

# THE CONTROL OF TILLERING IN THE BARLEY PLANT

## II. THE CONTROL OF TILLER-BUD GROWTH DURING EAR DEVELOPMENT

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### *Summary*

The interaction between grain number and the level of mineral nutrient supply in the control of tiller-bud elongation has been examined in two varieties of barley (cv. Pirolina, free tillering; cv. CI. 3576, restricted tillering). It was found in Pirolina that the level of the nutrient supply did not alter the effect of the grains, although a considerable increase in tillering at all levels of grain removal resulted from an increase in the mineral nutrient supply. In CI. 3576, on the other hand, increasing the nutrient supply decreased the influence of the grains although it required an extremely high nutrient supply to completely suppress the grain effect. The hypothesis that tillering in this variety was primarily controlled by competition between the grains and tiller buds for a limited nutrient supply was supported by an examination of the nitrogen contents of the grains and emerging tillers.

The leaves were found to be without influence on the number of tiller buds which elongated except under conditions of reduced light intensity. Removing green leaves on the main shoots reduced tiller dry weight, however, indicating that carbohydrates from the mature leaves contribute to the growth of the tillers, at least in the early stages of growth.

The mature shoots on an intact plant have been shown to influence the elongation of tiller buds on other shoots on the same plant. This effect is dependent upon a vascular connection between the tillers and is additional to intershoot competition for light or nutrients in the rooting medium. The nature of the substances moving between shoots in this manner is unknown, but indirect evidence indicated that foliar-applied nitrogen could be so translocated.

The data are discussed in the light of current theories of apical dominance.

### I. INTRODUCTION

The tillering pattern of barley from germination to maturity has been shown to be largely determined by the level of the external mineral nutrient supply (Aspinall 1961). The developing grains also play a part, however, as decapitation generally produces a marked increase in tillering. It has been shown that, at an early stage of growth, the effects of this decapitation can be reversed by an application of  $\alpha$ -naphthaleneacetic acid (Leopold 1949), and this has been used as evidence for the theory that the apex directly inhibits the tiller buds through an auxin system. It seems appropriate, however, in the light of accumulating evidence of the importance of nutrient supply in apical dominance (Gregory and Veale 1957), to examine the influence of the level of nutrient supply on the effect of the apex. It is difficult to perform the type of treatments required on the barley apex before emergence but the

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young ear provides a very useful experimental subject. The level of bud inhibition is generally still high at anthesis, although it drops later in development, and a response to additional mineral nutrients can be elicited. Furthermore, the system at this stage of development has the added advantage that the "apex" can be subdivided in that different numbers of developing grains can be removed from the ear. This allows experiments to be designed in which both factors (apex influence and level of mineral nutrient supply) are varied over a range of values.

Other organs besides the ear may contribute to the control of tillering and in Part I (Aspinall 1961) it was speculated that senescent leaves may act as a source of nutrients for tillering late in the development of the plant. This hypothesis has been examined by the removal of these leaves at various stages of growth and senescence, and the interaction of this factor with ear control has been explored.

The barley plant at anthesis has a number of large flowering tillers, the total depending upon the previous nutritional history of the plant. These tillers have been treated as individual entities in previous experiments and intershoot effects ignored. There is a considerable body of evidence (e.g. Thorne 1962*a*), however, which indicates that this is an oversimplification of the system and that there is a considerable level of interaction between tillers. This system has been examined with the mature barley plant and special emphasis has been placed on determining whether the effects are external (i.e. competitive, which could occur between closely adjacent individuals) or internal.

## II. EXPERIMENTAL METHODS

### (a) *Effect of Grain Number and Mineral Nutrition on Tillering*

Two varieties of two-row barley (*Hordeum vulgare* L.) were compared, cv. Pirolin with a high, and cv. CI. 3576 with a low tillering capacity. The plants were grown under glasshouse conditions with the majority of the mineral nutrient supplied before germination, in sand culture in the initial experiment with Pirolin and in John Innes compost in the subsequent experiments. No further nutrients were applied during vegetative growth. When the majority of the main shoots on the plants came into ear a further varying amount of nutrients was supplied to the plants, the same nutrient solution being employed as in previous experiments.\* At this same stage grain numbers were reduced on the emerging ears by removing surplus spikelets with forceps, leaving both the sterile lateral florets and the appropriate number of fertile spikelets spaced over the length of the rachis. The several ears on any one plant did not emerge simultaneously but the majority could be treated within 1 week.

The plants were grown for a further 3–4 weeks and the new tillers were then harvested, counted, and oven dried at 80°C. Dry weights of the ears on the mature shoots and of the new tillers were obtained and nitrogen contents were assessed in the initial experiment with CI. 3576 by a macroKjeldahl procedure.

\* Constituents of standard nutrient solution (100% solution), g/plant:  $\text{NaNO}_3$ , 1.82;  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ , 5.13;  $\text{KNO}_3$ , 1.58;  $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$ , 3.14;  $\text{MgSO}_4$ , 1.85;  $\text{FeC}_6\text{H}_5\text{O}_7 \cdot 5\text{H}_2\text{O}$ , 0.12; traces of  $\text{H}_3\text{BO}_3$ ,  $\text{MnSO}_4$ ,  $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ ,  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ , and  $\text{MoO}_3$  (see Aspinall 1961).

(b) *Influence of the Mature Leaves on Tillering*

The effect of the leaves was investigated in cv. Pirolina only. In two experiments the plants were grown through to anthesis of the early formed shoots before any treatments were applied. All combinations of complete defoliation (severing the leaves at the junction of lamina and sheath) and decapitation were compared in the initial experiment. These treatments were repeated in the second experiment in combination with a third variable, the addition or not of a supplementary amount of nutrient solution (20% of the standard solution). The newly formed tillers were counted and, in the second experiment only, harvested and weighed following oven drying 2 weeks after treatment of the plants.

These initial experiments involved the removal of green as well as senescent leaves at a specific stage of growth. A further experiment was designed to ascertain whether the removal of leaves as they became senescent would influence tillering. Leaves were removed weekly at two stages of senescence, namely, when the tip of the lamina became yellowed or when half of the blade was yellow. In a third treatment, all leaves showing any trace of yellow were removed at anthesis. In the twelfth week, when the plants were well advanced in the non-tillering growth phase (Aspinall 1961), half of the plants in each treatment were decapitated. Defoliation and the recording of tiller numbers were continued for a further 8 weeks.

(c) *Translocation of the Control of Tiller-bud Elongation between Mature Tillers*

All the plants used in this series of experiments (cv. Pirolina and cv. CI. 3576) were grown in John Innes compost. Basically the treatments imposed consisted of applying the appropriate conditions (decapitation, foliar nitrogen application, lamina removal, or decapitation followed by 3-indolylacetic acid (IAA) application) to a number of the mature tillers on a plant and recording the new tillers stimulated to emerge both on the treated tillers and the remainder of the tillers on the plant. All treatments were commenced at anthesis of the majority of the ears, but treatments were imposed on all the appropriate tillers at the same time whether the tiller treated was in anthesis or not. Foliar nitrogen applications were made by spraying the green leaves of the treated tillers with a 10% solution of  $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$ . Care was taken to avoid spraying the untreated tillers and to prevent any run-off from reaching the soil. The plants were sprayed at 3-4-day intervals from anthesis to harvest. Auxin applications of 0.1% IAA in lanolin were made to the freshly decapitated tillers. The treatments were renewed every 3-4 days by slicing away a small section of the stem and applying fresh auxin paste.

In order to demonstrate that the effects observed were dependent on a stem connection between the tillers and could not be explained as being due to root interactions or competition, a technique was employed in two experiments which allowed the tillers on a mature plant to be separated. Commencing at approximately 6 weeks after emergence, the young tillers were pinned flat to the soil surface and covered lightly with sand. This treatment was renewed weekly and the layer of sand gradually increased. Six tillers were retained on each plant, the remainder being removed as they developed. At anthesis, the majority of these layered tillers had produced a

substantial adventitious root system from nodes away from the centre of the plant. The tillers could then be severed below these adventitious roots, rendering them independent of the rest of the plant.

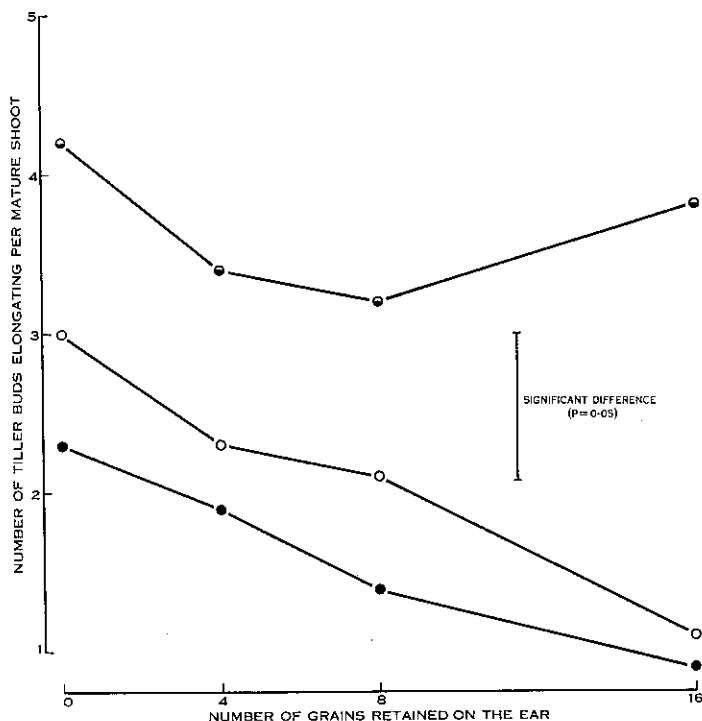


Fig. 1.—Effect of grain number and nutrient supply on tillering in barley (cv. Pirolina): ● no added nutrients; ○ 2% of standard amount added; ◐ 20% of standard amount added. Significant difference ( $P = 0.05$ ) between means shown.

### III. EXPERIMENTAL RESULTS

#### (a) Effect of Grain Number and Mineral Nutrition on Tillering

(i) *cv. Pirolina*.—Two experiments were carried out with this variety, at an initially high (sand-culture) or an initially low (John Innes compost, unfertilized) mineral nutrient status. Essentially the same results were obtained in both cases, however, so only the data from the second experiment will be commented upon in detail. In this experiment the intact ears had some 16 grains and in other treatments grain numbers were reduced to 8, 4, or 0. Nutrients were applied at anthesis at the rate of 0, 2, or 20% of the standard solution.

These two factors showed no interaction in the control of tiller-bud elongation (Fig. 1). The addition of increasing amounts of nutrients successively increased the number of tillers produced at each level of grain removal, although the data at the highest level were variable. There was no evidence for any difference in the effect

of the additional nutrients at different grain numbers. Similarly, there was no interaction of the effects of these treatments in the initial experiment although the grains had a smaller overall effect on tiller elongation (24 grains, 2.4 tillers; 12, 2.7 tillers; 4, 2.8 tillers; 0, 3.2 tillers).

The increase in mean dry weight of the new tillers was not as sensitive to ear removal or nutrient supply as the number of tillers which elongated. In the initial experiment tiller dry weight was unaffected by treatment but in the second the presence of grains on the ear did have an effect, tiller dry weight being depressed by

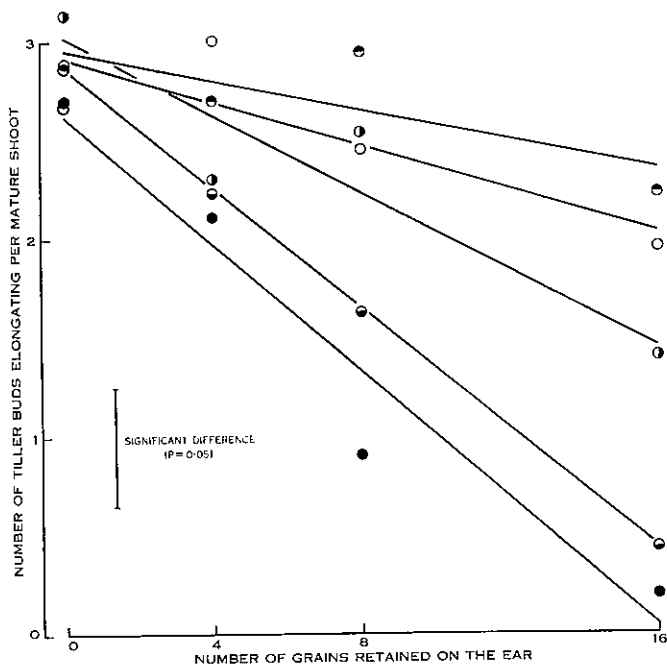


Fig. 2.—Effect of grain number and nutrient supply on tillering in barley (cv. CI. 3576) grown in an initially high nutrient regime: ● no added nutrients; ◐ 1% of standard amount added; ◑ 10% of standard amount added; ○ 50% of standard amount added; ⊗ 100% of standard amount added. Significant difference ( $P = 0.05$ ) between means shown.

the presence of 16 grains in comparison with other treatments ( $\log_{10}$  tiller dry weight (mg): 0 grains, 2.319; 4, 2.291; 8, 2.307; 16, 2.139; significant difference ( $P = 0.05$ ), 0.139). The addition of nutrients did not relieve this effect and, indeed, nutrient levels had very little effect on any of the tiller dry weights.

Grain dry weights were determined to ascertain whether the treatments affected grain growth which might in turn influence the ability of the ears to control tillering. Variations in mineral nutrient supply were without effect, however, and the influence of grain removal was small (4 grains retained, 40.7 mg; 8 grains, 40.3; 16 grains, 38.7) so that variations in the influence of the grains from this source is likely to be unimportant.

The results of both experiments suggest that, in this variety, the principal effect of an increase in nutrient supply at flowering is to produce a general increase in the rate of tillering and not to relieve the relatively weak effect of the developing grains.

(ii) *cv. CI. 3576*.—In the initial experiment with this variety, fertilized compost was used as the growing medium. Four levels of grain removal (0, 4, 8, and 16 grains remaining on the ear) and five levels of mineral nutrient supplementation were imposed at anthesis (0, 1, 10, 50, and 100% of the standard amount).

In contrast to the data obtained with Pirolina, the effects of grain removal and nutrient supply on tiller formation interacted very markedly (Fig. 2). The number of tillers produced when all grains were removed was unaffected by the nutrient supply, whereas with increasing grain numbers per ear the nutrient supply

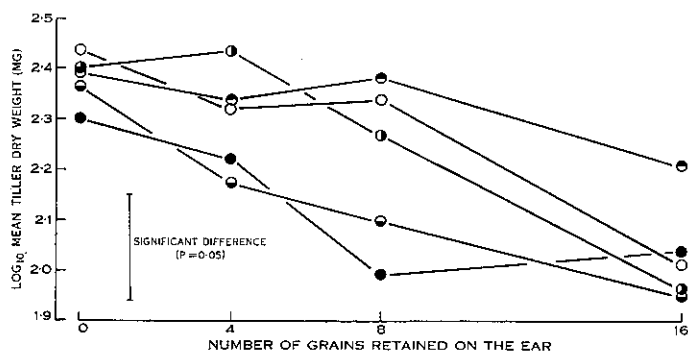


Fig. 3.—Effect of grain number and nutrient supply on mean tiller dry weight in barley (*cv. CI. 3576*): ● no added nutrients; ◐ 1% of standard amount added; ◑ 10% of standard amount added; ⊗ 50% of standard amount added; ○ 100% of standard amount added. Significant difference ( $P = 0.05$ ) between means shown.

had an increasing effect. This resulted in the influence of grain number being reduced at the higher nutrient levels, although even at the highest nutrient level complete grain removal significantly increased the number of tillers which developed. All the data could be described by linear regressions on grain number and the slope of these lines decreased progressively with increasing nutrient level.

The effects of the treatments on mean tiller dry weight (Fig. 3) were similar to those on tiller number except that here grain number had a proportionally larger effect than the nutrient supply. There was some evidence for an interaction of these effects, as the grain number effect was not significant at the highest level of nutrient supply. The result of these two effects, on tiller number and tiller weight, was that the total dry weight of new growth made by the plants following anthesis was considerably influenced by both nutrient supply and grain number. For example, at the lower nutrient supply there was nearly a 10-fold increase in dry weight production following upon complete decapitation, and at high grain numbers per ear, the maximum nutrient supply produced a five- to sixfold increase.

In this experiment the ears were harvested at the same time as the tillers, oven dried, and weighed. Nutrients had no effect on the weight of these ears at any level of grain removal. Mean grain weights were calculated on the assumption that the rachis and infertile spikelet weights obtained from the treatments where all grains were removed were representative of all treatments. The mean grain weight was lower (16 grains, 37.9; 8 grains, 47.0; 4 grains, 46.2 mg) where all the grains were left on the ear although the reduction was not large and it is unlikely to have affected the tiller-bud : grain number relationship.

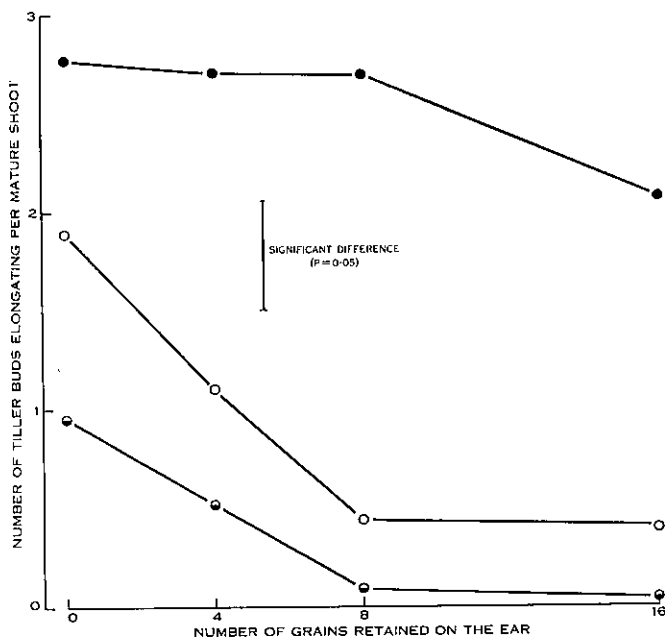


Fig. 4.—Effect of grain number and mineral nutrient supply on tillering in barley (cv. CI. 3576) grown in an initially low nutrient regime: ● no added nutrients; ○ 2% of standard amount added; ◐ 20% of standard amount added. Significant difference ( $P = 0.05$ ) between means shown.

When CI. 3576 plants were grown in initially *unfertilized* soil, an apparently different relationship between tiller growth and grain and nutrient treatments resulted (Fig. 4). At low levels of nutrient application (0 and 2%) a reduction of the number of grains on the ear by 50% (from 16 to 8) did not affect the suppression of tiller growth. At the high level (20%), however, there was an increase in the number of tillers developed with a change from 16 to 8 grains per ear. This interaction was significant. At all levels of grain removal there was also a general increase in the tillering in response to nutrient application as in the Pirolina experiment, but it should be noted that only at the highest level did the tillering rate reach that in totally decapitated plants in the previous experiment. Despite these apparent differences, a careful consideration of the data leads to the conclusion that the same

general relationships were developed in this as in the previous experiment. Thus the slopes of the tiller number/grain number relationships are comparable with those in the previous experiment, if tiller numbers (which are very low) at high grain numbers per ear and low nutrient levels are disregarded.

The tiller dry weights were smaller than in the previous experiment, suggesting a general shortage of nutrients. At the two higher levels of nutrient supply, dry weight fell with increasing grain numbers (from 129 to 51 mg per tiller) but where no nutrients were added, too few tillers elongated to give a reliable estimate of tiller weight. The ears were divided into grains and remainder before drying and weighing.

TABLE 1  
NITROGEN CONTENT OF NEW TILLERS FOR cv. CI. 3576  
Significant difference ( $P = 0.05$ ) for comparisons with eight  
samples = 0.56

No. of Grains per Ear	Nutrients Supplied at Anthesis (% basic amount)	Total Nitrogen (% dry wt.)	No. of Samples
16	0	1.24	2
	2	1.58	4
	20	2.99	8
8	0	3.16	1
	2	2.31	3
	20	3.37	7
4	0	2.85	4
	2	2.20	8
	20	3.21	8
0	0	2.14	6
	2	2.00	8
	20	3.25	6

Nutrient supply had no effect on the weight of either the grains or the rest of the ears. As before, grain removal led to an increase in the weight of the remaining grains (16 grains/ear, 30.6 mg, 8, 37.1 mg; 4, 39.7 mg; significant difference ( $P = 0.05$ ), 5.1). As there was no indication of any effect of nutrient supply on this relationship it is likely that competition for photosynthetic materials was occurring between the individual grains on the ear.

The total nitrogen contents of the new tillers and the ears were determined in this experiment. Owing to the low rate of tillering in several of the treatments, a complete analysis of the effects of the treatments on the nitrogen content of the tillers was impossible. However, nitrogen content increased with increasing nutrient supply and also, although the number of samples available at the higher grain



numbers were insufficient to establish significance (Table 1), with reduction of the number of grains on the ear. Percentage nitrogen content was unchanged by a small increase in nitrogen supply but a further 10-fold increase in the supply resulted in a rise of 1%, despite the concurrent production of considerably more tiller dry weight.

For the ear assay, grains and the rest of the ear were combined and more samples were available. It is clear that both grain number and nutrient supply influenced the nitrogen content of the ears and that there was a considerable interaction of their effects (Table 2). Where all the grains were removed, the nitrogen content of the rest of the ear was unaffected by the nutrient supply. On the other

TABLE 2  
NITROGEN CONTENT OF EARS AND CALCULATED NITROGEN CONTENT OF  
GRAINS FOR cv. CI. 3576

Significant difference ( $P = 0.05$ ) between means = 0.21

No. of Grains per Ear	Nutrients Supplied at Anthesis (% basic amount)	Nitrogen Content of Ears (% dry wt.)	Calculated Nitrogen Content of Grains (% dry wt.)
16	0	1.42	1.48
	2	1.55	1.63
	20	2.21	2.37
8	0	1.56	1.71
	2	1.70	1.85
	20	2.11	2.38
4	0	1.75	2.09
	2	1.77	2.13
	20	1.89	2.34
0	0	1.01	
	2	0.97	
	20	1.08	

hand, when grains were present the nitrogen content varied with both grain number and nutrient supply. At low levels of nutrient supply the nitrogen percentage increased with decreasing grain numbers per ear whereas at a high level of supply it decreased. In view of the lack of effect of nutrient supply on the nitrogen content of the totally degrained ears it is likely that this was due to changes in the nitrogen content of the grains alone. These have been calculated assuming the non-grain portion of the ears to have a constant nitrogen content of 1%. The results indicate that at low nutrient levels there is considerable competition between the grains for the available nutrient supply whereas at the highest level there is no competition.

*(b) Influence of Mature and Senescing Leaves on Tillering*

In an initial experiment on plants grown in a shaded glasshouse it was found that complete defoliation at anthesis reduced tillering on both decapitated and undecapitated plants (mean number of new tillers per mature shoot: control, 1.76; defoliated, 0.53; significant difference ( $P = 0.05$ ), 0.12). These treatments were repeated and extended in a further experiment where another variable was introduced in that two levels of external nutrient supply were given. In this experiment there was no significant effect of defoliation on the numbers of new tillers produced although there was an effect on their weight (Table 3). Decapitation and additional nutrition both increased the number of tillers produced but there was no interaction of the effects of any of these factors. Mineral nutrient supply had only a small effect on tiller weight but decapitation had a much larger effect, comparable with that of the leaves.

TABLE 3  
EFFECT OF EXTERNAL NUTRIENT SUPPLY, OF EAR REMOVAL, AND OF  
DEFOLIATION AT ANTHESIS ON THE SUBSEQUENT TILLER PRODUCTION OF  
BARLEY, cv. PIROLINE

Ears	Leaves	Nutrients Added	New Tillers Produced per Plant	Log <sub>10</sub> Dry Weight (mg) per Tiller
Present	Present	None	3.2	1.75
		20%	13.7	1.81
	Absent	None	6.3	1.55
		20%	14.0	1.67
Absent	Present	None	12.2	1.98
		20%	18.9	1.98
	Absent	None	9.1	1.69
		20%	18.4	1.81
Significant difference ( <i>P</i> = 0.05)			3.9	0.20

In both these previous experiments the leaves were removed at anthesis whether they had reached the stage of senescence or not and inevitably any assessment of the role of the leaves as reserves of mineral nutrients would be confused with their role as photosynthetic organs. This was avoided in the final experiment by progressively removing the leaves as they became senescent. The most severe treatment, in which leaves were removed when they showed the initial signs of senescence, undoubtedly removed functional photosynthetic tissue but this loss was negligible in the remaining two treatments. There were no consistent differences in tillering pattern in these plants due to the removal of leaves, either in the earlier stages of growth or after anthesis and whether ears were removed or not (Table 4). It must

be concluded, therefore, that it is very doubtful whether senescent leaves play any role in the control of tillering and there is certainly no evidence to suggest that they act as a significant source of mineral nutrients during post-flowering tillering.

(c) *Interrelationships of Mature Tillers on the Plant*

(i) *Experiments 1 and 2.*—In the initial experiments in this series there were three basic treatments: (1) the plants remained intact, (2) all the ears were removed, and (3) 50% of the ears were removed from each plant. In additional treatments, one tiller alone was decapitated in the first experiment and all but one tiller were so treated in the second. Total decapitation produced a marked promotion of tillering

TABLE 4  
EFFECT OF PROGRESSIVE DEFOLIATION AND EAR REMOVAL ON TILLERING OF BARLEY, cv. PIROLINE

Treatment		No. of Tillers Present at Anthesis	New Tillers Formed per Mature Shoot 8 Weeks after Anthesis
No leaves removed	Ears present	20.0	0.3
	Ears removed at anthesis		1.5
Leaves removed when showing a trace of yellow	Ears present	19.3	0.1
	Ears removed at anthesis		1.3
Leaves removed when half yellow	Ears present	18.7	0.2
	Ears removed at anthesis		1.3
All yellow leaves removed at anthesis	Ears present	17.0	0.2
	Ears removed at anthesis		1.2
Significant difference ( $P = 0.05$ )		3.9	0.5

(Table 5). Decapitation of half of the ears on a plant resulted in an increase in tiller production on both the treated and the untreated tillers, the stimulation being greater on the decapitated tillers. Removing one ear had little effect, whereas removing all but one resulted in a marked promotion of tillering, but there was a large difference between tiller-bud elongation on intact tillers as compared with those decapitated. Where only half of the ears were removed, fewer new tillers were produced *per plant* than where all ears were removed. These results demonstrate that, although overall tiller-bud elongation on the plant is dependent on the number of ears present, each mature shoot has a certain degree of autonomy in this regard and the ear can still depress the growth of the tiller-buds despite a marked lifting of suppression in the plant as a whole.

(ii) *Experiment 3.*—Following upon these results, the effects of defoliation in addition to decapitation were examined. The plants were reduced to four tillers at

anthesis and a pair of shoots was treated as a unit, every combination of defoliation and decapitation of each pair of tillers being made. Defoliation had no effect on the number of new tillers produced (Table 6) as before, but decapitation of the parent or of the other shoots on the plant had a profound effect. Once again the largest number of tillers was produced on plants which were totally decapitated, and in this case the number of tillers produced per plant was linearly related to the number of ears which were decapitated (0 ears, 9.8; 2 ears, 5.8; 4 ears, 1.2 new tillers per plant).

TABLE 5  
RELATIONSHIP BETWEEN MATURE TILLERS IN THE CONTROL OF TILLER-BUD ELONGATION IN EXPERIMENTS 1 AND 2

Treatment	No. of New Tillers per Mature Tiller		No. of New Tillers per Plant	
	Expt. 1	Expt. 2	Expt. 1	Expt. 2
(1) Control: ears intact	0.41	0.73	10.3	13.8
(2) All ears removed	2.24	1.93	29.0	23.4
(3) Half of ears removed:			17.5	17.4
Ears intact	0.92	0.80		
Ears removed	1.15	1.55		
(4) One tiller decapitated:			3.3	
Ears intact	0.21			
One ear removed	0.25			
(5) All but one tiller decapitated:				27.8
Ears intact		1.40		
Ears removed		2.63		

(iii) *Experiment 4.*—The finding that decapitation of a number of the tillers can lead to at least a small increase in tiller-bud elongation on intact tillers on the same plant (compare the level of tillering in these cases with the level of tillering on control, i.e. completely undecapitated plants (Tables 5 and 6)) may be interpreted as being due to a lessened competition for nutrients between the roots of the plant or to some influence acting within the plant. This choice of interpretation may be resolved by severing connections between tillers and allowing them to subsist on adventitious roots developed from higher nodes. The amount of rooting obtained in this manner is variable and accordingly replication has to be high (15-fold in the present experiment). This necessarily reduces the number of treatments which can be compared.

All the plants were reduced to six tillers from early in development and the ears of three of these tillers were removed at anthesis. At this same time half of the plants were severed at the internode below the site of adventitious root formation.

Subsequent tillering demonstrated that this operation had no deleterious effect on nutrient or water uptake by the plants as the total number of tillers formed per plant

TABLE 6

TILLER PRODUCTION ON PARENT SHOOTS FOLLOWING EAR REMOVAL AND DEFOLIATION TREATMENTS OF BOTH PAIRS OF SHOOTS IN EXPERIMENT 3

Mean number of tillers per mature shoot given. Significant difference ( $P = 0.05$ ) between these means = 0.82

Remaining Shoots	Parent Shoots				Mean of Means
	Ears Intact, Leaves Intact	Ears Intact, Defoliated	Ears Removed, Leaves Intact	Ears Removed, Defoliated	
Ears intact, leaves intact	0.45	0	2.05	1.50	1.00
Ears intact, defoliated	0.20	0.50	2.15	1.70	1.30
Ears removed, leaves intact	1.30	0.95	2.10	2.25	1.65
Ears removed, defoliated	0.80	1.15	2.50	2.90	1.85
Mean of means	0.70	0.65	2.20	2.10	

was practically identical in both treatments (Table 7). The distribution of these tillers between intact and decapitated shoots was considerably affected, however.

TABLE 7

EFFECT OF TILLER EAR REMOVAL AND OF SEVERING THE PARENT SHOOTS ON ELONGATION OF TILLER BUDS

Treatment of Parent Shoots	No. of Tiller Buds Elongating per Mature Shoot		Total No. of Tillers Formed per Plant
	When Tillers Intact	When Tiller Ear Removed	
Shoots intact	0.59	1.13	10.32
Shoots severed	0.08	1.56	9.84
Significant difference ( $P = 0.05$ )	0.38	0.39	—

Where shoots were united, the number of tiller buds elongating was less on decapitated tillers and more on intact tillers in comparison with plants in which the shoots were separated. This demonstrates that the influence of the presence (or absence) of an ear can be translocated through the junction between the mature shoots of a plant.

Nevertheless, the shoot must retain a substantial degree of autonomy in the control of tiller-bud elongation since, as in the previous experiments, the decapitated shoots always produce more new tillers even on intact plants.

(iv) *Experiment 5.*—The separation of tillers was repeated in a further experiment in which additional treatments were introduced in the form of auxin applied to half of the tillers on a plant in the presence or absence of ears on the remaining tillers. Where auxin was not applied similar results (Table 8) were obtained to those of the

TABLE 8

NUMBERS AND MEAN DRY WEIGHT OF NEW TILLERS PRODUCED FOLLOWING TILLER EAR REMOVAL FROM INTACT AND SEVERED MATURE SHOOTS, AND SUBSEQUENT AUXIN\* TREATMENT (EXPT. 5)  
Significant difference ( $P = 0.05$ ) between tiller numbers = 1.6, between tiller weights = 0.433

Treatment of Tillers	Mature Shoots Severed		Mature Shoots Intact		No. of New Tillers per Plant
	No. of New Tillers per Shoot	Log <sub>10</sub> of Mean Dry Weight (mg) of New Tillers	No. of New Tillers per Shoot	Log <sub>10</sub> of Mean Dry Weight (mg) of New Tillers	
Ear intact	1.4	1.992	2.1	2.187	17.6
Ear removed	3.0	2.128	2.3	2.163	
Ear removed	3.7	1.830	3.4	2.256	23.8
Ear removed, auxin applied	2.1	1.982	2.7	2.284	
Ear intact	1.2	1.945	2.7	1.906	17.8
Ear removed, auxin applied	2.5	1.977	2.5	2.070	

\* 3-Indolylacetic acid.

previous experiment, in that separation of the tillers tended to confine the stimulatory effects of decapitation to the shoots so treated. The auxin treatments had only a small and inconsistent effect; in the absence of ears the auxin application reduced tillering on treated shoots, particularly where the shoots were separated, but the level of tillering in the plants as a whole was considerably higher than where ears were present on 50% of the shoots. This demonstrates that auxin could not, in this experiment, replace the effect of the ear. The dry weights of the new tillers were also taken and, whilst there was a tendency for shoot separation and the presence of an ear to reduce tiller dry weight these effects were not consistent.

(v) *Experiment 6.*—Mineral nutrients supplied during flowering have been shown to stimulate tillering and there is a strong possibility that the effects so far described are the result of the transport of mineral nutrients between shoots. The extent of this transport within the plant was explored by applying calcium nitrate solution to the leaves of 50% of the tillers on plants of the varieties Pirolina and

CI. 3576. A decapitation treatment was also included to test whether this had any influence on the distribution of the nitrogen. Pirolina produced many more new tillers than CI. 3576 but in both varieties nitrogen application and decapitation both stimulated tillering (Table 9). Although there was a trend towards more tillers being produced on the sprayed tiller in Pirolina, but not in CI. 3576, this trend did not anywhere reach significance. Two explanations are possible for this result, either foliar-applied nitrogen is very completely transported throughout the plant or there was a significant amount of run-off which supplied nitrogen to the roots of the unsprayed tillers. Precautions were taken to reduce this contamination to a minimum but the possibility cannot be excluded.

TABLE 9  
EFFECT OF FOLIAR APPLICATION OF CALCIUM NITRATE SOLUTION ON TILLERING IN TWO VARIETIES OF BARLEY

Significant difference ( $P = 0.05$ ) between plant means = 3.1, between shoot means = 2.0

Treatment of Tillers	cv. Pirolina		cv. CI. 3576	
	New Tillers per Shoot	New Tillers per Plant	New Tillers per Shoot	New Tillers per Plant
Ears present				
No nitrogen applied (control)	—	9.8	—	3.0
Nitrogen applied to 50% of shoots				
Treated shoots	2.7	} 15.3	1.1	} 6.2
Untreated shoots	2.4		1.0	
Ears removed				
No nitrogen applied (control)	—	17.2	—	6.0
Nitrogen applied to 50% of shoots				
Treated shoots	3.9	} 20.4	1.4	} 9.2
Untreated shoots	2.9		1.6	

#### IV. DISCUSSION

The paramount importance of the level of mineral nutrient supply in the control of tillering stressed previously (Aspinall 1961) has been confirmed for the later stages of plant growth. In previous experiments the development of the shoot apex was not correlated with the control of tiller-bud elongation and it was suggested that the critical factor was the supply of nutrients rather than the demand from the developing grains. The release of inhibition of tillering which generally occurs late in plant development would then be due to an increase in the supply rather than to a decrease in the competition for these nutrients. Senescing leaves were suggested as a source for this increase in supply.

The experiments carried out with the same variety (Pirolina) in the present study have tended to confirm that grains do not compete directly with tiller buds for mineral nutrients. Although the data are variable, the relatively small influence of

the grains is maintained despite an increase in the concentration of the external nutrient solution. This argues against any quantitative competition between the two sites of utilization, and it is possible that the grains are having a direct influence on tiller-bud elongation or that competition for some other substance (e.g. carbohydrate) is involved. Some support for this conclusion is found in the fact that tiller dry weight was unaffected by nutrient supply but was reduced by the presence of grains in one experiment. This indicates that some effect other than competition for nutrients is involved. The small effect of grain removal on subsequent grain growth renders it unlikely that there was very marked competition for carbohydrates within the plant and that this factor is of importance in the initiation of tiller-bud elongation. It seems possible, therefore, that a direct rather than a competitive effect of the grains is implicated. Nevertheless, it must be stressed that tiller-bud elongation was principally controlled by the level of mineral nutrients and that, although competition could not be demonstrated, their availability at anthesis largely determined the development of the buds. It is not impossible, however, to envisage a system of control wherein the grains inhibit tiller-bud elongation within the limits set by the level of nutrient supply. This being so, the hypothesis that the mobilization of mineral nutrients from senescent organs leads to a lifting of the inhibition of the buds would seem to be reasonable. Thorne (1962*a*) has presented indirect evidence that both nitrogen and dry weight (presumably in the form of carbohydrate) are transported from senescent to growing shoots during the later stages of growth of barley plants. The present experiments involving leaf removal, however, demonstrate unmistakably that the senescing leaves do not contribute to this effect. It is clear that further investigation is required to clarify the reasons for the partial lifting of the inhibition on tillering at flowering.

The controlling system in CI. 3576 appears to be much more intimately concerned with competition for mineral nutrients within the plant. The evidence from the interaction of nutrient supply and grain number on the ear and from the nitrogen contents of the ears and tillers supports the view that intense competition for these substances takes place between the ears and the tillers. Furthermore, the ears would appear to be very much more efficient in obtaining limiting nutrients than the tiller buds (Tables 1 and 2).

The relationships between numbers of tillers elongating and grain numbers remaining on the ear were found to be linear (Fig. 2) and the slopes were a function of the nutrient supply. The computed regression coefficients are inversely linearly related to the *logarithm* of the external nutrient concentration (Fig. 5) and thus it requires an apparently disproportionally high nutrient solution concentration to completely overcome the influence of the grains. The nitrogen content of the grains was unaffected by the level of grain removal at a level of supply equal to 20% of the standard nutrient supply (Table 2) and yet a definite grain influence can be detected at five times this concentration (Fig. 2). Part of the explanation of this anomaly may lie in the relationship between nutrient concentration and nutrient uptake by the plant. Although this approaches linearity when the plant is young and growing rapidly (Gregory 1937) the percentage uptake declines at higher levels of nutrient supply when the plants are grown for a longer period (Slater and Goodall 1957). It



is therefore probable that the relationship demonstrated in Figure 5 would be somewhat different if plotted against the internal nutrient content of the plant rather than the concentration of the external supply.

It is unlikely, however, that the data can be completely explained by a simple competition mechanism. Several other mechanisms are possible, each in combination with a direct competition mechanism which is dominant at the lower rates of nutrient supply. Firstly, there may be some direct hormonal influence of the grains on the

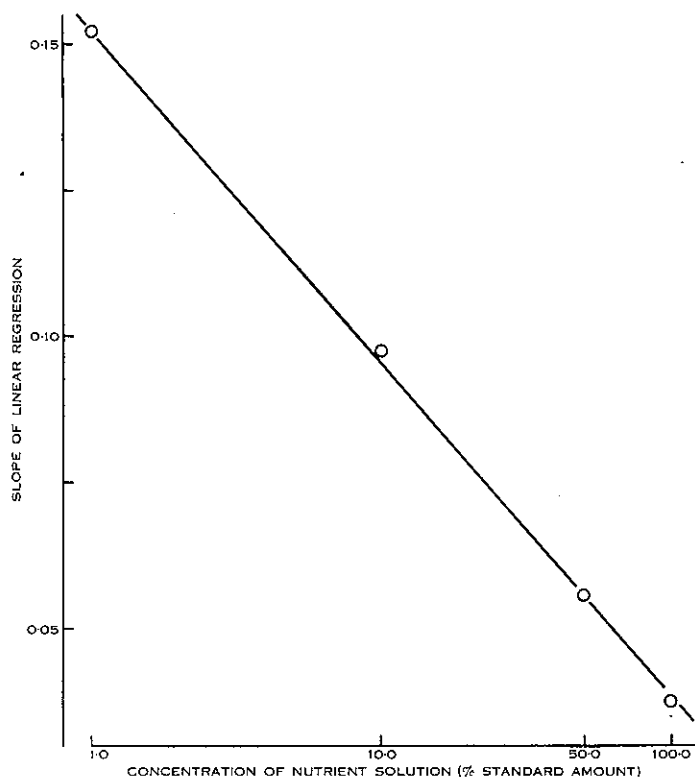


Fig. 5.—Effect of the level of nutrient supply on the relationship between tiller number and the number of grains on the ear for cv. CI. 3576 grown in an initially high nutrient regime.

tiller buds, as discussed in relation to the mechanism of control in Pirolina. Alternatively, nutrient uptake by the tillers may be limited by a hormone action of the grains irrespective of the level of nutrition, or the carbohydrate supply may become limiting, possibly accentuated by self-shading at the very high nutrient levels.

There is some evidence that grain removal increased the dry weight of the remaining grains and this is indirect evidence for competition for carbohydrates within the plant (Buttrose and May 1959). Similarly, the proportionally larger effect of grain removal on tiller dry weight than on tiller numbers (Fig. 3) also suggests that competition for carbohydrates was occurring. As the effect of complete removal

of the green leaves was solely on the size of the tillers rather than on their numbers (Table 4), however, it appears unlikely that competition for carbohydrates could be of paramount significance in determining tiller numbers on an intact plant.

Thorne (1962*b*) has also obtained an increase in tillering at ear emergence with an increase in nutrient supply and has contrasted this effect in pot culture with the response of cereals in the field where an increase in nutrient supply at flowering results in increased grain yield but no increase in tillering (Watson 1939). She considers that the lack of increase in grain yield in pot culture is due to competition from the new tillers for the added nutrients, but this is unlikely in view of the marked increase in grain nitrogen without increase in dry weight which occurs under similar conditions (Table 2).

A cereal plant normally consists of a number of more or less comparably sized tillers but there is a tendency to consider each individual tiller as a unit and to overlook the relationships between tillers on the same plant. Several workers have demonstrated intereffects between tillers on grain formation and yield (Smith 1933; Miller 1949; Hashimoto, Takiguchi, and Isoda 1956; Labanauskas and Dungan 1956) but many of their observations could be explained in terms of competition for nutrients or light which could equally well occur between individual plants growing in close proximity. The present results demonstrate clearly that vascular connections between the shoots are essential to obtain the full effect of companion tillers on tiller-bud elongation. Although intertiller competition between roots and between leaves undoubtedly also occurs there is an important component which is dependent on the transport of some substance or substances from one tiller to the other. The nature of this substance is unknown and may even vary, depending upon the state of the plant. The evidence that substances can be so translocated is supported by the effects of foliar-applied nitrogen (Table 9) and by more definitive results with foliar-applied  $^{32}\text{P}$  (Zabluda and Prosteva 1956), but growth substances or carbohydrates could be equally easily translocated around the plant.

In the intact plant there may be much less movement between tillers than in the experimentally modified system (some tillers decapitated, defoliated, or sprayed etc.) but the potentiality for this movement exists, and must be taken into account in considering the growth of cereals. As an example, nutrients which may be remobilized upon the senescence of individual tillers could be freely translocated to other shoots and utilized in growth (Thorne 1962*a*). For this reason, tillers which do not produce ears and senesce before maturity may not be completely wasted in terms of contributing to plant yield. On the other hand, it is possible that heavily shaded tillers may also draw on available carbohydrates from other shoots via the same route.

The lack of effect of applied IAA on tillering is contrary to the findings of Leopold (1949) but supports the results of Thorne (1962*a*). In both the present experiment and that of Thorne the auxin applications were made late in development whereas Leopold used much younger plants. This may account for this discrepancy, but much further study is required to establish a role for auxin in the control of tillering in cereals.

The present evidence reinforces the conclusion drawn in the previous paper (Aspinall 1961) that, whatever system of apical dominance is operative within the barley plant, the distribution of mineral nutrients is vitally involved. A theory which takes account only of direct effects of auxin (Thimann 1937) is insufficient to describe the data. On the other hand, a purely competitive hypothesis would also appear to be inadequate. Some type of interaction between growth substances and level of nutrient supply is more likely (van Overbeek 1938; Went 1939; Gregory and Veale 1957). In this connection the recent evidence of auxin influences on the rate and direction of translocation (Booth *et al.* 1962; Hill 1962) is of foremost importance. If nutrients, both mineral and carbohydrate, are preferentially translocated to regions of high auxin content, then the high competitive ability of the grains, at least in CI. 3576, may be due to a high production of auxin. There is every reason to suppose, by analogy with other seeds (Leopold 1955), that the developing grains contain a high concentration of growth substances.

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