Gaps in the canopy: the missing dimension in vegetation dynamics

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Abstract

Canopy gaps are important as entry points for new genotypes and new species into many types of vegetation, yet little is known about them in any type of vegetation but forests. Forest gaps are too large for manipulative experiments to be readily undertaken, and hitherto grassland gaps have been too small to be easily mapped. Preliminary results from mapping small (> 1 cm) grassland gaps with a new fibre-optic device suggest that experiments need to be performed at a smaller physical scale than has hitherto been achieved.

Introduction

In most types of vegetation outside the arid regions of the world, gaps in the canopy appear to be essential for new genotypes and new species to enter plant communities (e.g. Brokaw 1985; Goldberg & Werner 1983; Collins & Pickett 1987; Martinez-Ramos & Alvarez-Buylla 1986; Miles 1974; Wells & Haggar 1984). Furthermore, it has been suggested that different species have different requirements for the kind of gap they are able to colonize and that this provides one or more dimensions in which niche separation may take place (Denslow 1980; Grubb 1977; Silvertown & Wilkin 1983). Irrespective of whether equilibrium or non-equilibrium conditions apply, gaps are a fundamental feature of the working mechanism (sensu Watt 1947) of plant communities. A considerable amount is now known about the creation, size frequency distribution, timing of appearance and disappearance of gaps – or what might be called ‘gap demography’ – in forests (e.g. Faälle et al. 1984a & b; Foster & Reiners 1986; Lang & Knight 1983) but there is almost no experimental test of the role played by gaps in determining the species composition or community structure of forests. The reason for this lack is obvious: the physical scale of forest vegetation makes experimental treatments difficult to replicate sufficiently and the long lifespan of trees requires extended periods of study. Grasslands offer an alternative system in which to study the role of gaps in plant communities, but here we have the converse problem: there are many experimental studies of colonization (e.g. Fenner 1978; Gross 1980; Hillier 1986; Rusch 1988; Silvertown & Wilkin 1983) and almost no information on the demography of gaps. The reason for this is that the small physical scale of grassland plants demands a scale of measurement beneath the vegetation canopy which has not hitherto been achieved in the field. In this paper we describe preliminary results obtained from the use of a new instrument designed to map gaps in grassland.

Methods

Maps of grassland gaps

Leaves selectively absorb red light and transmit near infra-red. Measurements of the ratio of light intensi-
Correlations between germination and R/IR ratio measured at individual sowing positions were determined using the GLIM statistical package (Payne 1986) with models appropriate for binomial data. The following model was run for each of the 16 quadrats:

\[
\text{GERMINATION} = \frac{\text{QUADRAT}}{(\text{ROW} + \text{COLUMN})} + \text{RATIO}
\]

in which the term \(\frac{\text{QUADRAT}}{(\text{ROW} + \text{COLUMN})}\) determines the effect of spatial correlation (if any) on the germination of seeds sown in the same row or column of the planting grid within a quadrat.

Results

R/IR maps and gaps

An example of a contour map of R/IR is shown in Fig. 1. Few entirely bare areas (R/IR > 1) were present in the twelve quadrats: only 13 gaps in the

Germination in grassland gaps

Seeds of *Geranium dissectum* L. were sown individually with forceps at 2 cm intervals into 16 25 cm x 25 cm quadrats, 121 seeds per quadrat. Before sowing, each quadrat was mapped as described above. Four of the quadrats were at Milton Keynes (MK) and the remaining 12 in a 20-year-old grassland ley on a nature reserve at Little Wittenham, Oxfordshire (LW). The quadrats at Little Wittenham were situated in nine 0.25 ha paddocks grazed by sheep. Sheep grazing in each paddock is controlled to produce differences in sward height between paddocks. Sowing locations in each quadrat were reinspected and germination was scored one month after sowing.
was 100%, but in the field germination ranged between 25 and 70% per quadrat. There was significant spatial correlation in one of four quadrats at MK and in 5 of 12 quadrats at LW. There was no significant relationship between R/IR ratio and germination in any quadrat at MK and a significant positive relationship ($\chi^2 = 9.9$, d.f. = 1, $p < 0.005$) in only one of the twelve quadrats at LW.

Percent germination in quadrats at LW was significantly positively correlated with mean R/IR ratio per quadrat and was highest in paddocks with the heaviest grazing (Fig. 3).

Discussion

The size distribution of gaps clearly depends upon how a 'gap' is defined and upon the scale at which measurements are made. Size distributions of gaps in forests often show a skew towards smaller gap-sizes (e.g. Brokaw 1982; Faille et al. 1984a; Foster & Reiners 1986), similar to the pattern observed in our grassland quadrats at Milton Keynes (Fig. 2). The modal size-class of gaps at this site was 1–2 cm$^2$ which is significantly smaller than the size of gap generally created in experimental studies in grasslands. If the results of this preliminary study prove to be representative of other grasslands, then the gap dynamics of grasslands need to be studied at a much smaller physical scale than has hitherto been attempted. Gaps may be the missing dimension that is needed to understand the mechanism of vegetation dynamics.

The question of what the appropriate physical scale is on which to study grassland gap dynamics is crucial if we are to uncover the mechanism(s) of grassland vegetation dynamics. In order to answer this question, we first need to know how plants themselves respond to gaps of different size. Our results indicate that, in the case of Geranium dissectum, germination is not sensitive to plant cover at the scale of 1 cm$^2$ within quadrats, though between quadrats there is a correlation between percent germination and mean R/IR ratio (Fig. 3). It appears that this species, which has relatively large seeds weighing 2.75 mg, is responding to a coarser grain of environmental variation than the 1 cm$^2$ resolu-
tion of our R/IR measurements. *Geranium dissectum* is a ruderal species which, although found in grasslands in our study areas, is perhaps not typical of grassland dicots in general. Further studies of germination and survival in relation to R/IR ratio should reveal precisely where the threshold lies between invadable and non-invadable microsites for this species. Our ultimate objective is to identify this threshold for a group of grassland species and to be able to predict the potential for invasion into pastures from a knowledge of the gap dynamics of the grassland and the behaviour of individual species.

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References