THE BEHAVIOUR OF SEEDS IN SOIL

I. THE HETEROGENEITY OF SOIL SURFACES AND ITS ROLE IN DETERMINING THE ESTABLISHMENT OF PLANTS FROM SEED

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INTRODUCTION

This paper describes experiments made to determine the influence of variations in the microtopography of soil surfaces on the establishment of seedlings. The experiments derived from the realization that at the size scale of most seeds, the soil surface on which they are dispersed is highly heterogeneous and that this heterogeneity of the soil is likely to provide microsites offering widely different conditions for germination. Seeds often possess highly specific germination requirements and when seeds are dispersed on to soil surfaces, it seems reasonable to suppose that both the numbers and proportions of species establishing may be determined by the sort of micro-environment in which each seed lands. Unfortunately, the measurement of variations in the micro-environment at the appropriate scale is scarcely possible, and it may be for this reason that the ecological significance of soil surface microtopography has not been seriously considered.

EXPERIMENTAL

In the following experiments we have examined the influence of various artificial modifications of soil microtopography on the establishment of seedlings. The experiments fall into two groups:

(a) A study of the effects on seedling establishment of artificial topographical modifications introduced on to a fine seed bed. For this experiment three species of *Plantago*, *P. lanceolata*, *P. media* and *P. major*, were used.

(b) Studies of the influence of soil surface texture on seedling establishment in which an attempt was made to express variations in surface microtopography quantitatively. For these experiments a range of species including *Bromus* spp., *Chenopodium album* and *Brassica oleracea acephala* 'green marrow stemmed kale' were used.

1. *The influence of small modifications of soil microtopography on the germination of seeds of* Plantago *spp.*

A series of attempts to establish populations of *P. lanceolata*, *P. major* and *P. media* in open plots under field conditions showed that establishment frequently bore very little relationship to the germination capacity of the seed samples as shown by laboratory tests. Moreover, germination was very erratic from place to place within plots. On one occasion the experimental plots were trodden by pigs and there was rapidly produced a stand of *Plantago* seedlings wherever hoof marks had been made. This suggested that disturbance of the soil surface had created special conditions suitable for seedling establishment.

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An experiment was designed to test the influence of various kinds of soil disturbance on the ability of *Plantago* seeds to germinate in the soil. An artificial seed bed was constructed, 150 cm square and 30 cm deep, overlying a free draining gravel soil surface. The

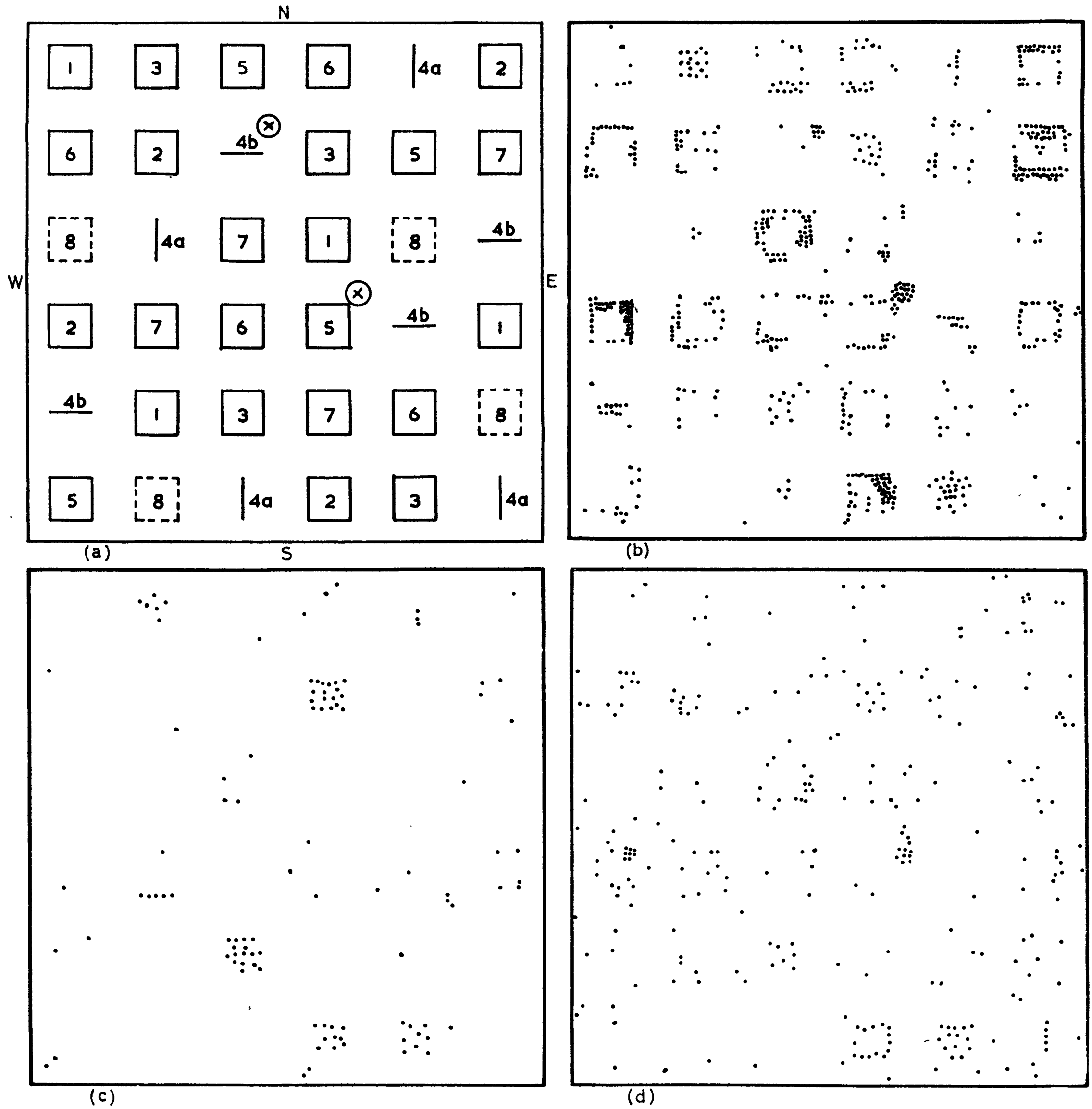


FIG. 1. (a) Plan showing the distribution of various types of objects placed on a soil surface sown with seeds of *Plantago* species (see text and Phot. 1). ⊗ = worm casts. (b) The distribution of seedlings of *P. lanceolata* in relation to objects and depressions on the soil surface. Combined records of 1 May and 11 June 1959; all seedlings were counted and removed on each date. (c) As (b) for seedlings of *P. media*. (d) As (b) for seedlings of *P. major*.

seed bed was prepared from John Innes Compost No. 2, finely sifted, with the coarse particles at the bottom of the seed bed and with a fine crumb soil to a depth of 2 in. at the surface. The seed bed was watered frequently after preparation.

Each plot was sown evenly with 500 seeds of each of the three species, *P. lanceolata*, *P. media* and *P. major*. The seed used had been collected from the Ridgeway on the Berkshire Downs in 1958, and stored in the laboratory throughout the winter of 1958–59. The area was divided into four blocks, each of nine plots, which were treated as follows:

(1) A hole 12·5 cm square and 1·25 cm deep was made by pressing a square of glass to the required depth and then removing it.

(2) A hole 12·5 cm square and 2·5 cm deep was prepared as in (1).

(3) A sheet of plate-glass 12·5 cm square and 0·6 cm thick was placed horizontally on the soil surface.

(4a) A sheet of plate-glass 12·5 cm long and 3·75 cm high was inserted vertically into the soil to a depth of 1·25 cm, thus leaving 2·5 cm standing vertically above the soil surface. The glass was aligned from north to south.

(4b) As (4a) but with the glass aligned east to west.

Table 1. *The emergence of seedlings of* Plantago *species in relation to the distribution of various modifications in the soil surface*

All seedlings found within the treated area (12·5 × 12·5 cm) and including a 2·5 cm broad surrounding border were regarded as associated with a treatment. Figures are means of four replicates accumulated over two sampling dates, 1 May and 11 June 1959.

Treatment	Percentage of total emergence for each species		
	P. lanceolata	*P. media*	*P. major*
1. Hole 1·25 cm deep	7·3	4·8	8·0
2. Hole 2·5 cm deep	23·5	11·4	18·5
3. Glass sheet flat on surface	9·6	46·7	11·6
4a. Glass sheet vertical N–S	2·3	2·9	3·3
4b. Glass sheet vertical E–W	3·8	1·9	2·2
5. Box 2·5 cm above surface	10·6	3·8	4·7
6. Box 1·25 cm above surface	11·0	4·8	8·7
7. Box 0 cm above surface	23·2	13·3	12·0
8. Control—no treatment	0·4	0·0	3·3
9. Seedlings not associated with treatments 1–8 (43·5% of total sown area)	8·3	10·5	27·9
Total number of seedlings emerged	689	105	276

(5) A thin walled wooden box 12·5 cm × 12·5 cm without top or bottom and with sides 3·75 cm high was pressed 1·25 cm into the soil, leaving 2·5 cm projecting above the soil surface.

(6) A similar wooden box with sides 2·5 cm high was pressed 1·25 cm into the soil, leaving 1·25 cm projecting above the soil surface.

(7) A similar box with sides 1·25 cm high was pressed 1·25 cm into the soil leaving the top of the box flush with the soil surface.

(8) A control plot received no special treatment.

The layout of this experiment is shown in Fig. 1(a) and Phot. 1. The seed was sown and treatments applied on 14 April 1959, and the experiment received only natural rainfall from that time. Seedlings started to emerge on 1 May 1959, and 9 days later the position of all emerged seedlings was recorded and the seedlings were removed. A second flush of seedlings was mapped and removed on 11 June 1959. Maps of the distribution of seedlings from these two harvesting dates are presented together in Fig. 1(b, c and d). It is apparent that the seedlings were not evenly distributed throughout the sown area, but arose in close relation to the objects placed on the surface. Apart from the pattern of seedling distribution associated with applied treatments, two worm casts were formed on the soil surface during the course of the experiment and a mass of seedlings of both *P. lanceolata* and *P. major* appeared in association with these. Table 1 summarizes the establishment of seedlings of the three species under the various treatments.

A first and obvious conclusion is that *c.* 90% of the seedlings of *P. lanceolata* and *P. media* developed close to the objects or depressions on the surface. In contrast, the distribution of *P. major* was largely independent of the distribution of objects. The emergence of all species was increased by compressing the soil, but the most striking increase was of *P. lanceolata* and *P. major*. In contrast, seedling emergence of *P. media* was greatly favoured under a glass sheet lying flat on the soil surface, but this had relatively little effect on *P. lanceolata* and *P. major*. The establishment of *P. lanceolata* and *P. media* was increased by the presence of boxes placed on the soil surface and the effect was greatest when the boxes scarcely projected above the soil. It was least with the most projecting boxes. This difference is interesting as all boxes were pressed to an equal depth in the soil—the extent of projection above the soil was the only variable. The effect of glass sheets placed on edge was much the same as one side of a box with no difference between N–S and E–W orientation.

2. *A study of the establishment of a variety of species on artificially prepared soil surfaces of varied texture*

The topography of soil surfaces varies not only with the frequency of obstructions, but also with the condition of the soil itself. In nature, variations in the wetting and drying cycles to which the soil has been exposed result in varied degrees of cracking. The activities of the soil fauna result in variations in the tilth of the soil surface, the presence and decay of leaf litter provides a changing soil surface and the activities of man may provide a variety of tilths as a result of cultivation.

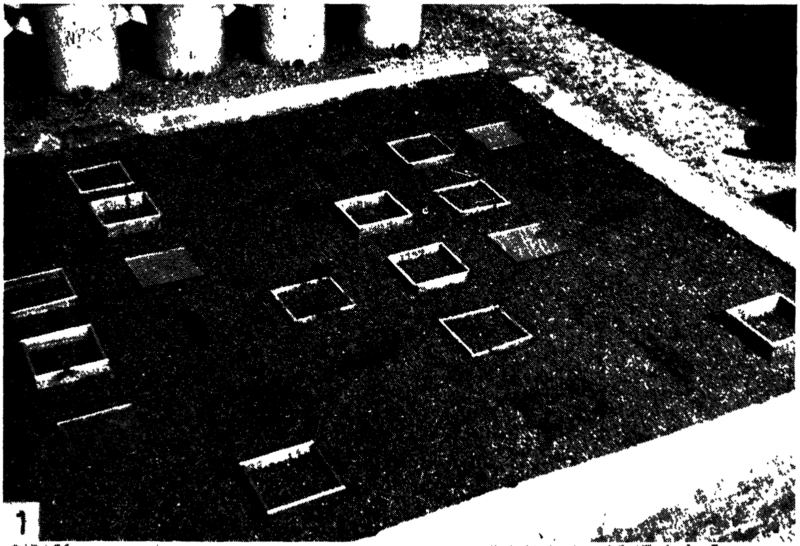
An attempt was made to provide a graded series of soil surfaces. It was considered important to avoid sifting the soil as this results in a separation of fractions which differ not only in structure but also in nutrient content (Hammerton 1961). Large clumps of soil were therefore taken and broken by hand into fragments of the required size and these were used to form seed beds on which seeds of various species were sown. Seeds were dropped on to the soil surface from 30 cm height to simulate natural dispersal.

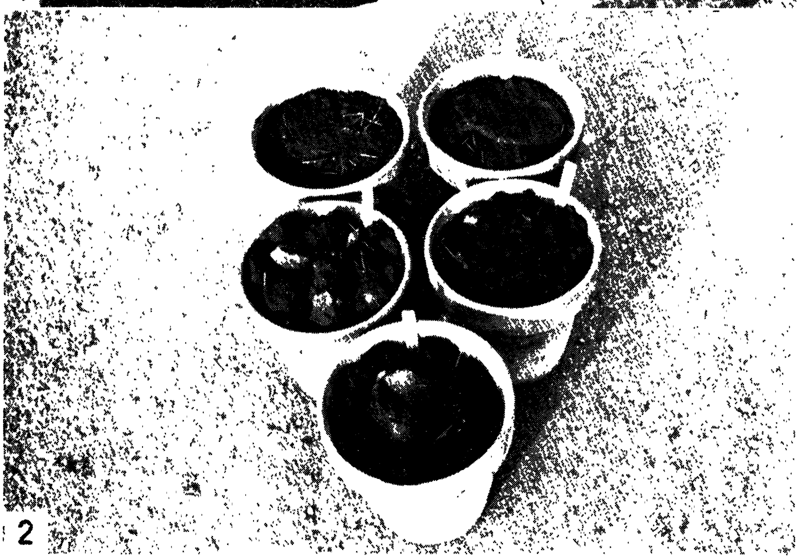
(a) *The establishment of species of* Bromus *on Yolo silty loam*

Plant pots 20 cm diameter were filled to within 10 cm of the rim with a 3 to 1 mixture of fine sand and Yolo silty loam. Yolo silty loam was available in a dry caked condition, having been stored wet and allowed to dry. From this a series of soil surfaces of graded structure was prepared. The large clods of soil, many of which were originally >30 cm in diameter, were broken by hand to give four grades:

(A) A large grade in which the unit clods were *c.* 5 cm diameter.
(B) A slightly smaller grade 3–5 cm diameter.
(C) A grade of soil clods 2–2·5 cm diameter.
(D) In which the large lumps were broken into fragments 1·25 cm diameter or less.

Sufficient large clods of grade A were placed on top of the soil–sand mixture to bring the average level of the soil to the top of the plant pot. The same weight of soil of the remaining grades was added to other pots. Eight pots were prepared from each soil





PHOT. 1. The arrangement of objects on a soil surface sown with seeds of *Plantago* species (compare with Fig. 1a).

PHOT. 2. Various soil surfaces, prepared from Yolo silty loam, on which seeds of *Bromus* species have been dropped. The long awns of *B. rigidus* are conspicuous on the surface.

grade except grade D from which sixteen pots were prepared. Eight pots of grade D were watered heavily and then allowed to dry for 3 weeks to give a fifth type of surface, E, hard capped with deep cracks (Phot. 2).

The soil surfaces prepared for the experiments were superficially similar to many of the soil surfaces observed on the coastal ranges of central California. Frequently soil disturbance results in clod sizes comparable with grades A, B and C. Grade E corresponded to soil surfaces which had been rained on and then cracked during drying. Simple equipment was designed to permit measurement of the roughness of the soil surface. This consisted of a frame holding a line of ten pins arranged so that they were free to move vertically. The tops of the pins were fitted with pointers which rested against a graph paper scale (Fig. 2). The frame was lowered horizontally on to the soil surface until the points of all the pins rested on the soil. Readings were then taken of the heights of the pointers. Three such sets of ten readings were taken from each pot of soil. The absolute

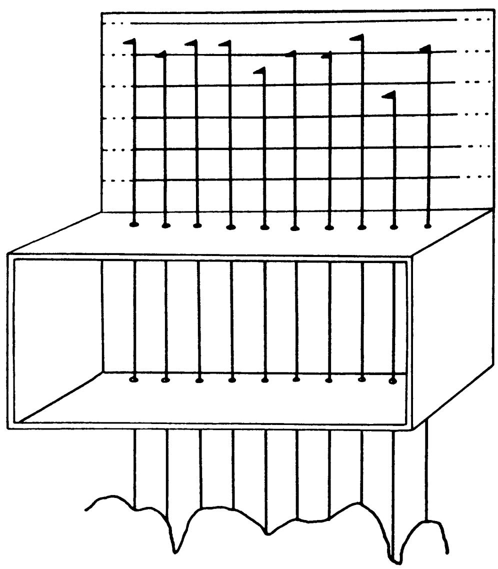


FIG. 2. Ten-pin frame used for the measurement of soil roughness.

values obtained from such readings have no very useful meaning but the variance of the values gives a measure of the soil microtopography. This parameter may be called 'soil microtopographical variance' (S.M-T.V.). The values for S.M-T.V. represent the error variance in an analysis of variance of pointer readings, after partitioning and removing the variance due to differences between replicate pots and due to differences between the three positions of the aligned pins in each pot. Determination of the S.M-T.V. in this way makes it irrelevant whether or not the apparatus is held at the same height for every set of ten readings, and makes this measurement possible as a field operation. It is of course essential that the frame is horizontal when readings are taken.

There was a high degree of constancy in the variance obtained from eight pots of similar soil grade. The S.M-T.V. of the five grades was as follows: (A) 189·48 mm^2, (B) 166·49 mm^2, (C) 60·59 mm^2, (D) 6·43 mm^2, (E) 2·78 mm^2.

Seeds of *B. rigidus* and *B. madritensis* were sown on the varied soil surfaces. Both species are annuals. They differ in vigour of growth, *B. rigidus* being the more vigorous (see Harper, Clatworthy, McNaughton & Sagar 1961), and they differ in shape and size of the dispersal unit. The grains are dispersed together with enclosing lemma and palea and the lemma of *B. rigidus* bears a straight awn. The grain of *B. madritensis* is smaller and lighter and the awn is slightly curved. It was obvious on scattering the grains on the soil that those of *B. rigidus* often fell like darts, entering the cracks and crevices between soil clods and leaving only the awn showing. In contrast, grains of *B. madritensis* fell more slowly and the slight winging of the grains seemed to cause them to land horizontally more often than vertically on the surface of the soil. Sowings were made at four densities of ten, thirty, sixty and 100 seeds per pot and each density was obtained from a mixture of seeds of the two species in equal proportions by number.

The design of the experiment was therefore as follows: Five soil grades; four sowing densities; the whole being replicated twice. The soil was watered from above by simulant rainfall from a fine hose; 1·25 cm of rain was given immediately on sowing. Seven days later the soil had dried and no germination was observed. The equivalent of 2·5 cm of rainfall was then applied and followed by a further 2·5 cm a week later.

Rapid germination of both species was observed and when no further emergence occurred and the established seedlings had wilted, all seedlings were removed and counted. The results of this experiment are shown in Fig. 3, and the changes in relative proportion of the two species with soil microtopography are shown in Fig. 4. The effects of soil surface were significant at $P<0{\cdot}001$, and there were significant interactions between soil surface and species ($P<0{\cdot}05$), and between soil surface and sowing density ($P<0{\cdot}01$).

On the three soil surfaces with high values of S.M-T.V. there was a linear relationship between the number of seeds sown and the number of seedlings established. On the soil which had been watered and allowed to crack, a very different relationship developed. Here the population of seedlings was not increased by a further increase in sowing density from thirty to 100 seeds per pot, and it is concluded that on this soil surface there was a very limited number of sites suitable for establishment under the conditions of this experiment, and that the sites were quickly saturated by increasing the density of seeds sown. The model soils provided in this experiment illustrate two contrasting conditions which may be expected to occur in the field: one in which population sizes are not limited by the availability of suitable microsites within the range of densities examined and one in which a relatively low population size is maintained despite wide variations of sowing density.

Although seeds of the two species used in this experiment were sown in equal proportions at every density and on every soil surface, there were striking differences in the proportions of the two species in the seedling populations. There was a significantly higher proportion of *B. rigidus* on the soils of low S.M-T.V. and a higher proportion of *B. madritensis* on the rougher soils. This may perhaps be explained in terms of the different types of contact made by the grains with the soil surface. On the very rough soils the curved awn of *B. madritensis* ensures that the grain often comes to lie curved around a soil clod making good and close contact with the water supplying soil surface. Such contact is minimized on a flat surface. In contrast, *B. rigidus* lies flat and was apparently more efficient at making contact with a flat soil surface (or entering a very narrow crack or crevice).

(b) *The establishment of* Chenopodium album *and kale on heavy clay soil*

A heavy clay soil was obtained from Griffith's Crossing workings at Port Dinorwic, Caernarvonshire. Pots of 23 cm diameter were filled two thirds full with a 50/50 mixture

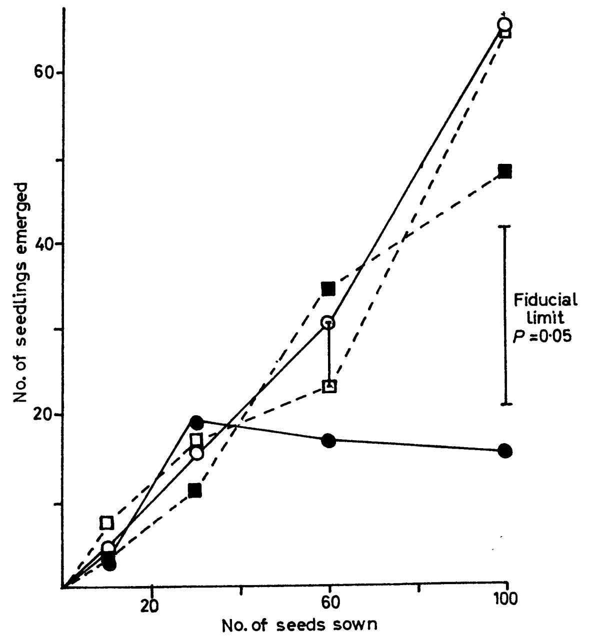


FIG. 3. The relationship between the numbers of seed of *Bromus* species sown and the numbers of seedlings establishing on soils of varied microtopography. A (□) Soil microtopographical variance = 189·5 mm²; B (○) = 166·5 mm²; C (■) = 60·6 mm²; E (●) = 2·8 mm².

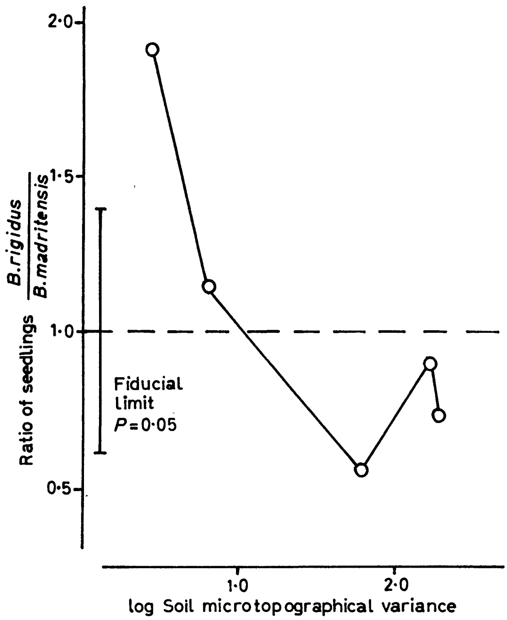


FIG. 4. The ratio of numbers of seedlings of *Bromus rigidus* and *B. madritensis* establishing from an equiproportioned mixture sown on soils of varied microtopography.

of the clay with John Innes Compost No. 2. Further samples of the clay were dried and broken by hand to give a range of clod sizes as in the previous experiment. Subsequent preparation and arrangement of the clods followed the procedure described for *Bromus* experiments. The range of surface roughness obtained in this experiment was (S.M-T.V. values) A, 214·47 mm^2, B, 74·39 mm^2, C, 29·31 mm^2, D, 7·20 mm^2 and E (dried and cracked from D as previously) 9·98 mm^2. One hundred seeds of kale and 100 seeds of *Chenopodium album* were broadcast on to each soil surface. The experiment was replicated five times and arranged as a randomized block within a cool glasshouse. The seeds were sown broadcast on to the soil surface and it was immediately obvious that the two species took up different positions of rest in the soil. The heavier kale seeds tended to roll down between the clods, although a few lodged on the sides of the larger clods. Seeds of *C. album* usually remained where they first landed and most became

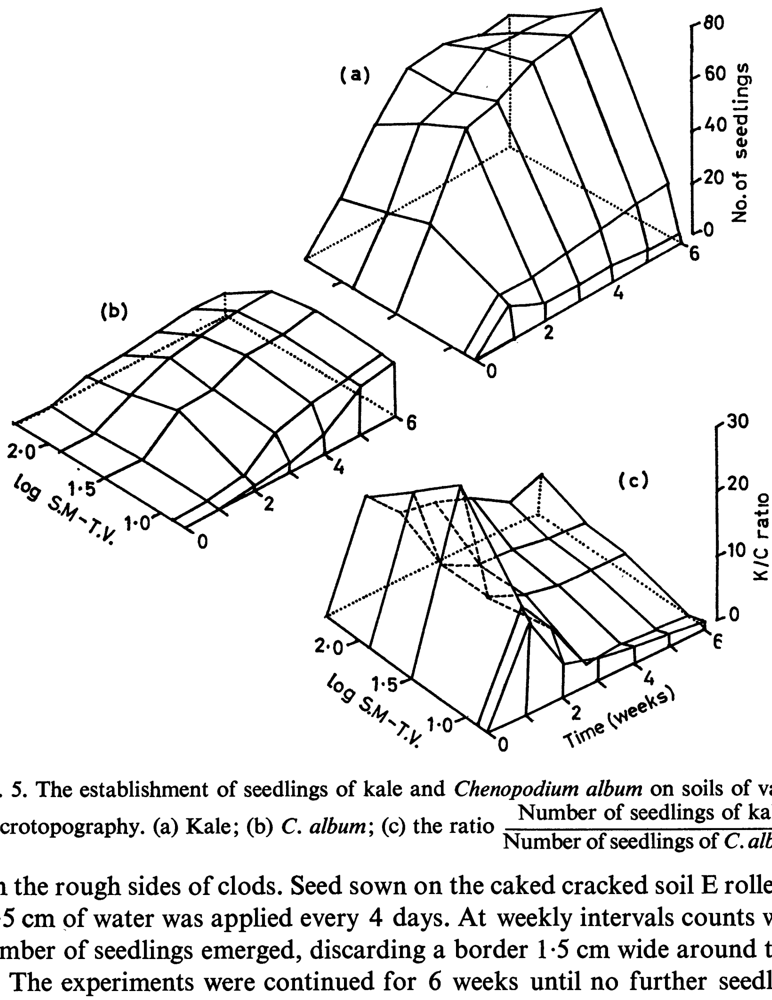


FIG. 5. The establishment of seedlings of kale and *Chenopodium album* on soils of varied microtopography. (a) Kale; (b) *C. album*; (c) the ratio $\frac{\text{Number of seedlings of kale}}{\text{Number of seedlings of } C.\ album}$.

lodged on the rough sides of clods. Seed sown on the caked cracked soil E rolled into the cracks. 2·5 cm of water was applied every 4 days. At weekly intervals counts were made of the number of seedlings emerged, discarding a border 1·5 cm wide around the side of each pot. The experiments were continued for 6 weeks until no further seedling emergence occurred in the experiments. The number of seedlings present at each count and the ratio between the two species is shown in Fig. 5. Seedlings of kale emerged more quickly than those of *C. album*. The most successful emergence of both the species was from the soil surface of variance 29·31 mm^2 and the worst emergence of kale was from the smoothest soil and of *C. album* from the roughest. Kale was much more sensitive to soil roughness than *C. album*. Because the species differed in the speed with which they germinated, the ratio of the number of seedlings of kale to *C. album* started high and then fell rapidly. More seedlings established on the soil which had dried and then cracked than on the fine soil surface from which it had been prepared, because the seeds falling into cracks tended to germinate quickly and regularly.

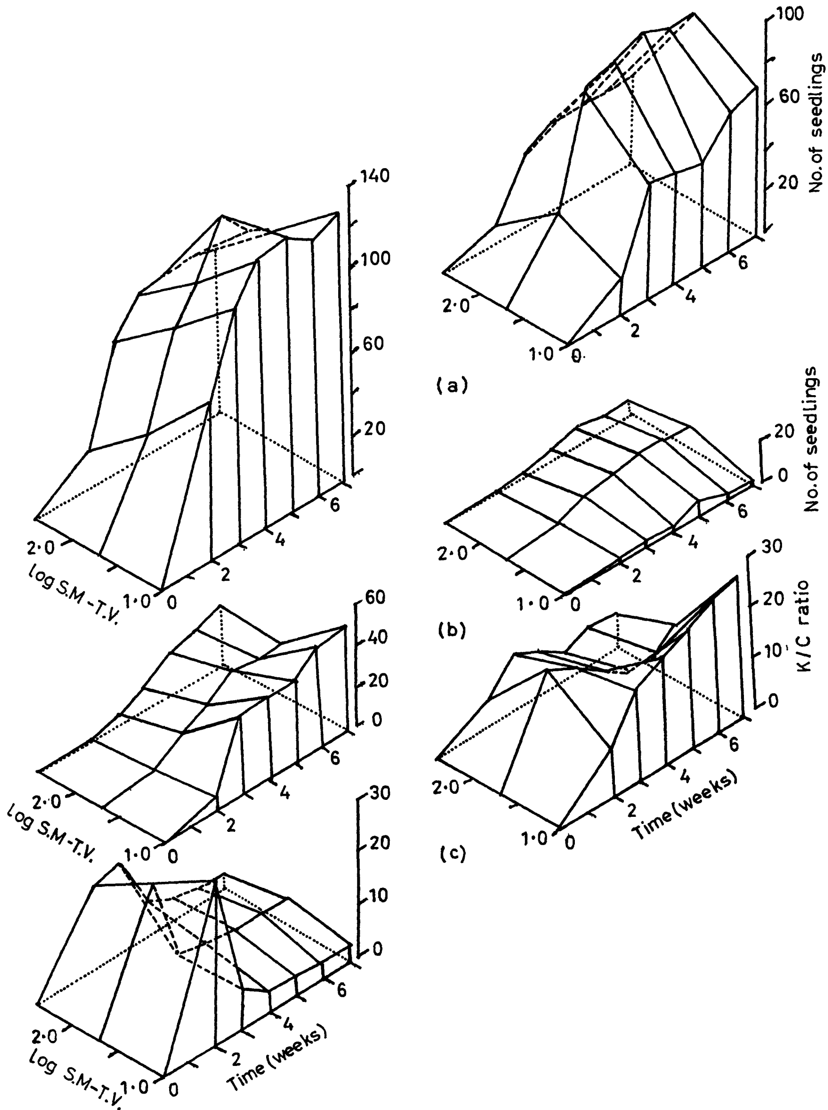


FIG. 6. The influence of surface compaction on the establishment of seedlings of kale and *Chenopodium album* on soils of varied microtopography. Left hand side—no compaction; right hand side—with compaction. (a) Kale; (b) *C. album*; (c) the ratio $\frac{\text{Number of seedlings of kale}}{\text{Number of seedlings of } C.\ album}$.

3. *Modification of soil microtopography by compaction or enclosure subsequent to seed dispersal*

Seed boxes, 100×62×37 cm deep, were prepared with three soil microtopographies corresponding approximately to A, C, and D in the previous experiments (S.M-T.V. =

258·50, 55·75 and 9·90 mm²). A mixture of 200 seeds of *C. album* and 200 seeds of kale were broadcast on each soil surface. After sowing the seed, the soil in one half of the boxes was compacted by rolling with a linoleum roller. The boxes were laid out as a ran-

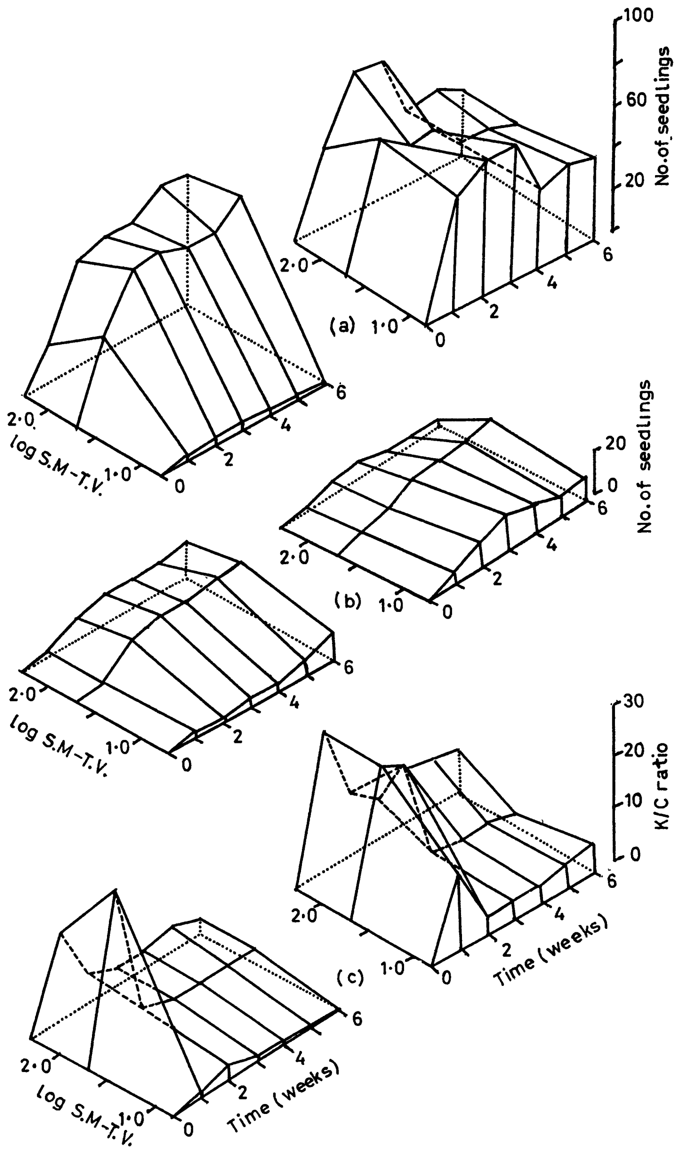


FIG. 7. The influence of surface protection on the establishment of seedlings of kale and *Chenopodium album* on soils of varied microtopography. Left hand side—no polythene; right hand side—with polythene. (a) Kale; (b) *C. album*; (c) the ratio $\frac{\text{Number of seedlings of kale}}{\text{Number of seedlings of } C.\ album}$.

domized block with five replicates each of six treatments. The boxes were placed in the open and received natural rainfall. There was a period of dry weather immediately after sowing and additional water was given at this time. The number of seedlings present at each count and the ratio between kale and *Chenopodium* is shown in Fig. 6. The establishment of *C. album* was greatly reduced by compaction but kale was much less affected, particularly on the rougher soils. Clearly the influence of soil roughness on seedling emergence can be modified by compaction. Not only were the number of potential germination sites altered by compaction, but the treatment affected the establishment of the species differentially.

One of the most obvious ways in which soil microtopography might be expected to influence seedling establishment is by determining the extent to which seeds are exposed to the atmosphere. If this is the case, then the effects of varied topographies might be reduced if the soil surface were protected by restricting evaporation from the surface. Three series of soil surfaces were prepared, S.M-T.V. 212·62, 56·23 and 6·08 mm². A mixture of 100 seeds of *C. album* and 100 seeds of kale was broadcast on each plot. Half of the pots were covered with clear polythene held tightly across the rim by rubber bands. The pots were laid out as a randomized block with five replicates of each of the six treatments. The pots were kept in a cool glasshouse and were buried to their rims in soil to avoid excessive drying of the side of the pots. 2·5 cm of water was applied to the soil surface every 4 days from a fine spray. A high relative humidity was maintained under the polythene covers, which carried a continuous film of water droplets. The covers were removed after 2 weeks. During bright sunlight the temperature of the soil at 5 cm depth under polythene covers was raised by between 2 and 3·1° C above that of uncovered soil. The mean number of seedlings present at each count is shown in Fig. 7.

The effect of the polythene covers was particularly marked on the emergence of kale, causing a much more rapid flush of germination and largely eliminating variations due to soil microtopography. The experiment was complicated, however, by much damping-off of seedlings which had emerged under polythene. The damping-off occurred 4 weeks after emergence even though the polythene had been removed after 2 weeks. The seedlings which had developed under polythene tended to be straggly and slightly etiolated. After 6 weeks the populations on the rough soils were smaller under polythene than without, but the populations on smooth soils were larger under polythene. The greater liability to damping-off on the rough soils may well be explained by the humid environment maintained around the hypocotyls as they elongated between the large soil clods (see Hammerton 1961). The seeds usually fell deep in such surfaces in contrast to their behaviour on fine soils where the hypocotyls were quickly free from the soil microenvironment.

The establishment of *C. album* was less influenced than kale by the presence of polythene covers, but in general, the effect of covering the pots with polythene was to reduce the differences due to soil microtopography. It is suggested that variations in soil microtopography affect the establishment of these species by determining the frequency on the soil surface of microsites sufficiently humid for germination.

4. *Water uptake by seeds and germination on four graded soil surfaces*

An experiment was designed to examine the rates of water uptake by seeds sown on soils of varied microtopography with the aim of determining whether this was correlated with seedling establishment on such soils. Four soil surfaces were prepared (S.M-T.V. = 332·27, 128·69, 63·94 and 8·40 mm²) and twenty seeds of kale and twenty seeds of *C. album* were broadcast on to each surface. The treatments were replicated four times and the pots arranged in a randomized block design. The pots were sunk to the rim in damp soil in a cool glasshouse and after sowing the seed the pots were given 2·5 cm of water from a fine spray. The seeds had been desiccated for 2 days over calcium chloride before sowing and they were recovered after 24 h in the soil, weighed and the percentage increase in weight was calculated. Immediately after recovering the seeds, a mixture of 100 seeds of kale and 100 seeds of *C. album* was sown on each of the soil surfaces to obtain a measure of seedling emergence from the same soils. Seedling emergence was recorded. The change in weight of the first batch of seeds sown in the soil and the ultimate emergence of seedlings from the second batch of seeds sown in the same soil are shown in Fig. 8. The soil roughness which was optimal for seedling establishment was different for the two species and the optima coincided with the optima for water absorption. The results of this experiment support the hypothesis that an important role of varying soil micro-

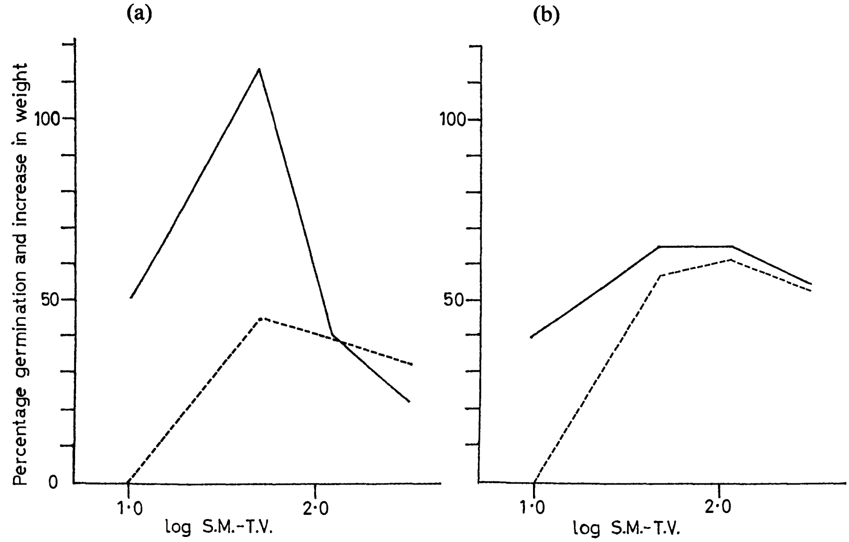


FIG. 8. Percentage increase in weight over 24 h (——) of seeds of (a) *Chenopodium album* and (b) kale sown on soils of varied microtopography. Plotted on the same graphs are percentage germination of these species sown on the same soils (- - -).

topography in seedling establishment is to determine the ease with which water is taken up by the seeds which fall in different positions and make different contacts in the various soil surfaces.

DISCUSSION

The experiments described in this paper are all concerned with the behaviour of seeds falling on a soil surface—imitating natural seed fall or the agricultural practice of 'broadcasting' seed. All the experimental results emphasize that the heterogeneities of a soil surface may determine the chance of a seed finding a suitable crevice for germination. It is obvious that in these experimental systems the density of the plant population is a function of the soil surface and the population may be said to be regulated by the frequency of 'safe sites' (Harper *et al.* 1961).

In all the experiments two or more species were sown on each type of soil surface, and the relative proportion of the species were changed with varying surface roughness. This suggests that there is considerable subtlety in the requirements of different species for 'safe sites'. The densities of species in a mixture may be independently determined for each species because of specialized requirements for germination which are satisfied at different places on a rough soil surface. This is particularly strongly suggested by the experiments with *Plantago* spp. in which the density of seedlings of each species was largely a function of the frequency of the different types of disturbance made on the soil surface.

A part of the effect of soil microtopography would seem to be due to the degree of protection of seeds against water loss—for protection of the soil surface with polythene removed much of the difference in seedling establishment on different soil surfaces. This could, however, have been due, in part, to the raised soil temperature under polythene. The observation that the different optimal topographies for establishment of *Chenopodium album* and kale corresponded with the different optimal topographies for water uptake by the seeds, supports the view that microtopography exerts its effects through modifying seed–water relationships.

It seems likely that subtle differences in seed shape and surface interacting with subtle variations in the structure of the soil surface may influence both the abundance of particular species and the balance between species. Unfortunately techniques are not available for the direct measurement of the physical properties of the minutely varying soil environment. The subsequent paper in this series analyses the behaviour of seeds in laboratory models on which the soil micro-environment of seeds may be rigidly controlled.

One feature of special interest concerns the manner in which plant population may be regulated. It is commonly argued that the regulation of densities of organisms must be by density-dependent processes (see for example, discussion by Haldane 1963), in which increasing density is responsible for reducing the chance of individual survival. In many of the model populations examined in this paper, the number of individuals becoming established is a direct function of the number of suitable or 'safe' microsites provided on the soil surface and a maximum population size is therefore determined directly by the physical environment. When the number of 'safe sites' is limited, the chance of a seed producing a plant will be reduced as the density of sowing is increased—giving the spurious impression that density is causal in controlling establishment. A suitable analogy is found in the sampling of an egg cup full of beans from a sack of beans—the sample is independent of the number of beans in the sack above a critical value (only the left-overs are density-dependent).

A further point of significance in these experimental results lies in the differential response of species to the configuration of microsites. Apparently the numbers of two species establishing from seed on a soil surface may be independently determined, because of different requirements of the seeds for suitable micro-environments for germination. Such factors may need to be taken into account in analysing fluctuations in natural populations and in accounting for the ability of several species to cohabit successfully within the same area.

SUMMARY

Seeds of different species differ in their requirements for conditions suitable for germination. The varied micro-environments provided on a soil surface act selectively on mixed seed populations and determine the numbers of 'safe' germination sites. Experiments involved placing various objects, or making depressions, on soil surfaces on which seed had been sown, and of creating artificial soil surfaces of varied microtopography.

Species used in the experiments were *Plantago lanceolata*, *P. major*, *P. media*, *Bromus rigidus*, *B. madritensis*, *Chenopodium album* and *Brassica oleracea acephala*.

A ten-point frame was used to obtain a measure of soil microtopography. It is argued

that the availability of suitable microsites on a soil surface may offer a means by which the numbers of plants establishing from seed is regulated and the relative abundance of different species is determined.

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