MEASURING PLANT DISTRIBUTION IN LIMESTONE PAVEMENT

By JONATHAN W. SILVERTOWN

Department of Biology, Open University, Walton Hall, Milton Keynes MK7 6AA

ABSTRACT

Limestone pavements contain a characteristic flora of woodland and rupestral plants. The compartmentalisation of this type ,of habitat into boxes of varying dimensions (grikes) makes it unusually suitable for studying the relative distribution of plant species. Appropriate sampling and experimental methods are described and illustrated with the results of a study undertaken in the Malham area.

INTRODUCTION

LIMESTONE pavements occur in several regions of Britain but are particularly a feature of the landscape of North Yorkshire (Ward and Evans, 1976). These pavements at one time were tree covered but now exist mostly in grazed areas and are devoid of trees. Pavements in the region of Malham are thought to have lost their tree cover during the Iron Age as a consequence of human activity (Pigott and Pigott, 1959). Some wooded pavements still exist such as those at Colt Park Wood (SD 774778) and Scar Close (SD 752777) National Nature Reserves.

The grikes (elongated hollows between the blocks of rock) of unwooded limestone pavements shelter a flora usually associated with woodlands together with some plants of rocky habitats. Some elements of this flora are to be found wherever grikes protect the plants in them from grazing. Where grikes are wide or shallow enough to allow sheep to graze, the "woodland flora" is replaced by the plants of limestone grassland. The "woodland flora" of limestone pavements is of interest to the ecologist from at least two points of view.

Firstly the flora is of intrinsic interest because it is probably a relict of the woodland phase in the vegetation history of the area. Of course that is not to say that it is identical to the historical woodland flora, either in species composition or relative species abundance. Nevertheless it is difficult to imagine how pavements, which are now isolated in a sea of sheep hostile to woodland plants, could have been colonised by these plants after grazing began. I believe that the flora must therefore be largely a relict one; though some ecologists might argue with this. Secondly, this flora is of interest because it now occupies a unique type of habitat, one which is divided into compartments.

Grikes vary in depth, width and length but all form compartments with measurable dimensions. Many grikes are interconnected with adjacent ones by transverse fissures but, by and large, grikes can be regarded as rectangular boxes of varying size. The dimensions of each box have a strong influence on the microclimate inside it as well as on the effects of grazing.

The limited aperture of a grike obviously produces a shaded environment and light intensity diminishes with depth. Grike depth also influences temperature and the diurnal fluctuation of temperature. Some measurements of these fluctuations made in the pavement at Highfolds (SD 895676) are shown in Figure 1. Note that temperature is much more stable at the bottom of grikes than at the top. Temperature is stabilised in a similar way in woodland. Measurements of humidity made in grikes in limestone pavement in the Burren have shown similar values to
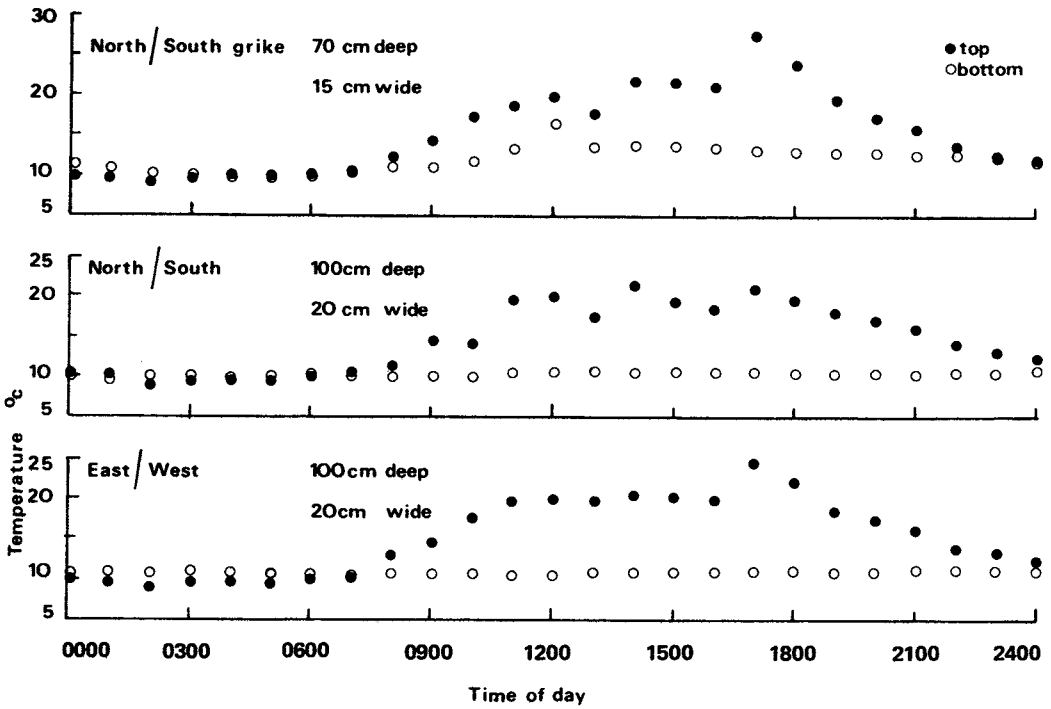
FIG. 1.
Diurnal temperature variation in limestone pavement at Highfolds.

those which occur in the herb layer of woodland in the same area (Heslop-Harrison, 1960; Dickinson *et al.*, 1974).

A simple rule of thumb describes the relationship between grike dimensions and grazing within limestone pavements. For grikes which are not wide enough to allow a sheep to enter bodily, sheep can only graze to a depth equal to grike width (Ward and Evans, 1976). This is demonstrated later in this paper.

The distribution of individual species of the grike flora also varies with depth. In pavements in the Malham area, Wallrue *Asplenium ruta-muraria*, Wall Lettuce *Mycelis muralis* and Herb Robert *Geranium robertianum* are found near the top of grikes, whilst Wood Sanicle *Sanicula europaea*, Dogs Mercury *Mercurialis perennis* and Harts Tongue Fern *Phyllitis scolopendrium* are amongst those occurring lower down. Grazing appears to have an influence on the upper limits of the distribution of the latter three of these species. Nearly all species also have lower limits to their distribution in grikes.

A common approach of ecologists studying the distribution of plants is to measure a number of environmental variables such as light, temperature and humidity and to attempt to correlate these with plant abundance or plant performance. The problem with this approach is that correlated factors are not necessarily directly related to the causes of plant distribution. Without performing experiments we can never know whether what we are measuring is really of relevance to the organism itself. Ideally what is required is a "plant's-eye view of the environment" (Turkington and Harper, 1979). This may be easier to achieve than the comprehensive data on all the environmental variables usually measured in plant ecology.

Plants do not respond to temperature, light, humidity etc. as independent variables but as interacting influences on growth, reproduction and survival. A grike 100 cm deep, 30 cm wide and 15 m long has a characteristic environment in which temperature, humidity and grazing are all dependent upon those dimensions. A plant growing at 100 cm depth and another at 30 cm depth will experience correlated differences in several environmental variables. It would be artificial to pick out one of these (such as light) and to measure this alone. Because so many variables are all related to grike dimensions, neither is it necessary to measure a dozen environmental variables. All we need to do is to measure the physical dimensions of the grike itself and the position of plants within it.

Microclimate and grazing certainly influence plant distribution but other factors may also be involved. In habitats such as grassland, woodland, and rocky shores, plant distribution is also influenced by interactions between species and there are also features of population dynamics and habitat disturbance which have to be taken into account (Silvertown, 1982). Nevertheless, once the distribution of different species has been defined in relation to grike dimensions we can begin to assess the importance of those other processes. Limestone pavement and woodland may have many species in common but it is infinitely easier to study the relative distribution of plants in the former. The compartmentation of the habitat allows the relative distribution of plants in relation to niche space to be clearly defined. In limestone pavement we can specify the frequency with which Herb Robert, for instance, occurs in grikes of different depths and we can compare this frequency distribution with that for other species and with the overall frequency distribution of grike depths. The only way this could be achieved in a woodland would involve multivariate analysis of many environmental variables (e.g. Yarranton and Beasleigh, 1968, 1969; Yarranton, 1970), unless a gradient could be found in a single "important" environmental variable. These alternative methods still beg the question of what really counts in the life of plants themselves. By using the dimensions of habitat space (or niche space) to define plant distribution and by the use of experiments we may avoid this problem. This paper outlines some of the methods which have been used in such a study.

METHODS

Grikes in the pavement around Malham are generally orientated North-South or East-West. Microclimate in both types of grike is determined by the same factors (e.g. see Figure 1) but there may be seasonal differences related to the difference in orientation. The investigation described here was confined to North-South grikes.

The vegetation in grikes was recorded within a 25 cm long sample. Species were recorded as present or absent in each sample and the rooted depth of species and grike depth and width were measured.

The object of this sampling was to produce a description of overall plant distribution in relation to the depth and width of grikes, which was within reasonable limits of the true situation. The structure of grikes introduces a number of possible sources of error which must be avoided. Firstly, adjacent grikes are sometimes physically interconnected by transverse fissures and, secondly, grikes may extend for tens of metres in length.

The interconnections may allow plants from one grike to colonise others nearby. If this happens each grike cannot be regarded as an independent sample. Ivy, *Hedera*

helix, is the plant which most often seems to spread in this way. Many of the wood-land plants of limestone pavement are rhizomatous and spread along the length of grikes. Thus samples taken within the same grike cannot safely be treated as independent. A simple sampling procedure avoids both these problems.

For each pavement studied the length of fifty to one hundred grikes was measured. This was then used to draw up a frequency histogram of grike lengths. From this histogram the inclusive length of 95 per cent of all grikes was read. Transects were then set up across the pavement, at right angles to the grikes being investigated and at the 95 per cent inclusive distance apart. Samples taken along adjacent transects therefore had a 95 per cent chance of being from different grikes. The effect of transverse fissures on most of the vegetation in the pavements studied was considered to be small. Any bias may be avoided by taking samples only from every second or third grike along a transect.

This sampling procedure may be used in two ways depending on the purpose of the investigation. If only information about the distribution of individual species in relation to grike dimensions is required, the quickest way to gather it is to sample every grike (or every second grike) along a transect and to ignore those where the species is absent. If, on the other hand, information is required about species inter-actions, for instance how often two species occur together and apart, then every sampled grike must be taken into account, including those where the relevant species are totally absent. We will consider the two types of investigation separately.

1. The distribution of individual species

The simplest hypothesis about plant distribution is that plants are distributed at random within their habitat. If this were true then species would be distributed in grikes like balls tossed into a collection of boxes and the frequency with which plants were found in deep and shallow grikes would be in direct proportion to the frequency of deep and shallow grikes available. We may set up the null hypothesis that the distribution of plant and grike depths is the same and test this by com-paring the two distributions with a chi square. The frequency distribution of plant depths is obtained by the method outlined above. The frequency distribution of grike depths in a pavement may be obtained in the same way but without the need to allow for the effect of transverse spread of plants between grikes. The caution about double-sampling the same grike still applies.

The width of grikes also affects plant distribution and should ideally be included in any analysis. In practice, as long as all grikes sampled are deeper than they are wide, useful information can be obtained by considering depth distributions on their own and ignoring grike widths.

The depth distributions of species sampled from the same pavement may be directly compared with each other by chi square. Species distributions obtained from different pavements may only be compared directly if the frequency dis-tribution of grike depths in the different pavements is also the same.

2. Interactions between species

Sampling and data collection by the more complete method provides the kind of data which are required to test for association between species. Data on grike depths are ignored and each sample is treated like a conventional quadrat. A *n* species times

n species contingency table (Everett, 1977) is produced, chi square values calculated and tested in the usual way (Sokal and Rohlf, 1969).

Another type of test for association may also be used. The straightforward type of association test reveals the tendencies plants may show to "avoid" occurring together in the same quadrat. Plants in limestone pavement may also "avoid" each other by growing at different depths within the same grike. Effects of this kind can be detected by comparing the depth distribution of two species when they occur on their own (allopatric samples) and when they occur together (sympatric samples). If interference is occurring between plants in sympatric samples their depth distributions should be less similar in these than in allopatric ones.

Phytometer Experiments

Surveys of plant distribution in limestone pavement frequently show that particular species are absent or under-represented in grikes above or below a certain depth. The implication of such distributions is that some environmental or biotic factor(s) confine plants within restricted zones. A phytometer experiment may give us a "plant's-eye view" of conditions inside and outside the observed range of a species distribution. Test plants (phytometers) are transplanted to sites across the normal range of distribution and their fate is observed. The simplest information derived from a phytometer experiment is the probability of an adult plant dying. In the longer-term, phytometers may give information on the probability of plants reproducing and forming self-sustaining populations over a range of conditions.

A phytometer experiment employing Herb Robert and Dog's Mercury was set up at Malham in July 1980. Seventy-five plants of each of these two species were placed in pots at a range of grike depths in the pavement of Highfolds (SD895676) which is protected from grazing. Another fifty phytometers of each species were placed at a range of grike depths in pavement on adjoining land which is grazed. This experimental design allowed the effects of grazing and depth of grike to be assessed independently for both species. All phytometers in the experiment were inspected and their fate was recorded in May 1981. No maintenance of the plants was given between July 1980 and May 1981.

Results and Discussion
Scar Close

The distribution of nine species was measured by the first (simplified) method separately in grazed and ungrazed areas at Scar Close National Nature Reserve. The distribution of grike depths themselves (niche space) and of plants sampled independently is shown for each area in Figure 2. In the ungrazed area all plants except *Polystichum aculeatum* were distributed non-randomly with respect to grike depth. All except this fern species were significantly under-represented in the deeper parts of grikes. *Actaea spicata, Thalictrum minus* and in *P. aculeatum* were totally absent from the grazed area. All plants in the grazed area except *Phyllitis scolopendrium* and *Mercurialis perennis* were non-randomly distributed with respect to grike depth. *Dryopteris filix-mas* was significantly under-represented in shallow grikes.

The distribution of plants at Scar Close shows a number of interesting features. In the ungrazed area, where the deepest grikes occur, *P. aculeatum* seems indifferent to the depth at which it grows. On the other hand *Actaea spicata* and *Thalictrum minus*,
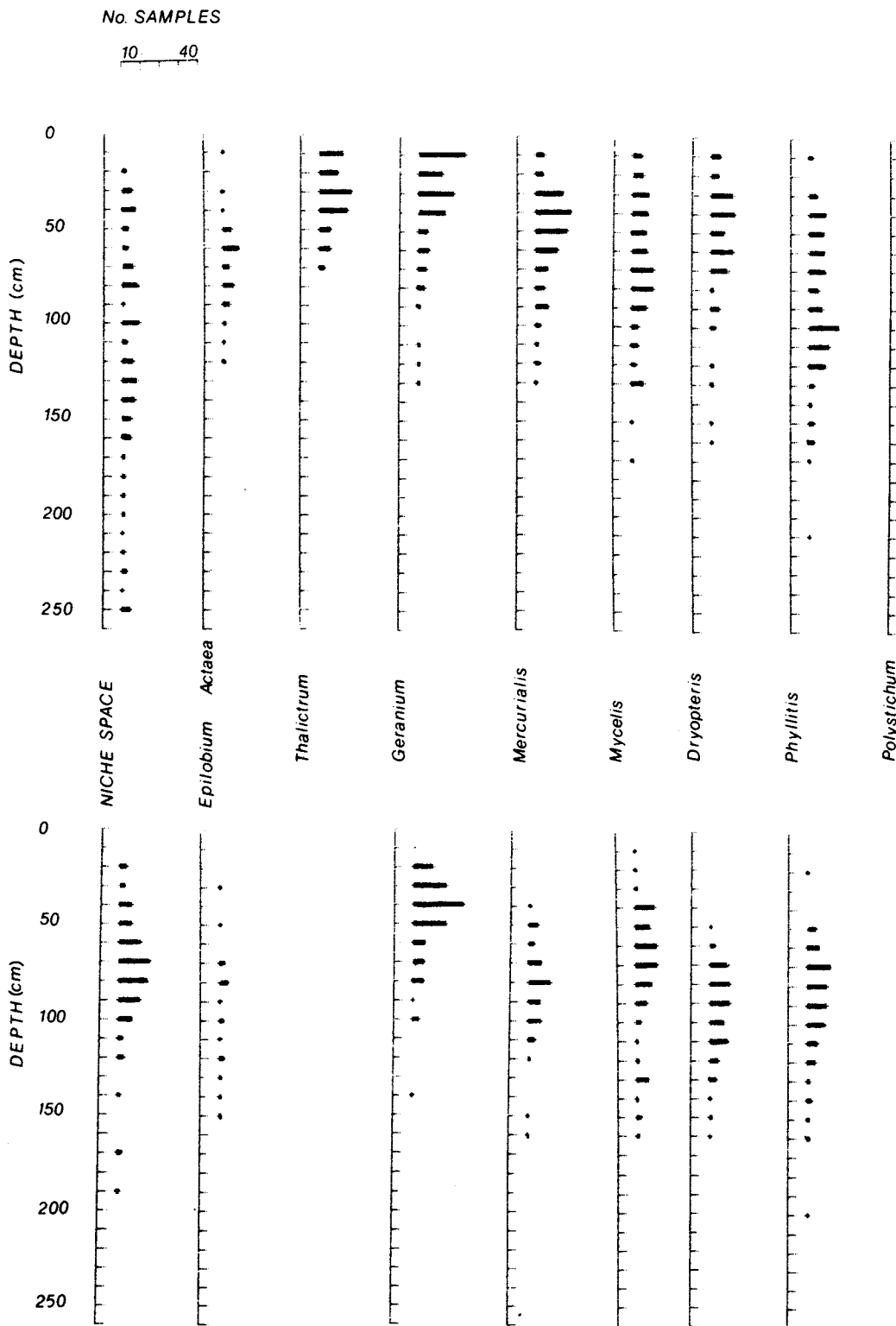
FIG. 2.

Frequency distributions of grike depths and species depths occurring in ungrazed (top) and grazed (bottom) areas of limestone pavement at Scar Close N.N.R.
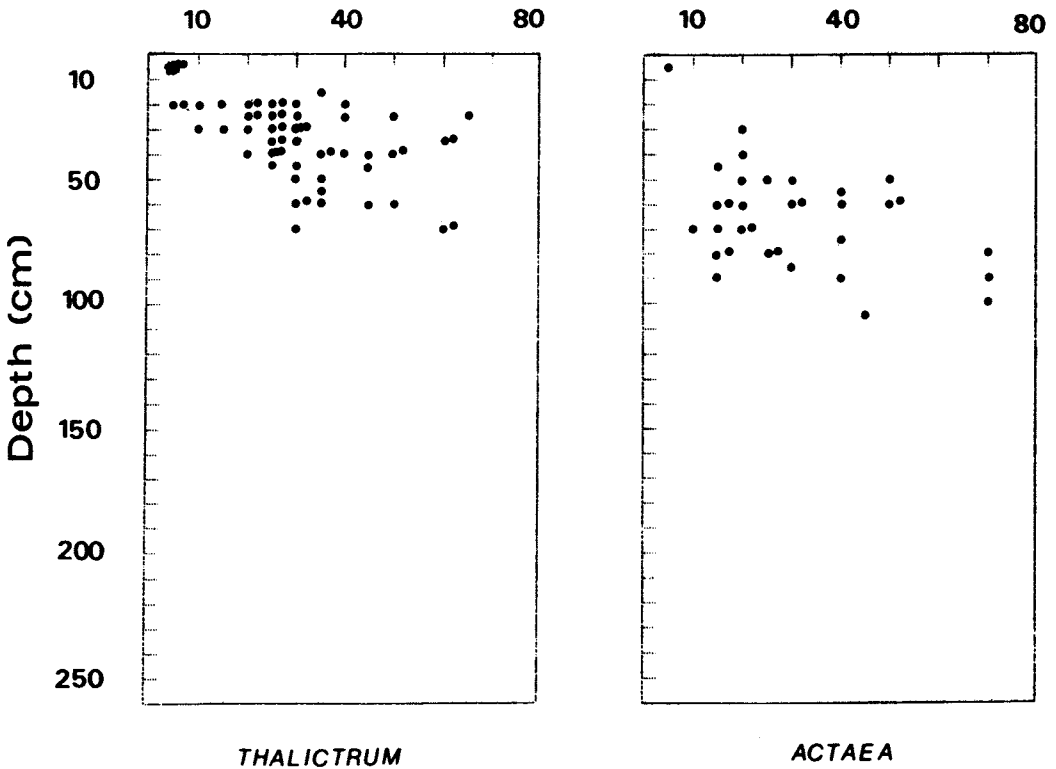
FIG. 3.
The distribution of plants of *Thalictrum minus* and *Actaea spicata* in the ungrazed area at Scar Close, plotted by rooted depth and width of grike.

two species which are entirely absent from the grazed area, are confined to the shallower grikes. The distribution of these two species, plotted by width as well as depth, falls largely within zones which are prone to grazing (Figure 3). Grazing may eliminate species such as these from an area in two ways. By outright removal of all plants or by lowering the density of plants to such a level that those individuals remaining are too sparsely distributed to sustain a self-replacing population (Carter and Prince, 1981). Some indication of the effect of grazing on the distributions of other species may be obtained by comparing the diagrams for grazed and ungrazed areas (Figure 2).

Unfortunately, a direct comparison of species' distribution in the grazed and ungrazed areas cannot be made and tested by chi square because the distributions of grike depths in each area are significantly different. Nevertheless *circumstantial evidence* can be obtained by comparing within modal groups of the same depth i.e. 10–20 cms, 20–30 cm deep etc., grazed v. ungrazed. It is clear that *D.filix-mas* is absent from shallow grikes in the grazed area although it occurs in these in the absence of grazing (Figure 4). *M. perennis* also shows this trend to some extent. It is slight or absent in *G. robertianum* and *Mycelis muralis*.
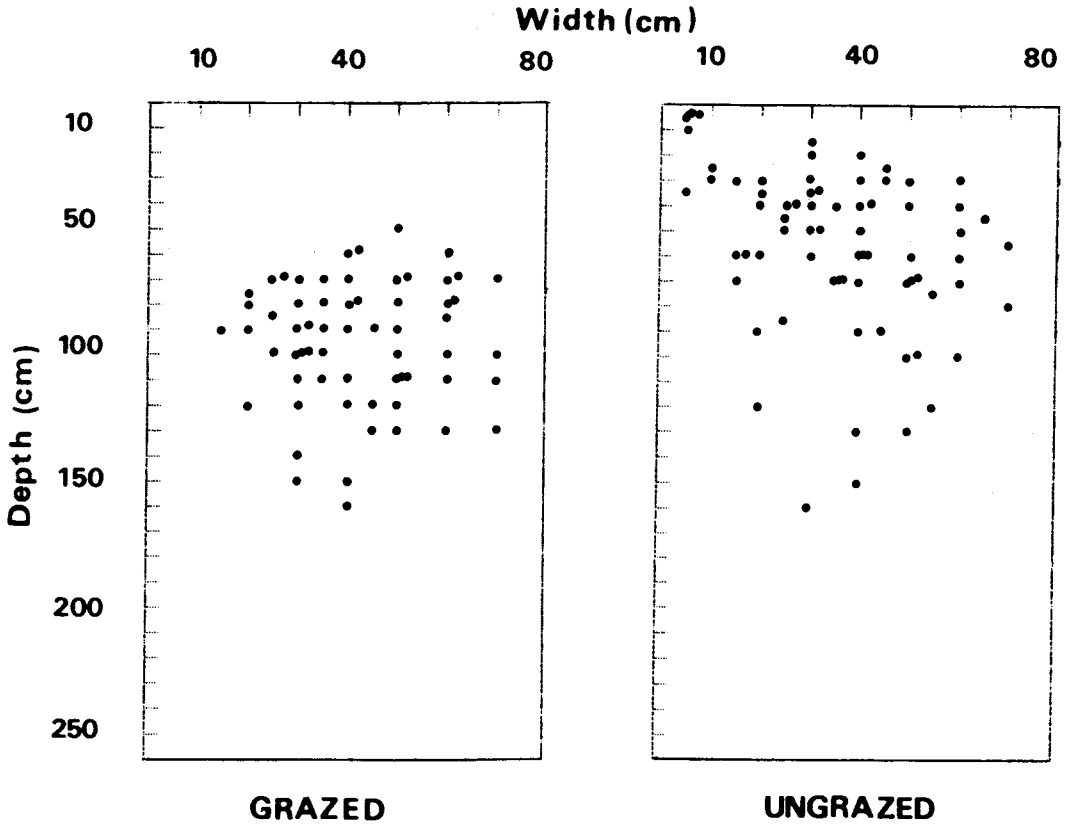
FIG. 4.
The distribution of plants of *Dryopteris filix-mas* in the grazed and ungrazed areas of Scar Close plotted by rooted depth and width of grike.

Ing Scar

A complete analysis of plant distribution was made at Ing Scar pavement (SD894645) which was sampled at 375 points chosen by the methods described above. These data were used to compile a contingency table from which species' association was determined. Twelve species of angiosperm and seven ferns were encountered of which six and four species respectively were found in more than fifteen samples. No statistically significant positive or negative associations between these species were detected. Pairs of species distributions were also analysed for differences between allopatric and sympatric samples but no differences were found.

The depth distributions of most of the species in this pavement did not depart significantly from the distribution of grike depths. The exceptions were the rupestral ferns *Asplenium ruta-muraria, A. trichomanes* and *A. viride* (Figure 5) and Herb Robert *Geranium robertianum* (Figure 6), all of which were under-represented in deeper grikes. The three *Asplenium* species occur largely on the walls of grikes; *G. robertianum* occurs on the walls and floor.

Seedlings of *G. robertianum* were also present in the pavement at Ing Scar during the survey but their distribution did not depart significantly from the distribution of niche space (Figure 6). The difference between seedling and adult distributions suggests that mortality selectively removes those seedlings of *G. robertianum* that
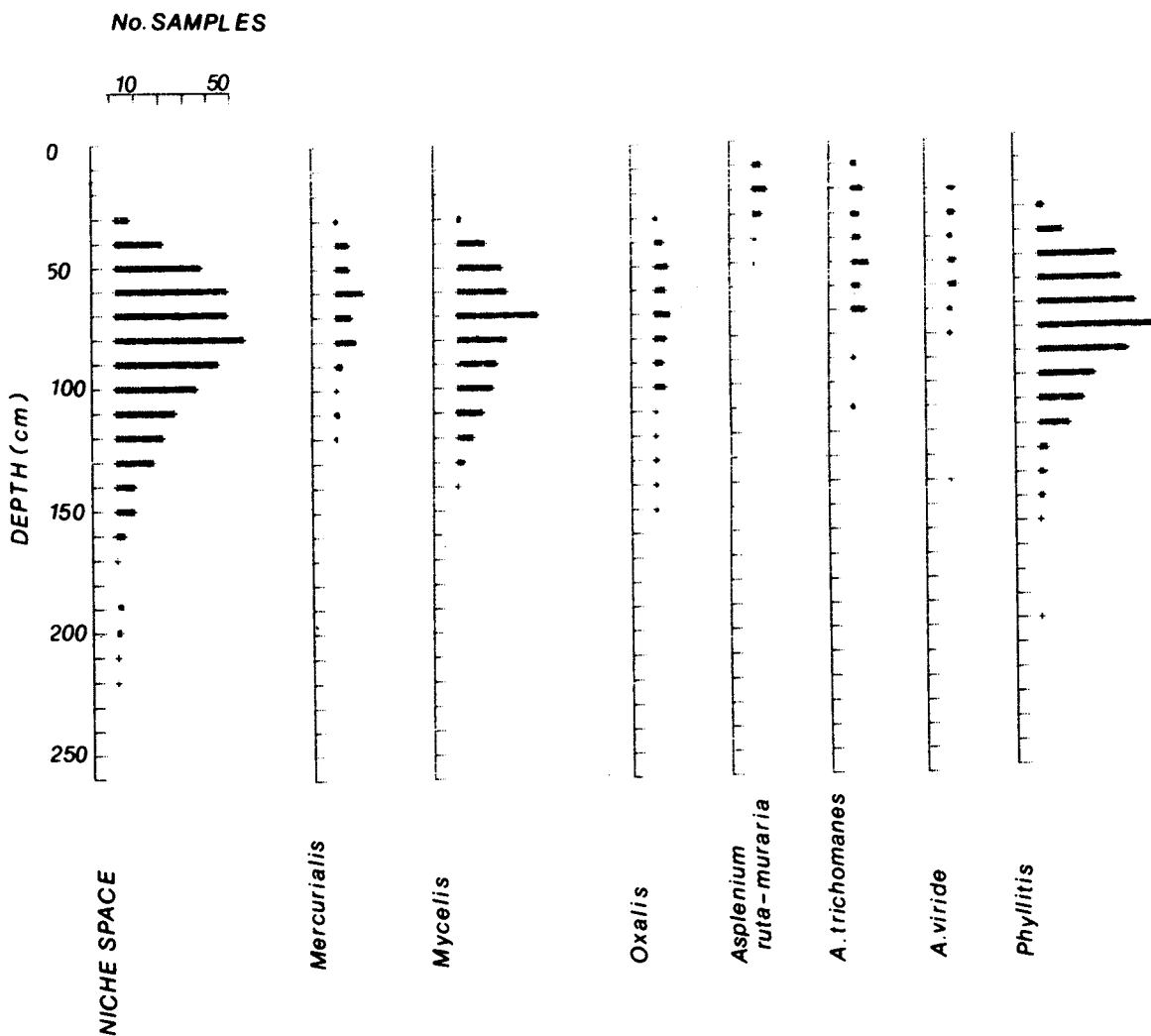
FIG. 5.
Frequency distributions of grike depths and species depths occurring in limestone pavement at Ing Scar.

appear at lower levels. This conclusion is supported by the results of the phyto-meter experiment at Highfolds.

Highfolds Phytometer Experiment

Phytometers of each species at each site were divided into upper and lower samples defined by their position in relation to the median depth at which each set of phytometers was placed. The proportion of phytometers dying in each sample is shown in Table 1. Deep grikes (~1 metre) were present in the ungrazed but not in the grazed area. Therefore, although the median depth of placement was approxi-mately the same (~60 cm) for both areas, the phytometers of the lower sample were placed deeper in the ungrazed area than in the grazed area. This puts limitations on the comparisons which may be drawn between grazing treatments.
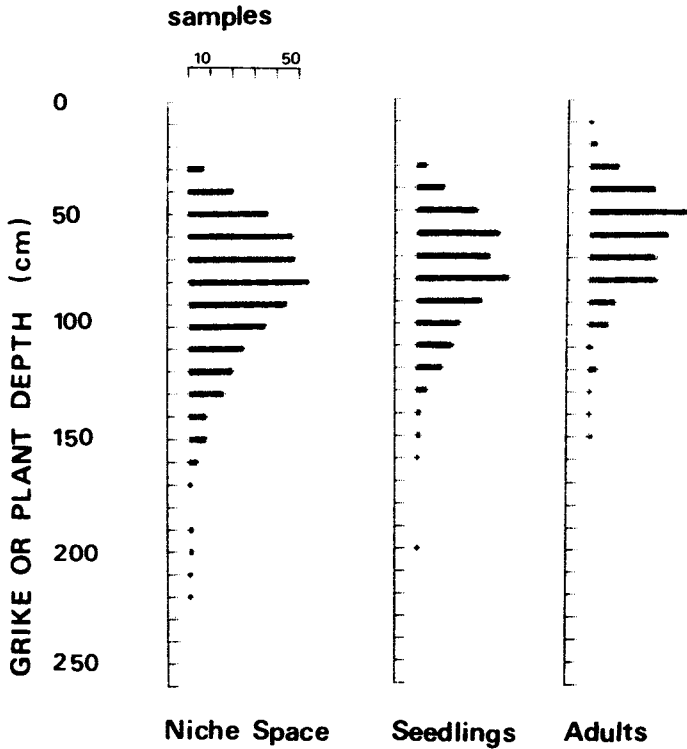
FIG. 6.
Frequency distributions of grike depths and of rooted depth of seedlings and adult plants of *Geranium robertianum* at Ing Scar.

Comparisons of mortality within grazing treatments

In ungrazed pavement, *Mercurialis perennis* suffered the same degree of mortality in upper and lower samples but in grazed pavement mortality was significantly higher in upper samples than in lower ones $(G = 5.01, p < 0.05)$. *Geranium robertianum* suffered greater mortality in lower samples than in upper ones in ungrazed pavement $(G = 6.07, p < 0.02)$ but no significant difference in mortality was found between sampling depths in grazed pavement.

Table 1. Mortalities of *Mercurialis perennis* and *Geranium robertianum* as a proportion of the phytometers placed in each treatment

Sample	Grazing treatment		Species
	Ungrazed	Grazed	
Upper	0.32[acf]	0.48[df]	*M. perennis*
Lower	0.35[a]	0.18	
Upper	0.34[ce]	0.33[bde]	*G. robertianum*
Lower	0.67	0.55[b]	

Mortalities sharing the same superscript are not significantly different from each other at the 0.05 level. Contingency tables were analysed by a G test (Sokal and Rohlf, 1969). The G statistic is approximated by chi square.

FIG. 7.
Scar Close NNR from the East, showing the grazed (foreground, in front of wall) and ungrazed (rear, behind wall) areas of limestone pavement.

Comparing the mortality of the two species at each depth in the ungrazed treatment, in the upper sample the species suffered the same mortality. In the lower sample, *Geranium robertianum* suffered substantially greater mortality in the ungrazed treatment than *Mercurialis perennis* (G = 111.48, p≪0.001). The same patterns of relative mortality in each species occurred in the grazed pavement though the difference between them in the lower samples was less significant (G = 6.50, p<0.02). This is not surprising since fewer very deep grikes were present in the grazed area.

Comparisons of mortality between grazing treatments
 The difference in the number of deep grikes between grazing treatments limits the number of valid comparisons that may be drawn between them. Despite this difference, median values of grike depth for the two areas were nearly the same (60 cm ungrazed, 55 cm grazed) so that mortality in the upper samples of both treatments may validly be compared. This is not the case for lower samples but does not greatly affect the interpretation of results since grazing effects are only likely to be observed in the upper samples, which are in the depth zone accessible to sheep.
 No significant difference in mortality between grazing treatments was observed for either *M. perennis* or *G. robertianum* although non-significant trends suggest *M. perennis* suffered a little from grazing whilst *G. robertianum* did not (Table 1).

CONCLUSIONS
 Grike depth and grazing are important influences on plant distribution within pavements. Grazing effects are related to grike dimensions so that these alone may be used as an integrated measure of a species' distribution. Grazing and grike depth

both influence species differentially. For instance the distribution of *Polystichum aculeatum* appears insensitive to grike depth at Scar Close whilst that of *Thalictrum minus* is highly sensitive. The distribution of *Geranium robertianum* appears relatively insensitive to grazing at Scar Close and in the Highfolds experiment whilst the distribution of *Mercurialis perennis* is sensitive. These results might suggest that the different species of the limestone pavement flora have different niches and that this facilitates their coexistence by reducing competition between them. For instance *G. robertianum* and *M. perennis* might conceivably "avoid" each other in this way. In fact the association analyses at Ing Scar show that these plants are not negatively associated in any detectable way. Furthermore, there is a relatively large amount of empty growing space in the pavement so that competition for space may be unimportant in determining species' distributions. In the light of these results more attention should be paid to the factors which control plant density, including the processes of colonisation and extinction of local populations.

REFERENCES

CARTER, R. N. and PRINCE, S. D. (1981). Epidemic model used to explain biogeographical distribution
   limits. *Nature*, 293, 644–645.
DICKINSON, C. H., PEARSON, M. C. and WEBB, D. A. (1974). Some microhabitats of the Burren, their
   micro-environments and vegetation. *Proceedings of the Royal Irish Academy*, 63B, 291–302.
EVERETT, B. S. (1977). *The analysis of contingency tables*. Chapman and Hall.
HESLOP-HARRISON, J. (1960). A note on the temperature and vapour pressure deficit under drought
   conditions in some microhabitats of the Burren limestone, Co Clare. *Proceedings of the Royal Irish
   Academy*, 61B, 109–114.
PIGOTT, M. E. and PIGOTT, C. D. (1959). Stratigraphy and pollen analysis of Malham Tarn and Tarn
   Moss. *Field Studies*, 1, (1), 1–18.
SILVERTOWN, J. W. (1982). *Introduction to plant population ecology*. Longman, London.
SOKAL, R. R. and ROHLF, F. J. (1969). *Biometry*. W. H. Freeman. San Francisco.
TURKINGTON, R. and HARPER, J. L. (1979). The growth, distribution and neighbour relationships of
   Trifolium repens in a permanent pasture. IV, Fine-scale biotic differentiation. *Journal of Ecology*, 67,
   245–254.
WARD, S. D. and EVANS, D. F. (1976). Conservation assessment of British Limestone pavements based
   on floristic criteria. *Biological Conservation*, 9, 217–233.
YARRANTON, G. A. (1970). Towards a mathematical model of limestone pavement vegetation III.
   Estimation of the determinants of species frequencies. *Canadian Journal of Botany*, 48, 1387–1404.
YARRANTON, G. A. and BEASLEIGH, W. J. (1968). Towards a mathematical model of limestone pavement
   vegetation I. Vegetation and microtopography. *Canadian Journal of Botany*, 46, 1591–1599.
YARRANTON, G. A. and BEASLEIGH, W. J. (1969). Towards a mathematical model of limestone pave-
   ment vegetation II. Microclimate, surface pH, and microtopography. *Canadian Journal of Botany*,
   47, 959–974.