# オーチャードグラス個体群における個体の生長と枯死III


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# Mortal Response and Growth of Individual Plants in a Population of Orchardgrass (*Dactylis glomerata* L.)

## III. Relationship between tiller density and tiller weight

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## Introduction

Studies on the self-regulation of plant numbers in populations of grass species have made rapid progress recently. However, the ultimate causes of the density-dependent death are still obscure. Most of the studies on population which have been made on plants in natutal and artificial populations suggest that mortality is a continuing risk through the life of the plant, continually adjusting the plant numbers in the population in relation to the increasing size of the plants[1,9,15]. A very important aspect of these works is that they examine both the response of numbers and of individual plant size (i. e. both mortality and plasticity) to changing density.

In previous papers[12,13], we reported that changes in tiller numbers per plant could be termed plant plasticity, and self thinning might occur initially by tiller mortality rather than by plant mortality. This change in number of tillers per plant is commonly observed at all densities, but is more pronounced in higher densities. These results is helpful to reinforce the observation of NAYLOR[9] that high density grass populations become increasingly dominated by small number of heavy, well-tillered individuals, so that the distribution of number of tillers per plant is positively skewed, i. e. most individuals have tillers smaller than the mean tiller number. In this case, a large proportion of dead material may occur in both large or small plant, but plants with fewer tillers must have a smaller chance of survival. Some weeker plants with fewer tillers may gradually reduce the number of tillers under continued stress, then tiller and plant mortality must finally become identical for these weaker plants as is stated previous paper[13]. Because of undergoing extensive self-thinning in a population, it is usually the smallest members of the hierarchy that are eliminated[5].

As a part of a series of investigations on the self regulation of plant populations, tiller production, development and mortality have been examined with orchardgrass (*Dactylis glomerata* L.)

## Meterials and Methods

Orchardgrass (*Dactylis glomerata* L.) was used as the material in the present experiment.

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The seeds were sown on 10 May 1974 in regular square disposition with spacing of 10.0 cm, 7.7 cm, 5.0 cm, 3.8 cm, 3.3 cm, 2.5 cm and 1.7 cm in both directions, i. e. 100, 169, 400, 676, 900, 1600 and 3600 plants/m$^2$ in plant density, respectively. These plots were abbreviated as 100-D, 169-D, 400-D, 676-D, 900-D, 1600-D and 3600-D, respectively. Their areas were 1.5 m×0.75 m (1600- and 3600-D), 1.5 m×1.5 m (676- and 900-D), 1.5 m×2.0 m (400-D), 1.5 m×3.0 m (169-D), and 1.5 m×5.0 m (100-D), and randomized block layout with three replications was used. The field soil was sufficiently fertilized with chemical fertilizers prior to sowing.

Harvest was started on 7 June, and hence was carried out every 7 days until 26 July. Mean tiller number, leaf area and dry weight per plant were measured for thirty randomly selected plants within each plot. The measurement was the same as used in the previous experiment[13].

The experiments were carried out at the experimental field in Ayashi, Miyagi Town, Miyagi Prefecture in 1974.

## Results

The mean weight per plant and the surviving density are shown in **Fig. 1**. The mean plant weight at the first harvest on 7 June slightly was reduced with decreasing density. (It appears that during the early stage of growth there was some cooperative interaction at high densities.) However, individual plant weight progressively reduced with increasing density, differences in the mean plant weight among different densities became apparent toward the end of the experiment. As is shown in Fig. 1, the higher the sowing density, the earlier was the onset of plant mortality, and the time sequence of thinning in the highest density indicated a rather constant death rate over the period of the experiment. Self-thinning were

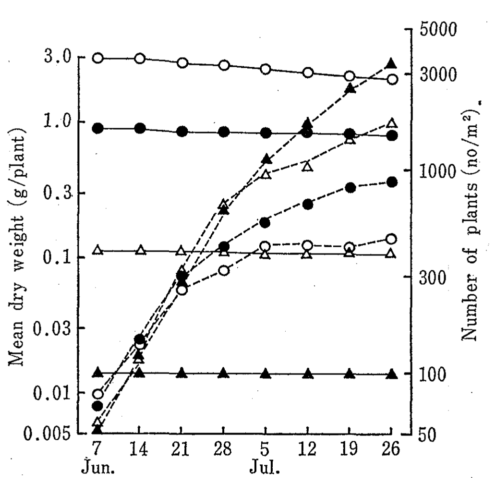


Fig. 1. Effect of plant density on changes in numbers (continuous line) and dry werght (broken line) of plant with time. (○) 3,600 plants/m$^2$, (●) 1,600 plants/m$^2$, (△) 400 plants/m$^2$ and (▲) 100 plants/m$^2$.

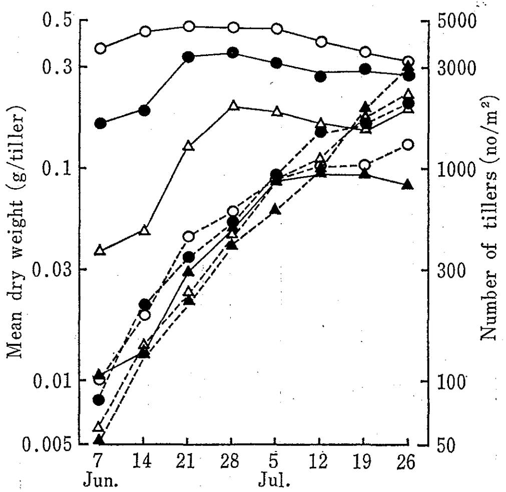


Fig. 2, Effect of plant density on changes in numbers (continuous line) and dry weight (broken line) of tiller with time. (○) 3,600 plants/m$^2$, (●) 1,600 plants/m$^2$, (△) 400 plants/m$^2$ and (▲) 100 plants/m$^2$.

not recognized in plots where the initial plant density was lower than a certain level; the critical level was around 400 plants/m$^2$.

**Figure 2** illustrates the time course of the changes in the number of tillers and the mean weight per tiller. Total tiller numbers started to decline after the third harvest (on 21 June) in the highest density (3600 plants/m$^2$), and after the fourth harvest (on 28 June) in the intermediate densities (1600 and 400 plants/m$^2$). Very rapid tillering was observed, in contrast, in the lowest density (100 plants/m$^2$). Towards the end of the experimental period, however, the rate of reduction of tillers in each density had become relatively independent of initial plant density. The number of tillers at each havest was correlated with the corresponding initial plant density. In early stage of growth, mean tiller weight in high densities were higher than those in lower densities, and after the fifth harvest the growth rate considerably declined in high densities.

The ralationship between the mean weight per plant and the surviving density is given in **Fig. 3** on log/log co-ordinates. The intensity of competition as indicated by mean plant weight rose with increasing density and mean plant weight became remarkably increased with decreasing density. These relationships between the surviving plant density and the mean plant weight at each harvest supported the existence of the C-D (Competition-Density) Effect[6] except for the highest density plot. However, it was not observed that the rate of growth of the survivers was positively related to the plant death, and the relationship between the surviving plant density and the mean plant weight conformed with the 3/2 thinning law was not recognized. On and after 19 July, in the highest density plot (3600-D) the decline in plant numbers and the increase in mean plant weight with time were recognized only slightly.

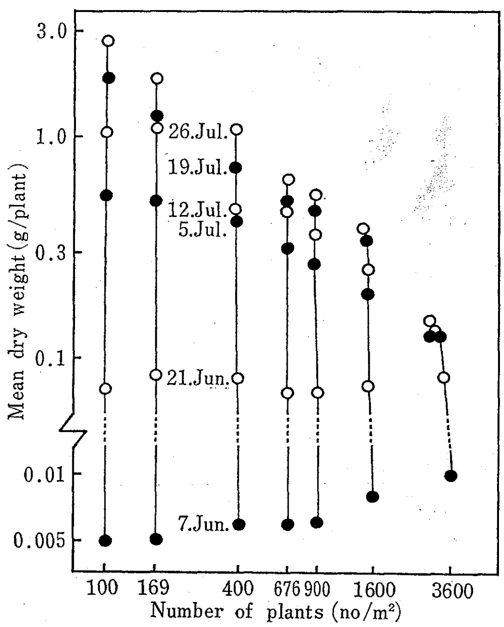


Fig. 3. Changes in numbers and individual plant weight with time.

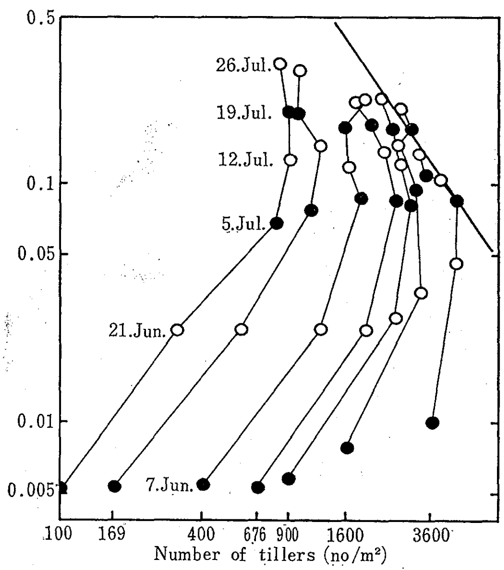


Fig. 4. Changes in numbers and weight of tillers with time. The thick line illustrates the theoretical −1.5 slope predicted by the thinning low.

**Figure 4** shows the relationship between tiller weight and tiller number in populations of seven different densities. Each population was not free from influence of the initial plant density. From the variation in growth exhibited on the graph, it appears, therefore, that no single thinning process would suffice for all densities. In the later stage of the experiment, however, the thinning process started to conform strikingly to the thinning line of the gradient value of $-1.5$ after the fifth harvest (5 July) in the highest density, after the seventh harvest in the plot of 1600-D and at the final harvest in the plot of 900-D.

## Discussion

Self-thinning, the term used by YODA *et al.*[15] to describe mortality of plants in a population under overcrowded conditions, takes place when the environmental capacity of a habitat is exceeded by a population development. The relationship between the number of surviving individuals and their mean dry weight may be derived from a simple geometrical model relating weight to the area a plant occupies[15]. The area occupied by an individual plant (S) is proportional to a linear dimension of the plant (L) as $S \propto L^2$. The weight of an individal (W) is also proportional to L, i. e. $W \propto L^3$, therefore, $W \propto S^{3/2}$. The area S is also proportional to density (P), assuming that thinning occurs when the total stand cover exceeds 100% and operates to maintain 100% cover, as $S \propto 1/P$. From the above argument the relationship $W = C \cdot P^{-3/2}$ is readily derived. However, no confirmatory study has been made of grasses or other vegetatively reproducing species.

In a series of these experiments with orchardgrass (*Dactylis glomerata* L.) grown under a wide range of densities, it was found that there was the above mathematical relationship between the length of tiller (h) and the dry weight of a tiller (w) at least in the first nine weeks as shown in **Fig. 5**. The leaf area of a tiller (s) was also proportional to a linear dimension of the length of tiller (h) as $s \propto h^2$ in these experiments. This fact may be an evidence to support the interpretation that tillers are also the unit of population regulation in grasses.

NAYLAR[9] showed that nevertheless the total number of tillers in the high density perennial ryegrass (*Lolium perenne* L.) populations started to decrease in the later stage, the larger individuals still continued to grow and produced more tillers, while the majority of individuals either lost tiller or, at best, produced no new tiller. A similar pattern in the frequency distribution was also observed for plant weight in his experiment. Several workers have described a change from normality to positive skewness in weight distribution with advence of population growth[7,10,11]. They showed that the degree of skewness increased with time and was

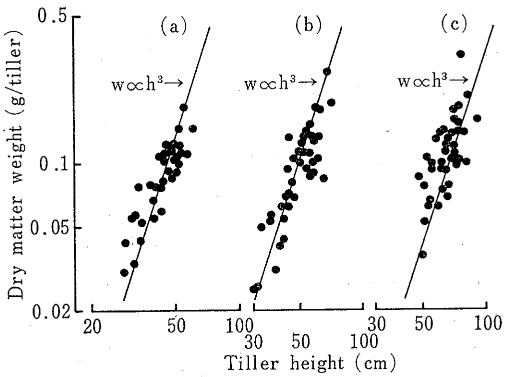


Fig. 5. Relationship between tiller weight (w) and tiller height (h) after 60 days from sowing in population of *Dactylis glomerata* sown at three densities: (a) 36 plants/m², (b) 100 plants/m², and (c) 400 plants/m².

greater in higher densities. WHITE and HARPER[14] working with populations of rape (*Brassica napus* L.) and radish (*Raphanus sativus* L.), and FORD and NEWBOULD[2] working with coppice shoots of *Castanea sativa* showed that, under stress conditions that resulted in thinning, the smallest individuals in a population were the first to die. The mortality of tillers, however, may occur on the majority of individuals in the population[9]. Under continued competitive conditions at higher densities, therefore, a chance of survival of small plant with fewer tillers may be smaller than that of larger plants. In the present investigation, the higher the plant (genet) density, the earlier was the onset of tiller mortality (Fig. 4), and the majority of individuals in the highest density plot (3600-D) had consisted of only a single tiller throughout the whole period of the experiment. Taking together the data of the present experiment with those of WHITE *et al.*[14], FORD *et al.*[2] and NAYLOR[9], it is suggested that the mortality of tillers is directly related to the rate of growth of the surviving tillers that eventually tiller and plant mortality become synonymous in higher densities. Weaker individuals in high density populations continued to lose their tillers under continued stress, and would finally consist of only a single tiller. However, during this stage (after the start of extensive growth), there was very little increase in mean weight per plant (genet) (Fig. 3), with no apparent density-induced thinning. Thus the plant did not conform to the $-1.5$ power equation through time, although the relationship between mean plant weight and density conformed to the competition-density equation. In cotrast, the relationship between tiller weight and tiller numbers in higher densities conformed considerably with the power equation. The conclusions of KAYS and HARPER[5] that plants (genets) of *Lolium perenne* follow the $-1.5$ thinning relationship, but that tillers do not, must therefore be reconsidered by the present serial experiments with plants of other vegetatively reproducing species. HARPER[4] has pointed out that the populations are adjusting the effective density of tillers per plot throughout the experiment and the number of tillers at any time is the consequence of (i) differential mortality of genets, (ii) differential birth rates of tillers per genet and (iii) differential death rates of tillers.

In the present experiment, the populations were allowed to develop without cutting under full daylight in experimental field. LANGER, RYLE and JEWISS[8] showed that the death risk of individuals and tillers in the population of timothy (*Phleum pratense* L.) and meadow fescue (*Festuca elatior* L.) was much reduced when cutting of the sward was frequent, and that higher densities of both tillers and plants (genets) was maintained under a frequent cutting regime than under hay and aftermath treatment. Their data suggest that plant (genet) and tiller mortality are mainly related to the rate of growth of the survivors. This concept, therefore, contradicts Darwin's view[3] to an extent that mortality is concentrated in the seedling stage. If the number of surving tillers is strictly related to their mean weight in accordance with the 3/2 power law of YODA *et al.*[15] in a grass population, the possible maximum density of tillers for a given average tiller weight brought about by self-thinning can be calculated from the power equation.

During the period of vegetative growth, the tiller death is obviously attributable to the development of the population exceeding to the environmental capacity of the habitat, but the tiller death subsequent to this vegetative phase is probably not related to the power equation. The rise in height of the flag leaf canopy in a flowering sward creates a new shaded environment under which the vegetative tillers are intercepted from sun light, so that the time of tiller death coincides with the period of grass flowering (cf. KAYS and HARPER[5]).

## Summary

Orchardgrass (*Dactylis glomerata* L.) were grown at various densities in experimental field. The development of plant (genets) and tillers in each density were investigated.

Although the relationship between mean plant weight and density had a tendency to conform to the so called competition-density law, the development of the plant population in higher densities was not conformed to the $-1.5$ power law through time. Tiller death took place in the majority of individual plant in the population and the rate of growth of surviving tillers was related to the tiller death. Consequently, the changes in tiller densities in various plant densities were showed to follow the common thinning line in the period of vegetative growth. However, during the reproductive phase and under a frequent cutting treatment, it was considered that the relationship between mean tiller weight and tiller density might alter with the lapse of time, with no density-induced thinning.

The results were discussed by comparing with those obtained from other studies on grass populations.

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# オーチャードグラス個体群における個体の生長と枯死

## III. 分けつ密度と平均分けつ重の相互関係

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## 要　約

本試験は，オーチャードグラス実験個体群を用い，7段階の密度処理のもとで，株数減少と茎数変化との相互の関係を調べ，個体群内におけるいわゆる natural thinning 現象がどの様に起っているのかを明らかにせんとして行われた。

各密度区間において，平均個体（株）重と現存株密度との間に，競争密度効果とみなしうる相互関係は認められたが，高株密度側において個体（株）重の増加に伴う密度の減少経過の現われ方が不明瞭であり，ここでの現存株密度が，3/2 乗則の場合の個体密度に相当しているかは明らかでない。

一方，個体（株）の重量増加は，茎数増大と密接に関係しており，特に高株密度の側で単位面積あたり現存分けつ密度と平均分けつ重との両者間の経時的な軌跡が，傾きほぼ −1.5 の直線に沿って得られたことから，既報[12]で指摘したように，イネ科牧草個体群内における密度の調節は，株数に対するそれよりも，各 shoot に対する調節を先行させている可能性が大きい。

しかし，こうした密度調節の可能性が，生殖生長の段階や再生長の場面で存在するのか，存在するとすればどの様な存在様式をとるのかは今後の問題点として残された。

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