

THE REGULATION OF PLANT AND TILLER DENSITY IN A GRASS SWARD

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Populations of higher plants may react to stress by variations in growth rate or by mortality (Harper 1961). Mortality tends to be a continuing process throughout the life of dense populations and Yoda *et al.* (1963), working with a variety of dicotyledonous species, showed that there was a formal mathematical relationship between the mean size of the surviving plants and the residual density at various stages in the development of a population. The number of surviving individuals is related to their mean weight as $w = cp^{-3/2}$, where w is the mean dry weight per plant, p the density of plants remaining in the community and c is a constant which varies with the species.

More recently it has been shown that this relationship applies to a wider range of species than originally considered by Yoda *et al.* and that even the rules followed by foresters guiding optimal thinning policy conform essentially to the same relationship (White & Harper 1970). However, no comparable study has been made of grasses or other vegetatively reproducing species.

A higher plant is, in a sense, itself a population. A classical interpretation of the shoot system is of a population within which the leaf with its axillary bud constitutes the unit: '... the whole plant is thus a matriarchal tribe of shoots, many generations of individuals living together, in dependence upon one another. In the upshot this leads inevitably to a certain competition between the generations, which profoundly influences their morphology' (Arber 1950, p. 136). The size of a plant is largely determined by variations in the number of these branching units rather than by large variations in the size of the units. In vegetatively reproducing species branches develop distinct root systems and may acquire a degree of or complete independence from one another with eventual severance from the parent plant. It is of much interest to determine how population regulation occurs in such a system where the size of a population may be reflected in the numbers of the genetic individuals (genets) present, or the number of vegetative units—tillers or ramets.

The exploitation of resources by plants in a community depends on their ability to make rapid physiological adjustments to changing conditions. The growth of neighbours itself constitutes such a change in the environment. It appears that characteristically a dominance hierarchy is established within mono-specific communities of plants which results in the frequency distribution of genet weights becoming skewed with time and approaching a log-normal 'hierarchical' distribution (Koyama & Kira 1956; Obeid, Machin & Harper 1967). In a population undergoing extensive self-thinning it is usually the smallest members of the hierarchy that are eliminated (Harper & White 1972). Ross & Harper (1970) have shown that in a grass population the hierarchy is largely determined by quite small differences in emergence time of simultaneously sown seed resulting in differing success of the various genets in the capture of space \equiv resources).

Grasses are appropriate experimental material for studies of population regulation in vegetatively reproducing species. The basal branching habit, whether intra- or extra-vaginal, is responsible for the development of a population of tillers. Tillers may die on plants that remain alive—some tillers may flower and die and others on the same plant may remain vegetative and continue to form daughter tillers. In such a situation it is of interest to discover whether there is any formal relationship between tiller density and tiller size or between genet density and genet size.

The tillers of *Lolium perenne** grow from within the sheath of the subtending leaf. Tillers may in turn give rise to secondary tillers and the degree of inter-dependence between these is complex. Before the formation of an adventitious root system, the young tillers are clearly dependent on the parent. After the root system has been formed the tiller may function as an independent unit but revert in times of stress, for example defoliation, to a degree of dependence on the parent plant (Marshall & Sagar 1965). However, the tiller, particularly in a sward, may be shaded by the leaves of its parent's shoot and *vice versa*, so that as the tillers become independent a struggle for existence might be expected to develop between them.

Thomas & Stepler (1971) have shown that in *Dactylis glomerata* and *Phleum pratense* there is a very regular relationship between the density at which a grass is sown and the rate at which its ramets multiply and grow in size. They considered only the first 8 weeks of growth from seed and extrapolation of their data suggests that populations would converge, irrespective of sowing density, at some common tiller density and tiller size if grown for longer periods. As part of a series of investigations on the regulation of plant populations tiller production, development and mortality have been examined in *Lolium perenne*.

EXPERIMENTAL METHODS

Populations of *Lolium perenne* (S23) were sown in plots 30 × 30 cm of sandy loam soil c. 1 m deep, in glasshouse beds at four initial densities (3.2×10^2 , 1×10^3 , 3.2×10^3 and 1×10^4 plants/m²), and at three light intensities obtained by the use of Tygan screens which gave (by selenium cell measurement) approximately 100%, 70% and 30% of full light intensity at ground level. The experiment involved a split plot design with four replications. Seed was sown on 12 February 1972 and harvests made on 3 and 24 March, 14 April, 2 June and 21 July. At harvest the central area of each plot, 20 × 20 cm, was taken and measurements were made of genet density, tiller density and mean genet dry weight. Mean tiller number and mean dry weight per genet were estimated from twelve randomly selected plants from within each replicate. The seedling shoot was counted as the primary tiller and secondary and subsequent tillers were counted as soon as they reached the two-leaf stage.

RESULTS AND DISCUSSION

The yields of dry matter per unit area are shown in Fig. 1(a–d). The growth rate declined at each harvest interval and negligible growth was made between the last two harvests when some populations actually lost weight. The growth rate was less in the reduced light intensities and under these conditions a lower 'plateau' value was obtained at the last harvests. Differences in the yield at different densities were apparent early in the growth

* Nomenclature follows Clapham, Tutin & Warburg (1962).

of the population but, as expected, became insignificant towards the end of the experiment. (It appears that at the lowest light intensity there was some real slight advantage of high sowing density.)

Yield is the product of the mean weight per genet and the number of genets per unit area, or the mean weight per tiller and the number of tillers per unit area—all four relevant measures change with time. Fig. 2(a-c) illustrates the changes in tiller and genet densities. In full daylight (Fig. 2a) there was very rapid tillering. Genets at low density produced, on average, twenty-three tillers per plant, but tillering was only slight at high densities (1.65 tillers per plant at the highest sowing density). Tillering was followed by

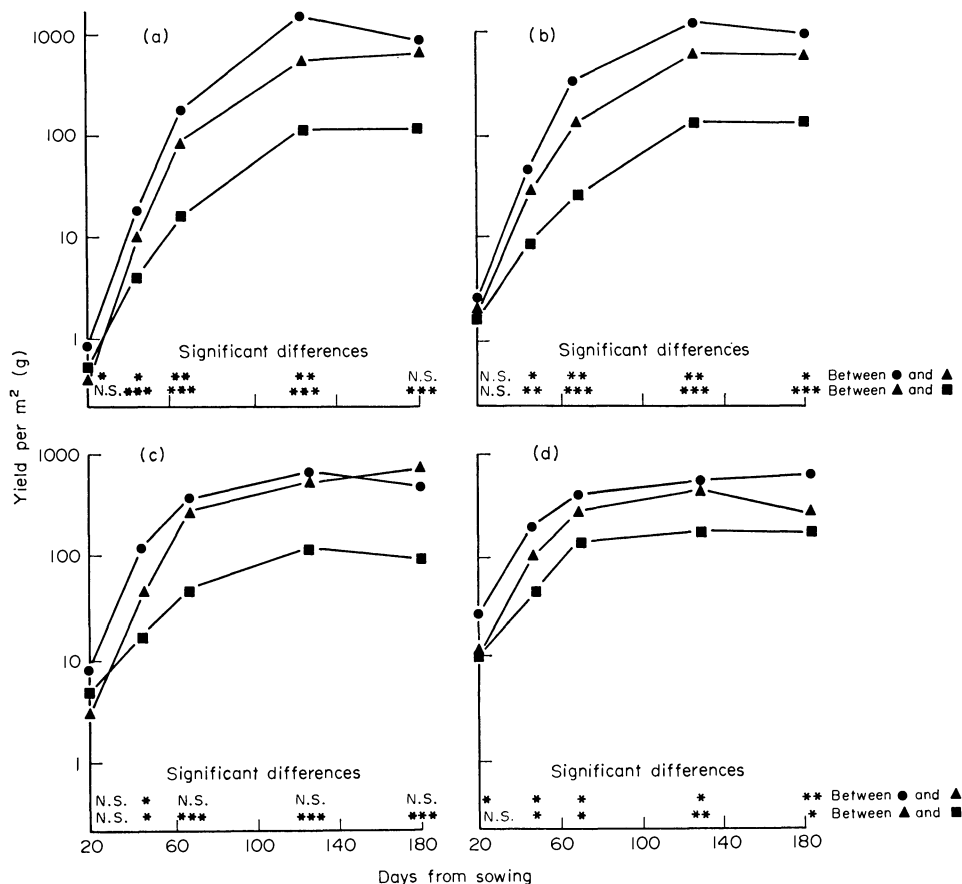


FIG. 1. The time course of production of dry matter by populations of *Lolium perenne* in full daylight (●), 70% (▲) and 30% (■) light intensity. (a) 320 seeds/m², (b) 1000 seeds/m², (c) 3200 seeds/m² and (d) 10 000 seeds/m² (note log scales).

(and probably overlapped with) tiller and genet death and the actual number of tillers present is the resultant of the two processes of multiplication and mortality. Total tiller numbers started to decline after the second harvest in the high density plots, after the third harvest in the intermediate densities and after the fourth harvest at the lowest density. The differential multiplication and mortality at the various sowing densities ensured that the 30.2-fold range of densities at the first harvest had become a 1.2-fold range by the fourth harvest (when there was no significant difference in tiller density). By

the final harvest there was a slight widening in the range of tiller densities as a degree of over-compensation occurred—the plots sown at low densities now had the slightly higher tiller densities.

At lower light intensities (Fig. 2a–c) tillering was reduced and in the lowest light

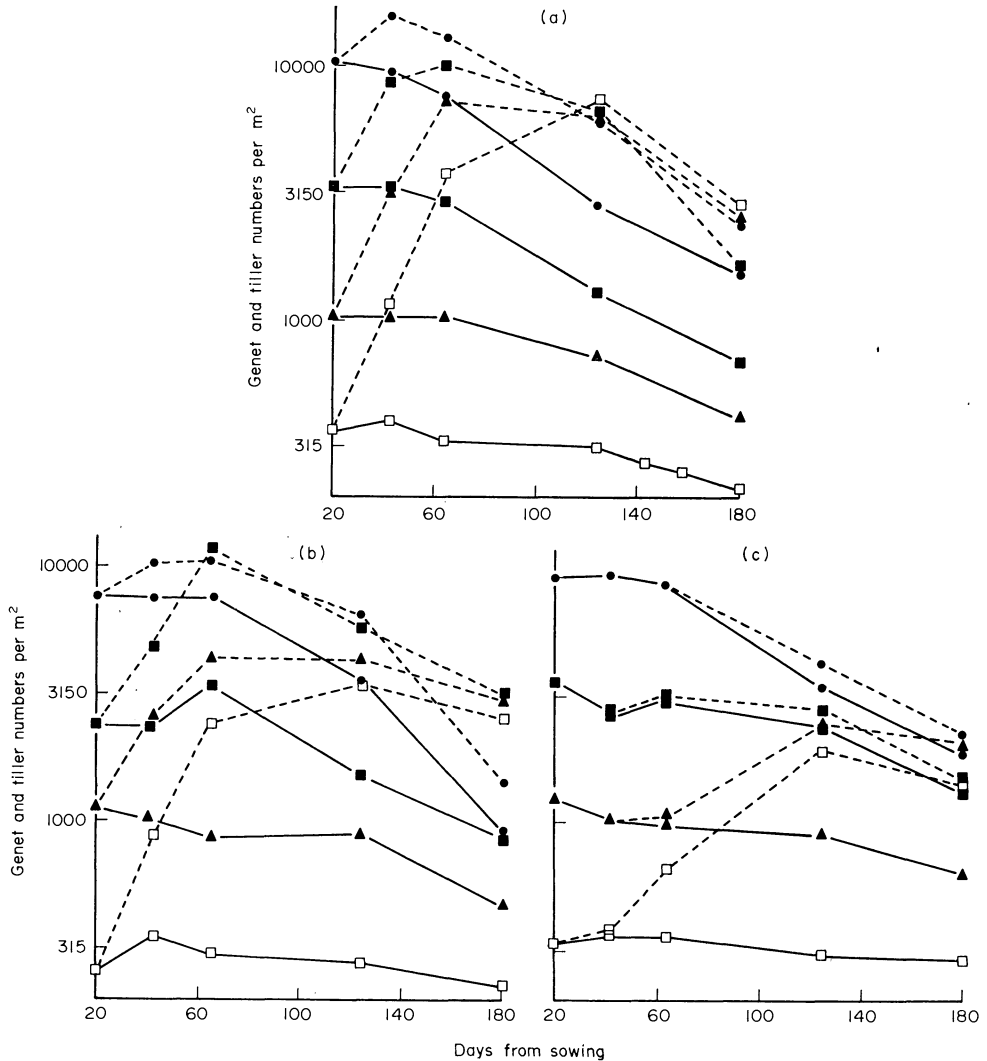


FIG. 2. Changes in the density of genes (continuous line) and tillers (broken line) of *Lolium perenne* sown at four densities: 320 (\square), 1000 (\blacktriangle), 3200 (\blacksquare) and 10 000 (\bullet) seeds/m². (a) Full daylight, (b) 70% light intensity, (c) 30% light intensity (note log scales). After 180 days from sowing, density of tillers is not significantly different, at the different sowing densities, at $P = 0.05$ in (a), (b) or (c). After 180 days from sowing, density of genes is significantly different, at the different sowing densities, as follows: (a) $P = 0.0001$, (b) $P = 0.001$, (c) $P = 0.0001$.

regime only at the two lowest sowing densities did the tiller density rise above the starting seed density. However, even at the highest sowing density, at which tiller numbers declined steadily from the second harvest, there was some tillering: whole genes were being lost from the population at a faster rate than the survivors produced new daughters

and the decline in overall tiller density occurred while there was an increase in the number of tillers per genet.

During the whole period of the experiment mean tiller weight was increasing at all light intensities. The changes in density and mean tiller weight are brought together in Fig. 3(a–c) and show how each population converges towards a tiller density–tiller weight value characteristic of the light intensity but remarkably free of influence of the initial sowing density. The whole process of compensation for differences in sowing density involved the integration of three effects: (1) a mortality of genets; (2) a differential multiplication of tillers; and (3) a differential mortality of tillers.

The mortality of genets can be assessed separately from that of tillers because during the whole length of the present experiment the identity of what were originally seedlings could still be recognized, though with increasing difficulty. The decline in genet numbers

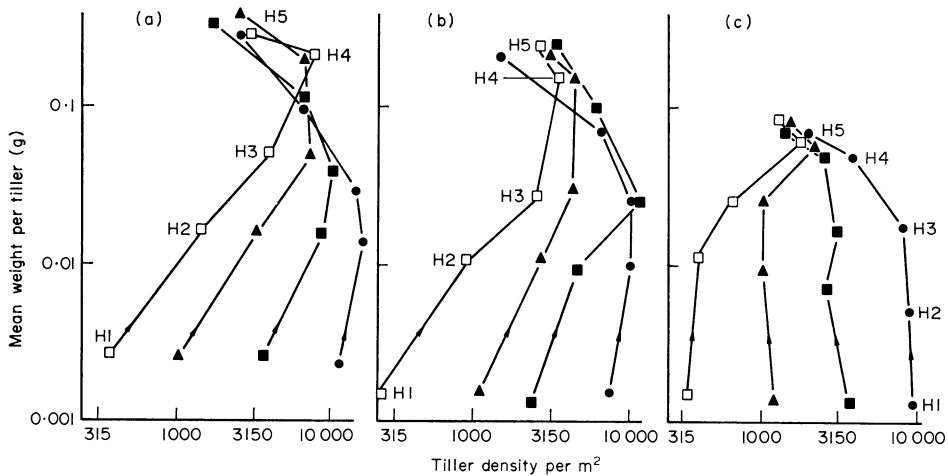


FIG. 3. The relationship between changing tiller weight and tiller density in populations of *Lolium perenne* sown at four densities: 320 (\square), 1000 (\blacktriangle), 3200 (\blacksquare) and 10 000 (\bullet) seeds/m² followed through five successive samplings H1–H5. (a) Full daylight, (b) 70% light intensity, (c) 30% light intensity (note log scales).

with time is shown in Fig. 2(a–c). The higher the sowing density, the earlier was the onset of genet mortality, but towards the end of the experiment in full light, the rate of elimination of genets had become relatively independent of density with a genet half-life of 6.5–9 weeks.

Fig. 4(a–c) shows the relationship between genet weight and genet numbers, which at full and 70% light intensity conforms strikingly with the $3/2$ thinning law. A thirty-fold range of sowing densities had narrowed in full light to a 6.3-fold range of genet densities by the final harvest and the increase in mean genet weight appears to be highly integrated with the rate of thinning. The grass genet is therefore behaving essentially like the genets of the dicotyledonous species without vegetative reproduction that had been studied previously. At the lowest light intensity (Fig. 4c), the thinning line lies at a slope of 1 or <1 . All populations that lie along a thinning slope of 1 have the same mean population weight so that any loss of individuals which occurs within such a population is only just compensated for by the growth made by the survivors. There is a comparable experiment on the effect of light intensity on the thinning process made by Hiroi & Monsi (1966)

and analysed by White & Harper (1970). The experiment involved the growth of sunflower and a typical $3/2$ thinning line was obtained at full light intensity but the slope of the thinning line was *c.* 1.0 at low light intensities. Such an influence of light intensity on the slope of the thinning line suggests that it is reduced light intensity within a sward that creates the stress responsible for the elimination of individuals. If a treatment such as nutrient application simply has the effect of changing the intensity of the stress but is not in itself the causal stress factor, the effect will be simply to move points up or down a constant thinning line. Only if it is the stress factor itself that is altered is the slope of the thinning line likely to be changed (White & Harper 1970).

Langer, Ryle & Jewiss (1964) followed the changes in plant, genet and tiller populations of swards of *Phleum pratense* and *Festuca pratensis* over 3 years in experimental populations out-of-doors. They noted a rapid loss of genets from their populations and a very marked seasonal rhythm of loss, elimination being fastest in the peak growing season, March–June; negligible loss occurred in the winter months. Their data suggest that there

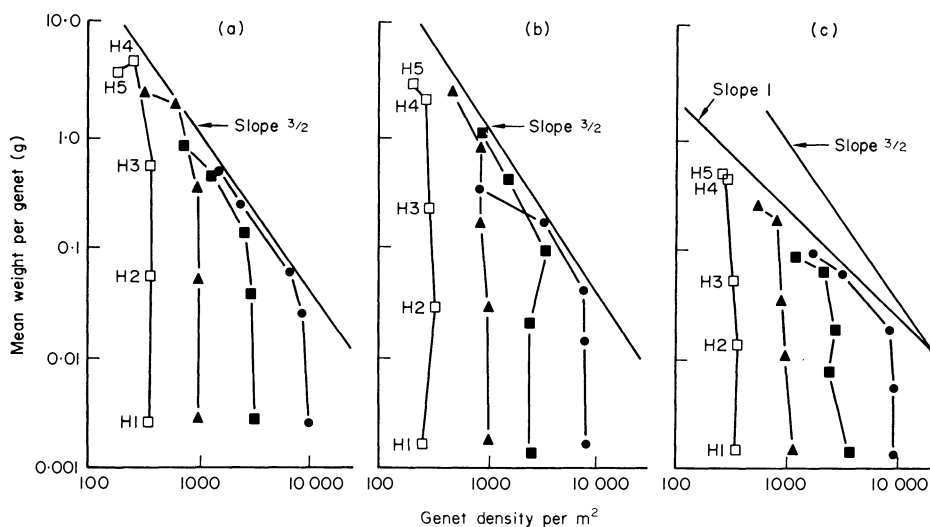


FIG. 4. The relationship between changing genet weight and genet density in populations of *Lolium perenne* sown at four densities: 320 (\square), 1000 (\blacktriangle), 3200 (\blacksquare) and 10 000 (\bullet) seeds/m² followed through five successive samplings H1–H5. (a) Full daylight, (b) 70% light intensity, (c) 30% light intensity (note log scales).

is a relatively constant annual risk of death to genets in the population on which is superimposed a marked seasonal rhythm. A similar pattern in the mortality risk was found by Antonovics (1972) for the grass *Anthoxanthum odoratum* and by Sarukhán & Harper (1973) for *Ranunculus* spp. In the experiments of Langer *et al.* (1964) the death risk was much reduced when cutting of the sward was frequent and higher densities of both tillers and genets were maintained under a frequent cutting regime than under hay and aftermath treatment. Taken together, the data of the present experiment with those of Langer *et al.* and Antonovics strongly suggest that it is density stresses in the sward that are responsible for controlling the death rates of genets and that these stresses are at their most intense during the period of active growth. It is perhaps surprising that genet death is so precisely related to the rate of growth of the survivors, suggesting that at least to the 20th week the genet is the effective unit of population regulation. The variation in

tiller numbers is comparable to the variation in branching and branch death in non-vegetatively reproducing species. The result of tillering, tiller death and genet death is to adjust the number of tillers to a density that is extraordinarily similar despite wide variations in sowing rate and light intensity. The experiments reported here were made under the artificial conditions of an unheated glasshouse in relatively small plots. Comparable thinning occurs on a field scale. Charles (1961) showed that in a sown pasture only 20% of the grass seedlings survived more than 2 months and survival had fallen to 10% before the swards were 12 months old. He sowed mixtures of strains of single species and was thus able to detect changes in the balance of genotypes within his population. He found a rapid change in the proportions of the strain depending on the frequency of defoliation and the fertilizer treatment applied.

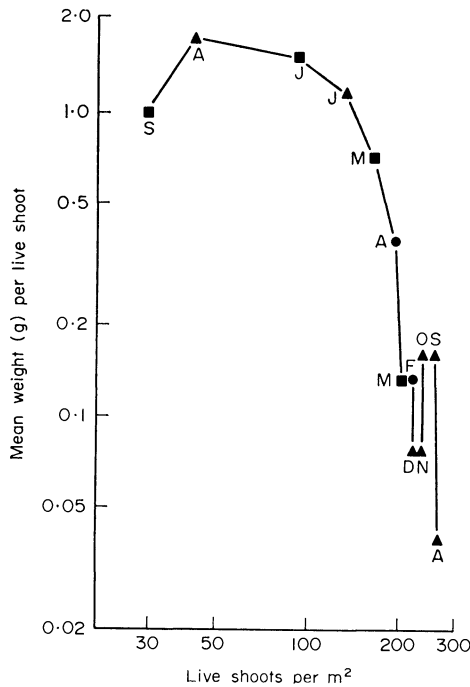


FIG. 5. The relationship between changing tiller weight and tiller density in a natural population of *Glyceria maxima* (calculated from data given by Matthews & Westlake 1969). The months of sampling are indicated: ▲, directly determined; ■, indirectly determined; ●, determined from previous year's data in part.

Most studies of death rates in grass populations have been made in deliberately sown swards. There is, however, interesting evidence that a similar thinning process occurs in natural populations of a wild grass. Matthews & Westlake (1969) estimated productivity in a population of *Glyceria maxima* and presented their data in a form which enables the relationship between tiller density and mean tiller weight to be calculated (Fig. 5). *Glyceria maxima* produces young shoots in the autumn at high density; their weight and number change only slightly during the winter but start into rapid growth between March and April. From April to July continued growth of tillers occurs synchronously with the elimination of tillers from the population. After July the plants make little extra growth in shoot dry weight and start to flower and senesce. The aerial parts then die back and new daughter shoots are produced in the autumn, again at very high density.

None of the experiments described in the present paper included plants that flowered—the populations remained vegetative through the growth period. Tiller death has often been reported as coinciding with the period of grass flowering (the grass tiller is monocarpic) but it may also be that the rise in height of the flag leaf canopy that occurs in a flowering sward creates a new shaded environment for the vegetative tillers and may be responsible for an increased death rate amongst them at this phase. Further experiments are required before the integration of the flowering process into the experimental model can be made effective.

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SUMMARY

Populations of *Lolium perenne* were sown at a wide range of densities and allowed to develop without defoliation under full daylight and under reduced light intensities. The multiplication of tillers, the growth in their mean weight and the death of genetic individuals (genets) acted together to regulate the character of the population and to determine that the density of tillers per unit area became independent of sowing density. The rate of elimination of genets from the population was related to the rate of growth of the survivors according to the 3/2 thinning law, but under low light intensities the thinning process was radically altered in a way that suggests that the density stress within the grass populations was caused by mutual self-shading.

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