MICRO-SPATIAL HETEROGENEITY AND SEEDLING DEMOGRAPHY IN SPECIES-RICH GRASSLAND

By JONATHAN W. SILVERTOWN*

School of Biology, University of Sussex, Falmer, Brighton, Sussex, U.K.

SUMMARY

It is suggested that spatial niche-separation between grassland species occurs in the regeneration phase and that the differential response of species to micro-variations in leaf cover may allow coexistence at high density. A technique for measuring heterogeneity in leaf-cover on a scale of 1-cm² units (micro-cover) and the demography of seedling cohorts of *Reseda lutea* and *Anthyllis vulneraria* in relation to this heterogeneity is described. Densities of seedlings were significantly higher in micro-sites of low micro-cover for *R. lutea* and for one of the three cohorts of *A. vulneraria* studied. No relationship was found between mortality and density of seedlings or micro-cover. The ultimate causes of these distribution patterns of seedlings and their consequences for the maintenance of species diversity in grassland are discussed.

INTRODUCTION

The high species density often found in plant communities appears to contradict the competitive exclusion principle (Gause, 1934; Williamson, 1957) which predicts that co-occurring species should not have the same limiting factor. This apparent contradiction reaches its most acute form in Britain in species-rich calcareous grasslands (Rorison, 1971; Lloyd, Grime and Rorison, 1971) where spatial niche-separation is limited principally to two dimensions in the horizontal plane and to differences in rooting depth in the vertical plane (Anderson, 1927). A superficial view of a typical species-rich chalk grassland habitat containing up to 25 species of higher plant in $\frac{1}{16}$ m² (Silvertown, 1979) would suggest that spatial heterogeneity in such habitats is far too low to reconcile the coexistence of so many species with the principle of competitive exclusion.

Harper *et al.* (1961), Harper, Williams and Sagar (1965), Grubb (1977) and Fagerström and Ågren (1979) have suggested that plant species respond differently to fine-scale spatial heterogeneity in the regeneration phase of the life cycle and that this may be an important factor contributing to the maintenance of high species density. Fine-scale spatial heterogeniety affecting regeneration may arise from physical differences in micro-topography (e.g. Harper *et al.* 1965; Oomes and Elberse, 1976) or from local variation in the abundance and specific identity of neighbouring leaves and plants (Harper, 1978). Mack and Harper (1977) examined the effect of the distance, weight and dispersion of neighbours on individual plant weight and fecundity in an experiment which demonstrated that nearly 70% of variations in these parameters could be accounted for by neighbour effects. Other experiments by Robocker, Curtis and Ahlgren (1952), Shultz, Launchbaugh and Biswell (1955), Foster, (1964), Caruso (1970), Holt (1972), Miles (1972), King (1975) and Fenner (1978) have examined the influence of variations in local

* Present address: Department of Biology, The Open University, Walton Hall, Milton Keynes MK7 6AA, U.K.

vegetation cover in grasslands on the regeneration of various species from sown seed and generally report that emergence or growth of seedlings is inhibited by the presence of ambient vegetation. An absence of observations in the field on the distribution of volunteer (unsown) seedlings in relation to local vegetation cover obscures the relevance of these experiments to the situation in the field. This article reports observations on the demography of natural populations of two species, *Reseda lutea** and *Anthylis vulneraria* in relation to local vegetation cover. The results of experimental sowings in grassland will be published in a subsequent paper (Silvertown and Wilkin, in preparation).

MATERIALS AND METHODS

Seedling demography

Thirty permanent plots (25 cm × 25 cm each) located by steel pins concreted into 2 cm auger holes were established inside fenced enclosures in chalk grassland on a west-facing hillside at Castle Hill National Nature Reserve, Sussex (TQ 376065). A pantograph, designed to allow accurate mapping of seedlings within plots (Silvertown, 1979), was bolted into position at monthly intervals and a record made of the identity and position of seedlings in each plot from 18 November 1976 to 21 December 1977. Seedlings of two species, *Reseda lutea* and *Anthyllis vulneraria*, occurred in sufficient numbers to allow cohorts within single quadrats to be treated separately for statistical purposes. Two adjacent quadrats with populations of *R. lutea* contained 167 and 109 seedlings, three other quadrats contained 103, 103 and 156 seedlings of *A. vulneraria*. Monthly tallies of new seedlings and deaths were made by a comparison of maps of seedlings and checked by ringing all seedlings (on the occasion they were first observed) with sections cut from plastic drinking straws.

Analysis of spatial heterogeneity

Vertical colour photographs of each quadrat were taken on the first three monthly mapping dates and micro-variation in leaf cover (micro-cover) within each quadrat was estimated from an analysis of colour transparencies which were projected life-size on to 25 cm × 25 cm sheets, ruled into 1-cm squares. Vegetation cover in each of these 625 units was estimated on a scale of 0 to 4 according to the number of quarters in each unit which contained a visible section of green leaf:

Micro-cover value	Green leaf visible in
0	No quarter of a unit
1	One quarter of a unit
2	Two quarters of a unit
3	Three quarters of a unit
4	All quarters of a unit

Seedlings visible in the photographs were ignored and did not contribute to the evaluation of micro-cover in units of the quadrats.

* Botanical nomenclature follows Clapham, Tutin and Warburg (1962).

Statistical treatment of the data

Occurrence of seedlings. The co-ordinates of seedlings in 1-cm units of the quadrats were placed on computer file. Separate computer files held data on the micro-cover values in each quadrat. A purpose-written computer program was used to tabulate the number of seedlings present in units of each micro-cover value, using values estimated in the month of peak seedling emergence. The distribution of micro-cover values changed between the first and last recordings of seedlings. However, it was not possible to take account of this in the analysis of observations.

Several problems arose in analyzing field observations for association between micro-cover and seedling occurrence and are discussed fully by Silvertown (1979). A non-parametric statistic was used to test for differences in density of seedlings between units of different micro-cover values. The mapping units falling into each class of micro-cover value were themselves divided by seedling density into groups containing 1, 2, 3 or > 3 seedlings per unit and micro-cover classes were then compared for differences in seedling density by a Simultaneous Test Procedure
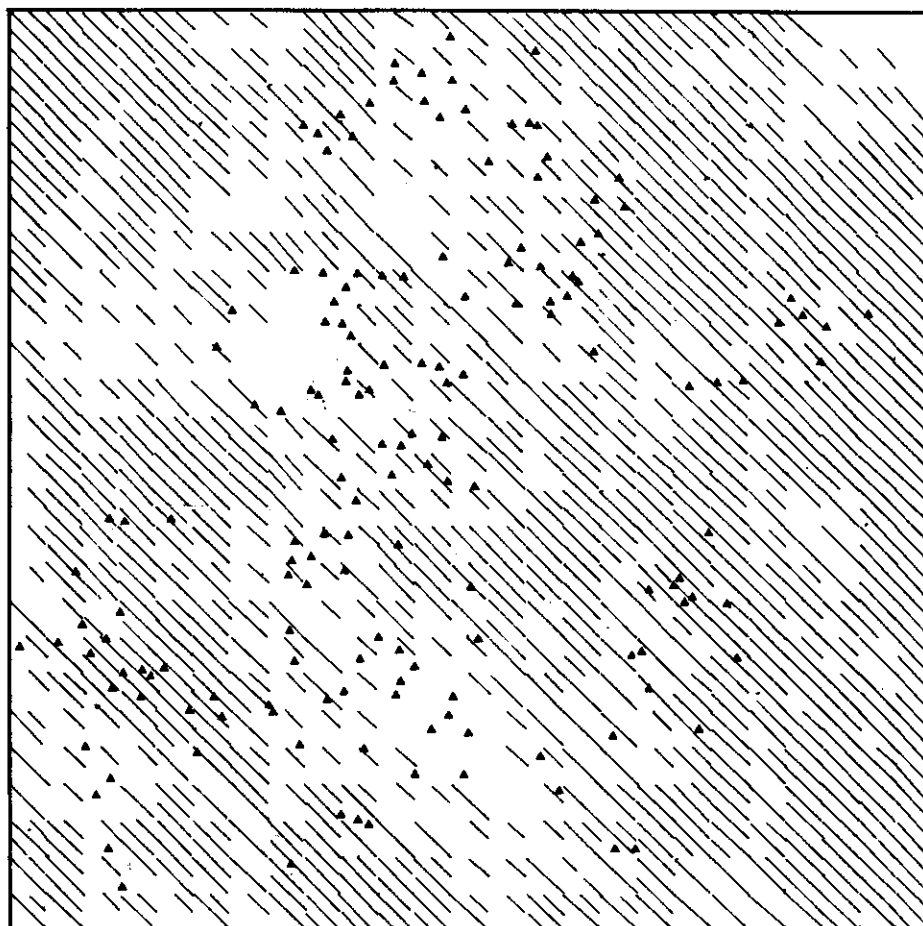

Fig. 1. The distribution of seedlings of *Reseda lutea* in quadrat 24 superimposed on a map of micro-cover. Seedlings and cover mapped on 18 November 1976. Micro-cover classes; □, 0; ▨, 1; ▨, 2; ▨, 3; ▨, 4.
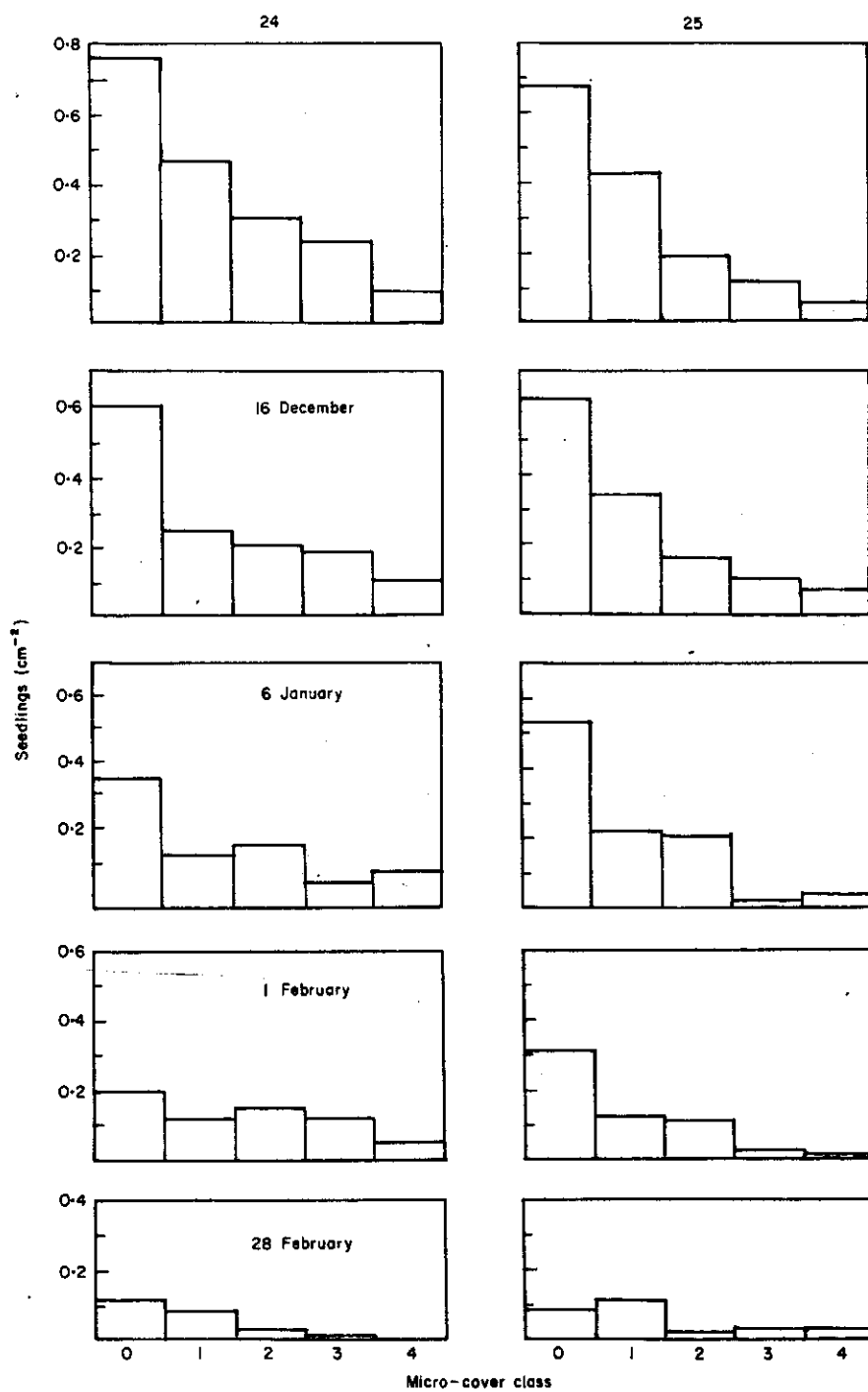
Fig. 2. The distribution of seedlings (seedlings cm⁻²) of *Reseda lutea* by micro-cover class in quadrats 24 and 25 from emergence in November 1976 to February 1977.
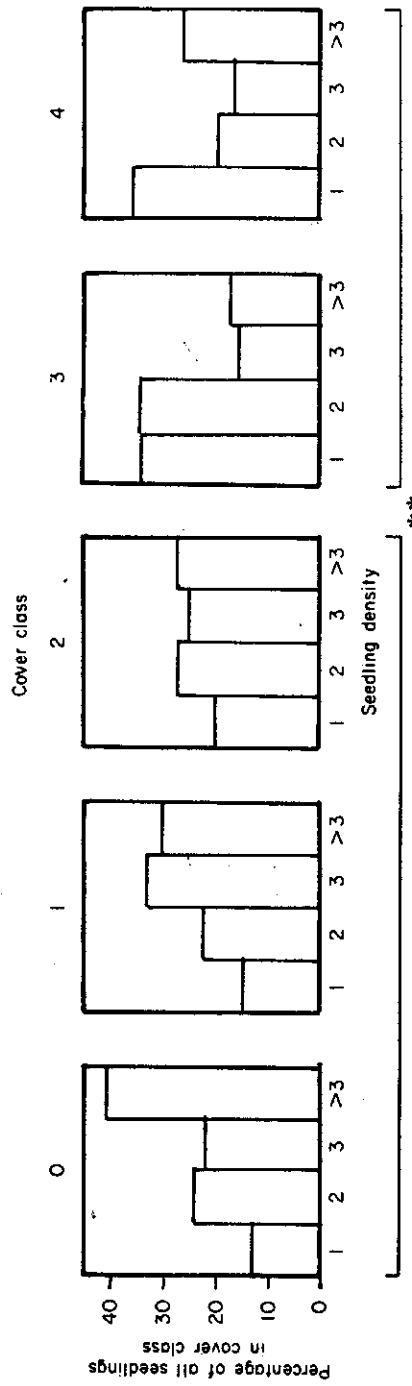
Fig. 3. The percentage of *Reseda lutea* seedlings by density and micro-cover class in quadrats 24 and 25 (November 1976). Micro-cover classes have been divided into maximally non-significant subsets by S.T.P. (See text for details.) ** $P < 0.01$.
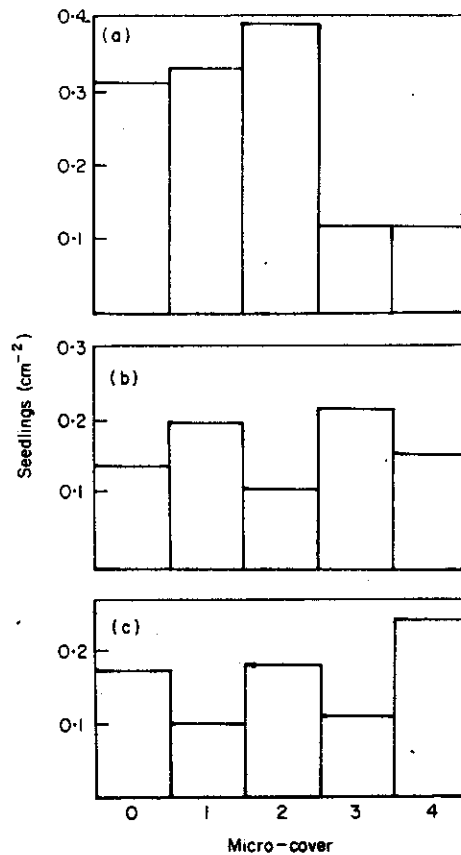
Fig. 4. The distribution of seedlings (seedlings cm^{-2}) of *Anthyllis vulneraria* by micro-cover class In quadrats 5, 11 and 14 at peak emergence in March and April 1977. (a) Quadrat 14, $n = 156$; (b) quadrat 11, $n = 103$; (c) quadrat 5, $n = 103$.

(S.T.P.; Sokal and Rohlf, 1969). Such a test was the nearest that could be approached to testing seedling occurrence × micro-cover value *per se*.

Mortality of seedlings. Non-parametric tests of association for mortality of seedlings, micro-cover value and density of seedlings were used in an investigation employing a multi-variate technique. A three-way G test (Sokal and Rohlf, 1969) was employed on the data of each quadrat to test the independence of micro-cover × mortality, density × mortality and density × micro-cover, and the inter-action of all three components: density × cover × mortality. Local density of seed-lings was determined for this purpose by a count of the number of seedlings occurring in a 2 cm diameter circle drawn around each seedling on the map produced at the peak of seedling emergence. The mortality of seedlings was determined from an overlay of the final seedling map on the initial one. Data on mortality × micro-cover obtained by this method could be compared with the output of the computer program at the two dates. This program was not designed to identify individual seedlings by their position and the form of data storage employed, with a resolution of only 1 cm², was not accurate enough for the purposes of a density × mortality × micro-cover analysis.
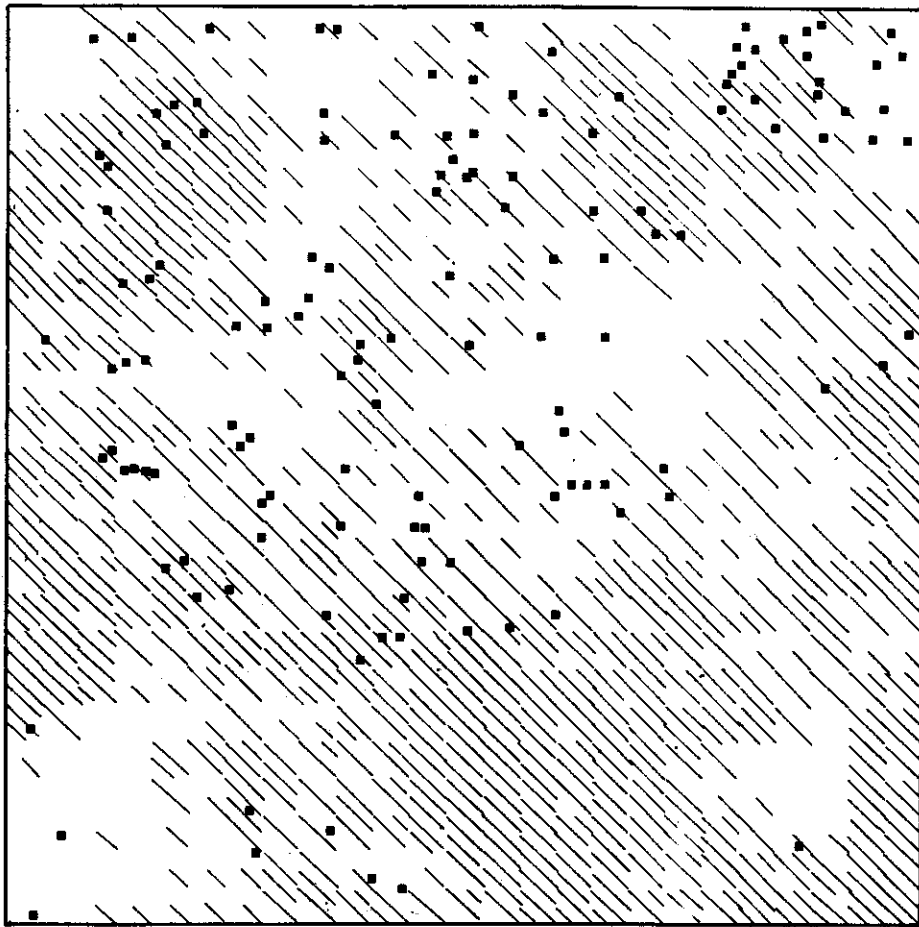
Fig. 5. The distribution of seedlings of *Anthyllis vulneraria* in quadrat 14 superimposed on a map of micro-cover. Seedlings and cover mapped in April 1977.

RESULTS

Seedling occurrence and micro-cover

Seedlings of *Reseda lutea* reached peak of emergence in November 1976. Figure 1 shows the distribution of these seedlings in one of the quadrats superimposed upon a map of micro-cover values for the area. The visual impression that seedlings are distributed predominantly in gaps in the vegetation is confirmed by the histograms of seedlings per cm² for units of different micro-cover values which are shown for both *R. lutea* quadrats in Figure 2. Statistical tests cannot be applied to these histograms (Silvertown, 1979) but an analysis of seedling density per unit × micro-cover for the combined data on *R. lutea* shows that seedling densities per unit (1 cm²) are significantly higher ($P < 0.01$) in units with micro-cover values of 0 to 2 than in units with values of 3 to 4 [Fig. 3]. Thus, seedlings of *R. lutea* occurred significantly more often in micro-sites with a low cover of green leaf than in more shaded micro-sites.
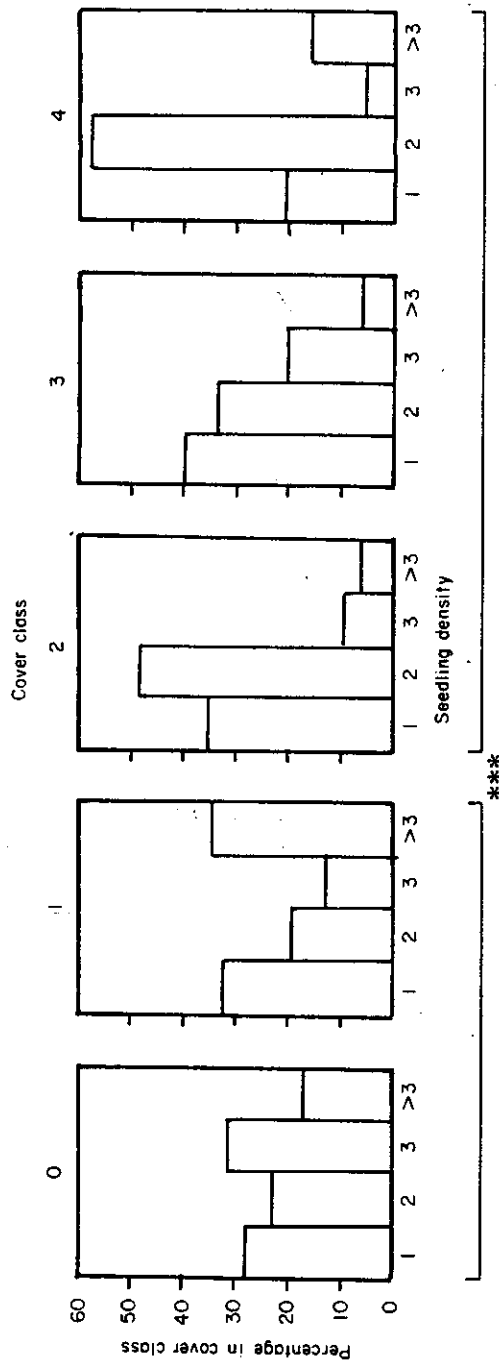
Fig. 6. The percentage of *Anthyllis vulneraria* seedlings by density and micro-cover class at peak emergence in quadrat 14 (April 1977). Micro-cover classes have been divided into maximally non-significant subsets by S.T.P. *** $P < 0.001$.

Table 1. *Results of a three-way analysis of seedling density × mortality × micro-cover for three cohorts of Anthyllis vulneraria seedlings and two cohorts of Reseda lutea. Statistically significant results are italicized*

Species	Period of observation	Quadrat number	No. seedlings in cohort	Null hypothesis				
				Micro-cover × mortality independence $P <$	Density × mortality independence $P <$	Density × micro-cover independence $P <$	Density × micro-cover mortality interaction $P <$
Anthyllis vulneraria	15.3.77 to 1.6.77	5	103	0·30	0·30	0·20	0·20
A. vulneraria	15.3.77 to 27.5.77	11	103	0·50	0·50	0·10	0·30
A. vulneraria	19.4.77 to 21.12.77	14	156	0·80	0·20	*0·01*	*0·70*
Reseda lutea	18.11.76 to 28.2.77	24	167	0·50	0·10	0·50	0·30
R. lutea	18.11.76 to 28.2.77	25	109	0·70	0·30	0·10	0·50
R. lutea (pooled data)		24+25	276	0·50	0·10	*0·05*	0·20

Histograms of the number of seedlings per cm² in units of different micro-cover value are shown for the three *Anthyllis vulneraria* quadrats in Figure 4. No association between seedling density and micro-cover occurred in two of the quadrats though the third (quadrat 14) showed a significantly higher density of seedlings in units with micro-cover values of 0 to 2 than in those with values 3 to 4 ($P < 0.001$). Figure 5 is a map of the distribution of seedlings and micro-cover in this quadrat and Figure 6 shows the data in the form of a seedling density × micro-cover analysis.

Seedling mortality, density and micro-cover

From a three-way analysis of seedling density × mortality × micro-cover for the five quadrats, no dependence between micro-cover and mortality, or density and mortality was found and there was no statistically significant interaction between density, micro-cover and mortality in any of the quadrats (Table 1). Densities, calculated as the number of seedlings in a circle of 2 cm diameter for this particular analysis (see above), were significantly greater in units of low micro-cover in quadrats 14 and 24. No significant differences in the density of seedlings occurred between quadrats 24 and 25 (G-test) whose pooled data showed a significant interaction between micro-cover and the density of *Reseda lutea* seedlings ($P < 0.05$). These results confirm those obtained from the two-way analysis of density (measured as seedlings per unit) and micro-cover reported above.

DISCUSSION

Reseda lutea clearly responds to micro-spatial differences in leaf cover and is likely to regenerate only from microsites with low levels of shading. This species is characteristic of disturbed sites (Grubb, 1976) and would appear to be restricted to these open areas by limitations placed on its distribution in the regeneration phase. The possible nature of some of these limitations is discussed below. *Anthyllis vulneraria* also showed a tendency towards higher density of seedlings in units of low micro-cover in one quadrat, though this association was not shown in two others. These results are consistent with the hypothesis that *A. vulneraria* is more likely to appear in shaded micro-sites than *R. lutea*, though the factors determining the distribution of the former species may vary from one quadrat to another.

Distribution of seedlings may be correlated with micro-spatial heterogeneity in leaf cover as a consequence of three causes: differential seed dispersal into some microsites, differential recruitment to the seedling population and differential seedling mortality. Differential dispersal of seed into microsites with different amounts of leaf cover could result in the seed pool beneath large leaves becoming impoverished if the soil surface remained impenetrably covered for a sufficient length of time. This hypothesis may be tested directly by sampling the seed pool beneath micro-sites with different micro-cover values or, circumstantially, by demonstrating that seed germination and survival are equally successful under all degrees of leaf cover. The spatial pattern of seeds in the soil may both influence, and be influenced by, the vegetation at the soil surface (Greig Smith, 1979). Enhanced germination in vegetation gaps may occur as a result of 'gap detecting mechanisms' (Grime, 1979) in seeds which are sensitive to fluctuations in temperature (Thompson, Grime and Mason, 1978) or changes in light quality (Silvertown, 1980) caused by variations in the density of leaf cover. *Anthyllis*

vulneraria is insensitive to changes in the spectral composition of light which cause induced dormancy in other grassland species when they are placed under a leaf canopy (Silvertown, 1980) and this must facilitate its ability to germinate equally well in units of high and low micro-cover in quadrats 5 and 11. No similar information on the response of *Reseda lutea* to quality of light is available.

The three suggested factors causing a correlation between distribution of seedlings and spatial heterogeneity are likely to place different degrees of constraint on the former. When acting alone, each factor can be expected to produce different degrees of 'error' in the correspondence between distribution of seedlings and microcover. Differential germination is likely to be the least elastic constraint because of its physiological basis which is likely closely to determine the germination requirements and habitat range of the plant. Differential seedling mortality is more likely to vary with seasonal conditions and to be important in some years but not in others (Grubb, 1977). Observations reported here have shown that mortality and micro-cover were independent in the five quadrats studied, though a significant inverse relationship between seedling mortality and micro-cover has been observed for seedlings of *Trifolium* sp. in the same habitat in a year of drought (Silvertown, 1979). Differential seed dispersal is likely to be the most capricious and unpredictable of all factors determining the relationship between micro-cover and seedling distribution because of the role of animals in seed dispersal (e.g., McRill and Sagar, 1973) and because of changes in vegetation cover caused by fluxes in plant populations.

The complexity of factors involved in determining the regeneration of different species hampers the interpretation of field observations since there is necessarily the minimum experimental control over the conditions under which these observations are made. The value of such observations lies in their power to generate hypotheses and experimental work. The present observations suggest differences in the regenerative behaviour of plants may may indeed provide a fruitful source of 'hidden' niche separation in species-rich grasslands and that a major source of heterogeneity in the habitat lies in the micro-distribution of leaves and plants themselves.

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