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OCCUPATION OF BIOLOGICAL SPACE DURING SEEDLING ESTABLISHMENT

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INTRODUCTION

As each individual in a population of seedlings germinates and becomes established, it gains access to resources necessary for its further growth and development. The term 'biological space' is used to cover this complex of resources. Such a simplification assumes that the requirements of individuals within a species are essentially similar.

The object of this paper is to show the importance of the position of an individual in the overall ranking of emergence times, and its spatial separation from neighbours, in enabling it to occupy space to the exclusion of its neighbours. Most information on the performance of an individual within a population has come from work with mixed populations and this literature warrants consideration.

A number of studies have been made on the temporal and spatial components of seedling interference, but the interaction of the two, interference in the dynamic context, has received less attention.

The relative times at which different species are introduced into a mixture has been shown by a number of authors to produce dramatic changes in the outcome of interference between the components. When Sagar (1959) sowed S23 *Lolium perenne* and *Plantago lanceolata* simultaneously, *Lolium* contributed 80% of the total plant dry weight at harvest. If *Lolium* were introduced 3 weeks before *Plantago*, the proportion contributed by *Lolium* rose to 90%, but, sown 3 weeks after *Plantago*, *Lolium* contributed only 6.4% of the total dry weight. A similar result was reported by Harper (1961) using two *Bromus* species. When *B. rigidus* and *B. madritensis* were sown simultaneously, the former contributed over 75% of the final dry weight of the mixture. If the introduction of *B. rigidus* were delayed for 3 weeks, then the contribution by this species dropped to approximately 13% of the total dry weight. Williams (1962) has repeated this effect in an agronomic context. He found that *Chenopodium album* reduced the yield of barley by 20% when the two were sown at the same time, but delaying barley sowing by 7 weeks allowed *Chenopodium* to reduce the yield of the barley by 45%. The same effect with one species was shown by Black & Wilkinson (1963) using subterranean clover. They delayed planting alternate seeds within a grid pattern by 0, 2, 4 and 8 days, thus considerably increasing the range of emergence times within swards. By recording the final yield of each individual, they showed that a 5-day delay in the emergence of an individual reduced its final weight by 50%, and a delay of 8 or 9 days, by at least 75%. These differences could not be accounted for solely by differences in growing times between emergence and harvest.

As early as 1938, Weaver & Clements described how an advantage gained by an individual over its neighbours was likely to be maintained or accentuated during subsequent

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growth. Since then a number of studies have been made to observe the effect of neighbours on the behaviour of an individual and to assess the effect of spatial arrangement on the outcome of interference between two species.

Sakai (1957) found that when a barley plant of one variety was planted in a pot surrounded by varying proportions of the same and a different variety in a hexagon, the yield of the centre plant was proportional to the number of the same variety represented in the surrounding hexagon. He found also that the arrangement of the surrounding plants, whether random or regular, did not significantly influence the result. Harper (1961), using 100 plants per treatment, thus considerably reducing any edge effect, did not find such a linear relationship between an individual and the number of neighbours of the same species in the surrounding circle of plants, when comparing two *Bromus* species. Furthermore, he concluded that the degree of aggregation of one species in a segment of the surrounding hexagon influenced their ability to suppress the plant in the centre. In a similar experiment where four different random arrangements of the two *Bromus* species were replicated, the result of interference between the two species differed significantly between the different random arrangements.

These reports illustrate situations in which individuals of one species are able to dominate those of an associated species. Within monospecific populations, Koyama & Kira (1956) have shown that a dominance hierarchy is set up which leads to the distribution of individual plant weights becoming skewed, eventually moving towards a log-normal weight distribution. More recently, White & Harper (1970), in an examination of plant weight distribution in monospecific populations undergoing self-thinning, have concluded that the dominance hierarchy leads to a removal of the smallest individuals according to the '3/2th rule' originally proposed by Yoda *et al.* (1963). This suggests that the survival of an individual is greatly dependent on its position in the dominance hierarchy.

The experimental work presented in this paper demonstrates the influence of seed size, emergence time, growth rate and proximity of neighbours in determining the position of individual cocksfoot plants in the dominance hierarchy.

EXPERIMENT 1

Method

Horticultural trays 22×38×5 cm were filled with sand and sown with cocksfoot (*Dactylis glomerata*) 'seeds' in a random arrangement, at a rate of 3.3 seeds per cm² except that, by using templates during sowing, circular areas were left unsown as illustrated in Fig. 1.

Two trays constituted each treatment, and four different layouts within each treatment were each replicated three times, giving twelve replicates of each main treatment. In the centre of the circles of different areas, four seeds from the same sample as those of the 'background' population were sown. Into circles of the same size, groups of four seeds were sown at varying distances from the centre of the circle, as shown in Fig. 1. The aim of sowing four seeds was to ensure that at least one survived, and only the first to emerge was allowed to survive, the others being thinned as soon as they emerged. Trays were placed on a capillary bench in a glasshouse, and given continuous access to full nutrient solution. Only four groups failed to produce a seedling, and these were treated statistically as missing values. The plant inside each circle was harvested, dried and weighed, 47 days after sowing.

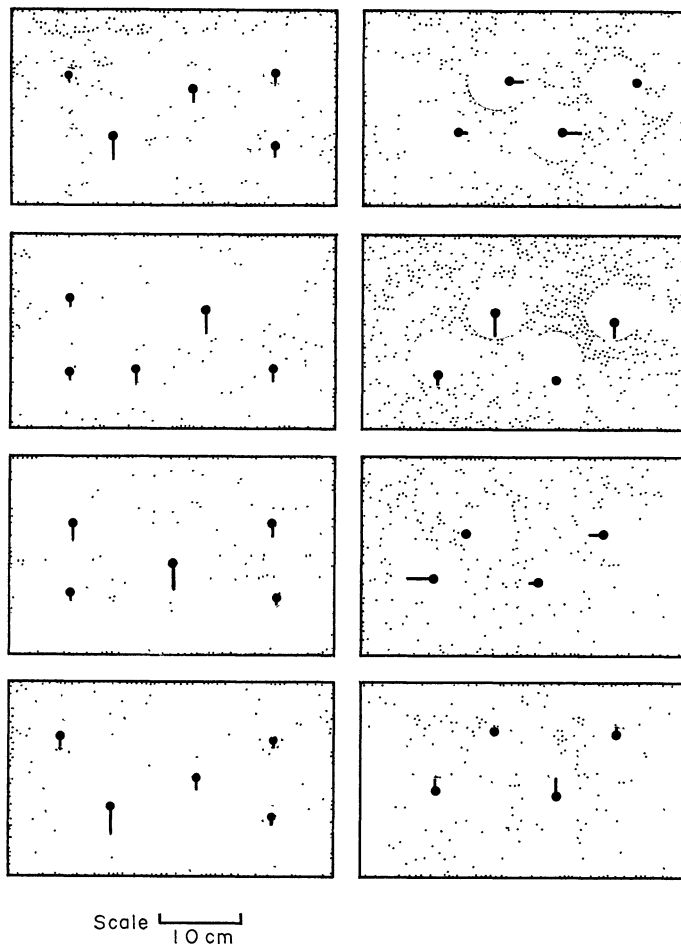


FIG. 1. Layout of plants in Expt 1. Left, four arrangements of different patch sizes; right, four arrangements of different distances from centre plants to patch perimeter.

Results

Within each treatment, two effects could be tested.

(1) Where the size of the patches varied, and the plant within the patch was always at the centre, the effect of patch size on the weight of the centre plant could be determined. The relationship accounting for the highest proportion of dry weight variance was found to be

$$W = 16.3 + 0.422 (r)^3 \quad (P < 0.01)$$

where W is the dry weight in milligrams and r is the patch radius (cm) implying that interference between plants is essentially three dimensional. Fig. 2(b) shows this relationship, and also gives the 95% confidence limits about the intercept value, showing that the intercept on the y axis is significantly above zero.

It might be expected that the intercept on this axis, representing the weight of a plant which has no space available to it, would approximate to zero. The significantly higher

value which was observed is probably due to the plant in the centre of each patch establishing, on average, slightly before the plants surrounding the patch. This happened because the centre seedling represented the earliest emerging of four seedlings. The time advantage given to the centre plant was directly manifest as a space advantage and, in this sense, biological space and geometric space have coincided.

(2) Where patches were of the same size, the effect on its dry weight of varying the distance of the centre plant from the edge of the patch could be determined. A significant ($P < 0.01$) regression relationship was found (Fig. 2a) such that

$$W = 36.4 + 1.31 d$$

where W is the weight of the centre plant in milligrams, and d is the distance (cm) from the edge of the patch. In Fig. 2 (a, b) the scales of the W axis on both graphs are the same.

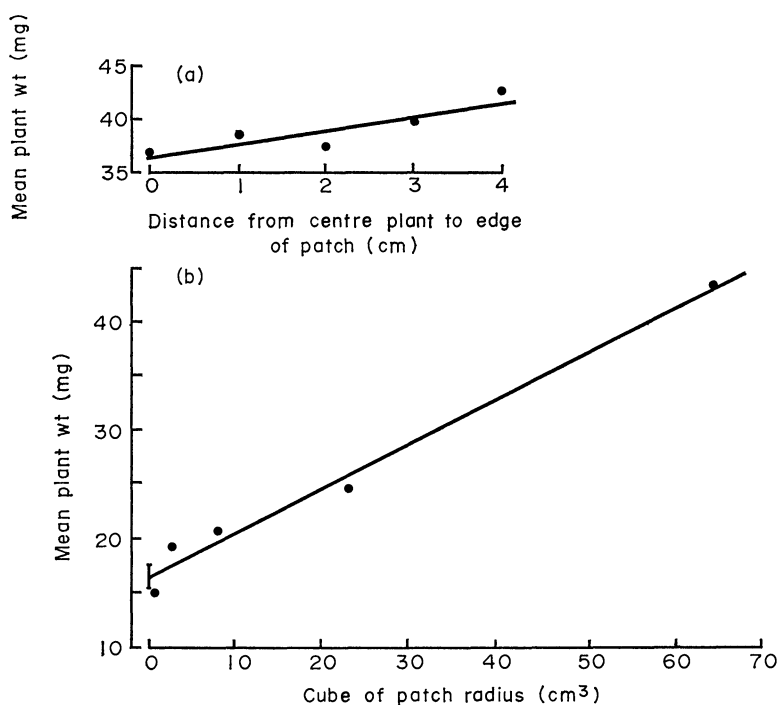


FIG. 2. Response of individual plant weight to (a) varying the distance of the centre plant from the perimeter of the patch; (b) varying sizes of patches.

It can be seen that the distance of the plant from the edge of the patch has relatively little effect on its weight, compared with the effect of patch size. This comparison suggests that the centre plant is able to compensate for interference from one direction by expanding in a direction of lesser interference.

EXPERIMENT 2

Since Expt 1 had indicated that the time at which a seedling germinated could markedly influence the amount of space it was able to occupy, Expt 2 was designed to examine more

closely the degree to which the weight of an individual, within a dense population, is influenced by the time at which it emerges. It had been noted in previous experiments that cocksfoot seedlings emerged over a considerable period of time, making it an ideal species for this experiment.

The co-ordinates of the position of each plant, as well as its emergence time and final dry weight were determined so that a thorough analysis of the time \times weight interaction could be made.

Method

Five trays, similar to those used in Expt 1, were sown with cocksfoot 'seeds', again in a random arrangement, to give a density of approximately three seeds per cm². Two of the trays were used as border trays at the end of the row and received no further treatment. On each of the remaining three trays, an area, of approximately 10 cm square, was marked out on the centre of each tray. The seeds were then covered with a 1-cm layer of fine vermiculite, and the trays placed on the capillary bench as in Expt 1. Twice each day the trays were examined for seedlings emerging within the specified area. When a group of approximately ten seedlings had emerged since the last observation, each of the plants in this group was appropriately marked and the time of emergence noted. Individual shoots were tagged with a 2-mm length of split coloured plastic drinking straw.

Seeds were sown on 9 March 1967 and the size and position of each plant were determined 53 days later using rectangular co-ordinates.

Results

Variation in the geometric mean of plant weights at harvest was found to be related to the number of days which elapsed between the emergence of seedlings in that group and final harvest (Fig. 3). The advantage to a seedling of early emergence is manifest. Where W is the mean log weight of plants in the group and t is the number of days from emergence to harvest, the regression accounts for 95% of the variance of W .

$$W = 0.2569 t - 2.0158 \quad (P < 0.001).$$

If the plants in the largest group had not suffered from interference, and the size of the plants in each group was directly related to the time from emergence, points would be expected to lie along the broken line in Fig. 3. The weights of later emerging groups fall well below this line, and the last groups to emerge consisted of plants which had barely exceeded their 'seed capital' (see Expt 3) 35 days after emergence. It is unlikely that even the plants in the earliest emerging groups had escaped interference, so that the real potential growth line is probably considerably steeper than that shown, and the proportionate suppression of the later emerging groups even greater than the graph indicates.

As an alternative to expressing the effect of actual emergence time on the performance of an individual, the position of that individual in the overall ranking of emergence times may be used. If comparisons are to be made between replicate populations, then the position of individuals in the emergence ranking of each population needs to be standardized. Here it has been expressed as the position which the individuals would have occupied had 100 seeds been sown ('percentage emergence ranking').

In this experiment, plants had been grouped according to emergence time, and the 'percentage emergence ranking' of each group was calculated from the time at which the median plant in each group emerged. Fig. 4 gives the relationship between the mean log plant weight for each group and the percentage emergence ranking for the group. The

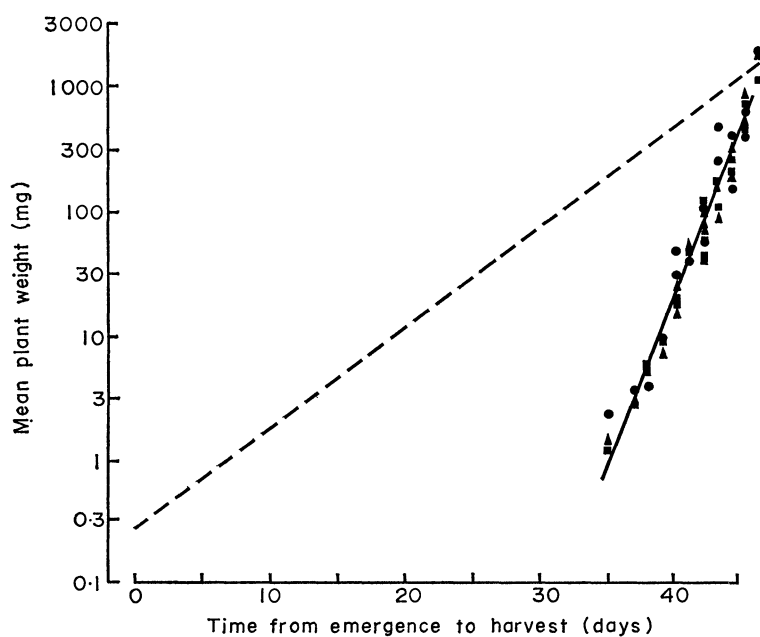


FIG. 3. Mean weight of groups emerging at different times. Replicated populations: ●, A; ▲, B; ■, C.

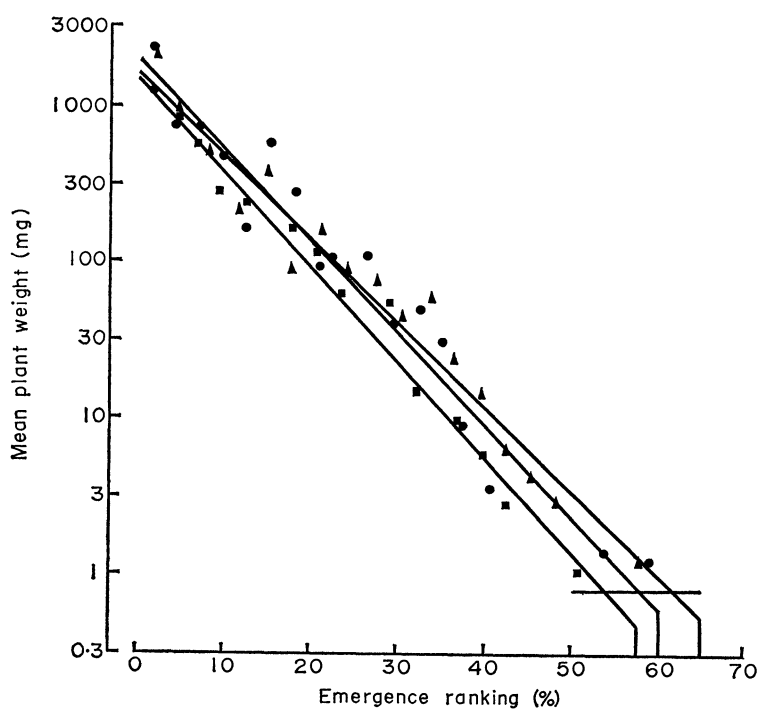


FIG. 4. Mean weight of emergence groups related to percentage emergence ranking of the group. Replicated populations: ■, A; ▲, B; ●, C.

method of representing the data shows that if an intercept, corresponding to the percentage of the sown seeds of each population which had emerged by harvest time, is extended to meet the regression line for that population, then the intercept point in each case falls within the 95% confidence limits of the initial 'seed capital' estimated from Expt 3. That this interception occurred may have been the result of a fortuitous selection of seedling density or harvest time. Alternatively, it may indicate that a dominance continuum exists, such that the last emerging seedlings are completely dominated, but still exert some pressure on those just up the hierarchy, and this is carried on, right up to the first emerging individuals.

It may be noted that, in data shown in Fig. 3, 95% of the variance in plant weight was accounted for by the number of days from emergence to harvest. This does not allow for any direct contribution from the spatial arrangement of the plants. Therefore, either the spatial arrangement is responsible for 5%, or less, of the weight variance, or the manifestation of spatial arrangement is confounded with the effect of emergence time.

Since the co-ordinates of each plant were known, it was possible to calculate, using a suitable computer program, the weight and number of neighbours in various concentric zones surrounding each individual. In testing the relationship between the weight of an individual and the weights or numbers of its neighbours, no consistent relationship could be found. This suggests that the zone of influence of most individuals by the time they were harvested was so extensive, and embraced so many neighbours, each adding to the total variance, that any underlying relationship was completely masked.

EXPERIMENT 3

It was established in Expt 2 that the advantage which early emergence confers on an individual is markedly greater than that which can be accounted for merely by the greater time for which it has been allowed to grow. It may be concluded that this advantage is due, at least in part, to the disproportionate occupation of space by the early emerging individuals, and that this advantage is at least maintained as the plant grows. In Expt 3 an attempt was made to estimate, in geometric terms, the advantage conferred by early emergence.

In order to avoid the limitations, particularly that of the constant direction of lighting, encountered in a growth cabinet the experiment was conducted in the glasshouse but precautions were taken to avoid unduly high background variance. So that emergence times of individuals would not be confounded with environmental fluctuations, four groups of seeds were sown at 3-day intervals. At a suitable date the most recently emerged seedlings were selected for the continuation of the experiment. This meant that in the combined population of quite uniform seedlings, those emerging late from the first population, a little earlier from the second and third populations, and the first emerging seedlings from the last sown population were represented. It also meant that when making comparisons between plants on the basis of time from emergence to harvest, the range of emergence times was increased beyond what would have been possible using a population of the same size in which all seeds were sown together.

Method

Two seedling cocksfoot populations termed 'restricted' and 'unrestricted' were grown throughout the course of the experiment. Plants in the unrestricted treatments arose from a single seed sown in the centre of a polythene pot of 7.4 cm diameter and 11 cm deep.

Plants in the restricted population also arose from a single seed sown in the centre of a pot and were free from neighbours for a radius of 2.1 cm, but, from this radius to the edge of the pot, a dense population of the same seeds was sown. A mechanical seeder gave a seeding rate of 2.5 seedlings per cm², and seeds were accurately covered with a further 1 cm of vermiculite.

Twice daily, the pots were examined for newly emerging seedlings appearing in the centre. The emergence ranking of seedlings within each group was noted, as well as the time at which the seedlings emerged. Within each group, the seeds in the centre of the pots and those around the perimeter were from the same seed source and germinated under similar conditions, so the same percentage emergence ranking which applied to central seeds within a group, also applied to the centre seed relative to the perimeter seeds. The mean number of seeds in the background population was 74.5 per pot, and provided a large enough sample to make meaningful the position of the central seed in the emergence ranking of seeds within each pot.

When the majority of the seedlings in the last sown group had emerged, the main growing period of the experiment started. From both the restricted and unrestricted populations, twenty-seven pots were taken from each sowing group, and three plants from each group were randomly allocated to each of nine harvest groups. Within the harvest groups, the three plants were allocated to blocks. Pots were then saturated with full nutrient solution and placed on the capillary bench.

Plants were usually harvested at 3-day intervals, the first harvest being taken when the plants were supplied with nutrient solution. At each harvest, the height and number of leaves were recorded, and the plant cut, just above the point of adventitious rooting, and the dry weight of the top taken.

Results

In a broad comparison of the restricted and unrestricted population (Fig. 5), it can be seen that after harvest 3 the two populations maintained markedly different growth rates. The unrestricted population, as might be expected, maintained exponential growth

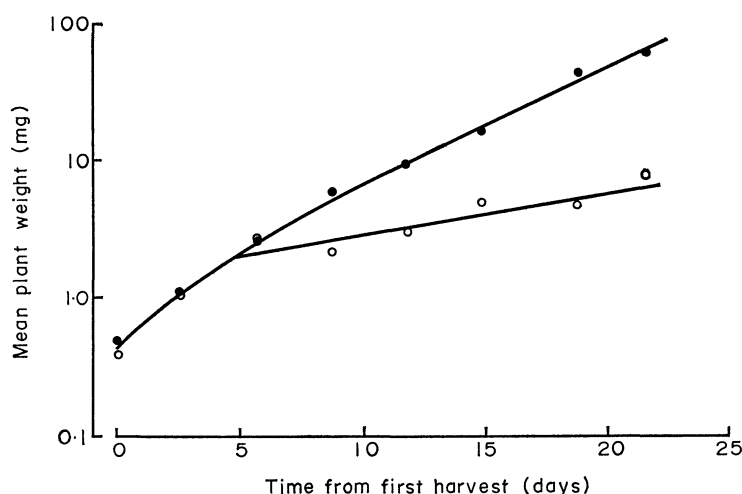


FIG. 5. Growth curves of 'restricted' (○) and 'unrestricted' (●) populations. The ordinate represents mean dry weight of above-ground parts (log scale).

throughout the period, while the growth rate of the restricted population departed from that of the unrestricted, but adopted a new exponential rate which it maintained. Such behaviour suggests that the decrease in relative growth rate (r), due to neighbours, occurs

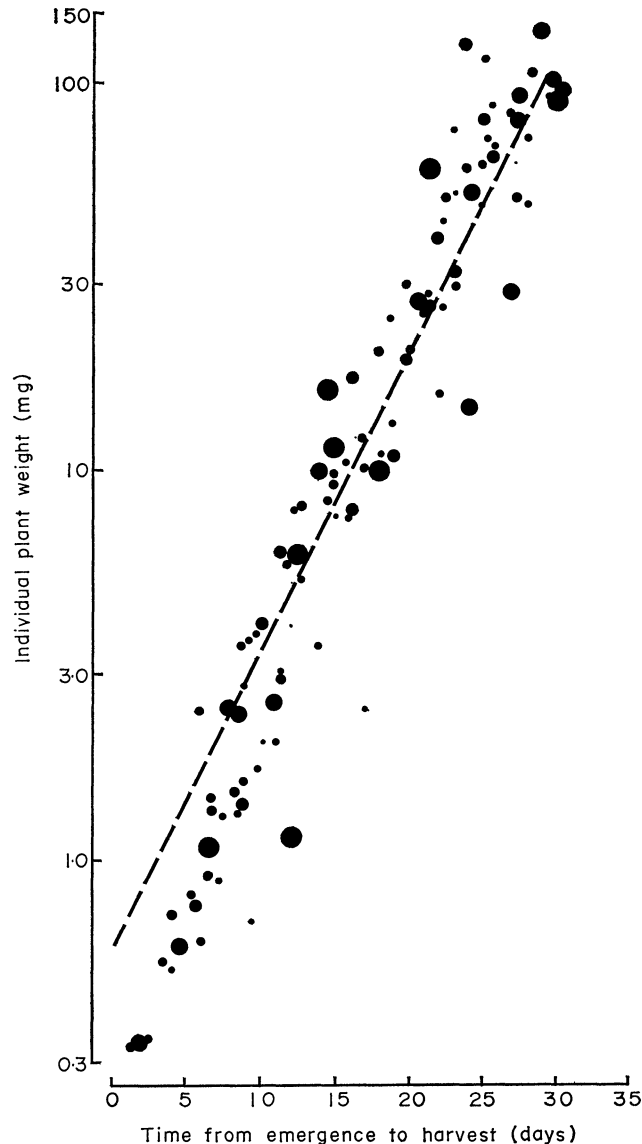


FIG. 6. Regression of weights of individual plants in the 'unrestricted' population on the time elapsed between emergence and harvest (see text).

early in the growth period. This is consistent with an hypothesis based on an early apportionment of 'space', which thereafter determines growth rate.

As illustrated in Fig. 6, the log weight of individual plants in the unrestricted population showed a significant regression on time from emergence to harvest. Where W is log plant weight at harvest, and t is days from emergence to harvest, the relationship is

$$W = 6.5618 + 0.1715 t \quad (P < 0.001).$$

In Fig. 6, point size represents emergence ranking, the larger points representing the earlier emerging plants. Points of different sizes are scattered evenly along the regression

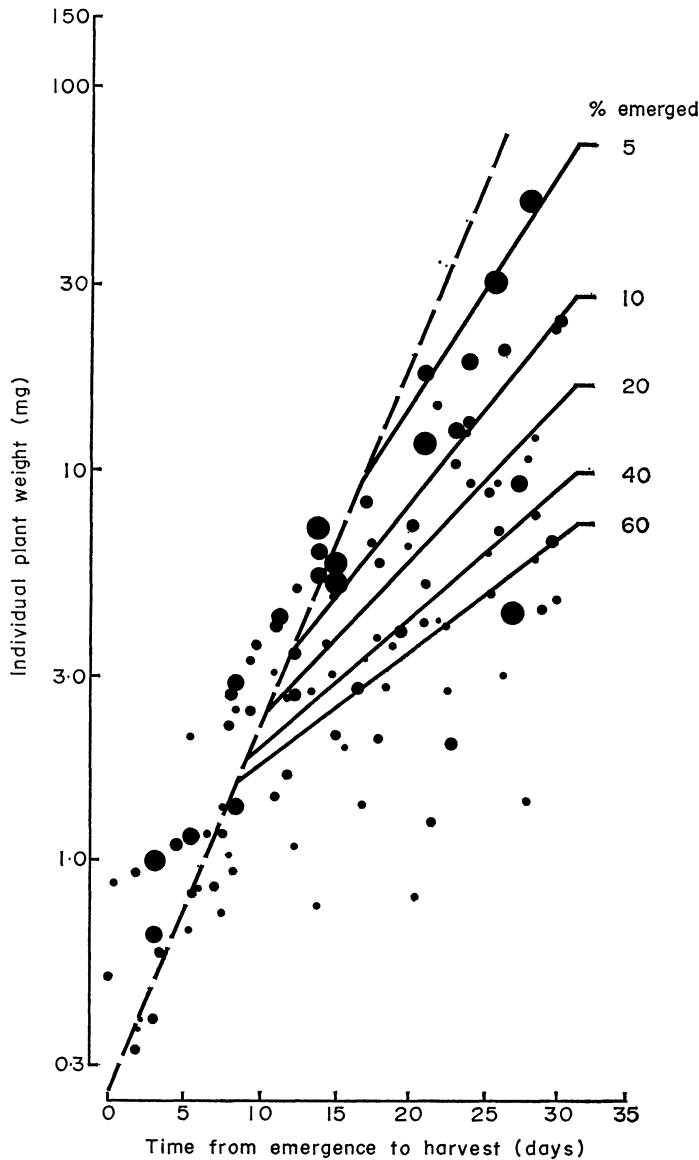


FIG. 7. Regression of weights of individual plants in the restricted population on the time elapsed between emergence and harvest (see text).

line, and emergence ranking does not account for significantly more of the harvest weight variance than is accounted for by t .

It can be seen from Fig. 6 that the intercept on the W axis, of the regression for harvests 4–9, gives an estimate of 'seed capital' at the date of emergence. When the mean seed intercept value (0.6642 mg) is divided by the mean seed weight (1.1108 mg), then an

estimate of the proportion of seed weight constituting 'seed capital' contributing to the weight of tops is obtained, and this is 59.8%.

In contrast with the unrestricted population, plants in the restricted population were markedly influenced by percentage emergence ranking, as well as the time which elapsed from emergence to harvest (Fig. 7). When the regression relationship from the unrestricted population (harvests 1–3) is superimposed on this graph, it can be seen that many of the points, particularly those representing early emerging plants, follow this line, and these represent plants which have experienced no interference. However, the majority of points deviate from this line. The continuous regression lines in Fig. 7 were obtained from multiple regression analysis in which time from emergence to harvest, and percentage emergence ranking, were the causal variables. As in Fig. 6, the larger points represent the earlier emerging plants. Fig. 7 shows that early emerging plants deviated from the unrestricted growth line late in their growth, and deviated only slightly. As plants emerged later, so they deviated earlier in their growth and deviations became more marked. Thus the dominance hierarchy is formed, with individual seed weights and early growth rates modifying the pattern to only a minor degree.

CONCLUSIONS

From this series of experiments it can be concluded that, during the emergence of a monospecific seedling population, a dominance hierarchy is set up, and this severely influences the future development of each individual.

Dominance by neighbours may be felt very early in the life of an individual. Fig. 7 shows that late-emerging seedlings deviated from their unrestricted growth rate after increasing their 'seed capital' only three times.

After the emergence of a seedling, the factor most influencing its future growth rate is the density of seedlings already emerged. Seedlings emerging subsequently may exert an influence, but to a considerably lesser degree. Weights of seeds from which seedlings emerged exerted a negligible effect in these experiments. Variation in the early growth rates of non-interfering individuals was much less than that produced by variation in emergence time. Seed weight, time of emergence and early growth rates of individual cocksfoot plants were not found to be significantly correlated.

The growth rate of individual seedlings was more directly related to emergence ranking than to the absolute time at which the individual emerged. Growth rate was also shown to be related to the three dimensional space available to the seedling. This suggests that an individual's potential for capturing resources is dictated by the number and proximity of neighbours already capturing resources.

Within the high density sward being considered, the zones of influence of individual plants appeared diffuse, with considerable overlap. The position of the plant within unseeded patches had little influence, suggesting that, wherever the plant was positioned, it was able to take considerable advantage of the unsown area. The failure to show any consistent relationship between the performance of a plant and that of its immediate neighbours also suggests that an individual is influenced by a large number of neighbours. Divergence of relative growth rates between early and late emerging individuals suggests that the earlier emergers continually increase their ability to capture resources at the expense of the later emergers, and in doing so increase their physical zone of influence. This appears to be the mechanism by which the distribution of plant weights within a

population becomes progressively skewed as the population grows (Koyama & Kira 1956), eventually leading to self-thinning, as observed by Yoda *et al.* (1963) and White & Harper (1970).

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SUMMARY

Capture of resources by individual seedlings during their establishment was studied in high density populations of *Dactylis glomerata*. Growth of each individual was most influenced by the density of previously emerged neighbours. Spatial distribution of neighbours exerted less influence and the effect of seed size was negligible.

The influence of emergence time in producing a divergence of individual growth rates following emergence is illustrated. Growth rates of individuals were also found to be directly related to the third power of their mean distance from neighbours.

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