THE CONTROL OF TILLERING IN THE BARLEY PLANT

I. THE PATTERN OF TILLERING AND ITS RELATION TO NUTRIENT SUPPLY

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Summary

The tillering patterns of barley plants were followed from germination until grain maturity under a variety of nutrient regimes. Where nutrients were supplied solely before germination, tiller emergence was restricted to two periods in the development of the plants, and the extent and duration of tillering in the first phase was governed by nutrient supply. The period of non-tillering which followed was not due to the absence of tiller buds and could be terminated at any time by the application of nutrients; the recommencement of tillering late in the development of the plant was not directly related to the development of the early tillers.

When nutrients were renewed throughout growth, tillering was essentially continuous. An early phase of tillering which approached an exponential rate at high nutrient levels was succeeded by a practically constant rate of tillering for the remainder of the experiment.

These relationships are discussed with respect to the control of tillering and the annual habit of growth.

I. INTRODUCTION

Since the pioneer studies of Engledow and Wadham (1923), the importance of tillering capacity as a determinant of cereal yield has been fully recognized. The control mechanisms governing tiller growth have also been frequently studied (Watson 1936; Gregory 1937; Leopold 1949) but no complete picture has emerged. Gregory (1937) stressed the importance of mineral nutrients as a primary factor in tillering and this has been borne out by agricultural experience (Hunter and Hartley 1938). Leopold (1949), on the other hand, provided evidence for the operation of a system of apical dominance in the cereal plant, the inhibiting influence of the apex on tillering being replaceable by an exogenous source of α-naphthaleneacetic acid. Several hypotheses have been advanced to integrate the effects of apical dominance system on the one hand and of the level of mineral nutrition on the other in dicotyledonous plants (van Overbeek 1938; Went 1939; Gregory and Veale 1957). These workers consider that auxin controls the distribution of "nutrients" (both mineral and otherwise) and that axillary bud growth is governed by the resulting nutrient availability. It would be of interest to ascertain whether a similar system operates within the cereal plant but two factors render this difficult to determine. Firstly the stem apices are concealed and hence difficult to manipulate and, secondly, the tillers rapidly produce adventitious roots and become, at least partially, independent of vascular connections with the remainder of the plant. This second factor results in the system under consideration being partially one of competition between a number of individuals.

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Perennial grasses present very similar problems and the relationships between initiation, growth, and senescence of tillers and the development of the tiller apices have been the subject of several reports (Cooper 1951; Lamp 1952; Langer 1956). The basic difference between these plants and cereals, the perennial habit, has been stated (Cooper and Saeed 1949) to be due to differences in the balance between a tendency to rapid floral initiation and subsequent tiller senescence and a tendency to slow vegetative development. Similar studies, involving the tracing of the life histories of individual tillers, have not been carried out with cereals, although Watson (1936) found that only fruitful tillers survived until harvest in the wheat plant. In his experiments, tillering was suppressed late in development despite adequate nutrition. This suggests that a progressive suppression of tillering with age also contributes to the annual habit of the cereal plant.

It seemed appropriate to initiate a study of the mechanisms controlling tillering in barley with a re-examination of the effects of nutrient supply, especially with reference to the influence of different rates and times of application in relation to development. Attention has been given to correlations between tillering and developmental stage to provide comparisons with the known relationships in perennial grasses, and to form the basis for a more complete understanding of the relationship between apical dominance, apical age, and nutrient supply.

II. EXPERIMENTAL METHODS

(a) Experiments 1 and 2

Barley plants (*Hordeum distichum* cv. Piroline (experiment 1), cv. Prior (experiment 2), were grown in 6-in. pots of compost (John Innes) in an open-sided glass-house. Plants in the first experiment were sown in January and grown until July; in the second experiment they were sown in July and harvested repeatedly until December. The tillers on plants in the first experiment were labelled weekly as they emerged from the sheath of the subtending leaf and the ears were later labelled with the date of anthesis; in the second experiment the tillers were counted weekly on one group of plants while sample plants were taken from another group for dissection. The total number of tiller "buds" (tillers less than the length of the subtending leaf sheath) visible to the eye was recorded from these plants. Replication was sevenfold in the first experiment and sixfold in the second, duplicate samples were taken for tiller-bud determinations.

(b) Experiments 3 and 4

Barley plants (cv. Piroline) were grown in 6-in. earthenware pots containing vermiculite, and resting on a larger container, in the same open-sided glass-house as in the previous experiments. Both experiments commenced in March and ran for approximately 20 weeks. The application of mineral nutrients was made in three basic ways:

(1) Total amount supplied pre-emergence, none subsequently.

(2) Total amount split into two or more fractions applied at different intervals through plant development.

(3) Nutrients replaced completely at weekly intervals.

In all cases the volume of solution applied was such that a certain proportion drained through the vermiculite and collected in the lower container. This solution was recycled through the vermiculite daily. Losses from transpiration and evaporation were corrected by making up the solution in the lower container to the initial volume at least once a week, when the solutions in treatment (3) were replaced, and more frequently when transpiration was rapid. The constituents (g/plant) of the nutrient solution used were as follows: $NaNO_3$, $1\cdot82$; $Ca(NO_3)_2.4H_2O$, $5\cdot13$; KNO_3, $1\cdot58$; $NaH_2PO_4.2H_2O$, $3\cdot14$; $MgSO_4$, $1\cdot85$; $FeC_6H_5O_7.5H_2O$, $0\cdot12$; H_3BO_3, $0\cdot014$; $MnSO_4$, $0\cdot007$; $ZnSO_4.7H_2O$, $0\cdot001$; $CuSO_4.5H_2O$, $0\cdot0004$; MoO_3, $0\cdot0005$; in
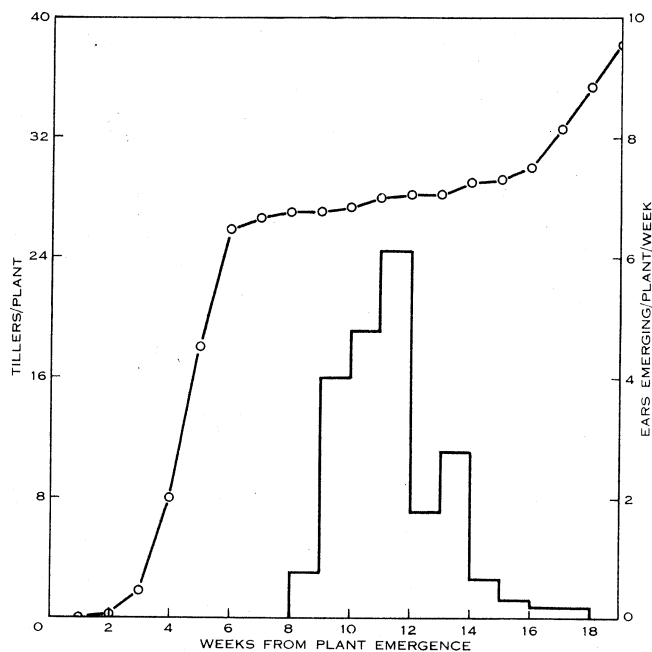

Fig. 1.—Tillering and ear emergence of barley (cv. Piroline) grown in potting soil, experiment 1. ○ Tiller numbers; histogram: number of ears emerging per plant per week.

500 ml of distilled water.* The total number of tillers and ears were counted weekly and senescent tillers, defined as tillers with all leaves dead, were recorded. Replication was sixfold in the case of experiment 3 and fivefold in experiment 4. Statistical analysis was carried out on the data following a logarithmic transformation and only significant ($P = 0\cdot05$) variations are discussed.

III. EXPERIMENTAL RESULTS

(a) Plants Grown in Soil

The barley plants, cv. Piroline (experiment 1), showed two clear phases of tiller production (Fig. 1). There was an early rapid rise in the rate of tillering reaching

* Standard solution, referred to subsequently as "100% solution".

a maximum at 5–6 weeks from germination and followed by an equally rapid decline. The plants then entered upon a phase of very slow production of new tillers which lasted for some 9–10 weeks. During this period, the majority of the early tillers came into ear, and finally there was a rapid increase in the rate of tiller production

Fig. 2.—Typical tillers produced on barley (cv. Prior) at the time of
ear emergence of the principal tillers.

in the last 3 weeks of grain ripening on the early tillers. The tillers produced in this late stage of growth had extremely reduced laminae on the first leaves (Fig. 2) and in only a few cases did they produce adventitious roots. Frequently they elongated from nodes on the parent tillers which were well above soil level and any roots which did develop were desiccated before reaching the soil. Ear emergence was rapid on these tillers and the ears had fewer spikelets than those on early tillers.

Barley plants (cv. Prior) grown in the second experiment also exhibited a two-phase type of tillering pattern (Fig. 3). Counts of unexpanded tillers and tiller buds were taken from the beginning of the phase of slow tillering. Throughout this phase, until the second increase in tillering rate, the numbers of unexpanded tillers remained relatively constant at between 25 and 35 per plant. The number declined slightly during the second peak of tillering and this decrease was accentuated by the senescence of a number of the tiller buds which did not expand during this period. Of the tiller buds and unexpanded tillers present on the plant at the end of the phase of reduced tillering, approximately one-third elongated in the second phase of tillering and one-third died during this final period. Tiller buds on the newly
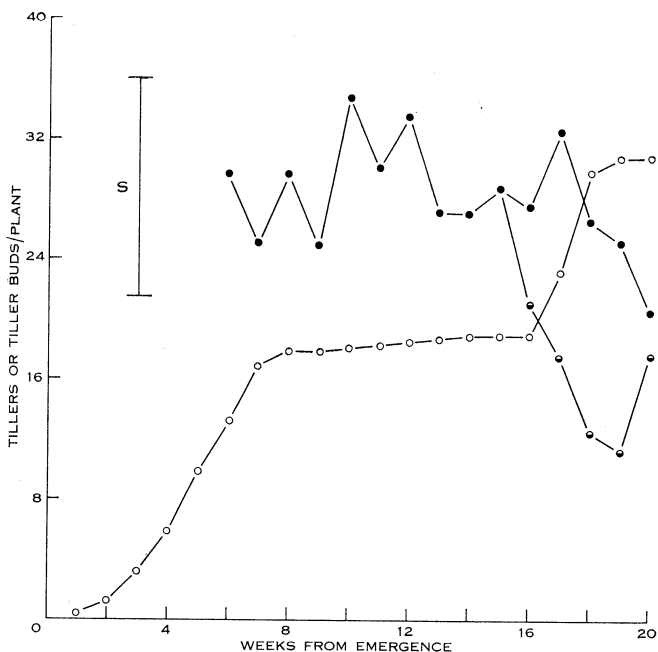

Fig. 3.—Tillers and tiller buds produced by barley (cv. Prior) grown in potting soil, experiment 2. ○ Tiller numbers; ● total number of tiller buds; ◒ number of living tiller buds. S, significant difference between tiller buds ($P = 0.05$).

emerged tillers had not developed sufficiently to materially contribute to these totals by the end of the experiment. It is clear that tillering during the 9-week period of inactivity was not limited by the number of tiller buds present on the plants.

(b) Plants Grown with Controlled Nutrition

(i) *Experiment 3.*—The nutrient treatments applied to the plants were as follows: (1) All nutrients (100% solution) applied before germination; (2) 50% solution applied initially, 50% solution towards the end of the first phase of tillering (6 weeks postgermination); (3) 50% solution applied initially, 50% solution during the phase of tiller inactivity (10 weeks postgermination); (4) 50% solution applied
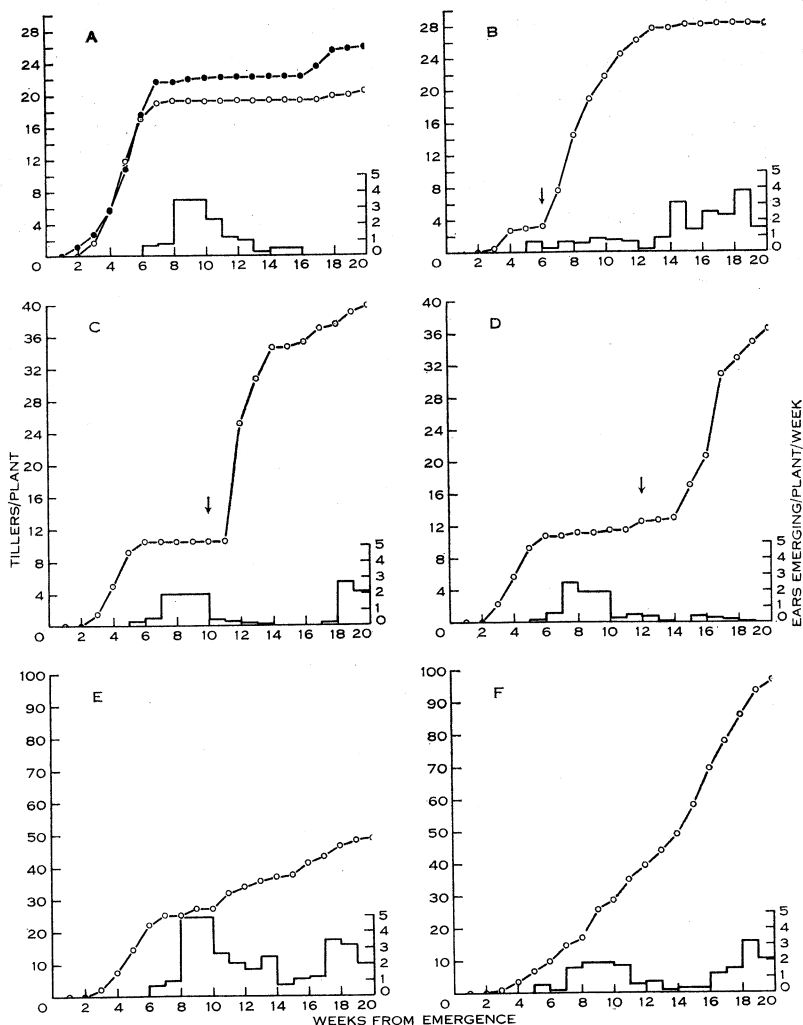
Fig. 4.—Tillering and ear emergence of barley (cv. Piroline) under varying nutrient regimes, experiment 3. *A*, 100% solution applied before germination. *B*, 50% solution before germination, 50% solution at 6 weeks. *C*, 50% solution before germination, 50% solution at 10 weeks. *D*, 50% solution before germination, 50% solution at 12 weeks. *E*, 5% solution each week. *F*, nutrients replaced completely each week by 100% solution. ○ Tiller numbers; histograms, number of ears emerging per week; ● (*A*), tiller numbers from plants in a previous experiment given a treatment identical to *A*. Arrows indicate the time of application of the second quantity of nutrients in *B*, *C*, and *D*.

initially, 50% solution at the beginning of the second phase of tillering (12 weeks postgermination); (5) 5% solution applied weekly for 20 weeks; (6) nutrients replaced weekly by an amount equivalent to 100% solution.*

Plants supplied with nutrients solely before germination behaved as did the plants grown in soil, giving a two-phase tillering pattern (Fig. 4, A). In this experiment, tillering activity in the second phase was slight, amounting to little more than one additional tiller per plant. The tillering curve for an identical treatment in an earlier experiment is given for comparison (Fig. 4, A) and here there was greater tillering activity during this second phase. In both cases, this tillering followed upon a prolonged period of absolute inactivity and the tillers which did emerge were similar in appearance to those previously described. Where only half of the total nutrient supply was given initially the first tillering phase tended to cease earlier (Fig. 4, B, C, D). Tillering in this early phase was less in treatment (2) than in treatments (3) and (4) although all received the same nutrient supply initially. No explanation can be advanced for this and it did not apparently prevent subsequent tillering responses. The addition of the second amount of nutrients at any of the growth stages had the effect of increasing the tillering rate. The time taken for the plants to respond, however, increased with the age of the plant at the time the application was made. Six weeks after germination there was a response within a week, at 10 weeks this had increased to 2 weeks, and at 12 weeks there was a period of 3 weeks before there was any response. The plants with the least number of tillers at the end of the experiment were those to which all nutrients were applied pregermination. Approximately the same total number of tillers were produced by plants given two applications whenever the second application was made.

The plants given 5% of the total nutrient supply weekly (treatment (5), Fig. 4, E) produced many more tillers than plants given nutrients less frequently (although amounting to an identical total supply). These plants did not pass through any prolonged period of low tillering activity. Where the nutrient supply was maintained at a high level throughout (treatment (6), Fig. 4, F) the rate of tillering increased gradually with time. Initially the rate was lower than that of the plants in other treatments (excepting treatment (2)), presumably due to the supra-optimal concentration used for the first few weeks. There was little evidence for any of the tillering phases noted in other treatments or for an eventual cessation of tillering.

Tiller senescence was also influenced by the nutrient supply (Table 1). The criterion of senescence used was a conservative one as it was frequently noted that the upper leaves, and presumably the apical meristem, of a tiller senesced some time before the more mature lower leaves. No dead tillers were recorded on any plants prior to week 11 but thereafter there was a steady loss of tillers from plants supplied with nutrients in two or fewer applications. Few tillers died on plants supplied with nutrients throughout their development, whereas approximately one-third of the tillers were dead by the end of the experiment on plants supplied with nutrients before germination only.

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* It was found that this nutrient concentration caused slight wilting when applied; consequently, from the third week onwards it was diluted with a further 500 ml of distilled water per plant.

The time at which the first ear emerged on the plants was approximately the same (6–7 weeks after germination) in all treatments but the subsequent rate of ear emergence was considerably modified by the previous tillering history of the plant. In treatment (1), the majority of the ears emerged between 8 and 11 weeks after germination, during the phase of tiller inactivity. Where two applications of nutrients were made, ear emergence approached a two-phase pattern following the major tillering flushes (Fig. 4, *B*, *C*). In treatment (4), the experiment was terminated before the tillers induced to emerge by the second application of nutrients had come into ear (Fig. 4, *D*). Continuous applications of a low level of nutrient supply also resulted in a two-phase type of ear-emergence pattern, following closely upon the two early phases of tillering (Fig. 4, *E*). Continuous application of a high

TABLE 1

RELATIONSHIP BETWEEN NUMBERS OF EAR-BEARING TILLERS, THE NUMBERS OF
DEAD TILLERS, AND THE RATIO OF TILLERS FLOWERING IN 13 WEEKS OR LESS AT
THE TERMINATION OF EXPERIMENT 3

Treatment	Number of Ears Present on Plants, Week 21	Dead Tillers, Week 21	Ratio of Ear Number, Week 21, to Tiller Number, Week 8
1	14·3	6·0	1·0
2	22·2	2·7	1·3
3	17·0	5·5	2·8
4	9·8	5·0	1·4
5	33·2	1·2	0·8
6	19·3	0·2	0·7

level of nutrient supply gave a very prolonged period of ear emergence (Fig. 4, *F*) and it would appear that the period between tiller emergence and ear emergence was prolonged in this treatment as compared with the other lower nutrient levels (Table 1).

(ii) *Experiment* 4.—This experiment was designed to investigate the effects of different levels of nutrient supply, either applied initially or repeatedly, on the pattern of tillering and of ear emergence. The following treatments were applied: (1) All nutrients (100% solution) added before germination (as for treatment (1), experiment 3); (2) 50% solution applied pregermination, no further application; (3) 10% solution applied pregermination, no further application; (4) nutrients replaced weekly by an amount equivalent to 50% solution; (5) nutrients replaced weekly by an amount equivalent to 5% solution; (6) nutrients replaced weekly by an amount equivalent to 1% solution.

In all three treatments in which all the nutrients were applied before germination, the tillering pattern followed the same two-phase form found in previous experiments (Fig. 5, *A*). Reducing the amount of nutrition had the effect of reducing the number of tillers produced in the first phase, hastening the onset of the non-tillering phase and slightly reducing the number of tillers produced in the second phase. The time of emergence of the ears was not influenced by the amount of

nutrients applied but the length of time between tiller emergence and flowering and, in particular, the relationship between the flowering time and the timing of the second tillering phase was very different to that found in previous experiments. Ear emergence was delayed until some 16 weeks after germination and yet the second tillers appeared on the 15th or 16th week as in previous experiments.

The difference in flowering time is most probably due to climatic differences between the periods in which the experiments were carried out. Although experiments 3 and 4 were both sown in March, the temperature during the experimental periods differed in the two years. In 1959 (expt. 3) the mean monthly maxima and minima (°F) for the time of the experiment were: March 78·6, 60·5; April 72·7, 56·2; May 65·8, 50·3; June 68·3, 44·6; and in 1960 (expt. 4) they were: March 79·3, 63·0; April 67·3, 53·5; May 63·0, 45·8; June 57·1, 45·4. In addition the
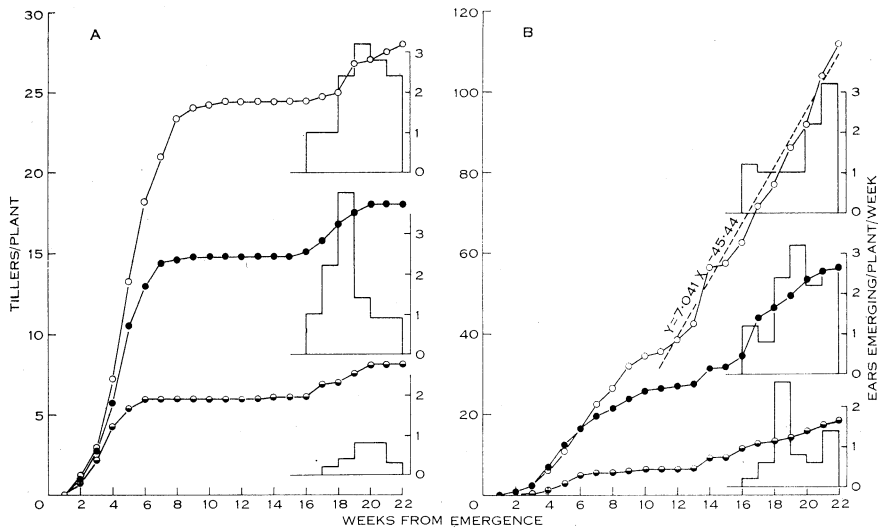

Fig. 5.—Tillering and ear emergence of barley (cv. Piroline) under varying nutrient regimes, experiment 4. A, all nutrients applied before germination: ○ 100% solution; ● 50% solution; ◐ 10% solution; histograms: number of ears emerging per week. B, nutrients replaced weekly: ○ 50% solution; ● 5% solution; ◐ 1% solution; histograms: number of ears emerging per week.

incident solar radiation differed considerably between the two years. The difference in the relationship between tillering and flowering, however, is more complex and implies that there can be no direct temporal correlation between ear emergence or stage of ear development and tillering.

Approximately one-third of the tillers produced had died by the end of the experiment in plants given all the nutrients initially (treatment (1) 10 died; (2) 6·2; (3) 3·2), the majority of these tillers reached the final stages of senescence between the 13th and 15th weeks although they had shown signs (e.g. death of upper leaves) of premature senescence at an earlier date.

Where the nutrient supply was replenished regularly, the tillering pattern was determined by the amount supplied (Fig. 5, B). At all three levels there was an initial rise in the rate of tillering followed by a fall to a minimal level at approximately 10 weeks postemergence. The tillering rate was not maintained at this minimal level for long, however, and subsequently there was another increase in tillering, being more pronounced at the high levels of nutrition. Ear emergence was not apparently delayed by the repeated application of nutrients, the first ears being recorded on all treatments at 10 weeks postemergence, although the proportion of the early emerging tillers which had flowered by the end of the experiment was lower in the high nutrition series. Tiller senescence was practically negligible in all treatments where nutrients were supplied weekly (treatment (4) 0·4 tillers died; (5) 1·6; (6) 0·6) and the tillers which did senesce did so at a later date (weeks 17–20) than those on plants given nutrients solely before germination.

IV. Discussion

The experiments which have been described in this paper simply provide a background of data against which any general hypothesis on mechanisms underlying tiller control may be judged. It has been confirmed that tillering is very largely controlled by nutrient supply, both with respect to the rate and the pattern of tillering. Thus any scheme which envisages the internal control of tiller-bud elongation by an apical dominance system, and it cannot be denied that such a system does operate in the barley plant (Leopold 1949), must account for the modification of control with changes in nutrient supply.

The pattern of tillering which was established where all nutrients were supplied before germination (e.g. Fig. 1) is similar to those described by Lamp (1952) for *Bromus inermis* and Langer (1956) in *Phleum pratense* and suggests the importance of competition for nutrients within the plant. In the initial phase of tillering, both the rate and number were influenced by nutrient supply (Fig. 5, A) and tillering ceased earlier where the nutrient supply was low. As the tillers which were already formed continued to develop, it may be supposed that they were better able to compete for nutrients than were the tiller buds. On the other hand, it is most likely that the death of the apices of a number of the developing tillers, but not of the buds, occurred at the end of the initial phase of tillering and that the senescence of these tiller apices was directly due to a shortage of nutrients as no comparable tiller senescence took place where nutrients were continually supplied. The higher resistance of bud meristems to episodes of nutrient stress is similar to the resistance of young grass seedlings to prolonged periods of nutrient or light stress (Chippindale 1948; Cooper 1948) and may be an inherent property of immature meristems of the Graminaea.

The suppression of tiller-bud development continued for a considerable period but could be relieved at any time by an increase in the nutrient supply (Fig. 4, B, C, D). Wheat plants exhibit a similar period of nutrient-controlled suppression of tillering (Watson 1936) but here, in contrast to the barley plant, the later the stage at which the nutrient supply was increased the fewer was the number of tillers promoted. Watson suggests that competition between the shoots may determine the

pattern, competition becoming more intense with age, but the present data suggests that the state of the inhibited tiller buds following different periods of inactivity should also be taken into account. Increasing the period of inhibition increased the time taken for the buds to respond to an increase in nutrient supply and buds which had withstood a prolonged period of suppression developed into abnormal tillers. These observations parallel data obtained by Mitchell (1953) with *Lolium* spp. and suggests that the difference in response between wheat in Watson's experiments and barley in the present experiments may be due both to the intensity of nutrient stress developed within the plants and to the comparative ability of inhibited tiller buds to withstand such a stress.

The release of tiller-bud suppression during the later stages of growth also indicates the contrast between the situation in barley and in wheat. This release cannot be closely correlated with the development of the early tillers and, hence, it would appear unlikely that the nutrient requirement of the developing ears is the primary factor in its occurence. Although a decline in nutrient requirement with grain growth could contribute to the effect, some source of nutrients must be tapped to support late tiller growth. The most likely source for the new supply would seem to be the senescing leaves and tillers although there is no direct evidence for this assertion.

No clear phasic pattern of tillering was present in plants supplied with nutrients continuously and the week by week tillering rate was highly irregular, the fluctuations being of a greater magnitude than in the one-application treatments. In no case was an exponential rate of tillering produced, even initially at high nutrient levels, and it cannot be concluded that nutrient availability was even here limiting tillering as (Fig. 5, *B*) a tenfold increase in nutrition did not produce a closer approach to an exponential rate of tillering. A still further increase in nutrient level (Fig. 4, *F*) in a separate experiment caused some inhibition of tillering over this early phase. It is likely that some other factor, for example the number of tiller buds or a progressive change in apical auxin synthesis must initially limit tillering. A reduction in nutrient status to a very low level, however, reduced the tillering rate in this same period, delaying the emergence of even the first tiller (Fig. 5, *B*).

The tillering rate of these plants declined, following the initial rapid phase, at a time which corresponded to the beginning of the non-tillering period in plants grown on nutrients supplied prior to germination. A high nutrient demand by the elongating internodes may account for this decrease as certainly the effect was greater at the lower nutrient levels. Whatever the controlling mechanism, however, its effects were confined to the early stages of internode elongation as tillering re-commenced some considerable time before ear emergence. The tillering rate at the highest non-inhibitory nutrient level was constant with time from the 11th week onwards ($y = 7 \cdot 041x - 45 \cdot 44$, $P = 0 \cdot 001$, see Fig. 5, *B*) but at the lower nutrient levels, although there was a general linearity, large individual variations in rate reduced the significance of the trend. The constancy of the rate of tillering at the highest level indicates a state of balance within the plants. If the plants can be considered as a collection of competing meristems, then the activation of a constant number weekly must entail a corresponding decrease in the nutrient requirements

of the older tillers. Another indication of this balance, at all nutrient levels, is the absence of premature tiller senescence indicating that competition between tillers never became sufficiently intense to cause the degeneration of established meristems.

The continued tillering of barley plants, given suitable nutrient regimes, up to and beyond grain maturation on the early tillers raises the question of what determines the annual habit in cereals. Cooper and Saeed (1949) have attributed perennation in *Lolium* spp. to the production of vegetative tillers following the flowering of the early tillers. There is no comparable return to vegetative growth in the barley plant and, indeed, later tillers produce ears more rapidly. On the other hand, the late tillers still produce axillary tiller buds and there is no progressive suppression of tillering with age as noted by Watson (1936). Late tillers which are produced at nodes some distance above ground and consequently produce no adventitious roots will clearly be at a disadvantage and capable of only limited growth but these constitute only a small proportion of the tillers on plants growing under a high constant-renewal regime. It is possible that the annual habit, in a freely tillering variety of cereal, is very largely conditioned by the environment, particularly nutrient supply, and that under certain conditions there may be an approach to perennation. The influence of nutrition on the tillering habit which has been shown to exist in the barley plant would seem to indicate that greater attention should be given to this variable in studies of tillering in perennial grasses. In particular, the great difference between a one-application and a continual-renewal regime may repay investigation in pasture grasses.

V. ACKNOWLEDGMENTS

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