

Gaps in the canopy: the missing dimension in vegetation dynamics

Jonathan Silvertown & Bridget Smith

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

Accepted 24.5.1988

Keywords: Canopy gap, Grassland, Plant demography

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 & Haggard 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. Faille *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 rea-

son 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-

ty in non-overlapping wavebands in the red and near infra-red (R/IR) made beneath the grassland canopy are directly correlated with leaf area index (Jordan 1969; Frankland & Poo 1980). A field-portable, microcomputer-controlled instrument (Silvertown *et al.* 1988) with a fibre-optic probe was used to record the R/IR ratio at 1 cm intervals in a grid pattern in grassland quadrats at the campus of the Open University in Milton Keynes, Buckinghamshire. Twelve quadrats 25 cm × 25 cm each in a ca 6 cm tall grassland of *Lolium perenne* were mapped in this fashion on 18 August 1987. Contour maps of R/IR ratio were produced on a VAX computer system using the UNIRAS graphics package. These provide a quantitative picture of the distribution of gaps in each quadrat.

Because R/IR data provide a quantitative picture of the grassland canopy, exactly what is meant by a 'gap' can be defined quantitatively too. Gaps were identified and counted by a computer algorithm which operated on the matrix of raw R/IR ratios as follows. Each point in the matrix was checked in turn. Points with a R/IR ratio above a predetermined threshold value for a gap were identified and all adjacent points checked. The coordinates of adjacent points which qualified were entered in a list of points belonging to the same gap. This procedure was repeated on all coordinates in the list until the boundaries of the gap were encountered.

Germination in grassland gaps

Seeds of *Geranium dissectum* L. were sown individually with forceps at 2 cm intervals into 16 25 cm × 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 re-inspected and germination was scored one month after sowing.

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:

$$\text{GERMINATION} = \text{QUADRAT}/(\text{ROW} + \text{COLUMN}) + \text{RATIO}$$

in which the term QUADRAT/(ROW + 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

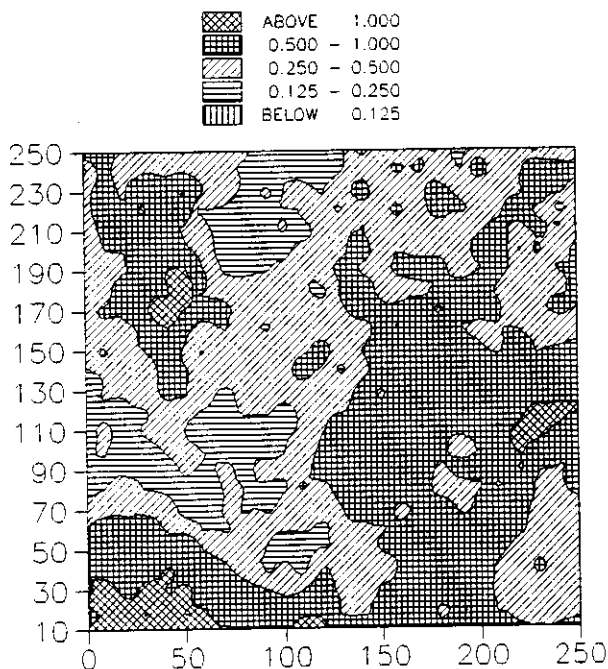


Fig. 1. Contour map of R/IR ratio in a representative quadrat mapped in Milton Keynes.

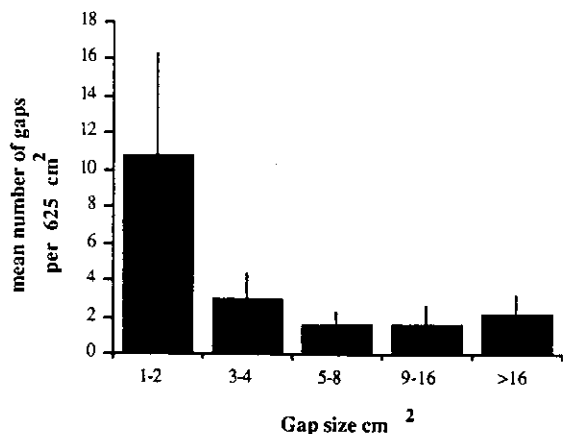


Fig. 2. Mean number of gaps per 625 cm² in five size classes at Milton Keynes. Bars show standard deviations, $n=12$.

1–2 cm² size-class and one gap in the size-class 3–4 cm² were recorded in the entire sampling area of 0.75 m². Defining gaps with a threshold R/IR ratio > 0.5 yielded 130 gaps and 36 gaps in these two size-classes respectively. The full size-class distribution of gaps (R/IR > 0.5) in twelve quadrats is shown in Fig. 2.

Germination in grassland gaps

Laboratory germination of *Geranium dissectum*

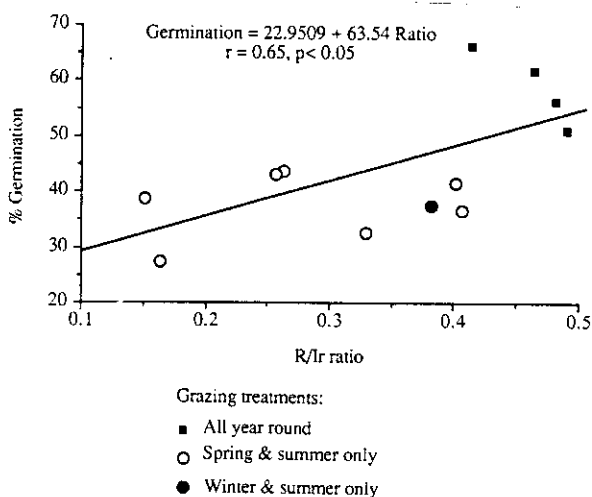


Fig. 3. Relationship between percent germination of *Geranium dissectum* and mean R/IR ratio in twelve grazed quadrats at Little Wittenham.

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 cm² 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 cm² 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 cm² 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.

Acknowledgements

We thank Jo Treweek and Trudy Watt for their assistance at Little Wittenham Nature Reserve and the Northmoor Trust for permission to work there. We thank Kevin McConway for statistical advice and we acknowledge financial support from the Natural Environment Research Council and the Open University Research Committee.

References

- Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14: 158–160.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- Collins, B. S. & Pickett, S. T. A. 1987. Influence of canopy openings on the environment and herb layer in a northern hardwood forest. *Vegetatio* 70: 3–10.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* (Suppl.) 12: 47–55.
- Faille, A., Lemée, G. & Pontailier, J. Y. 1984a. Dynamique des clairières d'une forêt inexploitée (reserves biologiques de la forêt de Fontainebleau) 1. Origine et état actuel des ouvertures. *Acta. Oecol. Oecol. Gen.* 5: 35–51.
- Faille, A., Lemée, G. & Pontailier, J. Y. 1984b. Dynamique des clairières d'une forêt inexploitée (reserves biologiques de la forêt de Fontainebleau) 2. Fermeture des clairières actuelles. *Acta. Oecol. Oecol. Gen.* 5: 181–199.
- Fenner, M. 1978. A comparison of the abilities of colonizers and closed turf species to establish from seed in artificial swards. *J. Ecol.* 66: 953–963.
- Foster, J. R. & Reiners, W. A. 1986. Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio* 68: 109–114.
- Frankland, B. & Poo, W. K. 1980. Phytochrome control of seed germination in relation to natural shading. pp. 357–366. In: J. De Greef. (ed.), *Photoreceptors and plant development*. Antwerpen University Press, Antwerpen, Belgium.
- Goldberg, D. & Werner, P. A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia* 60: 149–55.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old field in Michigan: experiments on the effects of vegetation. *J. Ecol.* 68: 919–928.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities. The importance of the regeneration niche. *Biol. Rev.* 52: 107–145.
- Hillier, S. H. 1986. A quantitative study of gap recolonization in two contrasted limestone grasslands. Ph. D. Thesis Univ. Sheffield.
- Jordan, C. F. 1969. Derivation of leaf-area index from quality of light on the forest floor. *Ecology* 50: 663–666.
- Lang, G. E. & Knight, D. H. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecology* 64: 1075–1080.
- Martinez-Ramos, M. & Alvarez-Buylla, E. 1986. Seed dispersal, gap dynamics and tree recruitment: the case of *Cecropia obtusifolia* at Los Tuxtlas, Mexico. In: Estrada, A. & Fleming, T. H. (eds), *Frugivores and seed dispersal*.
- Miles, J. 1974. Effects of experimental interference with stand structure on establishment of seedlings in Callunetum. *J. Ecol.* 62: 675–687.
- Payne, C. D. (ed.) 1986. *The Generalized Linear Interactive Modelling system*. Release 3.77. Numerical Algorithms Group, Oxford.
- Rusch, G. 1988. Reproductive regeneration in grazed and ungrazed limestone grassland communities on Öland. Preliminary results. *Acta Phytogeogr. Suec.* 76: 113–124.
- Silvertown, J. & Wilkin, F. R. 1983. An experimental test of the role of micro-spatial heterogeneity in the co-existence of congeneric plants. *Biol. J. Linn.* 19: 1–8.
- Silvertown, J., Prince, S. D. & Smith, B. A. 1988. A field-portable instrument for mapping the micro-environment within grass canopies. *Functional Ecology* 2: (in press).
- Watt, A. S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1–22.
- Wells, G. J. & Haggard, R. J. 1984. The ingress of *Poa annua* into perennial ryegrass swards. *Grass Forage Sci.* 39: 297–303.