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A six-year experimental restoration of biodiversity by shrub-clearing and grazing in calcareous grasslands of the French Prealps

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Abstract. The conservation of dry calcareous grasslands in the French Prealps strongly depends on the maintenance of low-intensity farming systems supported by agri-environmental schemes. An experimental assessment of the effect of current agro-pastoral management on the biodiversity of plant communities was conducted during a six-year permanent plot survey in four sites with contrasting habitat conditions (mesic to xeric). Analyses of species changes showed: (i) a strong increase in species richness and open grassland species frequencies four years after shrub-clearing, and (ii) a noticeable recovery of rare annuals and perennial species of conservation interest establishing in gaps created by grazing. At the community level, the restoration effect was evaluated by a between-year Correspondence Analysis, explaining 10.9% of the total floristic variability versus 29.5% for the site effect (between-site CA). Species ordination by between-year CA showed similar trajectories of vegetation changes during restoration despite different habitat conditions and grazing regimes between sites. The successful restoration of prealpine calcareous grasslands was explained by the availability of seed sources during the study in adjacent grazed or mown grasslands. Thus, restoration assessment should focus on dispersal possibilities and functional roles of species rather than species richness only. Finally, the spatial (i.e. the area of patches that need to be restored) and temporal (i.e. the frequency of shrub-clearing) implications for the large-scale conservation of prealpine calcareous grasslands by current agro-pastoral management are discussed.

Key words: biodiversity, calcareous grasslands, grazing, restoration, shrub-clearing

Introduction

Increasing shrub encroachment following reduction or abandonment of traditional use by livestock is a major conservation problem for typical plant, invertebrate and bird communities occurring in calcareous grassland ecosystems throughout western Europe (Dolman and Sutherland 1992; Fischer and Stöcklin 1997; Niemelä and Baur 1998). Experimental restoration of calcareous grasslands by tree and shrub clearing, as well as invasive *Brachypodium pinnatum* control by different grazing or cutting regimes, have been undertaken in different biogeographic areas (Bobbink and Willem 1993; Kiefer and Poschlod 1996; Zobel et al. 1996; Dzwonko and Loster 1998; Muller et al. 1998).

The particular importance of dispersal processes, seed rain and soil seed bank composition and longevity for successful restoration has been pointed out by many authors (Dutoit and Alard 1995; Willems 1995; Bakker et al. 1996a; Kollmann and Poschlod 1997; Willems and Bik 1998). Moreover, it has been demonstrated that optimal management should often include the restoration of traditional shepherding linking different sites of calcareous grasslands, in order to allow dispersal of species by sheep flocks (Fischer et al. 1996; Poschlod et al. 1998).

In submediterranean French Prealps, important areas of dry calcareous grasslands are still used by low-intensity livestock farming, in contrast with most of other western European countries (Barbaro and Cozic 1998). The study area may consequently provide useful examples for large-scale conservation management of rural submediterranean mountain landscapes by current agro-pastoral practices through agri-environmental schemes. The Vercors Natural Regional Park, located in the French Prealps, was one of the first three areas in France where an agri-environmental program was applied. It has been running since 1991, with special attention to the conservation or restoration of dry calcareous grasslands by agro-pastoral practices (grazing and cutting regimes). Dry calcareous grasslands of the Vercors provide suitable habitats for rare and legally protected orchids (*Ophrys drumana*, *Gymnadenia odoratissima*, *Orchis tridentata*), butterflies (*Zygaena rhadamanthus*, *Parnassius apollo*), and many passerines of high conservation interest (e.g. woodlark *Lullula arborea*, tawny pipit *Anthus campestris*, rock sparrow *Petronia petronia*, ortolan bunting *Emberiza hortulana*, and rock bunting *Emberiza cia*).

Most of the rare species of plants, birds and invertebrates depend on open short vegetation with patches of bare ground due to grazing and cutting disturbance for establishment (e.g. annual plants), foraging (e.g. birds), or laying eggs (e.g. grasshoppers and butterflies) (Dolman and Sutherland 1992). Moreover, an increasing risk of local extinction has been reported for species with particular life traits, i.e. short-lived taxa with no vegetative regeneration (Fischer and Stöcklin 1997).

The impact of current agro-pastoral practices on the conservation of the highly-valued biodiversity of prealpine dry grasslands of south-eastern France has been poorly studied compared to the northern part of France and Europe (Muller et al. 1998). The effect of an experimental restoration of prealpine calcareous grassland communities by a combination of shrub-clearing and various grazing regimes was therefore studied by means of permanent plots survey from 1992 to 1997.

In this work, two questions concerning the possibilities of calcareous grassland restoration by current agro-pastoral practices were considered: (i) does the combination of shrub-clearing and grazing significantly affect species richness and floristic composition, and especially target species of conservation interest? (ii) are there significant differences between sites, and is it possible to distinguish between site and year effects on changes in calcareous grassland communities after restoration?

Materials and methods

Study site

The study site is the limestone massif of the Vercors (Figure 1), located in the southwestern part of French Prealps (Drôme and Isère districts). The bioclimatic limit between mediterranean and medio-european regions runs through the study area and implies complex patterns of vegetation communities depending on elevation, slope, aspect and lithology. Annual rainfall varies within the study area from 900 to 1200 mm yr⁻¹ and average annual temperature from 7 to 11 °C.

Dry calcareous grasslands and shrublands occur on nutrient-poor and shallow rendzina soils and lithosols between 300 and 1300 m. Lithology is the main factor determining differences in habitat conditions, especially decreasing edaphic stress from Urganian calcareous bedstones of the plateau to more mesic marly and colluvial soils on the lower part of the slopes. Stages of shrub encroachment and grassland dynamics depend on current agro-pastoral management, and especially regular or irregular cutting or shrub-clearing, livestock type, grazing season and stocking rates (Barbaro and Cozic 1998).

Four calcareous grasslands with contrasting habitat conditions were chosen for experimental restoration (Figure 1 and Table 1):

- the site of Choranche (05°23'30" E, 45°04'04" N) is a mesotrophic *Mesobromion* grassland dominated by *Bromus erectus* co-occurring with *Dactylis glomerata*,

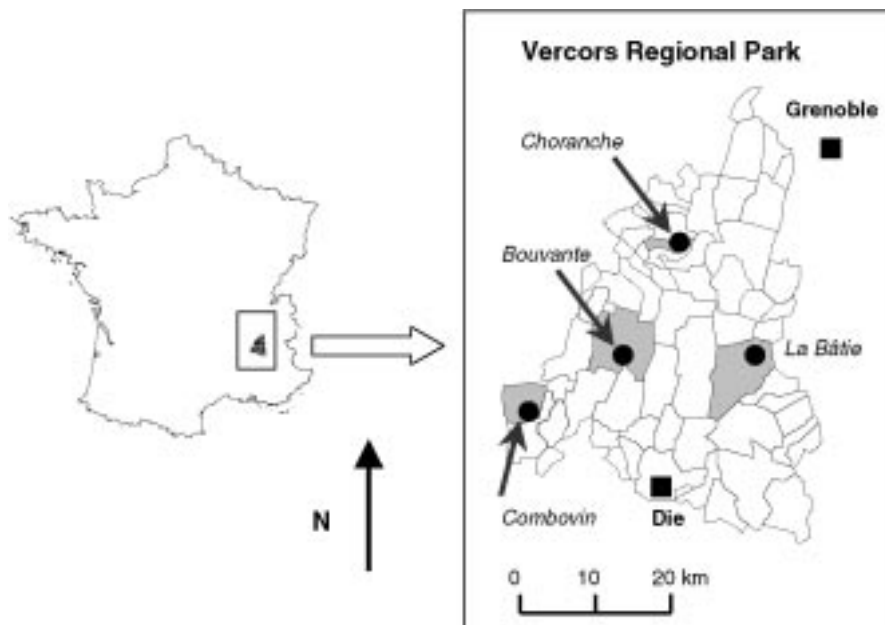


Figure 1. Location of the four experimental restoration sites (in italic).

Table 1. Habitat conditions and vegetation types for the four study sites.

Site	Elevation (m)	Aspect	Lithology	Soil depth (cm)	Habitat conditions	Dominant grasses	Dominant shrubs and trees
Choranche	350	South	Colluvium	40	Mesic	<i>Bromus erectus</i> <i>Dactylis glomerata</i> <i>Poa pratensis</i>	<i>Rosa canina</i> <i>Rubus fruticosus</i> <i>Ulmus campestris</i>
Bouvante	750	South-East	Marly limestone	30	Mesoxeric	<i>Bromus erectus</i> <i>Festuca ovina</i> s.l. <i>Briza media</i>	<i>Genista cinerea</i> <i>Juniperus communis</i> <i>Prunus spinosa</i>
Combovin	850	South	Urgonian limestone	10	Xeric	<i>Bromus erectus</i> <i>Festuca curvula</i>	<i>Buxus sempervirens</i> <i>Genista cinerea</i>
La Bâtie	1150	East	Marl	12	Mesoxeric	<i>Brachypodium pinnatum</i> <i>Bromus erectus</i> <i>Brachypodium pinnatum</i> <i>Briza media</i>	<i>Juniperus communis</i> <i>Juniperus communis</i> <i>Prunus spinosa</i> <i>Pinus sylvestris</i>

- Poa pratensis*, *Lotus corniculatus* and many forbs and annuals. Patches of Rosa-ceae shrubs and small individuals of *Ulmus campestris* are colonizing from the hedgerows, even under relatively high cattle grazing pressure;
- the site of Bouvante (05°16'17" E, 44°57'55" N) is a mesoxeric grassland-scrub mosaic, with characteristic taxa of both medio-european *Mesobromion* and sub-mediterranean *Aphyllantion* communities, following the phytosociological nomenclature of Gaultier (1989). It is dominated by *Bromus erectus*, *Festuca ovina* s.l., *Briza media*, *Brachypodium pinnatum*, *Carex flacca* and *Carex hallerana*, and partially colonized by a mixed *Genista cinerea-Juniperus communis* shrubland;
 - the site of Combovin (05°04'44" E, 44°52'29" N) is the driest site with a short *Xerobromion* grassland on stony Urgonian limestone with *Bromus erectus*, *Festuca curvula*, *Brachypodium pinnatum* and *Teucrium chamaedrys*, and patches of *Buxus sempervirens*, *Genista cinerea* and *Juniperus communis* shrubland;
 - the site of La Bâtie (05°34'03" E, 44°54'11" N) is a *Mesobromion* grassland established on marl at higher elevation than the other sites, with *Bromus erectus*, *Briza media*, *Brachypodium pinnatum*, *Festuca ovina* s.l. and *Carex hallerana*. In 1992, it was colonized by a dense shrubland of *Juniperus communis* and *Crataegus monogyna* with some sparse *Pinus sylvestris*.

Permanent plots survey

In each site, one paddock was selected in which three permanent plots of 10 × 10 m were established in 1992. All the experimental plots were located within dense shrubland patches, that were no more visited by livestock at the starting date of the experiment. In each of the four paddocks, there was one plot out of the total of three with 25% initial shrub cover in 1992 and the remaining two plots with 50% initial shrub cover.

Shrub-clearing was performed manually with the help of farmers between autumn 1992 and early spring 1993 (Table 2), in order to increase sward accessibility for livestock. All scrub and shrub species were removed until a final cover of less than 5% was obtained, but trees were conserved in Choranche (a tall individual of *Crataegus monogyna*) and La Bâtie (*Pinus sylvestris*). Vegetal remains were removed from the plots, but not stumps, so that some individuals of re-sprouting shrubs were able to grow back during the survey (e.g. *Buxus sempervirens*, *Genista cinerea*, *Prunus spinosa*). Shrub-clearing was not repeated later, and grazing was thereafter the only management regime applied.

Grazing management varied for each site, from mesic grasslands grazed by cattle (heifers) at higher stocking rate (Choranche) to xeric grasslands grazed by a mixed flock of sheep and hardy goats at lower stocking rates (Combovin) (Table 2). Mesoxeric marly grasslands were grazed both by cattle (Bouvante) and sheep (La Bâtie) at low stocking rates. Annual stocking rate is expressed throughout the study in

Table 2. Date of initial shrub-clearing and grazing management for the four study sites. Annual stocking rate is expressed in Livestock Units-days ha⁻¹.

Site	Date of shrub-clearing	Paddock area (ha)	Grazing species	Grazing season	Annual stocking rate
Choranche	Early spring 1993	3	Cattle	Spring to autumn	400
Bouvante	October 1992	15	Cattle	Spring to autumn	180
Combovin	April 1993	10	Sheep and goats	Late summer to winter	260
La Bâtie	Early spring 1993	3	Sheep	Spring to autumn	220

Livestock-Units days ha⁻¹. Grazing season was only different for the drier site (Combovin), which was grazed from late summer to early winter. Grazing management did not change during the whole period of study.

Vegetation survey was performed annually in late spring from 1992 (before shrub-clearing) to 1997 with a permanent linear transect across the diagonal of each plot, marked with wooden stakes. Species frequency and percentage cover of bare ground and stone was measured for each sample by noting presence-absence at 50 point-quadrats, at 20-cm intervals along the 10-m long transect (Bullock 1996). For the site of La Bâtie, there was initially three permanent plots, but the survey of one plot was discontinued because vegetation changes were biased by nitrogen input due to the vicinity of the sheepfold.

Data analysis

Changes in floristic composition following shrub-clearing were analysed both by univariate and multivariate analysis. The effect of restoration on species richness, number of annuals and rare perennials, species mean frequency, bare ground and stone cover were analysed by one-way ANOVA. When the treatment effect was significant, pairwise mean comparisons were performed with a Fisher's Least-Square-Difference test to identify significant differences between years.

Year-to-year variations in the ordination of plant communities under grazing or cutting disturbance have been studied by plant ecologists using direct or indirect gradient analyses (ter Braak and Wiertz 1994). A review of the literature in ordination methods shows that three-dimensional data table (site × species × time) can be analysed according to four ordination options: separate (i.e. all dates are analysed separately), mixed (i.e. all dates are mixed in a unique table), between-groups (i.e. between and within-dates analyses) and partitioning (i.e. discriminant) analyses (Dolédec and Chessel 1997).

In this study, we first performed a Correspondence Analysis (CA) on a 62 samples × 106 species × 6 years table and second, between and within-classes CA

to respectively take account of and eliminate spatial and temporal effects. The first eigenvalues of the following analyses were compared in order to decompose the total variability into 'site' effect and 'year' effect (i.e. restoration): total CA, within-year CA (elimination of year effect), within-site CA (elimination of site effect), between-year CA (taking account of year effect) and between-site CA (taking account of site effect) (Dolédec and Chessel 1997). Multivariate analyses were performed with ADE-4 software (Thioulouse et al. 1997).

Results

Changes in species richness

Species richness was significantly different between sites (Table 3), and pairwise mean comparisons (Fisher's LSD test) showed a significantly lower richness in xeric conditions (Combovin, 20 species) than mesic and mesoxeric ones (three other sites, 27 species). Year effect (i.e. restoration) was highly significant when considering all sites ($n = 62$) and for Choranche ($n = 16$), Bouvante ($n = 18$) and Combovin ($n = 16$). For La Bâtie, year effect on species richness was less significant, which may be related to the smaller sample ($n = 12$, Table 3).

Pairwise mean comparisons between years showed that shrub-clearing increased species richness from a mean richness of 16 species per sample before cutting to a mean of 30 species 4 years after cutting (Table 4). According to differences between sites, maxima for species richness were reached earlier (three years after cutting) for mesotrophic grassland grazed by cattle than for other sites. For mesoxeric to xeric grasslands, maximal species richness was reached later (4 years after cutting for

Table 3. Site effect for all years, year effect for all sites and year effect for each site on species richness between 1992 and 1997.

Effect	<i>d.f.</i>	MS	<i>F</i> -ratio	Significance
Site (all dates, $n = 62$)	3	193.68	5.33	**
Error	58	36.32		
Year (all sites, $n = 62$)	5	308.92	15.13	***
Error	56	20.41		
Year (Choranche, $n = 16$)	5	73.02	11.65	***
Error	10	6.27		
Year (Bouvante, $n = 18$)	5	134.06	22.34	***
Error	12	6.00		
Year (Combovin, $n = 16$)	5	72.19	20.05	***
Error	10	3.6		
Year (La Bâtie, $n = 12$)	5	92.33	7.1	*
Error	6	13.00		

One-factor ANOVA with * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$.

Table 4. Changes in mean species richness between 1992 (before shrub-clearing) and 1997.

	1992	1993	1994	1995	1996	1997
All sites	15.6 ^a	24.0 ^b	23.9 ^b	29.0 ^{bc}	30.0 ^c	28.2 ^{bc}
Choranche	17.7 ^a	–	25.0 ^b	31.3 ^b	29.3 ^b	29.3 ^b
Bouvante	18.0 ^a	23.7 ^a	24.0 ^a	32.7 ^b	35.0 ^b	32.3 ^b
Combovin	12.3 ^a	–	18.0 ^b	25.0 ^c	25.7 ^c	19.7 ^{bc}
La Bâtie	14.0 ^a	27.0 ^a	31.0 ^b	26.0 ^a	30.0 ^b	33.0 ^b

Different letters denote significant differences between means according to a Fisher's LSD test at a significance level of $P \leq 0.005$. Missing data are indicated by –.

Bouvante and Combovin, 5 years after cutting for La Bâtie). For all sites, richness was almost doubled during the restoration process.

Changes in dominant perennials and shrubs

For the mesotrophic grassland of Choranche, the combination of shrub-clearing and cattle grazing at 400 L.U.-days ha^{-1} led to a significant increase in frequency of rosette species such as *Bellis perennis*, *Prunella laciniata*, *Hieracium pilosella*, *Plantago media*, *Taraxacum officinale*, and forage grasses such as *Poa pratensis* (Table 5). Significantly, *Rosa canina* disappeared after shrub clearing, probably due to high stocking rate following cutting intervention (Table 5). For all grasses and forbs showing a significant increase, frequency was significantly higher 5 years after cutting than the other years, except for *Poa pratensis*, reaching significantly higher frequency three years after cutting.

A significant increase in the frequency of perennial grasses and legumes occurred in the mesoxeric grassland of Bouvante during the study, especially for *Briza media*, *Bromus erectus*, *Carex flacca*, *Festuca ovina* s.l., *Lotus corniculatus* and *Carex hallerana* (Table 6). Some rosette species also increased (*Plantago media* and *Cirsium acaule*) after shrub-clearing and cattle grazing at stocking rate of 180 L.U.-days ha^{-1} . For most dominant perennials, maximal frequency was reached in 1996, 4 years after shrub-clearing (Table 6).

Dominant perennials increased significantly in the xeric grassland of Combovin under sheep and goat grazing at 260 L.U.-days ha^{-1} , including *Teucrium chamaedrys*, *Carex hallerana* and *Koeleria pyramidata* (Table 7). *Juniperus communis* disappeared after shrub-clearing, a significant response in accordance with no re-sprouting after cutting, whereas *Buxus sempervirens* showed a non significant decrease one year after cutting and maintained important frequencies the following years, due to strong re-sprouting. For most dominant perennials (except *Carex hallerana*), maximal frequencies occurred earlier during the survey (i.e. 3 years after cutting) compared to other sites and despite drier habitat conditions.

Table 5. Changes in mean frequency for the main species, total number and sum of frequency of annuals, and cover of bare ground during restoration (Choranche, $n = 16$).

Species	1992	1994	1995	1996	1997	Significance
<i>Bellis perennis</i>	0.7 ^a	1.3 ^a	2.3 ^a	9.0 ^{ab}	21.0 ^b	***
<i>Brachypodium pinnatum</i>	8.3	5.0	8.0	4.7	7.3	NS
<i>Bromus erectus</i>	23.3	29.7	36.0	33.7	39.0	NS
<i>Hieracium pilosella</i>	1.0	0.7	0.3	1.7	4.7	*
<i>Plantago media</i>	0.3	0.7	2.7	2.0	3.7	*
<i>Poa pratensis</i>	0.0 ^a	4.7 ^{ab}	23.3 ^b	13.0 ^{ab}	2.0 ^a	***
<i>Prunella laciniata</i>	0.0 ^a	1.3 ^a	6.0 ^a	11.0 ^b	10.0 ^b	**
<i>Rosa canina</i>	17.7 ^a	0.0 ^b	0.0 ^b	0.0 ^b	0.0 ^b	***
<i>Taraxacum officinale</i>	0.0	0.0	2.3	0.0	3.7	*
<i>Catapodium rigidum</i>	0.0	0.0	3.0	3.0	0.3	NS
<i>Malva alcea</i>	0.0 ^a	0.0 ^a	2.3 ^{ab}	5.0 ^b	0.0 ^a	*
<i>Trifolium campestre</i>	5.3 ^{ab}	0.0 ^a	7.7 ^{ab}	9.7 ^b	4.3 ^{ab}	*
Number of annuals	2.3 ^a	2.3 ^a	8.3 ^b	7.3 ^b	6.7 ^b	***
Σ frequency of annuals	12.0 ^a	13.3 ^a	48.3 ^b	45.7 ^b	28.3 ^a	**
Bare ground cover	0.0 ^a	4.7 ^b	0.7 ^{ab}	1.7 ^{ab}	0.0 ^a	*

Significance level according to one-way ANOVA is indicated as follows: NS = non-significant, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.005$. When date effect was significant, a pairwise mean comparison between dates has been performed using a Fisher's LSD test. Different letters denote significant differences at $P \leq 0.005$.

In the mesoxeric grassland of La Bâtie, perennial species that showed a significant increase after shrub-clearing and sheep grazing at 220 L.U.-days ha⁻¹ were *Carex hallerana*, *Lotus corniculatus*, *Festuca ovina* s.l., *Hippocrepis comosa*, *Sanguisorba minor* and *Trifolium repens* (Table 8).

Table 6. Changes in mean frequency for the main species, total number and sum of frequency of annuals and rare perennials, and cover of bare ground during restoration (Bouvante, $n = 18$).

Species	1992	1993	1994	1995	1996	1997	Significance
<i>Brachypodium pinnatum</i>	13.7	8.7	9.7	16.0	17.7	16.7	NS
<i>Briza media</i>	4.7 ^a	5.3 ^a	2.0 ^a	27.0 ^b	36.7 ^b	15.0 ^{ab}	***
<i>Bromus erectus</i>	17.7 ^a	27.3 ^a	29.3 ^a	44.7 ^b	48.3 ^b	47.0 ^b	***
<i>Carex flacca</i>	2.0 ^a	8.7 ^{ab}	9.3 ^{ab}	29.7 ^b	20.3 ^b	14.3 ^{ab}	***
<i>Carex hallerana</i>	0.0 ^a	0.7 ^a	2.0 ^{ab}	3.3 ^{ab}	12.3 ^{ab}	15.3 ^b	*
<i>Cirsium acaule</i>	3.0 ^{ab}	0.0 ^a	7.0 ^{ab}	12.0 ^{ab}	16.0 ^b	9.3 ^{ab}	*
<i>Festuca ovina</i> s.l.	0.0 ^a	11.0 ^{ab}	4.0 ^a	28.0 ^b	32.0 ^b	15.0 ^{ab}	***
<i>Genista cinerea</i>	11.3	3.7	4.0	2.3	2.0	3.3	NS
<i>Lotus corniculatus</i>	3.3 ^a	2.0 ^a	3.3 ^a	8.3 ^{ab}	13.7 ^b	10.3 ^b	***
<i>Plantago media</i>	3.0 ^a	1.3 ^a	3.3 ^a	12.0 ^b	8.0 ^{ab}	6.0 ^{ab}	**
<i>Cerastium pumilum</i>	0.0 ^a	1.0 ^a	1.0 ^a	4.0 ^b	0.0 ^a	3.0 ^{ab}	**
<i>Daucus carota</i>	0.7 ^a	0.7 ^a	0.3 ^a	4.0 ^{ab}	8.7 ^b	4.7 ^{ab}	*
Number of annuals + rare	0.7 ^a	2.3 ^{ab}	1.7 ^{ab}	3.3 ^{ab}	3.7 ^{ab}	4.0 ^{ab}	*
Σ frequency of annuals + rare	0.7 ^a	4.3 ^{ab}	2.3 ^{ab}	10.7 ^b	15.7 ^b	11.7 ^b	***
Bare ground + stone cover	2.7	4.7	2.3	1.7	0.7	0.3	NS

Significance levels as in Table 5.

Table 7. Changes in mean frequency for the main species, total number and sum of frequency of annuals and rare perennials, cover of bare ground and stone during restoration (Combovin, $n = 16$).

Species	1992	1994	1995	1996	1997	Significance
<i>Brachypodium pinnatum</i>	15.7	29.7	30.0	29.3	19.0	NS
<i>Bromus erectus</i>	16.0	26.3	38.0	36.7	30.7	NS
<i>Buxus sempervirens</i>	26.0	7.0	7.0	9.0	9.0	NS
<i>Carex hallerana</i>	0.0 ^a	6.7 ^{ab}	13.0 ^{ab}	9.0 ^{ab}	21.0 ^b	*
<i>Juniperus communis</i>	5.7 ^a	0.0 ^b	0.0 ^b	0.0 ^b	0.0 ^b	*
<i>Koeleria pyramidata</i>	0.0 ^a	2.0 ^{ab}	5.3 ^b	4.0 ^{ab}	0.3 ^{ab}	*
<i>Teucrium chamaedrys</i>	16.3 ^a	26.7 ^b	30.7 ^b	24.0 ^{ab}	28.3 ^b	***
<i>Bombycilaena erecta</i>	0.0	0.0	0.0	1.0	0.3	NS
<i>Bupleurum baldense</i>	0.0	0.0	1.0	2.7	0.0	NS
<i>Ononis minutissima</i>	0.0	0.0	0.0	1.3	1.0	NS
<i>Petrorhagia prolifera</i>	0.0 ^a	0.0 ^a	0.0 ^a	1.7 ^b	0.0 ^a	*
Number of annuals + rare	0.0 ^a	1.3 ^{ab}	5.3 ^{ab}	6.3 ^b	4.0 ^{ab}	*
Σ frequency of annuals + rare	0.0 ^a	3.0 ^{ab}	13.7 ^b	14.3 ^b	7.0 ^{ab}	*
Bare ground cover	0.0 ^a	1.7 ^b	0.7 ^{ab}	0.0 ^a	0.7 ^{ab}	*
Stone cover	1.3 ^a	3.0 ^{ab}	2.3 ^{ab}	2.7 ^{ab}	5.0 ^b	*

Significance levels as in Table 5.

In none of the four study sites the mean frequency of *Brachypodium pinnatum* was affected significantly by restoration, due to its high competitive ability. Except for *Rosa canina* in Choranche and *Juniperus communis* in Combovin, restoration effect on shrub species was not significant although decreasing trends were noticeable for *Genista cinerea* in Bouvante, *Crataegus monogyna* and *Juniperus communis* in La Bâtie.

Table 8. Changes in mean frequency for the main species, total number and sum of frequency of annuals and rare perennials, and cover of bare ground during restoration (La Bâtie, $n = 12$).

Main species	1992	1993	1994	1995	1996	1997	Significance
<i>Brachypodium pinnatum</i>	21.0	17.5	26.5	27.5	19.5	25.5	NS
<i>Briza media</i>	6.0	1.5	4.0	6.5	9.0	14.0	NS
<i>Bromus erectus</i>	32.5	18.0	21.5	17.0	17.0	16.0	NS
<i>Carex hallerana</i>	0.0 ^a	2.0 ^a	13.0 ^b	22.0 ^b	17.0 ^b	14.5 ^b	***
<i>Crataegus monogyna</i>	13.0	0.5	0.5	0.0	0.0	1.5	NS
<i>Festuca ovina</i> s.l.	0.0 ^a	2.0 ^{ab}	2.5 ^{ab}	17.5 ^b	6.5 ^{ab}	3.0 ^{ab}	*
<i>Hieracium pilosella</i>	2.5	2.0	1.5	4.5	6.5	10.5	NS
<i>Hippocrepis comosa</i>	0.0 ^a	0.0 ^a	0.0 ^a	6.0 ^{ab}	11.0 ^b	5.0 ^{ab}	*
<i>Juniperus communis</i>	18.0	3.0	3.5	5.0	4.0	5.0	NS
<i>Lotus corniculatus</i>	0.0 ^a	2.0 ^{ab}	4.5 ^b	4.5 ^b	2.0 ^{ab}	5.0 ^b	*
<i>Sanguisorba minor</i>	6.0 ^{ab}	1.0 ^{ab}	0.0 ^a	8.0 ^b	1.0 ^{ab}	2.5 ^{ab}	*
<i>Trifolium repens</i>	0.0 ^a	0.0 ^a	1.5 ^{ab}	0.0 ^a	1.0 ^{ab}	3.5 ^b	*
Number of annuals + rare	0.5 ^a	3.5 ^{ab}	4.5 ^{ab}	4.0 ^{ab}	3.5 ^{ab}	6.0 ^b	*
Σ frequency of annuals + rare	1.0	5.5	6.5	8.5	6.0	10.5	NS
Bare ground + stone cover	0.0 ^a	2.5 ^{ab}	1.5 ^{ab}	7.5 ^{ab}	11.0 ^b	8.0 ^{ab}	*

Significance levels as in Table 5.

Changes in annuals and rare species

Several annual species occurred at Choranche during the experiment, most of them being absent before shrub-clearing (Table 5). Increasing frequency was only significant for *Malva alcea* and *Trifolium campestre*, but number of annuals and total frequency of annuals showed significant changes during the study, as well as bare ground cover. Bare ground cover was higher 2 years after cutting than the other years, although data are missing for the first year after shrub-clearing. Total number and frequency of annuals were higher 3 years after cutting, i.e. 1 year after maximum bare ground cover (Table 5). For most of the annuals, including taxa of conservation interest (*Catapodium rigidum*, *Malva alcea*, *Trifolium scabrum* and *Vulpia ciliata*), maximal frequency occurred 3 or 4 years after cutting, then decreased, although changes were not always significant because of low frequencies. In particular, *Vulpia ciliata* occurred only in 1995 (Table 5).

In Bouvante, the only annuals that significantly increased were *Cerastium pumilum* and *Daucus carota* (Table 6). The number of annuals and rare species and especially the total frequency of annuals and rare species also significantly increased, with a maxima four years after cutting. The increase in bare ground and stone cover was not significant but occurred the first year after cutting. Two species typical of *Aphyllantion* submediterranean communities (re)appeared 4 years after cutting (i.e. *Argyrolobium zanonii* and *Ononis cristata*).

In Combovin, changes in annuals and rare perennials (Table 7) were significant for *Petrorhagia prolifera*, but also for the number of annuals and rare perennials, the total frequency of annuals and rare perennials, the bare ground cover and the stone cover. Taxa of conservation interest (re)appeared three (*Bupleurum baldense*, *Trifolium scabrum*), or four years after cutting (*Bombacilaena erecta*, *Ononis minutissima*). Maximum bare ground cover occurred 2 years after cutting, and 5 years after cutting for stone cover. Here again, an increase in the flowering of annuals was noticeable in the 2 years following the maximum extent of bare ground (Table 7).

Finally, in La Bâtie, the number of annuals and rare perennials also significantly increased, as well as bare ground and stone cover (Table 8). Moreover, the rare *Chamaecytisus supinus* (re)appeared in 1997, 5 years after shrub-clearing, and maxima for the number of annuals and rare perennials also occurred in this year.

Site and year effects on community changes

Results of an initial CA produced a two-dimensional ordination of calcareous grassland communities on the gradients of edaphic stress and management intensity. In order to elucidate whether differences between sites or restoration effect was the most important factor in community ordination, between and within-classes CA were performed on the data set and their total inertia and first eigenvalues were compared (Table 9). Most of the total variability of the initial CA was maintained when

Table 9. Total inertia and first eigenvalues of multivariate analyses.

Analyses	CA	Within-year CA	Between-site CA	Within-site CA	Between-year CA
Total inertia	3.538	3.152	1.042	2.496	0.387
First eigenvalue	0.494	0.485	0.465	0.294	0.187
Monte-Carlo test	–	–	***	–	*

CA = Correspondence analysis. For between-classes CA, a Monte-Carlo test with 1000 permutations was performed to verify the significance of the effect, with *** $P \leq 0.005$, * $P \leq 0.05$.

removing the year effect with within-year CA (ratio of total inertias = 89.1%, Table 9), whereas more of this variability was lost when removing the site effect with within-site CA (ratio = 70.5%, Table 9).

Initial CA and within-year CA (removal of year effect) showed similar sample ordinations because contrasting habitat conditions were masking the restoration effect (Figure 2). In contrast, the removal of the site effect by within-site CA produced an ordination of samples on the restoration gradient (Figure 3). Between-site variations were eliminated, since all the samples of 1992 (before shrub-clearing) were located on the same side of the first axis of within-site CA, irrespective of the different sites (Figure 3).

This predominance of site effect over year effect (i.e. restoration) was confirmed by the results of between-site and between-year CA (Table 9). Taking account of site effect only by between-site CA explained 29.5% of the total inertia of simple CA, although taking account of year effect only by between-year CA explained less of the

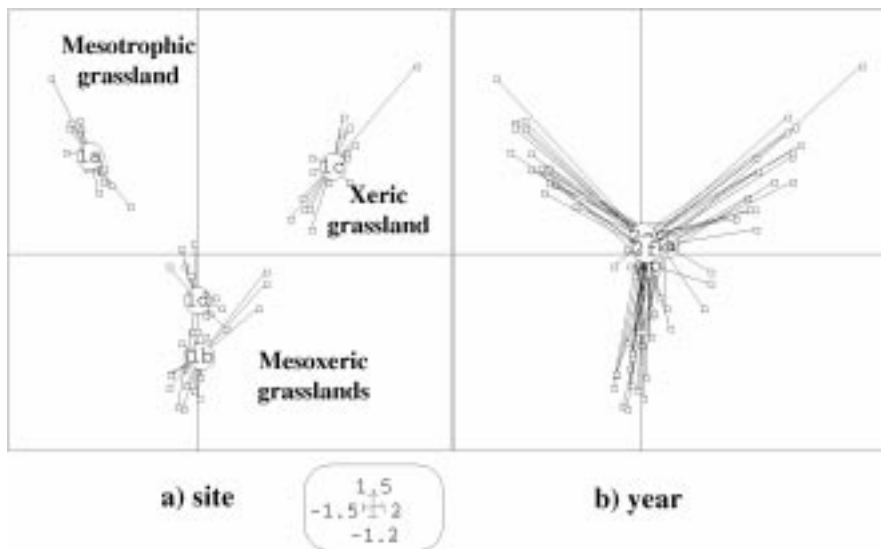


Figure 2. Elimination of year effect by within-year correspondence analysis. Samples are grouped by (a) sites: 1a = Choranche, 1b = Bouvante, 1c = Combovin, 1d = La Bâtie; and (b) years: 2a = 1992 (before shrub-clearing), 2b = 1993, 2c = 1994, 2d = 1995, 2e = 1996, 2f = 1997.

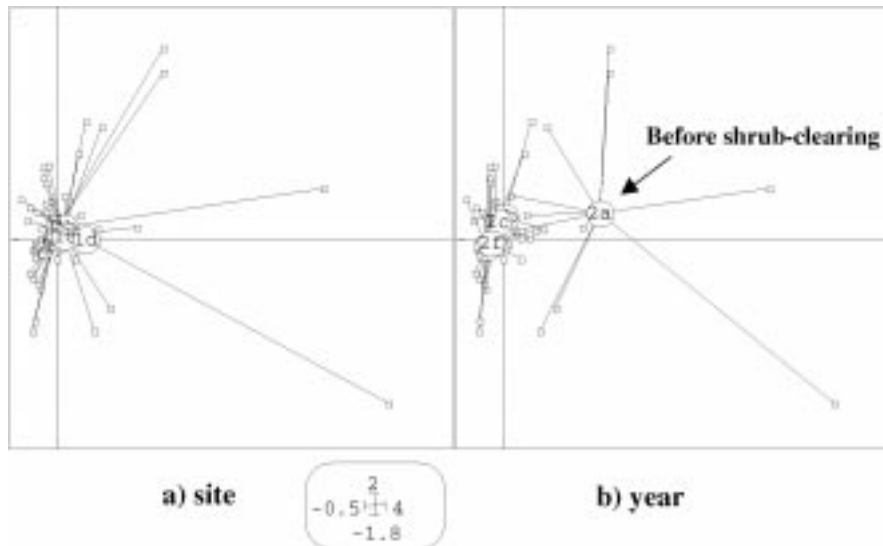


Figure 3. Elimination of site effect by within-site correspondence analysis. Samples are grouped by (a) sites: 1a = Choranche, 1b = Bouvante, 1c = Combovin, 1d = La Bâtie; and (b) years: 2a = 1992 (before shrub-clearing), 2b = 1993, 2c = 1994, 2d = 1995, 2e = 1996, 2f = 1997.

total variability of the data set (10.9%, Table 9). Moreover, if site effect was highly significant according to a Monte-Carlo test with 1000 permutations, year effect was less but still significant (Table 9).

Ordination of samples by between-year CA showed the detailed trajectories of changes in community composition, from initial stages before shrub-clearing (1992) to the most species-rich stages (1995–1996) with a higher number of annuals following increasing bare ground cover (Figure 4). All shrub species were grouped on the same side of axis 1 and most annuals and grazing-tolerant perennials were grouped on the opposite side, irrespective of contrasting nutrient and water requirements for different species (Figure 4).

Species ordination on the first axis of between-year CA was independent of habitat conditions and was considered as a restoration gradient following shrub-clearing. The second axis of between-year CA was a sward structure gradient from open short swards with many annuals to dense tall swards, depending on management intensity and especially grazing pressure (Figure 4).

Discussion

Although the duration of the survey (i.e. 5 years after initial shrub-clearing) did not allow definitive assumptions on long-term vegetation changes and especially clear distinctions between trends and fluctuations (Bakker et al. 1996b), it elucidated short-

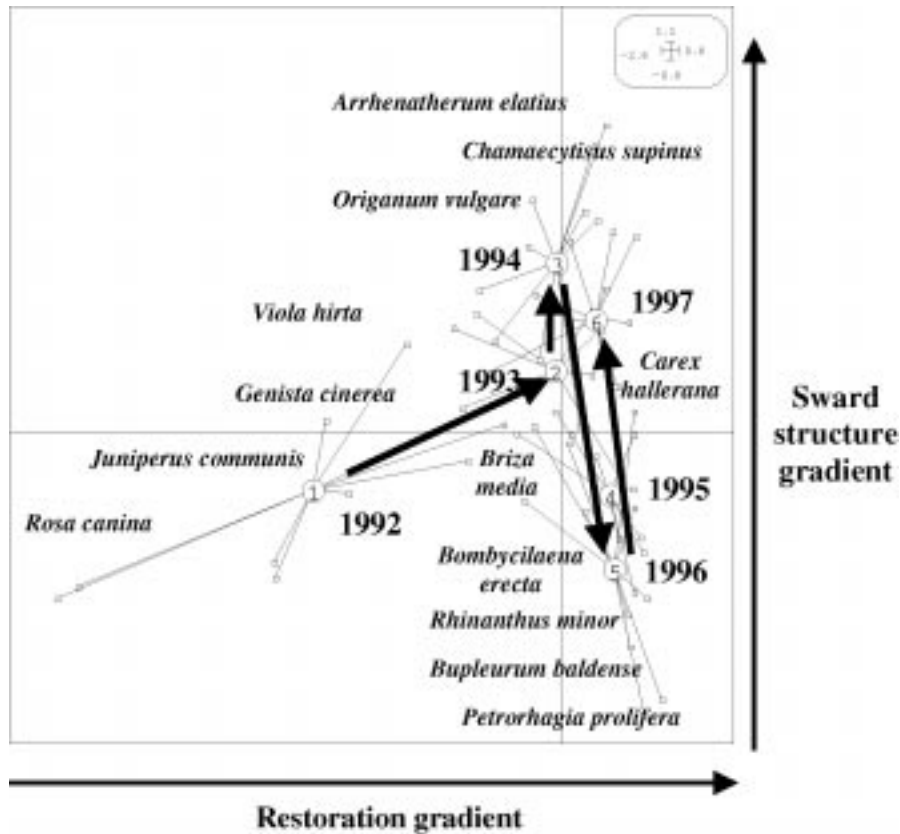


Figure 4. Trajectories of change in community ordination from 1992 (before shrub-clearing) to 1997. First factorial plane of between-year correspondence analysis: samples are grouped by years and positions of some characteristic species are indicated.

term patterns of changes in species richness and composition following shrub-clearing of grazed calcareous grasslands. Moreover, in comparison to long-term studies, the temporal scale used in this work is more in accordance with the frequency of agro-pastoral interventions for shrub control and grassland management (Watt et al. 1996; Bullock and Pakeman 1997).

An important result of the present experiment was the successful re-creation of species-rich grasslands, since the mean number of species was doubled 4 years after shrub-clearing. Such a positive effect on species richness was observed for all sites although initial species richness was lower in the driest site because of a more limited species pool in xeric conditions (Gigon and Leutert 1996). Differences in the rate of richness recovery were also noticeable between sites, probably because the different livestock types had distinct grazing behaviour. The hypothesis that mechanisms of species coexistence within calcareous grassland communities can be restored with the combination of shrub-clearing and grazing was validated,

and especially the spatio-temporal variation in opportunities for establishment and regeneration of species (Willems 1995).

Moreover, the central process following shrub-clearing is the re-colonization of bare ground by open grassland species, and particularly annual and biannual species of conservation interest (Ward and Jennings 1990; Bobbink and Willems 1993; Kollmann and Poschlod 1997). The effect of restoration on the abundance of different life-forms (forage grasses and legumes, rosette species, short rhizomatous or stoloniferous graminoids, annuals) reported from the present study, is a classical result in grazing experiments, in relation to increasing gap frequency within sward canopy (Ward and Jennings 1990; Bullock et al. 1994; Mitchley and Willems 1995; Watt et al. 1996). The rate of re-colonization by characteristic grassland species and recovery of species richness (i.e. between 3 and 5 years after initial shrub-clearing) was also similar to that observed in other restoration experiments (e.g. Bobbink and Willems 1993; Zobel et al. 1996).

As most grassland species have a transient seed bank not persistent under dense scrub canopy (Dutoit and Alard 1995; Willems 1995; Bakker et al. 1996a), the role of seed rain is considered as critical for the recolonization of bare ground by grassland species after shrub-clearing (Bullock et al. 1994; Kollmann and Poschlod 1997; Willems and Bik 1998). Nevertheless, distances of dispersal by seed rain rarely exceed 25 m for calcareous grassland species so that adjacent seed sources are needed for successful restoration (Stampfli and Zeiter 1999). The successful restoration of calcareous grasslands reported here was largely due to the availability of seed sources in other grazed grasslands being situated close to the experimental plots (Watt et al. 1996; Dzwonko and Loster 1998). The site of La Bâtie, where restoration process was slower than the other sites, is located near an abandoned shrubland, which probably induced a lack in the seed rain of open grassland species. This is in accordance with recent reviews showing the importance of the availability of propagules and dispersal processes in restoration ecology of calcareous grasslands (Mortimer et al. 1998; Poschlod et al. 1998).

In this study, the restoration effect explained a lesser part of floristic variation than the site effect. Nevertheless, there were similar trajectories of changes in community ordination, from initial high shrub cover to patches of short open swards with bare ground allowing the re-establishment of short-lived rare species. The effect of restoration was less obvious on shrub cover, especially re-sprouting species in xeric conditions (e.g. *Buxus sempervirens* at Combovin), except under higher stocking rates (e.g. *Rosa canina* at Choranche). There was no significant overall effect of treatment on *Brachypodium pinnatum* cover, in accordance with the high competitive ability of this species under low-intensity grazing and cutting regimes (Bobbink and Willems 1993; Mitchley and Willems 1995).

Finally, if successful restoration of prealpine calcareous grasslands is possible with the combination of grazing regimes and shrub-clearing, it is not possible with only shrub-clearing (Kiefer and Poschlod 1996; Zobel et al. 1996; Dzwonko and

Loster 1998; Stampfli and Zeiter 1999). However, cyclic trajectories with a progressive return to the initial stages were noticeable during this survey, and consequently a final decrease in gap frequency within the community through dominance of perennial graminoids and re-sprouting of shrubs. As a result, shrub-clearing is necessary every 5 or 6 years in dry prealpine grasslands to maintain an equilibrium between shrubland, grassland and bare ground patches of the mosaic (Ward 1990).

Another important question for conservation managers is the size of the area that needs to be restored (e.g. shrub-cleared) for the recovery of particular target species or communities, as well as for a landscape level management (Niemelä and Baur 1998). In this study, if the size of the restored area (permanent plots of 100 m²) has at least temporarily allowed the recolonization of several annual plant species of conservation interest, it is not obvious that it is the same for invertebrates and birds that need larger areas of restored grasslands as suitable habitats. Thus, a complete evaluation of restoration success should include the survey of multi-level indicators, that depend on different spatio-temporal scales and processes than plant communities (Mortimer et al. 1998).

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References

- Bakker JP, Bakker ES, Rosén E, Verweij GL and Bekker RM (1996a) Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *Journal of Vegetation Science* 7: 165–176
- Bakker JP, Olff H, Willems JH and Zobel M (1996b) Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science* 7: 147–156
- Barbaro L and Cozic P (1998) Organisation agro-écologique des pelouses et landes calcicoles du Parc Naturel Régional du Vercors. *Ecologie* 29: 443–457
- Bobbink R and Willems JH (1993) Restoration management of abandoned chalk grassland in the Netherlands. *Biodiversity and Conservation* 2: 616–626
- Bullock JM, Clear Hill B, Dale MP and Silvertown J (1994) An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology* 31: 493–507
- Bullock J (1996) Plants. In: Sutherland WJ (ed) *Ecological Census Techniques: A Handbook*, pp 111–138. Cambridge University Press, Cambridge

- Bullock JM and Pakeman RJ (1997) Grazing of lowland heath in England: management methods and their effects on heathland vegetation. *Biological Conservation* 79: 1–13
- Dolédec S and Chessel D (1997) Between- and within-groups principal component analyses. Documentation de la programmation ADE-4, University Lyon I
- Dolman PM and Sutherland WJ (1992) The ecological changes of Breckland grass heaths and the consequences of management. *Journal of Applied Ecology* 29: 402–413
- Dutoit T and Alard D (1995) Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. *Biodiversity and Conservation* 4: 939–950
- Dzwonko Z and Loster S (1998) Dynamics of species richness and composition in a limestone grassland restored after tree cutting. *Journal of Vegetation Science* 9: 387–394
- Fischer SF, Poschod P and Beinlich B (1996) Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. *Journal of Applied Ecology* 33: 1206–1222
- Fischer M and Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology* 11: 727–737
- Gaultier C (1989) Relations entre pelouses eurosibériennes (Festuco-Brometea) et groupements méditerranéens (Ononido-Rosmarinetea). Etude régionale (Diois) et synthèse sur le pourtour méditerranéen Nord-Occidental. PhD Thesis, University Paris XI Orsay
- Gigon A and Leutert A (1996) The dynamic keyhole-key model of coexistence to explain diversity of plants in limestone and other grasslands. *Journal of Vegetation Science* 7: 29–40
- Kiefer S and Poschod P (1996) Restoration of fallow or afforested calcareous grasslands by clear-cutting. In: Settele J, Margules CR, Poschod P and Henle K (eds) *Species Survival in Fragmented Landscapes*, pp 219–229. Kluwer Academic Publishers, Dordrecht, The Netherlands
- Kollmann J and Poschod, P. (1997) Population processes at the grassland-scrub interface. *Phytocoenologia* 27: 235–256
- Mitchley J and Willems JH (1995) Vertical canopy structure of Dutch chalk grasslands in relation to their management. *Vegetation* 117: 17–27
- Mortimer SR, Hollier JA and Brown VK (1998) Interactions between plant and insect diversity in the restoration of lowland calcareous grasslands in southern Britain. *Applied Vegetation Science* 1: 101–114
- Muller S, Dutoit T, Alard D and Gréville F (1998) Restoration and rehabilitation of species-rich grassland ecosystems in France: a review. *Restoration Ecology* 6: 94–101
- Niemelä J and Baur B (1998) Threatened species in a vanishing habitat: plants and invertebrates in calcareous grasslands in the Swiss Jura mountains. *Biodiversity and Conservation* 7: 1407–1416
- Poschod P, Kiefer S, Tränkle U, Fischer S and Bonn S (1998) Plant species richness in calcareous grasslands as affected by dispersability in space and time. *Applied Vegetation Science* 1: 75–90
- Stampfli A and Zeiter M (1999) Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *Journal of Vegetation Science* 10: 151–164
- ter Braak CJF and Wiertz J (1994) On the statistical analysis of vegetation change: a wetland affected by water extraction and soil acidification. *Journal of Vegetation Science* 5: 361–372
- Thioulouse J, Chessel D, Dolédec S and Olivier JM (1997) ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7: 75–83
- Ward LK (1990) Management of grassland-scrub mosaics. In: Hillier SH, Walton DWH and Wells DA (eds) *Calcareous Grassland: Ecology and Management*, pp 134–139. Bluntisham Books, Bluntisham, Huntingdon
- Ward LK and Jennings RD (1990) Succession of disturbed and undisturbed chalk grassland at Aston Rowant National Nature Reserve: details of changes in species. *Journal of Applied Ecology* 27: 913–923
- Watt TA, Treweek JR and Woolmer FS (1996) An experimental study of the impact of seasonal sheep grazing on formerly fertilized grassland. *Journal of Vegetation Science* 7: 535–542
- Willems JH (1995) Soil seed bank, seedling recruitment and actual species composition in an old and isolated chalk grassland site. *Folia Geobot. Phytotax.* 30: 141–156
- Willems JH and Bik LPM (1998) Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. *Applied Vegetation Science* 1: 91–100
- Zobel M, Suurkask M, Rosén E and Pärtel M (1996) The dynamics of species richness in an experimentally restored calcareous grassland. *Journal of Vegetation Science* 7: 203–210