seeds are from an unknown minimum number of mother plants; mean cover (C) in 1997-2000 per 15.84 m², asterisks indicate rare occurrence; emergence: number of seedlings (n) emerging in 1998-2002 per 0.54 m², percentage frequency of seedlings recorded in periods P₁-P₄, consistency of seasonal emergence (x/y: pattern confirmed in x out of y years with emerging seedlings); survival: number of seedlings of three annual age groups (n) with their percentage of survival (%) over 1 year.

| Species | Lf | Ss | Ms [mg] | C % | n | Emergence | | | | x/y | Survival | |
|--|----|----|-------------------|-------------------|-----|----------------|----------------|----------------|----------------|-----|----------|------|
| | | | | | | P ₁ | P ₂ | P ₃ | P ₄ | | n | % |
| Emergence in spring | | | | | | | | | | | | |
| <i>Anthyllis vulneraria</i> | f | 1 | 3.94 | 5.6 | 140 | 83 | 4 | 4 | 9 | 4/5 | 94 | 35.1 |
| <i>Campanula rotundifolia</i> ⁽¹⁾ | f | 2 | 0.07 | 1.2 | 124 | 81 | 10 | 2 | 6 | 5/5 | 54 | 9.3 |
| <i>Daucus carota</i> | f | 2 | ^b 0.82 | 0.8 | 69 | 78 | 22 | . | . | 5/5 | 53 | 22.6 |
| <i>Pimpinella saxifraga</i> | f | 2 | 0.67 | 10.2 | 292 | 69 | 16 | 1 | 13 | 4/5 | 200 | 32.0 |
| <i>Plantago lanceolata</i> | f | 1 | 1.88 | 17.8 | 479 | 94 | 4 | 1 | 1 | 5/5 | 373 | 13.1 |
| <i>Potentilla erecta</i> | f | 2 | 0.61 | 1.2 | 70 | 87 | 13 | . | . | 4/4 | 51 | 47.1 |
| <i>Prunella vulgaris</i> | f | 2 | ^a 0.52 | 14.6 | 324 | 61 | 27 | 4 | 8 | 3/5 | 264 | 32.6 |
| <i>Sanguisorba minor</i> | f | 1 | 5.61 | 1.7 | 30 | 93 | 3 | 3 | . | 5/5 | 27 | 48.1 |
| <i>Silene nutans</i> | f | 1 | 0.43 | 3.3 | 189 | 85 | 8 | 4 | 4 | 4/5 | 123 | 40.7 |
| <i>Solidago virgaurea</i> | f | 2 | ^a 0.72 | 0.6 | 74 | 77 | 22 | . | 1 | 4/4 | 64 | 23.4 |
| <i>Trifolium montanum</i> | f | . | 0.76 | 6.8 | 6 | 100 | . | . | . | 5/5 | 4 | 75.0 |
| <i>Trifolium pratense</i> | f | 1 | ^c 1.35 | 1.5 | 17 | 100 | . | . | . | 5/5 | 12 | 75.0 |
| <i>Trifolium repens</i> | f | . | ^c 0.56 | 7.7 | 25 | 100 | . | . | . | 5/5 | 18 | 16.7 |
| <i>Viola hirta</i> | f | 1 | ^c 2.81 | 0.6 | 69 | 93 | 7 | . | . | 5/5 | 43 | 65.1 |
| Emergence in autumn | | | | | | | | | | | | |
| <i>Anthoxanthum odoratum</i> | g | 1 | ^a 0.68 | 6.3 | 293 | 17 | 2 | 59 | 22 | 3/5 | 130 | 37.7 |
| <i>Arabis ciliata</i> | f | 1 | 0.11 | 1.8 | 150 | 3 | 3 | 73 | 21 | 5/5 | 119 | 31.1 |
| <i>Helictotrichon pubescens</i> | g | 1 | 3.33 | [*] 0.2 | 38 | 5 | . | 74 | 21 | 4/5 | 24 | 45.8 |
| <i>Briza media</i> | g | 0 | ^a 0.74 | 10.0 | 81 | 6 | 4 | 56 | 35 | 4/5 | 42 | 14.3 |
| <i>Bromus erectus</i> | g | 0 | 5.44 | 44.6 | 7 | . | . | 86 | 14 | 2/2 | 6 | 83.3 |
| <i>Festuca tenuifolia</i> | g | 0 | 0.36 | 35.5 | 43 | 12 | 5 | 40 | 44 | 2/4 | 21 | 19.0 |
| <i>Holcus lanatus</i> | g | 0 | ^a 0.31 | [*] 0.1 | 30 | 23 | . | 43 | 33 | 3/4 | 15 | 40.0 |
| <i>Hypochaeris radicata</i> | f | 1 | 1.39 | 6.7 | 133 | 9 | 14 | 69 | 8 | 3/5 | 100 | 13.0 |
| <i>Luzula campestris</i> | g | 1 | 0.66 | 5.4 | 79 | 5 | 1 | 56 | 38 | 4/5 | 35 | 22.9 |
| <i>Ranunculus bulbosus</i> | f | 1 | 4.32 | 1.5 | 86 | 6 | . | 34 | 60 | 4/5 | 17 | 52.9 |
| <i>Rumex acetosa</i> | f | 1 | 1.22 | 0.5 | 20 | 15 | . | 40 | 45 | 3/5 | 11 | 54.5 |
| <i>Salvia pratensis</i> | f | 1 | 2.22 | 3.5 | 9 | 11 | . | 89 | . | 3/4 | 6 | 16.7 |
| <i>Trisetum flavescens</i> | g | 0 | 0.11 | 0.3 | 11 | . | . | 73 | 27 | 3/3 | 3 | 33.3 |
| Emergence in cool season | | | | | | | | | | | | |
| <i>Achillea millefolium</i> agg. | f | 2 | ^a 0.08 | 1.2 | 7 | 57 | . | 14 | 29 | 4/5 | 5 | 40.0 |
| <i>Clinopodium vulgare</i> | f | 2 | ^a 0.43 | 1.0 | 205 | 47 | 3 | 2 | 48 | 5/5 | 80 | 43.8 |
| <i>Dianthus carthusianorum</i> | f | 2 | 0.65 | 3.8 | 92 | 20 | 10 | 1 | 70 | 3/4 | 82 | 63.4 |
| <i>Helianthemum nummularium</i> | f | 1 | ^a 1.11 | 26.8 | 195 | 67 | 8 | 6 | 21 | 4/5 | 135 | 10.4 |
| <i>Leontodon hispidus</i> | f | 2 | 1.14 | 1.4 | 105 | 50 | 12 | 6 | 32 | 3/5 | 37 | 35.1 |
| <i>Lotus corniculatus</i> | f | 1 | 0.89 | 3.0 | 5 | 60 | . | . | 40 | 2/2 | 0 | . |
| <i>Thymus pulegioides</i> | f | . | 0.16 | 19.1 | 63 | 57 | 5 | 17 | 21 | 3/5 | 32 | 9.4 |
| <i>Veronica arvensis</i> (annual) | f | 1 | ^c 0.11 | [*] <0.1 | 11 | 27 | 9 | . | 64 | 3/3 | 11 | 18.2 |
| Emergence not season specific | | | | | | | | | | | | |
| <i>Danthonia decumbens</i> | g | 0 | 2.16 | 21.4 | 29 | 17 | 31 | 38 | 14 | 3/5 | 18 | 38.9 |
| <i>Leucanthemum vulgare</i> | f | 1 | 0.45 | 1.6 | 28 | 54 | 11 | 25 | 11 | 1/4 | 15 | 40.0 |
| <i>Potentilla pusilla</i> | f | 1 | 0.12 | 7.4 | 46 | 37 | 26 | 7 | 30 | 4/5 | 26 | 26.9 |
| <i>Scabiosa columbaria</i> | f | 1 | 1.99 | 6.7 | 120 | 31 | 14 | 37 | 18 | 4/5 | 72 | 48.6 |
| Species with < 5 seedlings | | | | | | | | | | | | |
| <i>Agrostis capillaris</i> | g | 0 | . | 8.9 | 2 | 50 | . | 50 | . | ./1 | . | . |
| <i>Brachypodium pinnatum</i> | g | 0 | . | 26.0 | . | . | . | . | . | . | . | . |
| <i>Carex caryophylla</i> | g | 1 | . | 21.3 | 4 | . | 25 | 50 | 25 | ./3 | . | . |
| <i>Carlina acaulis</i> | f | 3 | . | 1.4 | 2 | . | 100 | . | . | ./1 | . | . |
| <i>Centaurea nigrescens</i> | f | 2 | . | 0.5 | 1 | 100 | . | . | . | ./1 | . | . |
| <i>Centaurea scabiosa</i> | f | 1 | . | 0.5 | . | . | . | . | . | . | . | . |
| <i>Dactylis glomerata</i> | g | 0 | . | [*] 0.3 | 1 | 100 | . | . | . | ./1 | . | . |
| <i>Festuca rubra</i> | g | 0 | . | 14.7 | . | . | . | . | . | . | . | . |
| <i>Galium verum</i> | f | . | . | 0.3 | 1 | 100 | . | . | . | ./1 | . | . |
| <i>Hippocrepis comosa</i> | f | . | . | 1.4 | . | . | . | . | . | . | . | . |
| <i>Koeleria macrantha</i> | g | 0 | . | 2.7 | . | . | . | . | . | . | . | . |
| <i>Primula veris</i> | f | 0 | . | 0.7 | 4 | 100 | . | . | . | ./3 | . | . |
| <i>Rumex acetosella</i> | f | 1 | . | 1.2 | 1 | 100 | . | . | . | ./1 | . | . |
| <i>Stachys officinalis</i> | f | . | . | [*] <0.1 | 1 | 100 | . | . | . | ./1 | . | . |
| <i>Thalictrum minus</i> | f | 2 | . | 6.7 | 2 | 100 | . | . | . | ./1 | . | . |
| <i>Veronica spicata</i> | f | 2 | . | 0.6 | . | . | . | . | . | . | . | . |

⁽¹⁾ Sums of *Campanula rotundifolia* may include few *Phyteuma betonicifolium* seedlings

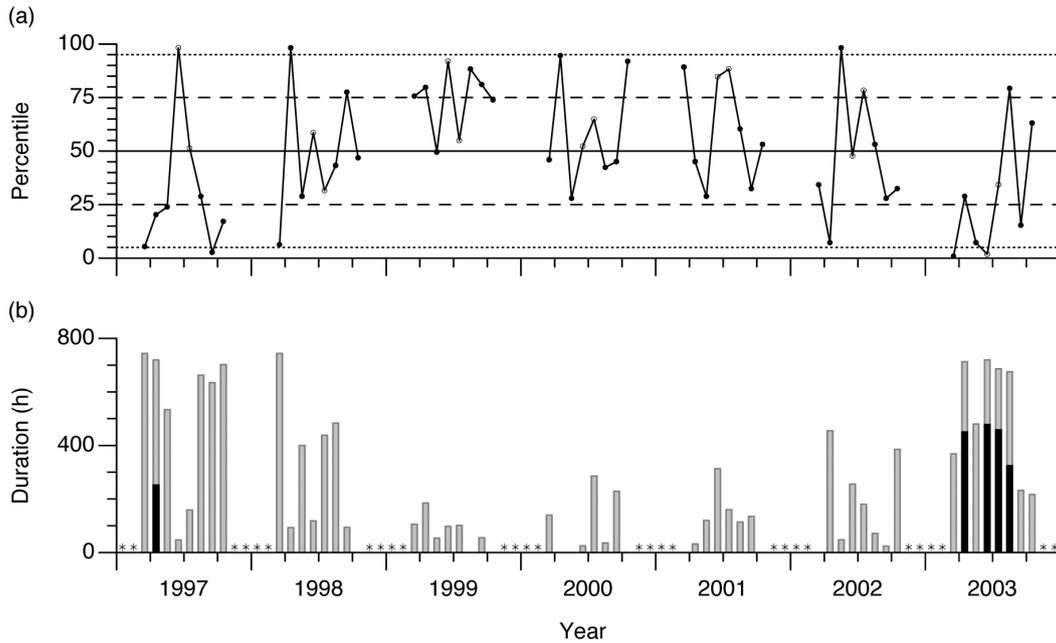


Fig. 4. Monthly weather-related variables across growing seasons (March-October) 1997-2003, asterisks indicating missing values (cold months). (a) Precipitation (at Comprovasco) as percentile of frequency distributions over 111 years (1893-2003) of monthly precipitation sums, medians (solid line), upper and lower quartiles (broken lines), 5- and 95-percentiles (dotted lines). (b) Duration of soil dryness (at Negrentino) defined as $\Psi_{\text{soil}} < -80 \text{ kPa}$ (grey bars) or $\Psi_{\text{soil}} < -200 \text{ kPa}$ (black bars).

All but one species confirmed their seasonal pattern in a majority of single years. Those with a spring preference showed a higher consistency than those with an autumn or cool-season preference (Table 1). About half of the forb species preferred emergence in spring, all graminoid species preferred emergence in autumn. Spring-emerging forbs supplied the majority of all herb seedlings.

Year-to-year variation of soil moisture and seedling emergence

The years 1997-2002 were characterized by dry and wet months in spring (Fig. 4). The March-May precipitation totals varied between 121.8 mm (in 1997) and 481.4 mm (in 1999) and represented a wide range of the frequency distribution (6-88 percentile) of the yearly March-May precipitation totals 1893-2003 (111-yr median: 304.2 mm). Soil moisture dropped in periods with low spring precipitation. In spring 1997 soil dryness prevailed during 1998 hours, i.e. 90.5 % of the time (Fig. 4b). The autumn period in the years 1998-2002 lacked dry months (Fig. 4a). The August-October precipitation totals varied between 279.1 mm (in 2002) and 709.5 mm (in 1999) and represented a relatively wet range of the frequency distribution (21-96 percentile) of the yearly August-October precipitation totals 1893-2003 (111-yr median: 427.8 mm). Consequently, soil dryness in this seasonal period did not exceed 578 hours, 26.2 % of the time in each year (Fig. 4b).

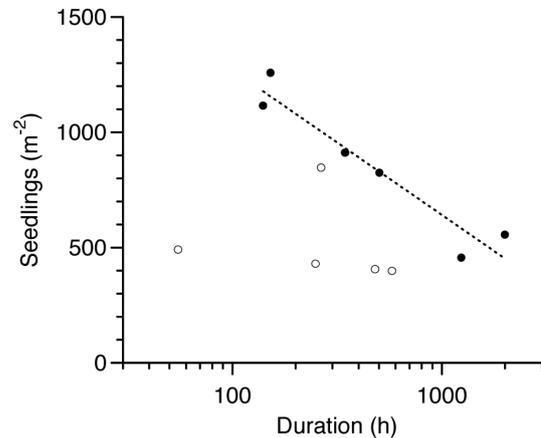


Fig. 5. Density of emerged seedlings in spring (6 years, 1997-2002, closed dots) or autumn (5 years, 1998-2002, open dots) and log duration of soil dryness ($\Psi_{\text{soil}} < -80 \text{ kPa}$) in germination period, relationship for spring (dotted line, $r^2 = 0.892$, $F = 42.3$, $p < 0.01$). Graminoids contributed 2.4-7.0 % (mean = 4.1 %) to annual spring and 6.0-60.6 % (mean = 32.5 %) to annual autumn totals.

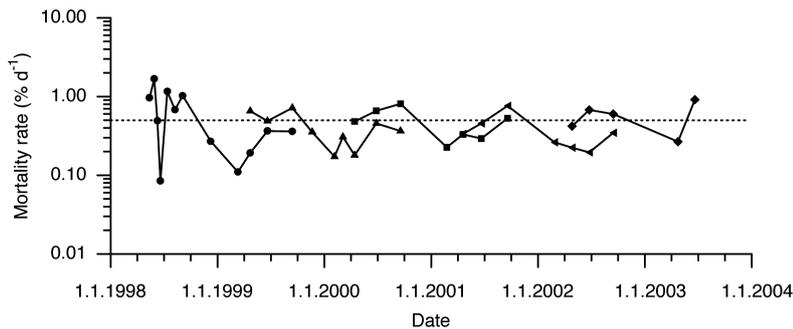


Fig. 6. Seasonal variation of average daily mortality rates (ADMR) of five annual age groups, 1998–2002 (symbols drawn at end of census intervals, those of same age group linked by lines), each from spring across ca. 1.5 years, calculated with all species with >6 individuals per census interval, arbitrary reference line at 0.5%. No mortality in first interval 1–23 April 1998 (not shown).

During spring periods (1997–2002) seedlings of 47 species arose, and during autumn periods (1998–2002) seedlings of 35 species. Total seedling emergence in spring was negatively related with log duration of soil dryness in the germination period, seedling emergence in autumn showed no relationship with this variable (Fig. 5). Separate analyses showed a stronger dependence of forbs ($r^2 = 0.895$, $p < 0.01$) than grasses ($r^2 = 0.447$, $p < 0.1$) in spring and no relationship for both life forms in autumn.

Seedling mortality: seasonal variability and weather influence

Average daily mortality rates (ADMR) of the five annual age groups showed similar seasonal oscillations across ca. 1.5 year (Fig. 6), a peak in the warm season (ADMR $> 0.5\% \text{ d}^{-1}$ between April and September) and a low in the cold season (ADMR $< 0.5\% \text{ d}^{-1}$ between October and March). Across four warm-seasonal intervals with 12 overlapping recording dates, the younger age group always showed a higher ADMR than the older age group. In the census interval 24 April–21 June 2003 when extremely dry weather prevailed (Fig. 4) the previous-year age group reached a maximal ADMR in their second summer ($0.91\% \text{ d}^{-1}$), twice to four times higher than in years without drought (Fig. 6).

The relative low ADMR in the cold season remained when ADMR was calculated with species showing a preference of emergence in autumn only, i.e. a selection

of younger individuals on average, and both curves were highly correlated ($r = 0.90$) across time ($n = 31$). A greater variation in ADMR in summer 1998 reflected the higher sampling resolution in that period.

The first half of 2003 revealed a precipitation total (174 mm) that was very close to the absolute 111-yr minimum (median of January–June precipitation total: 552 mm), only two days (30 April, 2 May) had > 10 mm of rain. Based on all recruits alive on 24 April ($n = 545$), forbs showed a higher resistance to the extreme drought in May/June than graminoids (-23.0% vs. -32.5% ; $\chi^2 = 4.6$; $p < 0.05$). The grass *Anthoxanthum odoratum* showed a relatively high mortality and had a strong effect on this result (Table 2). Older cohorts generally showed a higher resistance than younger cohorts (Table 2) but among older cohorts, forbs and graminoids did not differ in resistance (-12.8% vs. -16.7% ; $\chi^2 = 0.6$; n.s.).

In the wet period April 1998–October 2002 without long periods of intense soil drought (Fig. 4b) seedlings of 43 out of 46 species survived over 1 year (Table 1). One-year survivors of 28 species exceeded densities of 10 per m^2 . In multiple regression models with backward selection, life form was eliminated and log seed mass was retained as the only predictor for survival (Fig. 7). Log seed mass did not differ among life forms ($t_{31} = 0.30$) and had a positive effect on seedlings survival over 1 year ($F = 7.8$; $\text{df} = 1, 31$; $p < 0.01$). This effect remained significant when four species with missing local seed-mass data were excluded from the analysis ($F = 4.5$; $\text{df} = 1, 27$; $p < 0.05$).

Table 2. Individuals living in April 2003 (n) and resistance (R) during April–June 2003, for totals of forbs (29 species), graminoids (10 species), most abundant grass separately, χ^2 -tests (Yate's corrected for graminoid subcategories) for contingency tables with state (dead vs. alive) and age (two cohort categories).

| | Cohort 2002 | | Cohorts 1998–2001 | | χ^2 -test |
|------------------------------|-------------|---------|-------------------|---------|----------------|
| | n | R | n | R | |
| Forbs | 196 | –34.7 % | 226 | –12.8 % | $p < 0.001$ |
| Graminoids | 57 | –50.9 % | 66 | –16.7 % | $p < 0.001$ |
| <i>Anthoxanthum odoratum</i> | 41 | –53.6 % | 31 | –25.8 % | $p < 0.02$ |
| Other graminoids | 16 | –43.8 % | 35 | –8.6 % | $p < 0.02$ |

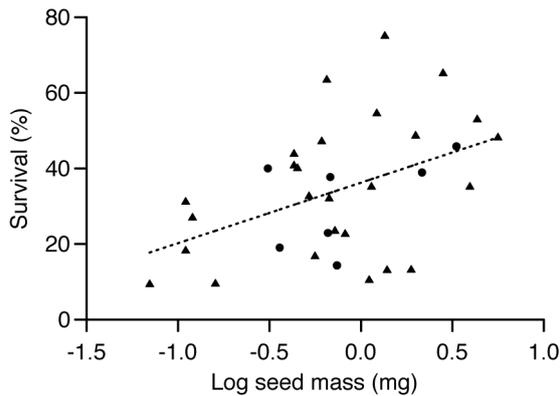


Fig. 7. Relationship between survival over 1 year and log seed mass ($r^2 = 0.200$) of species in years 1998-2002; graminoids (dots), forbs (triangles).

Discussion

Observations over 5 years in the ancient, semi-natural meadow revealed an imbalance of recruits among co-dominant graminoids and forbs. Low fecundity (*Brachypodium pinnatum*, *Carex caryophylla*, *Festuca rubra*), or a late maturation of seeds (*Agrostis capillaris*) contributed to poor recruitment in some abundant graminoids. Self-incompatibility and low genotype diversity can contribute to infertility in *B. pinnatum* (K. Thompson & T. Yardley pers. comm.), but a high capacity to spread vegetatively, particularly by long-lived belowground rhizomes with long internodes, and to increase in periods of low stress (Liancourt et al. 2005) can overcome low recruitment from seed. Low fecundity of abundant species of short stature such as *Carex caryophylla*, *Danthonia decumbens* and *Thymus pulegioides* may be due to suppression by taller plants (Silvertown et al. 2002).

In other species, such as *Bromus erectus*, low fecundity did not contribute to the observed poor recruitment; 'normally' developed seeds were produced in most years. However, very low fecundity in exceptional years can result in drawbacks if good opportunities for recruitment are missed by this species without persistent seeds. Two years (1990, 1998) with very low spikelet densities followed years with extremely dry autumns and reduced total precipitation for September and October (62 mm in 1989; 43 mm in 1997) compared to the 111-year median (266 mm). Autumn is likely the phenological period, in which *B. erectus* gains the threshold amount of resources needed to flower in the following season (Rathcke & Lacey 1985). Two principal grasses in mountain grassland showed an analogous response to unfavourable weather conditions in autumn (Herben et al. 1995): Over ten years, the number of flowering

shoots of *Anthoxanthum alpinum* or *Festuca rubra* was positively correlated with temperature in September or October of the preceding year.

From a community perspective, we infer a causal relationship between timing of mowing and the grass-forb ratio of recruits. In years with 'normal' weather, the majority of grass species come close to seed maturity when haymaking starts towards the end of June. Only a few grass species reach maturity. Moreover, many seeds presumably remain attached during the process of haymaking and are removed with the hay resulting in a strong imbalance between grasses and forbs in the seed rain. With regard to the dominant species *B. erectus*, this could explain the 55-fold reduction in number between viable seeds in June and seedlings emerging in autumn. These seedlings most likely emerge from seeds produced in the same year as sowing experiments with *B. erectus* showed that >90 % of its seeds germinate within 1 year after sowing (Stampfli & Zeiter 1999; Zeiter & Stampfli In press). Seed predators such as ants might also have contributed to the reduction of *B. erectus* seeds; however, from a nearby simultaneous sowing experiment (Zeiter & Stampfli In press) we estimate that seed predators reduced less than half of the *B. erectus* seeds.

Major structural shifts in community composition may result from failure of re-colonization in a period following frequent summer droughts (Stampfli & Zeiter 2004). Such changes are ultimately susceptible to the practise of land use. This conclusion is consistent with experimental findings in a more mesotrophic grassland in northern England where seed amounts were nearly balanced between grasses and forbs at the traditional date of cutting (Smith et al. 1996). With an earlier mowing, the quantity of seeds shed declined and forb seeds increased in relative abundance. When mowing was delayed, both, the quantity of seeds shed and the proportion of grass seeds increased. Varying the haymaking date would similarly affect the Negrentino meadow as many forbs have a distinctly earlier phenology of seed maturation than grasses and grasses almost exclusively set seeds in the first crop. The date of first cutting is likely to be a key factor controlling the grass proportion in semi-natural meadows. In such perennial herb communities, the uncovering of structural shifts resulting from changes in mowing date may require a long-term approach due to slow establishment rates (Zeiter et al. 2006).

Seedling emergence in years with 'normal' weather revealing a pattern with two principal seasons reflected the ability of immediate germination of grasses (autumn) and the more varied germination requirements of forbs, including those with a known responsiveness to chilling (spring) or dry storage (autumn). The unambiguous emergence preference of *Sanguisorba minor* or *Plantago lanceolata* in spring contrasted with germination

characteristics known from laboratory studies (Grime et al. 1981) and recalls that germination requirements may differ among ecotypes (van Groenendael 1986; Grime et al. 1988). Low soil moisture ($\Psi_{\text{soil}} < -80$ kPa) during half of a season clearly reduced the chances of seedling emergence by more than half. Effects of soil dryness were clearly apparent in a third of the years in spring but not in autumn. Year-to-year variation in autumn-seedling numbers reflected preceding processes such as seed production, seed rain, predation by ants, or gap formation, rather than soil moisture in the germination season. Droughts of the same intensity as in spring, however, could have a similar inhibitory effect on seedling emergence in autumn, and more serious consequences for populations without persistent seeds, such as those of most grasses (Thompson et al. 1997).

Desiccation is a well-known cause of seedling mortality in dry grasslands (Ryser 1993; Stampfli & Zeiter 1999). The lower resistance of graminoids, in comparison with forbs, to an early-seasonal drought could be due to different drought tolerances or to different ages that result from different germination phenologies of the previous-year cohorts. The lower resistance of younger (6-12-months old) compared with older seedlings may reflect their insufficient access to resource-supporting mycorrhizae networks in the soil (Kuyper & de Goede 2005). Another important cause of seedling mortality apart from desiccation is asymmetric competition for light from established plants because high seedling mortality occurred even in summers of relatively wet years. The positive relationship between seedling survival and seed mass came out when the turf was relatively dense with annual yields above average ($325 \text{ g.m}^{-2}.\text{a}^{-1}$ in 1999, ca. $400 \text{ g.m}^{-2}.\text{a}^{-1}$ in 2000-2002; A. Stampfli unpubl.). High seedling mortality in years with a lush growth of established plants is consistent with current theoretical ideas holding that the establishment of new species from seed depends on fluctuating (Davis et al. 2000) or unconsumed resources left by the established species (Tilman 2004) and empirical findings showing that spaces with reduced competition from established plants provide good opportunities for seedling establishment (Grubb 1977; Hillier 1990; Bullock 2000).

Seasonal droughts that coincide with a time window after a perturbation with reduced competition from established plants are likely to select between re-colonizing species of functional groups with different phenologies and may drive community structure towards a new 'equilibrium' state by displacing species of mismatching phenology. From seasonal patterns in seedling emergence and seedling mortality, we recognize three recruitment-related mechanisms by which 'equilibrium' states of vegetation structure in semi-natural meadows are susceptible to change. Under the assumption that

regular haymaking is continued and no invasive species is introduced we predict that (1) summer droughts (but also constantly wet conditions) tend to reduce species that depend on frequent recruitment from seed, hence favour long-lived clonally spreading species; (2) autumn droughts reduce grasses due to their germination preference in autumn, their lacking seed persistence and the more varied germination preferences of forbs; (3) spring droughts reduce graminoids due to their lower drought resistance among previous-year seedlings. A further, as yet speculative mechanism reducing grasses could be added if not only *B. erectus* but grasses in general show the restricted dependence on autumn resources for floral induction and forbs have a more varied timing.

Spring and autumn droughts converge in their negative effects on graminoid recruitment. These effects are likely to be stronger if droughts occur in successive years. If intense droughts increase in frequency, negative impacts on graminoids can be mitigated by changing management regimes with an influence on seed shedding, such as timing of first mowing and technique of haymaking.

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App. 1. Model for soil water potential (Author: Roman Zweifel).

The model for soil water potential (Ψ_{Soil}) is based on two key processes of the soil water balance: (i) the wetting of the soil by rain (P) and (ii) the drying of the soil by evapotranspiration (ET). Both processes are strongly determined by soil resistances, which themselves are dynamically changing with Ψ_{Soil} and P. The recursive model structure couples these two processes with Ψ_{Soil} .

The model (Fig. A1 below) can be formulated as:

$$\Psi_{\text{Soil}} = \Psi_{\text{Soil(oid)}} - \frac{f_1 * ET}{R_{\text{ET}}} + \frac{f_2 * P}{R_{\text{P}}} \quad (\text{A1})$$

where P is precipitation, ET is evapotranspiration, R_{P} is the wetting resistance, R_{ET} is the evaporating resistance and f_1 and f_2 soil-specific weighting parameters.

ET is calculated according to the energy-balance model by Penman-Monteith (Penman 1948; Monteith 1965) in which a constant mean stomatal resistance of the vegetation is preset and the boundary layer resistance dynamically depends on wind speed (Zweifel et al. 2002).

In a feedback loop, Ψ_{Soil} determines R_{ET} : the drier the soil is the bigger is the resistance to the withdrawal of water:

$$R_{\text{ET}} = (-\Psi_{\text{Soil}})^{f_3} \quad (\text{A2})$$

where f_3 is a soil-specific dehydration resistance parameter.

The penetration of water (rain) into the soil is determined by a dynamic resistance R_{P} , which proportionally changes with the sum of rain over the recent 12 hours ($P_{12\text{h}}$):

$$R_{\text{P}} = P_{12\text{h}} * f_4 + 1 \quad (\text{A3})$$

where f_4 is a soil-specific hydration resistance parameter. The reason for setting $P_{12\text{h}}$ proportional to R_{P} lies in the finding that the velocity of soil wetting mainly depends on the dryness of the uppermost soil layer between surface and measurement sensor and not so much on the absolute value of Ψ_{Soil} at the measurement depth. This ‘surface dryness’ was found to be described best by $P_{12\text{h}}$.

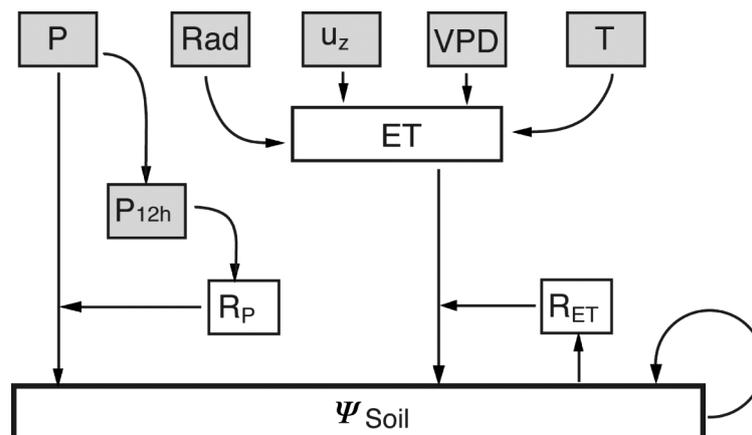


Fig. A1. Soil water potential model (Ψ_{Soil}). P = precipitation, $P_{12\text{h}}$ = sum of precipitation over the last 12 h, Rad = net radiation, u_z = wind velocity, VPD = vapour pressure deficit of the air, T = air temperature, ET = evapotranspiration, RP = wetting resistance, RET = evaporating resistance.

Sensitivity analysis

The sensitivity analysis covers two aspects: (i) the model sensitivity to variations in parameters f_1 to f_4 to test whether all the parameters are identifiable, and (ii) the degree of independence of individual parameters to test whether pairs of parameters are compensating each other.

(i) The model sensitivity $S(y_i)$ on each parameter was calculated according to (Steppe 2004) as:

$$S(y_i) = \frac{y_i(\theta + \Delta\theta) - y_i(\theta - \Delta\theta)}{2 * y_i(\theta)} \times 100 \quad (\text{A4})$$

where $y_i(\theta)$ is the model output at the time i with the original parameter value θ , and $\Delta\theta$ is the perturbation of θ . Perturbation was chosen to be 10 % of θ . Based on $S(y_i)$, the sensitivity measure δ^{meas} was calculated as:

$$\delta^{\text{meas}} = \frac{1}{N} \sum_{i=1}^N |S(y_i)| \quad (\text{A5})$$

where N is the number of $S(y_i)$ -values along the time axis. A high δ^{meas} for a certain parameter means a high sensitivity of the model on this parameter. A δ^{meas} close to zero means that the model does not depend on this parameter very strongly.

(ii) The dependence of pairs of parameters were tested with a correlation of the respective $S(y_i)$ -values.

Sensitivity analysis for data set “Compravasco 1999-2000”

The sensitivities of the model to the four parameters were ranked as follows: $f_3 \gg f_1 > f_2 \gg f_4$. High correlations were found between the parameter f_4 and f_1, f_4 and f_2 , and between f_1 and f_2 .

These findings led to the exclusion of f_4 from the parameterization process; f_4 was set to a constant value of 0.075, which was about the mean value obtained from several parameterization runs with different sets of data; f_1 and f_2 were retained as their exclusion resulted in a strong decrease of *EF* (see below).

Parameterization for data set “Compravasco 1999-2000”

Best-fit estimates for the parameters were found by an iterative procedure (Solver; Microsoft Excel 2000) that optimized the modelling efficiency factor (*EF*) for a set of measured data (Ψ_{Soil}). The modelling efficiency statistic was calculated according to Mayer & Butler (1993) and Hanson *et al.* (2004):

$$\text{EF} = 1 - \frac{\sum |y_i - \hat{y}_i|}{\sum |y_i - \bar{y}|} \quad (\text{A6})$$

where \hat{y}_i is the modelled value of Ψ_{Soil} at the time i , y_i is the measured Ψ_{Soil} at the time i , and \bar{y} is the measured average value of Ψ_{Soil} . To test the robustness of the model, the set of data used for calibration was varied and reduced and the resulting parameters compared (Table below). A robust model is expected to show a low sensitivity against reduced sets of data in terms of its output quality. The model proved to be very robust in terms of the choice of the calibration period, as *EF* did not much decrease and remained > 0.5 when the data used for calibration was reduced to 50 % or even 7 % (Table below).

The model produced unrealistically low Ψ_{Soil} values during periods with snow cover because evapotranspiration was withdrawing water from the snow layer and not from the soil.

Table A1. Parameters optimized for different sets of data (a-d) from Comprovasco to simulate soil water potentials 5 cm below surface at Negrentino: (a) 1 March-30 September 2000 plus 1 March-30 September 2001 (100 % of data), (b) 1 March-30 September 2000 (50 %), (c) 1 March-30 September 2001 (50 %), (d) 1-15 March 2000 plus 15-30 September 2001 (7 %). The four resulting sets of parameters were qualified on their ability to simulate the entire period a; f_4 was preset to 0.075. A modelling efficiency factor $EF > 0.5$ is very good.

| Parameter | Parameterization for period | | | |
|-----------------|-----------------------------|--------|--------|--------|
| | a | b | c | d |
| f_1 | 0.0933 | 0.0926 | 0.0964 | 0.1673 |
| f_2 | 3.606 | 2.704 | 3.927 | 1.9845 |
| f_3 | 0.8819 | 0.9508 | 0.8620 | 1.1812 |
| EF for period a | 0.63 | 0.59 | 0.61 | 0.52 |

App. 2. Determination of seed mass.

Seed mass of 26 species was collated from three studies in the southern Alps (Zeiter et al. 2006; B. Holzer unpubl.; A. Stampfli & M. Zeiter unpubl.) for which seeds were sampled in various years, 1998, 1999, and/or 2004, from a southerly exposed area of ca. 500 m² in the meadow around the nine permanent plots at Negrentino (820 m a.s.l.), or from such an area in a similar habitat situated at Pree (Monte Generoso, 45°53'58"N, 9°00'48"E, 980 m a.s.l.). Inflorescences with mature seeds from at least ten mother plants (except for *Pimpinella saxifraga*, *Prunella vulgaris*, *Solidago virgaurea*: at least five mother plants) were harvested in the field and stored in a dry cool room for a few weeks before pooled seed totals per species were cleaned from obviously predated or invalid seeds. Annual samples of 100-1000 seeds or indehiscent germinules per species were weighed. Seed mass was an average of the means of one to three annual samples. Seed mass for nine species was estimated based on a collection of 100-250 seeds (except for *Rumex acetosa*: 50 seeds) from an unknown number of mother plants sampled in 1 yr, 1995, 1997, 2004, or 2005, at one of the two sites, Negrentino or Pree (A. Stampfli & M. Zeiter unpubl.; Kupferschmid et al. 2000), except for *Daucus carota* seeds which were collected from a dry meadow, situated at San Michele (Monte Barro, northern Italy, 45°50'06"N, 9°23'26"E, 350 m a.s.l.).