# The influence of spatial heterogeneity on regeneration by seed in a limestone grassland

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**Abstract.** The spatial distribution of seedlings in fertilized and non-fertilized grassland patches (1 m × 2 m) was examined in alvar vegetation on the island of Öland, Sweden. We established whether variation in seedling distribution in grassland patches reflects the distribution of conspecific adults. We also established the significance of microsite turf attributes for prediction of seedling distribution at a small scale (10 cm × 10 cm), and the significance of conspecific adults abundance, assemblage of adult species and cover of lichens, mosses, litter and bare ground.

Our results indicate that fertilization reduces the importance of regeneration by seed of perennial species and enhances seedling recruitment of winter annuals and biennials. At the patch scale, enrichment does not affect species richness. Community patchiness contributes to the maintenance of diversity by providing a variety of environments with differential regeneration of the component species. Cover of lichens, mosses, litter and bare ground, accounts, in part, for the spatial variation in seedling numbers of certain species. The strong association of seedlings of some species with conspecific adults indicates that limitations in dispersal and/or the occurrence of a more suitable environment for emergence and/or establishment close to conspecific adult plants are likely to constrain the spatial distribution of new individuals in many cases. For other species, the lack of association of seedling densities with the cover of their conspecific adults, suggests that long-distance dispersal or a long-lived seed bank can play a role in counteracting the effect of short-distance dispersal.

**Keywords:** Alvar vegetation; Enrichment; Öland; Spatial pattern; Species diversity; Sweden; Turf structure.

**Nomenclature:** Tutin et al. (1964-1980).

## Introduction

Spatial structure in grasslands has often been described in terms of a matrix of dominant or 'core' species in which scattered subordinate or 'satellite' species occur which are the main contributors to the total species richness (Glenn & Collins 1990). At a regional scale, invasions and extinctions of 'satellite' species can be highly stochastic, as in the case of North-American prairies and, in the absence of physical environmental variation and disturbance, they become the main determinants of patch differentiation (Collins & Glenn 1991). At a local scale, colonization and extinction patterns appear also to be highly unpredictable. For example, subordinate species in European limestone grasslands often have high turnover rates (Rusch & van der Maarel 1992; van der Maarel & Sykes 1993), and colonization of individual species seems not to be restricted to particular grassland patches.

There is some evidence that colonization and extinction patterns within a community are not totally stochastic. Seed dispersal and the availability of seeds in the seed bank can influence the pattern. A recent example is provided by Salonen and co-workers (1992) who studied the origin of pattern caused exclusively by the distribution of propagules in a succession on bare peat surface. Limited dispersal will enhance aggregation by causing new individuals to establish closer to mother plants than would be expected by chance alone. At our study site on Öland, at a scale of 10 cm × 10 cm, both seedlings and seeds in the seed bank were highly clumped (Rusch 1992). This indicates that at least part of the spatial heterogeneity in the distribution of seedlings can be explained by fine-grained differences in the abundance of seeds.

Alternative causes for aggregation within species are the variety of sites for seedling emergence and establishment that the turf might provide, and environmental differences between grassland patches. Studies in Dutch calcareous grasslands show that the bryophyte layer can be important for the outcome of seedling establishment (van Tooren 1988, 1990), while a number of other studies provide evidence for the significance of litter (Goldberg & Werner 1983; Bergelson 1990) or the amount of open space (Rusch 1988; Hillier 1990; Ryser 1990). Accordingly, the turf, regarded as the environment of seeds and seedlings, can provide more or less suitable conditions for germination and establishment

(Gross & Werner 1982; Rusch 1988; Oesterheld & Sala 1990; van Tooren 1988, 1990).

Rusch (1992) showed that patches in alvar grassland varied in species composition and seedling density, while differing in turf structure (distance between rooting adult individuals, height and total cover of vascular plants) but the differences could not fully explain the variation in seedling numbers and species composition.

Colonization and extinction are processes closely related to mechanisms of maintenance of species diversity. While loss of diversity has been accounted for by limitation in recruitment of seedlings in experimental plots (Tilman 1993), high species richness at the community scale can be predicted from co-existence models based on small-scale aggregation of plant species in patchy environments where each species is dominant at a certain combination of environmental conditions (Levin et al. 1984; Chesson 1981, 1986; Chesson & Huntly 1988; Pacala 1986, 1987; Shmida & Ellner 1984; Comins & Noble 1985; Kadmon & Shmida 1990).

In the present study we assessed different aspects of the variation in spatial distribution of seedlings in grassland patches (1 m×2 m) which represent both the site's natural heterogeneity and fertilization treatments. We used fertilized plots to incorporate a wider range of floristic variation. First, we wished to know whether seedling distribution among floristically different grassland patches is similar to the distribution of conspecific adults. In this case, aggregation can be due to short-distance dispersal and/or species-specific environmental requirements within patches. Alternatively, the distribution of seedlings is affected by factors other than the proximity of conspecific adults, and long-distance dispersal and/or a persistent seed bank may account for differences between adult and seedling distributions.

We were also interested in assessing the contribution of colonization by seed in processes related to the maintenance of species diversity. Enriched environments often show low species diversity (e.g. Tilman & Pacala 1993; Rosenzweig & Abramsky 1993), and failure in colonization by seed may account for the loss of diversity along productivity gradients (Tilman 1993). Our objective was to relate species richness to variation in seedling emergence in terms of which species reproduce by seed, and the number of seedlings that emerge.

Lastly, we focused on the significance of small-scale turf attributes for prediction of seedling distribution, i.e. whether the cover of conspecific adults can predict variation in seedling numbers. We assumed that variation in turf structure at this scale provides a range of micro-environments for regeneration, the range being determined by the adult species assemblages, and the cover of lichens, mosses, litter and bare ground.

## Material and Methods

### Study site

The study was carried out in a limestone grassland community on Stora Alvaret, a vast limestone plateau on the Baltic island of Öland (Southeast Sweden). The vegetation belongs to the *Veronica spicata-Avenula pratensis* association (Krahulec et al. 1986) which occurs on soils that originate from glacio-fluvial sands and gravels (Königsson 1968; Rosén 1982; Bengtsson et al. 1988). The soils are 15 - 50 cm deep and weakly acid (pH 5 - 7). The vegetation is subject to frequent, long-lasting summer droughts which, together with grazing, maintain the open structure of alvar grassland (Titlyanova et al. 1988). The turf is short, 3 - 10 cm, with the grasses *Festuca ovina*, *Agrostis vinealis* and *Avenula pratensis* sharing co-dominance with many herbs. The study site, Gettlinge (56° 23' N 16° 27' E), is lightly grazed by cattle and a few horses. It has not been grazed between May and August since 1985.

### Sampling

In 1991, we recorded the number of seedlings per species in two 1 m× 2 m plots in three blocks: a, b and c, situated ca. 25 m from each other. The control plots Ca, Cb and Cc represent the community's natural patch variation; plots Fa, Fb and Fc have been fertilized since 1986 as part of a larger project on mechanisms of species co-existence (van der Maarel & Sykes 1993). The F- plots, which are 1 m away from their respective C-plots, receive yearly 67 kg N/ha, 37 kg K/ha, 29 kg P/ha, plus micronutrients (Mg, Ca, S, Mn, Mo, Fe, Cu, Zn, B). With these amounts the above-ground production was roughly doubled in summers without drought. Mean soil depth averaged 37 cm, 26 cm and 19 cm for blocks a, b, and c, respectively (R. Huber unpubl.). No environmental differences other than soil depth were evident between blocks, except that block b can sometimes be flooded for a short period in the spring. Since most species have germination peaks in either spring or autumn (Rusch 1988), seedlings were recorded in 48 10 cm×10 cm subplots per plot in early June ($n$=288), and in 40 such subplots (a subset of the 48) in October ($n$ = 240). The cover of adult plants was recorded in the same subplots, in June, when the vegetation is fully developed and both summer and winter annual species are found. Also, in each subplot, the cover of lichen, moss, litter and bare ground was estimated (5 % intervals, with an extra category for < 1 %) in June and October.

### Analysis

To assess differences in the distributions of adults and seedlings between treatments and blocks, we used a

two-step procedure. First, we tested for non-random distribution of species frequencies between plots using a $\chi^2$-test. Then, we grouped the species for which $\chi^2$-tests were significant according to the species response to treatment (fertilization vs. control), block, and interaction of treatment × block. A G-test (Zar 1984) was used to assess the association between treatment and block effects. When the G-test was non-significant, species were divided as positively or negatively associated with fertilization. When the test was significant, we concluded that there was a significant interaction between treatments and blocks, in other words, that the species response to fertilization varied across blocks. Two-way ANOVA was used to test for non-random distribution in seedling numbers between treatments and blocks. Data were square root ($\sqrt{y} + 0.5$) transformed to reduce the heteroscedasity resulting from counts of rare events (Sokal & Rohlf 1969). A Tukey test was used for multiple means comparisons.

The relationship between seedling emergence and adult-species composition, as well as the relationship between seedling emergence and a series of parameters that expressed features of the turf structure at the subplot scale (10 cm × 10 cm) were assessed with a least square multiple linear regression model. Independent variables were standardized to mean = 0 and SD = 1 and, prior to their inclusion in the regression model, tested for correlation. Independent variables were included in the model by stepwise selection when $p \le 0.05$. Seedling number, the dependent variable, was square root ($\sqrt{y} + 0.5$) transformed. The independent variables were (1) cover of conspecifics, (2) subplot floristic composition, (3) moss cover, (4) lichen cover, (5) bare ground and (6) litter. For these analyses we used procedures PROC· FREQ, PROC ANOVA, PROC REG; PROC MEANS and PROC CORR in SAS,version 6.04 (Anon. 1990).

We used CA, Correspondence Analysis (CANOCO, version 3.10; ter Braak 1990) to obtain an index of floristic composition of vascular plants that could be included in the multiple regression model as an independent variable. 'Cover of conspecific adults' and 'CA score' were based on June records for all species, whereas we used June records of moss, lichen, bare ground and litter cover for species emerging in spring, and October records for species emerging in autumn.

## Results

### Community patchiness

Adults of most species were non-randomly distributed (Table 1). Some showed significant associations with blocks, regardless of fertilization, e.g. *Anthoxan-*

*thum odoratum* and *Potentilla tabernaemontani* with block a, *Taraxacum* sectio *Erythrosperma* with block b and *Oxytropis campestris* and *Phleum phleoides* with block c, whereas others were significantly associated with either non-fertilized or fertilized plots, regardless of their spatial neighbourhood (groups B and C in Table 1). A final group (D in Table 1) had distributions which indicated an interaction of block and treatment effects (those whose response to fertilization varied between blocks). The fertilization treatment produced drastic floristic changes in blocks a and b, but only moderate ones in block c. Moss and bare ground were significantly associated with non-fertilized plots, while the distribution of lichen and litter was suggestive of an interaction between fertilization and block effects.

Seedlings of individual species also showed significant non-random distributions which did not always reflect the distribution of adults (Table 2), even though there were cases where both adults and seedlings were associated with the same plots, e.g. *Anthyllis vulneraria* with non-fertilized plots. These results are inconsistent with our null hypothesis that adult and seedling distribution vary in the same way among plots.

Seedlings of perennial species (*Festuca ovina, Potentilla tabernaemontani, Thymus serpyllum* and *Veronica spicata*) were negatively associated with fertilized plots, whereas adult plants of these species were evenly distributed between fertilized and non-fertilized plots (Tables 1 and 2). However, this pattern was not common for all perennial species. In the case of *Plantago lanceolata*, the occurrence of adults was positively associated with fertilized plots (group C, Table 1) while seedlings were associated with block b (group A, Table 2).

In fertilized plots, some winter annuals and biennials (e.g. *Arenaria serpyllifolia, Bromus hordeaceus, Cerastium semidecandrum*) had significantly higher frequencies, though the effect of fertilization often varied strongly between blocks (group D in Table 2).

Plots differed in species richness and in the number of species producing seedlings (Tables 1 and 2); plot Fc being richest with 38 species and plot Cb poorest with 32 species, but otherwise there were no clear differences in species richness between fertilized and non-fertilized plots, and between control plots from different blocks. The number of species that regenerated by seed was smallest in Fc (15 species) followed by Cc and Fa (19 species).

There was a significant block and treatment effect for mean number of seedlings per plot (Table 3). Block c had the smallest number of seedlings in both June and October. Blocks a and b differed significantly in June but not in October ($F = 48.10\ p < 0.0001$ and $F = 16.13\ p < 0.0001$ for June and October, respectively). Large seedling numbers in the non-fertilized plot Ca in June

**Table 1.** Number of 10 cm × 10 cm subplots ($n = 48$) where species occurred as adults in June, in control plots (Ca, Cb, Cc) and fertilized plots (Fa, Fb, Fc). **A.** Species varying in distribution between blocks, independent of fertilization. **B.** Species associated with non-fertilized plots. **C.** Species associated with fertilized plots. **D.** Species with a block-dependent response to fertilization (treatment-block interaction, G-test significant). **E.** Species for which no $\chi^2$ was calculated (expected values in any cell < 5) or with non-significant $\chi^2$. $P\chi^2$ = significance level of $\chi^2$ for equal distribution among plots. $P_G$ = significance level of G-test. P = Perennial. WA = Winter annual or biennial. SA = Spring annual or biennial.

| | | Ca | Cb | Cc | Fa | Fb | Fc | $P\chi^2$ | $P_G$ |
|---|---|---|---|---|---|---|---|---|---|
| **A** | *Anthoxanthum odoratum* | P | 21 | 1 | 1 | 34 | 0 | 0 | < 0.001 | 0.15 |
| | *Asperula tinctoria* | P | 3 | 0 | 18 | 0 | 0 | 13 | < 0.001 | 0.08 |
| | *Lotus corniculatus* | P | 13 | 15 | 19 | 12 | 10 | 30 | < 0.001 | 0.19 |
| | *Helianthemum oelandicum* | P | 3 | 3 | 37 | 0 | 2 | 9 | < 0.001 | 0.30 |
| | *Oxytropis campestris* | P | 0 | 0 | 21 | 0 | 0 | 10 | < 0.001 | - |
| | *Phleum phleoides* | P | 0 | 0 | 21 | 1 | 1 | 39 | < 0.001 | 0.43 |
| | *Potentilla tabernaemontani* | P | 41 | 21 | 20 | 40 | 27 | 24 | < 0.001 | 0.72 |
| | *Taraxacum* sectio *Erythrosperma* | P | 8 | 19 | 2 | 8 | 27 | 3 | < 0.001 | 0.82 |
| | | | | | | | | | | |
| **B** | *Anthyllis vulneraria* | P | 38 | 44 | 32 | 19 | 21 | 24 | < 0.001 | 0.43 |
| | *Briza media* | P | 11 | 6 | 20 | 2 | 0 | 7 | < 0.001 | 0.18 |
| | *Carex* spp. | P | 27 | 26 | 43 | 10 | 14 | 36 | < 0.001 | 0.14 |
| | *Filipendula vulgaris* | P | 43 | 45 | 32 | 23 | 31 | 15 | < 0.001 | 0.58 |
| | *Pulsatilla pratensis* | P | 29 | 6 | 33 | 3 | 0 | 7 | < 0.001 | 0.26 |
| | Mosses | | 38 | 32 | 25 | 0 | 0 | 1 | < 0.001 | 0.27 |
| | Bare ground | | 13 | 17 | 6 | 1 | 2 | 1 | < 0.001 | 0.87 |
| | | | | | | | | | | |
| **C** | *Achillea millefolium* | P | 36 | 35 | 35 | 47 | 40 | 44 | 0.002 | 0.91 |
| | *Bromus hordeaceus* | WA | 6 | 5 | 0 | 42 | 47 | 5 | < 0.001 | 0.51 |
| | *Myosotis stricta* | WA | 0 | 1 | 0 | 8 | 2 | 1 | < 0.001 | 0.71 |
| | *Plantago lanceolata* | P | 25 | 29 | 20 | 43 | 44 | 18 | < 0.001 | 0.27 |
| | *Ranunculus bulbosus* | P | 7 | 11 | 0 | 15 | 38 | 1 | < 0.001 | 0.53 |
| | *Sedum acre* | P | 1 | 0 | 0 | 26 | 9 | 9 | < 0.001 | 0.60 |
| | *Veronica arvensis* | WA | 8 | 1 | 0 | 15 | 9 | 0 | < 0.001 | 0.12 |
| | | | | | | | | | | |
| **D** | *Arenaria serpyllifolia* | WA | 4 | 0 | 0 | 39 | 46 | 14 | < 0.001 | 0.03 |
| | *Avenula pratensis* | P | 47 | 41 | 45 | 6 | 4 | 42 | < 0.001 | > 0.001 |
| | *Cerastium semidecandrum* | WA | 29 | 10 | 1 | 39 | 42 | 31 | < 0.001 | > 0.001 |
| | *Galium verum* | P | 21 | 6 | 27 | 45 | 26 | 11 | < 0.001 | > 0.001 |
| | *Helianthemum nummularium* | P | 32 | 41 | 28 | 15 | 11 | 35 | < 0.001 | > 0.001 |
| | *Linum catharticum* | SA | 45 | 26 | 14 | 3 | 7 | 6 | < 0.001 | 0.03 |
| | *Thymus serpyllum* | P | 27 | 30 | 43 | 0 | 2 | 7 | < 0.001 | 0.04 |
| | *Trifolium campestre* | WA | 20 | 14 | 2 | 39 | 29 | 19 | < 0.001 | 0.002 |
| | *Trifolium repens* | P | 2 | 0 | 2 | 14 | 40 | 0 | < 0.001 | > 0.001 |
| | *Trifolium striatum* | WA | 3 | 1 | 3 | 27 | 2 | 0 | < 0.001 | 0.002 |
| | Lichens | | 16 | 1 | 9 | 0 | 2 | 2 | < 0.001 | > 0.001 |
| | Litter | | 10 | 3 | 12 | 3 | 10 | 6 | 0.03 | 0.01 |
| | | | | | | | | | | |
| **E** | *Agrostis vinealis* | P | 46 | 47 | 44 | 44 | 45 | 47 | - | - |
| | *Agrostis tenuis* | P | 0 | 3 | 0 | 0 | | 8 | - | - |
| | *Antennaria dioica* | P | 5 | 16 | 2 | 0 | 0 | 0 | - | - |
| | *Arabis hirsuta* | P | 0 | 0 | 0 | 0 | 0 | 1 | - | - |
| | *Avenula pubescens* | P | 0 | 0 | 19 | 0 | 0 | 4 | - | - |
| | *Campanula rotundifolia* | P | 0 | 0 | 3 | 1 | 0 | 5 | - | - |
| | *Erophila verna* | WA | 0 | 0 | 0 | 1 | 0 | 0 | - | - |
| | *Festuca ovina* | P | 47 | 48 | 48 | 40 | 41 | 48 | - | - |
| | *Galium boreale* | P | 0 | 0 | 5 | 0 | 0 | 0 | - | - |
| | *Hieracium pilosella* | P | 0 | 0 | 12 | 0 | 0 | 2 | - | - |
| | *Luzula campestris* | P | 17 | 11 | 16 | 6 | 11 | 14 | 0.12 | 0.19 |
| | *Orchis ustulata* | P | 0 | 0 | 0 | 1 | 0 | 0 | - | - |
| | *Poa pratensis* | P | 0 | 0 | 0 | 3 | 12 | 0 | - | - |
| | *Sieglingia decumbens* | P | 6 | 0 | 1 | 0 | 0 | 3 | - | - |
| | *Saxifraga tridactylites* | WA | 0 | 0 | 0 | 0 | 4 | 0 | - | - |
| | *Trifolium dubium* | WA | 2 | 0 | 0 | 0 | 0 | 0 | - | - |
| | *Veronica spicata* | P | 8 | 16 | 8 | 4 | 10 | 8 | 0.06 | 0.64 |
| | *Vicia hirsuta* | P | 0 | 0 | 0 | 0 | 5 | 0 | - | - |
| | | | | | | | | | | |
| | Number of species | | 35 | 32 | 36 | 35 | 33 | 38 | | |

**Table 2.** Number of 10 cm × 10 cm subplots where the species occurred as seedlings in June ($n = 48$) and in October ($n = 40$), in the control plots Ca, Cb and Cc, and the fertilized plots Fa, Fb and Fc. **A.** Species for which seedling frequency varied among blocks, independent of fertilization. **B.** Species for which seedlings were associated with non-fertilized plots. **D.** Species with block-dependent response to fertilization (treatment-block interaction, G-test significant). **E.** Species for which no $\chi^2$ was calculated out (expected values in any cell < 5) or with non-significant $\chi^2$. $P\chi^2$ = significance level of $\chi^2$ for equal distribution among plots. $P_G$ = significance level of G-test. P = Perennial; WA = Winter annual or biennial; SA = Spring annual or biennial.

| | | | Plot | | | | | | $P\chi^2$ | $P_G$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Ca | Cb | Cc | Fa | Fb | Fc | | |
| A | *Plantago lanceolata* | P | 6 | 12 | 2 | 6 | 9 | 1 | 0.006 | 0.85 |
| B | *Anthyllis vulneraria* | P | 5 | 11 | 7 | 1 | 3 | 6 | 0.03 | 0.28 |
| | *Euphrasia stricta* | SA | 31 | 7 | 0 | 1 | 1 | 0 | < 0.001 | 0.33 |
| | *Festuca ovina* | P | 16 | 25 | 10 | 1 | 2 | 3 | < 0.001 | 0.30 |
| | *Thymus serpyllum* | P | 14 | 25 | 14 | 0 | 1 | 1 | < 0.001 | 0.51 |
| | *Veronica spicata* | P | 4 | 20 | 1 | 0 | 3 | 1 | < 0.001 | 0.26 |
| D | *Arenaria serpyllifolia* | WA | 15 | 6 | 5 | 25 | 30 | 28 | < 0.001 | 0.04 |
| | *Bromus hordeaceus* | WA | 6 | 0 | 0 | 28 | 27 | 3 | < 0.001 | 0.02 |
| | *Cerastium semidecandrum* | WA | 8 | 1 | 0 | 7 | 5 | 19 | < 0.001 | < 0.001 |
| | *Linum catharticum* | SA | 42 | 16 | 5 | 8 | 14 | 0 | < 0.001 | 0.003 |
| | *Potentilla tabernaemontani* | P | 21 | 2 | 2 | 3 | 0 | 4 | < 0.001 | 0.02 |
| E | *Trifolium* spp.(1) | | 12 | 7 | 1 | 18 | 22 | 12 | 0.08 | 0.06 |
| | *Achillea millefolium* | P | 1 | 3 | 0 | 1 | 5 | 0 | - | - |
| | *Antennaria dioica* | P | 1 | 1 | 0 | 0 | 1 | 0 | - | - |
| | *Agrostis vinealis* | P | 0 | 1 | 1 | 0 | 1 | 0 | - | - |
| | *Avenula pratensis* | P | 1 | 0 | 1 | 0 | 0 | 0 | - | - |
| | *Briza media* | P | 0 | 0 | 1 | 0 | 0 | 0 | - | - |
| | *Cirsium acaule* | P | 0 | 2 | 1 | 0 | 0 | 0 | - | - |
| | *Filipendula vulgaris* | P | 6 | 6 | 3 | 1 | 0 | 0 | - | - |
| | *Galium verum* | P | 2 | 1 | 3 | 10 | 0 | 3 | - | - |
| | *Helianthemum nummularium* | P | 5 | 4 | 0 | 1 | 0 | 0 | - | - |
| | *Helianthemum oelandicum* | P | 0 | 2 | 11 | 0 | 0 | 1 | - | - |
| | *Hieracium pilosella* | P | 0 | 0 | 3 | 0 | 0 | 2 | - | - |
| | *Lotus corniculatus* | P | 2 | 3 | 2 | 2 | 6 | 0 | - | - |
| | *Myosotis stricta* | WA | 1 | 0 | 0 | 3 | 5 | 0 | - | - |
| | *Phleum phleoides* | P | 0 | 0 | 0 | 0 | 0 | 2 | - | - |
| | *Pulsatilla pratensis* | P | 0 | 0 | 1 | 0 | 0 | 0 | - | - |
| | *Ranunculus bulbosus* | P | 0 | 0 | 0 | 0 | 1 | 0 | - | - |
| | *Sedum acre* | P | 1 | 0 | 0 | 0 | 3 | 0 | - | - |
| | *Taraxacum* sectio *Erythrosperma* | P | 5 | 4 | 0 | 1 | 1 | 3 | - | - |
| | *Trifolium campestre* | WA | 3 | 2 | 0 | 13 | 2 | 0 | - | - |
| | *Trifolium repens* | P | 0 | 0 | 0 | 0 | 8 | 0 | - | - |
| | *Trifolium striatum* | WA | 0 | 0 | 0 | 4 | 0 | 0 | - | - |
| | *Veronica arvensis* | WA | 6 | 1 | 0 | 12 | 4 | 0 | - | - |
| | Number of species | | 24 | 23 | 19 | 19 | 23 | 15 | | |
| | Subplots without seedlings in June | 0 | 1 | 9 | 20 | 16 | 26 | < 0.001 | 0.002 | |
| | Subplots without seedlings in October | 5 | 9 | 20 | 9 | 5 | 2 | < 0.001 | 0.005 | |

(1) Including seedlings of: *Trifolium arvense*, *T. campestre*, *T. dubium*, *T. pratense*, *T. repens* and *T. striatum*, which could not be identified.

were mainly due to *Linum catharticum* and *Euphrasia stricta*, two short-lived species, while plots Cb and Cc had mainly seedlings of perennial species.

Non-fertilized plots had larger number of seedlings than fertilized plots in June, while the opposite result was obtained in October (Table 3) ($F = 161.18$, $p < 0.0001$ and $F = 86.47$, $p < 0.0001$, respectively). In the fertilized plots (mainly in Fa and Fb), winter annuals (in particular *Bromus hordeaceus*) were responsible for the higher seedling numbers in October. In general, fertilized plots had significantly more subplots without

seedlings in June and fewer in October (Table 2).

*Correspondence Analysis of subplots*

Axis 1 of the CA explained most of the floristic variation of the 288 subplots (eigenvalues 0.61, 0.31 and 0.26 for Axis 1, 2 and 3 respectively). Roughly, scores corresponded to a sequence from Cc (non-fertilized, block c) through Ca , Cb (non-fertilized, blocks a and b) and Fc (fertilized, block c) to Fa and Fb (fertilized, blocks a and b). Axis 1 clearly represents variation

due to fertilization. In order to remove the fertilization effect, which we had previously analyzed (Tables 1 - 3), we conducted two independent CA ordinations for fertilized and non-fertilized plots (Fig. 1a and b). Fertilized plots a, b and c formed three relatively distinct groups in the diagram of axes 1 and 2 (eigenvalues = 0.54, 0.32 and 0.23 for Axis 1, 2 and 3 respectively), whereas the ordination of non-fertilized subplots only separated plot c from the rest (eigenvalues = 0.36, 0.28 and 0.25 for Axis 1, 2 and 3, respectively). We included Axis 1 and 2 of the fertilized plots ordination, and Axis 1 of the non-fertilized plots in further analyses.

### Conspecific adults and turf structure at a subplot scale

We tested for correlation between the independent variables prior to including them in the regression model. In non-fertilized plots, correlation values were low (absolute values of Pearson $r$ ranged from 0.03 to 0.20, with the majority of the values < 0.1). On the other hand, scores on CA axis 1 of the fertilized plots were highly correlated with 'litter' and 'lichens' (Pearson $r = -0.54$ and $-0.36$, respectively) and CA axis 2, with 'lichens' (Pearson $r = 0.36$). Therefore, only CA axis 1 of the non-fertilized plots ordination was included in the model. A second restriction was that absolute Pearson $r$ values between 'CA Axis 1 score' and 'conspecific cover' of the individual species did not exceed 0.25.

The least square multiple regression models included any of the six independent variables, namely 'Cover of conspecific adults', 'CA Axis 1 score', 'Moss', 'Lichen', 'Bare ground' and 'Litter'. For each species, we conducted two independent regression analyses, for both fertilized and in non-fertilized plots. We conducted multiple regression for individual species when the total number of seedlings was > 20. Species that germinate mainly in spring attained this value only in non-fertilized plots (with the exception of *Plantago lanceolata*), whereas those emerging in autumn reached this value in fertilized plots. Multiple regression models were sig-

nificant for 16 species (Table 4). 'CA axis 1 score' explained the variation in seedling numbers in four species.

'Cover of conspecific adults' significantly explained the variation in seedling numbers in eight out of 16 species. This variable was not included in the model for *Euphrasia stricta* because in June, at the first recording date, the adult cohort had already died; nor for *Stellaria graminea* because this species did not occur in the subplots as adults.

Fertilized and non-fertilized plots differed largely in turf structure (Table 5). Subplot moss cover in non-fertilized plots ranged from 0 to 60 %, lichen 0 to 15 %, litter 0 to 25 %, and bare ground 0 to 20 %. The effect of
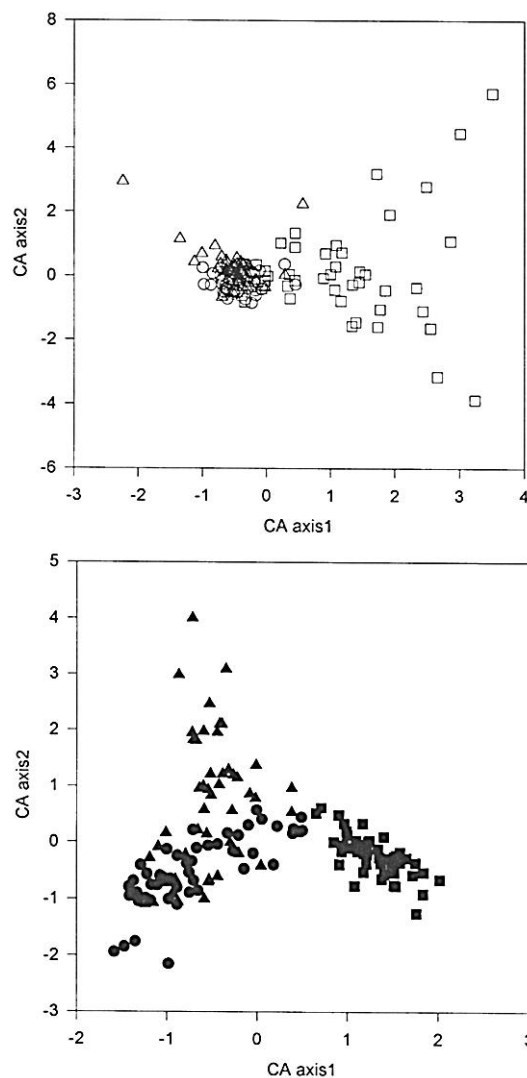


**Fig. 1.** Correspondence Analysis, diagram of axes 1 and 2; 144 non-fertilized (open symbols) and fertilized (filled symbols) subplots. Triangles, circles and squares correspond to blocks a, b and c, respectively.

**Table 3.** Treatment and block means of total number of seedlings per subplot obtained from June and October observations independently. Significance of differences established with a Tukey Studentized Range (HSD) test. Means with the same letter are not significantly different at $p < 0.05$.

| Source | June $n = 48$ | October $n = 40$ |
|---|---|---|
| Block a | 5.96 A | 23.51 A |
| Block b | 3.91 B | 17.14 A |
| Block c | 1.54 C | 3.19 B |
| Non-fertilized | 5.98 A | 2.25 A |
| Fertilized | 1.63 B | 26.98 B |

**Table 4.** Parameter estimate, partial $R^2$ and $F$-statistics of the independent variables in least squares multiple regressions on number of seedlings per subplot. Independent variables were selected by the STEPWISE procedure in SAS. The six independent variables are 'Conspecific': cover of adult conspecific species; CA axis 1 scores: subplot scores on Axis 1 resulting from the CA ordination of non-fertilized plots; and Cover of mosses, lichens, bare ground and litter. C = control; F = fertilized. J and O indicate the dates corresponding to records of the variables Moss, Lichen, Bare ground and Litter that were included in the model. Blanks indicate that the variable was not included in the model. Significance levels: $^* = p < 0.05$; $^{**} = p < 0.01$; $^{***} = p < 0.001$. Regressions were performed when total seedling number was > 20. Only species with significant regression models are presented.

| Species | Treatment | Date | Conspecific | | | CA Axis 1 scores | | | Moss | | | Lichen | | | Bare ground | | | Litter | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | E | R² | F | E | R² | F | E | R² | F | E | R² | F | E | R² | F | E | R² | F |
| *Anthyllis vulneraria* | C | J | | n.s. | | | -- | | | n.s. | | 0.04 | 0.03 | 3.99* | 0.05 | 0.03 | 4.82* | 0.04 | 0.03 | 4.74* |
| *Arenaria serpyllifolia* | F | O | | n.s. | | | -- | | | n.s. | | | n.s. | | | n.s. | | 0.42 | 0.13 | 17.22* |
| *Bromus hordeaceus* | F | O | 2.59 | 0.61 | 181.79*** | | -- | | | n.s. | | | n.s. | | | n.s. | | | n.s. | |
| *Cerastium semidecandrum* | F | O | | n.s. | | | -- | | | n.s. | | | n.s. | | | n.s. | | 0.13 | 0.06 | 8.23** |
| *Euphrasia stricta* | C | J | | -- | | -0.27 | 0.08 | 11.97*** | | n.s. | | 0.21 | 0.049 | 7.82** | | n.s. | | | n.s. | |
| *Festuca ovina* | C | J | | n.s. | | -0.10 | 0.05 | 7.80** | 0.07 | 0.03 | 4.64* | | n.s. | | | n.s. | | | n.s. | |
| *Helianthemum oelandicum* | C | J | 0.13 | 0.23 | 42.78*** | | -- | | -0.04 | 0.03 | 6.01* | | n.s. | | | n.s. | | | n.s. | |
| *Linum catharticum* | C | J | 0.13 | 0.04 | 6.55* | -0.15 | 0.10 | 15.06*** | | n.s. | | | n.s. | | 0.10 | 0.03 | 4.55* | | n.s. | |
| *Myosotis stricta* | F | O | 0.10 | 0.06 | 7.67** | | -- | | | n.s. | | | n.s. | | | n.s. | | | n.s. | |
| *Plantago lanceolata* | C | J | | n.s. | | -0.037 | 0.03 | 3.85* | | n.s. | | | n.s. | | | n.s. | | | n.s. | |
| | F | J | 0.05 | 0.05 | 6.66* | | -- | | | n.s. | | | n.s. | | | n.s. | | | n.s. | |
| *Potentilla tabernaemontani* | C | J | | n.s. | | | n.s | | | n.s. | | | n.s. | | 0.05 | 0.04 | 5.28** | | n.s. | |
| *Stellaria graminea* | F | O | | n.s. | | | -- | | | n.s. | | | n.s. | | | n.s. | | 0.16 | 0.07 | 9.19** |
| *Thymus serpyllum* | C | J | | n.s. | | | -- | | 0.06 | 0.03 | 3.6¹ | | n.s. | | | n.s. | | | n.s. | |
| *Trifolium campestre* | F | O | 0.03 | 0.04 | 6.30* | | -- | | | n.s. | | | n.s. | | | n.s. | | | n.s. | |
| *Veronica arvensis* | F | O | 0.17 | 0.20 | 28.86*** | | -- | | | n.s. | | | n.s. | | | n.s | | | n.s. | |
| *Veronica spicata* | C | J | 0.18 | 0.14 | 23.49*** | -0.08 | 0.023 | 3.91* | | n.s. | | | n.s. | | | n.s. | | | n.s. | |

¹ $p = 0.059$.

fertilization on turf structure was particularly evident in the autumn. In contrast to non-fertilized plots in June, we recorded no mosses in fertilized plots in October, and the mineral soil was completely covered, largely by litter (range = 0 to 65 %). Seedling numbers of four species were significantly explained by 'Litter'. 'Bare ground', 'Moss' and 'Lichen' were significant in three, three and two cases respectively.

## Discussion

### The spatial distribution of seedlings at the plot scale

Our results show that plots differed both in the total number of emergent seedlings and in the number and the identity of species that produced seedlings. They indicate large spatial variation in seedling emergence between grassland patches, which confirms earlier results at the same study site (Rusch 1992), and in other systems (e.g. Zimmergren 1980; Masuda & Washitani 1990; Aguiar et al. 1992).

Differences between plots in adult and seedling distributions lead us to doubt our first null hypothesis, i.e. that variation in seedling distribution between patches reflects only differences in the spatial distribution of adult plants. Firstly, we can attribute a large part of the spatial variation in seedling emergence to fertilization. For several perennial species, fertilization has a nega-

tive effect on emergence and/or survival of seedlings. However, some of them (e.g. *Plantago lanceolata*) have, as adults, either higher or equal frequencies in fertilized plots than in non-fertilized plots, suggesting that vegetative growth is not equally affected by this treatment. On the other hand, both seedling emergence and establishment of winter annuals is enhanced by fertilization.

Low species richness is a common feature in enriched grasslands which, to a large extent, can be accounted for by competitive interactions between already established plants (Goldberg & Miller 1990). Results from colonization experiments along productivity gradients have revealed loss of diversity with increases in productivity, which can be accounted for by a decline in the gain of perennial grass and forb species, and an increase in their rates of loss (Tilman 1993). Our results agree with fewer seedlings of perennial species emerging and/or establishing following fertilization. However, neither species richness nor the number of species which regenerate by seed declined with fertilization. Differences between fertilized and non-fertilized plots were instead due to the identity of the species that reproduced by seed and revealed a switch from perennial to annual species in fertilized plots.

Local fertilization through urine and faeces deposition is a common phenomenon in grasslands grazed by large herbivores. Patch enrichment can increase the diversity at the community scale ($\beta$-diversity) by increasing environmental heterogeneity. It will contribute

**Table 5.** Cover ranges of independent variables in June and October, in non-fertilized and fertilized plots.

| Independent variable | Non-fertilized/June | Fertilized June | Non-ferti-lized/Oct. | Fertilized Oct. |
|---|---|---|---|---|
| Moss | 0 - 60 % | 0 - 1 % | 0 - 55 % | 0 |
| Lichen | 0 - 15 % | 0 - 15 % | 0 - 25 % | 0 - 10 % |
| Bare ground | 0 - 20 % | 0 - 10 % | 0 - 15 % | 0 |
| Litter | 0 - 25 % | 0 - 15 % | 0 - 40 % | 0 - 65 % |

to patch formation by increasing the proportion of annual species in relation to perennials. Our results are consistent with the fact that annual species are generally confined to nutrient-rich environments. It is likely, therefore, that local enrichment will contribute to the maintenance of annual species populations in other grazed grasslands as well.

We could also detect spatial variation in seedling emergence due to natural heterogeneity (block effect), an effect which in some cases overrides the effect of fertilization and that in other cases interacts with it. The association of seedlings of *Festuca ovina* and *Thymus serpyllum* with non-fertilized plot b (Cb) (Table 2) could be partly attributed to the positive association of moss cover with this plot (Table 1) and the significance of these variables in explaining seedling numbers of these species (Table 4). Seedlings of *Euphrasia stricta* and *Linum catharticum* were positively associated with a non-fertilized plot in block a (Ca). Both species germinate only in spring, are short-lived (annual and biennial respectively) and are known to have similar regeneration requirements in the field (Rusch 1988). The fact that seedlings of both species were associated with plot Ca indicates that this patch might have had, in the spring, a fairly open structure that was particularly favourable for germination. This variation in regeneration among grassland patches supports predictions of co-existence models in patchy environments where plant species become dominant in different patches with a certain combination of environmental conditions.

*Seedling spatial distribution at the subplot scale*

We could reject our null hypothesis that seedlings are randomly distributed among subplots. At this scale, 'cover of conspecific adults' is the variable that explains the largest amount of variation in seedling numbers. This result indicates that either limitation imposed by short-distance dispersal and/or species specific environmental requirements, largely determines the distribution of new individuals. For other species, the abundance of conspecific adult plants weakly explained or did not explain at all the variation in seedling numbers, e.g. *Anthyllis vulneraria, Festuca ovina, Potentilla tabernaemontani* and *Thymus serpyllum*. Here, other factors

may be of importance such as long-lived seed banks, the environment affecting in a different way vegetative growth and seedling emergence and/or seed production, and turf structure features evaluated in our study.

For *Anthyllis vulneraria, Linum catharticum* and *Potentilla tabernaemontani*, 'bare ground' was a significant explanatory variable. Our results confirm earlier evidence of the importance of gaps in regeneration by seed in grasslands (Hillier 1990; Rusch 1988, 1993). The range of bare ground (0 - 20 %) shows that even small openings in the turf are important. In alvar grassland, small-scale disturbances as caused by small mammals (pocket gophers, prairie dogs, badgers etc. in North America) (Gibson et al. 1990) are not common. However, smaller-scale disturbances caused by ant and earthworm activities (Willems & Huijsmans 1994), in combination with summer drought, have similar effects on alvar grassland with its short (less than 10 cm) turf, leading to the death of tillers, ramets and individuals and the formation of very small gaps (a few cm$^2$). These gaps are important for seedling emergence.

The 'CA Axis 1 score' of non-fertilized plots explained the variation in seedling numbers in four species. The results mainly showed the negative relationship between the number of emergent seedlings of these species with subplots in plot Cc. As 'sample score' was not correlated with any of the other variables included in the model, the results suggest also that variation in seedling emergence and/or establishment is explained either by the turf structure conformed by the particular assemblage of species in the subplot (as an environment for seedlings), or by the expression in this assemblage of underlying environmental variation which was not explained by the variables we considered in the study.

'Moss cover' was a significant explanatory variable for seedling numbers of three species. It has been shown that the influence of the moss layer on germination and/or establishment of seedlings can be twofold. A moss cover can act as a 'seed trap' through retention of seeds (e.g. van Tooren 1988 for Dutch calcareous grasslands), but a thick moss layer can prevent seedlings from reaching the soil and hinder those with small seed reserves from successful establishment (van Tooren 1990). For *Helianthemum nummularium*, the relationship between seedling number and moss cover was negative, but for two other species, the 'seed trap' effect seems to have prevailed. Since we did not assess the fate of the seedlings after they had been recorded for the first time, we lack evidence about the possible negative effects of the moss layer on later stages of seedling development. Lichen cover explained the variation in number of seedlings of two species. We have often observed in the field that seedlings emerge within the lichen carpet (Rusch pers. obs.). The occurrence of lichens is likely to have a

similar effect in retaining seeds as the moss layer through, for example, reduced exposure to predation.

'Litter' significantly explained variation in seedling numbers of four species. Reports in the literature usually inidicate low emergence of seedlings under litter due to low light availability and a mechanical impediment due to the accumulation of a layer of several cm (Bergelson 1990; Goldberg & Werner 1983). However, non-fertilized plots at our study site are grazed, which keeps the turf short. As a result, the litter compartment constitutes only a small part of the grassland's aboveground biomass (ca. 25 %) (Titlyanova et al. 1988). In these plots, litter cover ranged from 0 to 25 %, usually forming a thin layer on the mineral soil. Even in the case that the litter layer was thin, a negative effect of litter on seedling growth and survival has been observed. This is probably due to a higher susceptibility to pathogen infections (Fowler 1988), but in our case this effect seems to have been of minor significance. A positive relationship between cover of litter and seedling numbers resulted for winter annuals as well, despite the high litter cover reached in fertilized plots (range 0 - 65 %). Positive effects of litter on seedling survival have also been reported (Fowler 1986), in particular due to the reduction of evapotranspiration in arid environments (Evans & Young 1970). In our study site, it is likely that litter is an expression of available space and of reduced competition from neighbours rather than an impediment to seedling emergence.

## Conclusions

Local fertilization in limestone grasslands is likely to change the relative importance of vegetative growth versus reproductive regeneration in perennial species, and the proportion of annual versus perennial species. This agrees with results obtained by others, where colonization by seed of perennial species is limited in enriched plots. However, it does not support a decline in species richness due to this limitation. Fertilization enhanced emergence of winter annuals and biennials which compensated for the loss of perennial species. Enriched plots supported a significantly different species assemblage, but with similar total numbers of species.

Within-community heterogeneity accounts for spatial variation in regeneration by seed. Community patchiness incorporates a variety of environments that differ in their ability to support regeneration of individual alvar species. Community heterogeneity does not seem to be completely stochastic, but patches provide different microsites suiting the regeneration requirements of individual species. Turf structure, in terms of the cover of lichen, moss, litter, turf and open soil accounts, in part,

for the variation in seedling numbers of some species. At the same time, the association of seedlings with conspecific adults indicates that limitations in dispersal, or the availability of sites suitable for seedling emergence and/or establishment close to conspecific adults, largely determine the distribution of new individuals. Part of the variation in seedling numbers is explained by variation extracted from subplot species composition which is not accounted for by fertilization or by the turf-structure features included in the study.

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