TILLERING PATTERNS IN WHEAT WITH SPECIAL REFERENCE TO THE SHOOT AT THE COLEOPTILE NODE

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[Manuscript received April 2, 1971]

Abstract

The production order, survival, and grain yields of individual tillers are described for four wheat cultivars grown at commercial planting densities under natural light and two controlled temperature conditions. One of the cultivars was also grown at wide spacing both in a growth room and outside.

Tiller appearance followed a well-defined pattern, being first the main shoot (M) followed more or less synchronously by T1 (first true-leaf tiller) and P (coleoptile node tiller), then by T2, T1P, and T3; the average contribution to grain yield by each shoot at close spacing was 27, 22, 12, 20, 8, and 8% respectively. The relatively low contribution by P was increased at a lower temperature.

Shortly before or at terminal spikelet formation on the main ear, tillering ceased in all cultivars and conditions, and by this time P was only half as heavy as T1 indicating that it is less well-positioned on the plant to receive assimilates. Grain yields for all tillers were in proportion to their dry weight at heading ($r = 0 \cdot 940$). In turn, grain yields were directly related to age for the primary true-leaf tillers, but the primary and secondary prophyll tillers were much lower yielders than expected from their age; in no case did grain production by P approach that of T2 which appeared much later.

It is suggested that as prophyll tillers, and particularly P, do not yield as well as synchronous true-leaf tillers, plants bearing only true-leaf tillers in rapid succession would be more-efficient grain producers.

I. Introduction

Field-grown wheat plants may produce up to 11 tillers under moderate to high levels of nutrition (Beech and Norman 1966), but a proportion of tillers die at or before emergence of the main ear and contribute nothing directly to grain yield (Engledow 1925; Smith 1933). Which tillers die is associated with time of appearance in relation to the main shoot, with late tillers being less productive (Krishnamurthy, quoted by Bunting and Drennan 1965), while the extent of tiller survival and yield differs with variety, soil fertility (Barley and Naidu 1964; Syme 1967), and the water status of the plant (cf. Hudson 1934 for an early review).

Cannell (1969*a*, 1969*b*) has shown that the primary tiller at the coleoptile node in barley is a shoot which is particularly sensitive to environmental conditions. It differs in its occurrence between varieties, giving a yield advantage to those varieties on which it has a higher frequency. The present study examines the importance of this and other tillers to yield in wheat under controlled conditions. From the

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findings it is suggested that wheat varieties which tend to produce only primary true-leaf tillers in rapid succession would give higher yields per unit area.

II. Materials and Methods

Tillering patterns of wheat plants were examined under three sets of conditions:

(1) At field planting densities, four cultivars were grown under either of two controlled temperature regimes and natural light.

(2) Under wide, non-competitive spacing, one of the cultivars was grown at constant temperature and light conditions.

(3) Under wide, non-competitive spacing, the cultivar from (2) was exposed to unfavourable high temperature conditions prior to heading.

(a) *Experiment 1*

Seeds of wheat cv. Triple Dirk, Heron, Gabo, and Mexico 120, sown at equidistant intervals to give a density of 192 plants per 1 m^2 (equivalent to 55 lb seed per acre), were grown in the Canberra phytotron. Plants were grown singly in pots containing a 50:50 mixture of perlite and vermiculite, and a modified Hoagland's nutrient solution and de-ionized water were supplied daily. Natural illumination was extended to a 16-hr photoperiod by low intensity incandescent lamps and the temperature was controlled at 21°C during the 8 hr of the "day" and 16°C at night, or at 15/10°C for the day/night periods.

Tiller appearance was noted every 2–3 days throughout growth on 20 plants taken from within the stand and dissections of the main shoot of two plants on each occasion showed the developmental stage of the ear. The dry weights of tillers were determined on 20 plants when the terminal spikelet of the main shoot had differentiated, when ears emerged, and at grain maturity. At the final harvest grain numbers and weights were measured for each tiller.

(b) *Experiment 2*

In this study plants of the semi-dwarf cv. Mexico 120 were spaced 1 ft apart in 2-litre pots containing nutrient solution in a growth chamber. The solution, which was changed twice weekly throughout growth, contained 27 p.p.m. nitrogen, 3 p.p.m. phosphorus, 88 p.p.m. potassium, 106 p.p.m. calcium, 52 p.p.m. magnesium, and essential micronutrients. Light of 3000 f.c. at pot level was provided for 16 hr per day from fluorescent and incandescent lamps while the temperature of the growth chamber was maintained at 18°C, intermediate between the two temperature treatments of experiment 1.

Tiller appearance was noted as in experiment 1, and a final harvest was made at maturity to examine the contribution of individual tillers to grain yield.

(c) *Experiment 3*

Tiller appearance was noted every 2–3 days on 36 plants grown 1 ft apart in the nutrient solution detailed under experiment 2; 4·8 litres of solution were available to each plant. This study was conducted outside under the high light and temperature conditions of the South Australian summer, the plants being sown on November 9, 1965. Temperatures were above 32°C for several days between jointing and ear emergence.

The growth of individual tillers was examined in detail from harvests taken approximately every 4 days until emergence of the main ear, but final grain yields were not determined.

(d) *Tiller Nomenclature*

Primary tillers in the axils of the first, second, third, etc. leaves on the main shoot were called T1, T2, T3, etc. while that at the coleoptile node was labelled P or prophyll tiller. Secondary tillers produced in the axils of the prophyll, first, second, and third leaves on primary shoots were termed T*n*P, T*n*1, T*n*2, T*n*3, respectively, where *n* is the group number; secondary tillers on P were labelled PP, P1, P2, P3. Tertiary shoots were labelled similarly (e.g. T*n.n.n.*) and M denoted the main culm.

III. Results

(a) *Experiment 1: Influence of Temperature on Tillering in Four Cultivars*

(i) *Total Tiller Number and Survival to Bear Grain*

Varieties differed appreciably in their maximum tiller number (Table 1) in spite of the close spacing of 192 plants per 1 m^2. However, differences between varieties in the number of ear-bearing tillers were much less, being only 14% at the lower temperature. Consequently the better tillering cultivars had a lower percentage survival of tillers than those which produced fewer shoots.

In all cases, tiller production ceased at or shortly prior to differentiation of the terminal spikelet on the main ear and it was between that time and ear emergence that tillers died on Mexico 120 plants (Fig. 1).

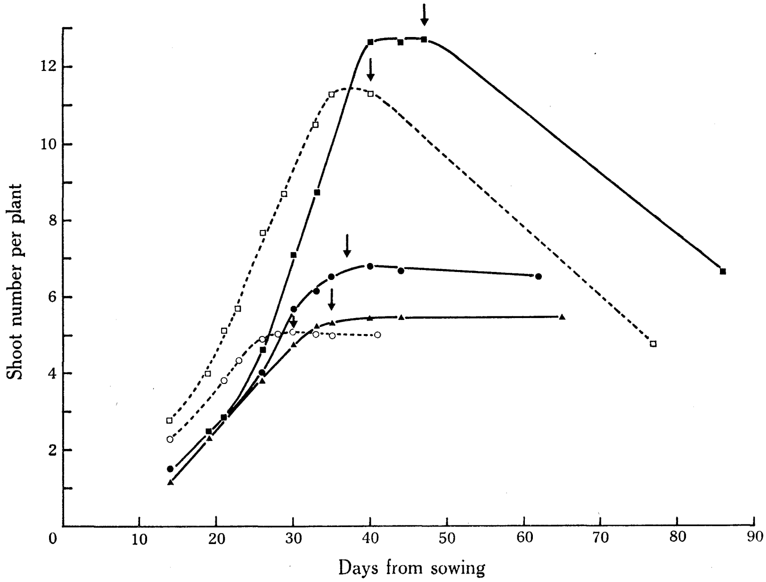


Fig. 1.—Shoot number per plant of wheat cv. Mexico 120 (■, □), Gabo (●, ○), and Triple Dirk (▲), grown either at 21/16°C (dotted lines) or 15/10°C (solid lines) and at approximate commercial sowing densities. For clarity on the graph data for cv. Heron are not shown. The last point on each curve is ear emergence and arrows point to terminal spikelet appearance.

(ii) *Individual Tiller Appearance and Grain Yield*

Main and first and second true-leaf tillers were the only shoots to be produced and survive on all plants under both temperature regimes (Table 2). The primary prophyll tiller and T3 and T1P were also important in all varieties, but most other tillers seldom survived to bear an ear.

Only the primary prophyll tiller and its subsidiaries were particularly influenced by temperature, appearing in most cases and having a much greater chance of survival at the lower temperature.

TABLE 1

SOME TILLER AND EAR CHARACTERISTICS FOR FOUR WHEAT CULTIVARS GROWN AT TWO TEMPERATURES

Values are means for 20 plants ± S.E.

Cultivar	21/16°C			15/10°C		
	Maximum Tiller No.	Ear No.	Tiller Survival (%)	Maximum Tiller No.	Ear No.	Tiller Survival (%)
Mexico 120	$11 \cdot 35 \pm 0 \cdot 48$	$5 \cdot 95 \pm 0 \cdot 22$	52·4	$12 \cdot 75 \pm 0 \cdot 59$	$5 \cdot 90 \pm 0 \cdot 16$	46·2
Gabo	$5 \cdot 50 \pm 0 \cdot 19$	$3 \cdot 85 \pm 0 \cdot 17$	70·0	$5 \cdot 45 \pm 0 \cdot 30$	$5 \cdot 05 \pm 0 \cdot 29$	92·6
Triple Dirk	$5 \cdot 10 \pm 0 \cdot 24$	$4 \cdot 30 \pm 0 \cdot 21$	84·3	$6 \cdot 80 \pm 0 \cdot 18$	$5 \cdot 40 \pm 0 \cdot 19$	79·4
Heron	$4 \cdot 35 \pm 0 \cdot 28$	$3 \cdot 90 \pm 0 \cdot 37$	89·6	$5 \cdot 40 \pm 0 \cdot 26$	$5 \cdot 10 \pm 0 \cdot 22$	94·4
Mean	$6 \cdot 67 \pm 0 \cdot 30$	$4 \cdot 00 \pm 0 \cdot 24$	72·9	$7 \cdot 60 \pm 0 \cdot 33$	$5 \cdot 36 \pm 0 \cdot 21$	78·1

TABLE 2

TILLER PRODUCTION AND SURVIVAL TO BEAR GRAIN FOR FOUR WHEAT CULTIVARS GROWN AT 21/16°C

Results for a selection of tillers grown at 15/10°C are also shown. Tiller numbers are expressed as a percentage presence on 20 plants. Tiller nomenclature as defined in the text

Shoot	Mexico 120		Gabo		Triple Dirk		Heron	
	Production	Survival	Production	Survival	Production	Survival	Production	Survival
				Temperature 21/16°C				
M	100	100	100	100	100	100	100	100
P	90	60	95	65	100	35	20	15
T1	100	100	100	100	100	100	100	100
T2	100	100	100	100	100	100	100	100
T3	100	80	80	5	60	45	70	30
T4	95	10			5	0	10	0
T5	15	0						
T1P	100	95	100	15	90	50	55	20
T2P	100	20	20	20	10	0	15	10
T3P	35	0						
T1.1	100	10	20	0	10	0	15	10
T2.1	70	0					10	0
T1.2	20	0						
P.P	45	0	15	0	20	0	5	5
P.1	50	0	20	0				
T1.P.P	40	0						
				Temperature 15/10°C				
P	100	85	100	100	100	100	100	65
P.P	95	10	50	10	75	5	15	10
P.1	90	0	40	0	40	20	20	0

The sequence of production of tillers did not differ greatly between varieties or between temperatures (Table 3); a generalized scheme would be M, T1/P, T2, T1P, T3 (P appeared with, slightly before, or slightly after T1). At the lower temperature there tended to be a longer interval between the appearance of the first three shoots and later tillers.

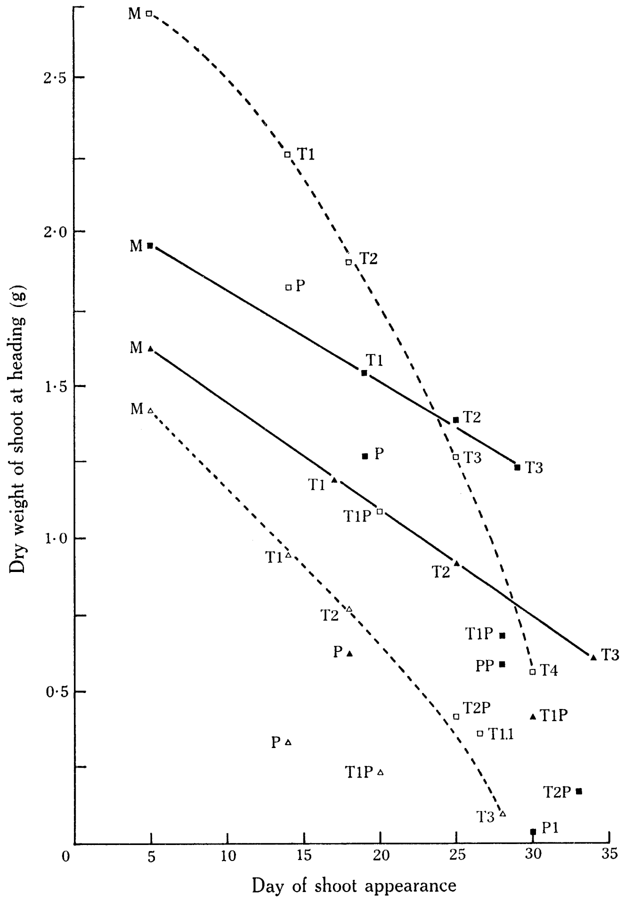


Fig. 2.—Dry weight at heading in relation to the day of appearance of shoots for Mexico 120 (■, □) and Triple Dirk (▲, △) grown at either 21/16°C (dotted lines) or 15/10°C (solid lines). Curves connect values for main and true-leaf tillers; each value is based on mean for 20 plants.

Grain yields per shoot (Table 4) were not entirely in relation to the time of production of a tiller. Although the main shoot was always the greatest contributor to total grain yield and by definition the first shoot to appear, the primary prophyll tiller was much less productive than would be predicted from its time of emergence. Even for cv. Gabo and Triple Dirk grown at 15/10°C, in which P appeared before T1 (Table 3) and had the same percentage survival (Table 2), the grain yields of P were appreciably lower than those for T1 (Table 4). In fact, for three of the cultivars P produced yields comparable with T3 which appeared up to 2 weeks later.

T1P was also a poor yielder, always appearing several days before T3 and having similar survival, but invariably yielding no better.

TABLE 3

DAY OF APPEARANCE OF TILLERS OF FOUR WHEAT CULTIVARS GROWN AT TWO TEMPERATURES

Tillers were considered to be present when they occurred on at least 50% of 20 plants

Day	21/16°C				15/10°C			
	Mexico 120	Gabo	Triple Dirk	Heron	Mexico 120	Gabo	Triple Dirk	Heron
	M	M	M	M	M	M	M	M
14	T1/P	T1	T1/P	T1			P	
17		T2		T2			T1	
18	T2	P	T2			P		T1
19					T1/P	T1		P
20	T1P		T1P					
23				T1P				
25	T3/T2P	T1P			T2		T2	
26						T2		T2
27	T1.1			T3				
28			T3		T1P/PP		PP	
29					T3			
30	T4	T3			P1		T1P	T1P
31						T1P		
33	T2.1				T2P			T3
34							T3	
35	P1							

TABLE 4

GRAIN YIELD PER PLANT AND PERCENTAGE CONTRIBUTION OF EACH TILLER IN FOUR WHEAT CULTIVARS GROWN AT TWO TEMPERATURES

Where total values are less than 100%, contributions from minor tillers have not been included. Each value is the mean for 20 plants

Shoot	Percentage Contribution at 21/16°C				Percentage Contribution at 15/10°C				Overall Mean
	Mexico 120	Gabo	Triple Dirk	Heron	Mexico 120	Gabo	Triple Dirk	Heron	
M	21·9	26·7	27·7	33·8	23·7	26·7	29·7	29·3	27·4
P	10·7	14·3	6·1	3·6	13·3	18·8	14·6	12·7	11·7
T1	19·6	24·9	23·8	24·5	17·2	21·0	20·8	22·2	21·7
T2	16·9	23·8	25·2	24·0	17·4	18·8	17·8	18·1	20·2
T3	10·6		8·5	6·1	15·3	1·3	10·6	8·5	7·6
T4	1·6				1·6				0·4
T1P	14·1	5·3	8·7	4·0	8·0	13·4	3·0	6·6	7·9
T2P	2·8			1·8	0·7		1·6		0·8
T1.1	1·6			2·0					0·4
Grain per plant (g)	10·708 ±0·833	4·323 ±0·220	4·449 ±0·259	4·249 ±0·387	9·502 ±0·679	6·216 ±0·230	5·415 ±0·223	5·592 ±0·338	

The tillers in their order of production together with their average yields for all cultivars and treatments give the summarized situation: M 27%, T1 22%, P 12%, T2 20%, T1P 8%, T3 8%.

(iii) *Biological and Economic Yield of Tillers*

There was an almost exact relationship between the time of appearance and the dry weight at ear emergence for main and primary true-leaf tillers (Fig. 2). Although there were differences of degree, this general relationship held for both cultivar and temperature. Prophyll tillers, on the other hand, whether primary or secondary in origin, had much lower dry weights than would be predicted for true-leaf tillers of the same age, and this applied for all treatments. Even by terminal spikelet formation, the primary prophyll tillers were on average only 52% of the weight of their near synchronous true-leaf tiller (T1). The mean dry weights (S.E. $\pm 13 \cdot 7$) for T1 and P tillers which were present at terminal spikelet formation under the 15/10°C treatment were respectively 289 and 104 mg for Mexico 120; 125 and 88 mg for Gabo; 185 and 104 mg for Triple Dirk; and 131 and 87 mg for Heron.

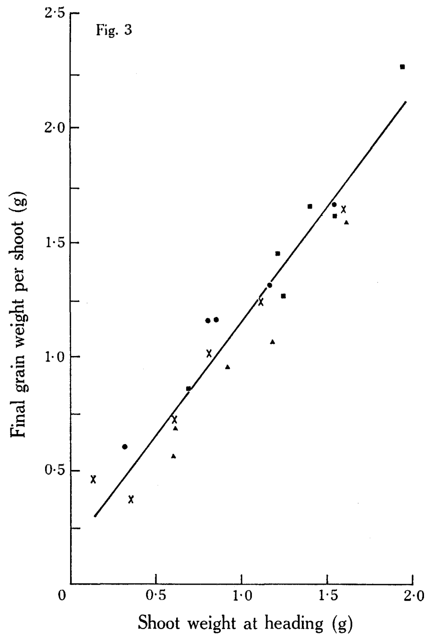
The necessity for a tiller to have a high dry weight at ear emergence so that it will yield well at maturity is seen on Figure 3, where $r = 0 \cdot 940$. Only the curves for 15/10°C are shown, as the same relationship was apparent for plants grown at 21/16°C, but under the higher temperature regime less grain was produced for shoots of a particular weight. For example, from the slope of the curve, 1 g of dry material at ear emergence was equivalent to $1 \cdot 075$ g grain at 15/10°C while the comparative value for the 21/16°C treatment (not shown) was $0 \cdot 825$ g. It is interesting that Mexico 120, which was the semi-dwarf cultivar in this trial, had the greatest dry weight per tiller in spite of its short stature, and also yielded most grain.

Regardless of the position on the plant and date of origin of a tiller, the harvest index of tillers (ratio of tiller total dry weight to grain weight) within each cultivar was the same in spite of a fourfold range in total weight per tiller at maturity (Fig. 4). Harvest index, taken at maturity, was highest in the semi-dwarf cultivar as shown by several other workers.

(*b*) *Experiment 2: Tillering of Mexico 120 under Wide Spacing*

No data are available for the primary prophyll tiller in experiment 2 as preliminary studies showed that it scarcely ever occurred under these conditions of low nitrogen; consequently it was excised if it appeared.

The pattern of tiller appearance differed only slightly from that at close spacing in that T1.1 was relatively earlier (compare Table 5 with values for Mexico 120 in Table 3). More tillers of secondary and tertiary origin were produced but, although several secondary shoots survived to bear grain, the sole contributing tertiary tiller was T1.P.P with an average of 187 mg grain per ear. Under wide spacing, tillers contributed more evenly to the total grain yield of the plant; 90% was produced by the main and primary tillers in experiment 1, but this was reduced to 56% under wide planting.



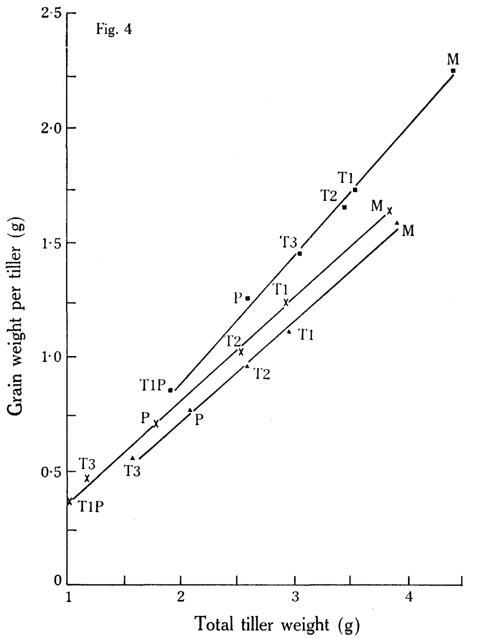


Fig. 3.—Grain production by shoots of different dry weight at heading for Mexico 120 (■), Triple Dirk (▲), Heron (×), and Gabo (●) grown at 15/10°C. Each value is the mean for 20 plants ($r = 0 \cdot 9399$).

Fig. 4.—Relation between grain yield and total dry weight for individual tillers of Mexico 120 (■), Triple Dirk (▲), and Heron (×) grown at 15/10°C. Each value is the mean for 20 plants.

TABLE 5

GRAIN YIELDS FOR THE MORE IMPORTANT SHOOTS OF MEXICO 120 PLANTS GROWN AT 18°C AND WIDE SPACING

Yields for Plumage Archer and Proctor barley plants (adapted from Thorne 1962) are also shown. Tillers are arranged in their sequence of appearance, both barley cultivars following the same pattern

Mexico 120			Barley Cultivars		
Shoot	Grain Weight per Ear ± S.E. (mg)	% of Grain Yield	Shoot (both barley cultivars)	Pl. Archer: % of Grain Yield	Proctor: % of Grain Yield
M	746±43	13·6	M	13·3	14·7
T1	628±49	11·4	T1	12·2	14·2
T2	625±22	11·4	T2	12·7	13·0
T1P	382±40	7·0	T1P	10·6	11·2
T3	567±52	10·3	T3	11·1	12·1
T1.1	461±44	8·5	T2P	8·6	7·6
T2P	364±39	7·0	T1.1	7·2	5·7
T4	509±50	9·3	T1P.P	5·4	0·2
T1.P.P	187±20	3·4	T4	6·8	8·9
			P*	4·9	11·6

* P was the third shoot to appear in Thorne's study, but was excised in Mexico 120. These values for P include its subsidiary tillers.

As was observed for dense sowing, the grain yield of shoots was not in exact relation to their age. The primary tillers usually yielded well and the prophyll tillers yielded less well than their true leaf counterparts. For example, T4 was the eighth tiller to emerge yet had the fifth highest grain production. Both T1P and T2P appeared earlier than T4 but yielded less (Table 5, also compare with barley).

(c) *Experiment 3: Survival of Tillers of Mexico 120 under High Temperature*

In this study of Mexico 120 plants grown at a spacing of 1 ft in nutrient solution, conditions were extremely favourable for rapid tillering during the early weeks after sowing. Tillers emerged in a similar order to that shown for experiment 2 (Table 5) but more were produced. However, after jointing or terminal spikelet formation, temperatures rose to high levels, causing the plants to shed tillers, so that by earing only seven of the 28 shoots remained alive. Of these 3·8 were primary (including M), 3·1 were secondary, and 0·1 were tertiary tillers, based on counts of 36 plants (Fig. 5).

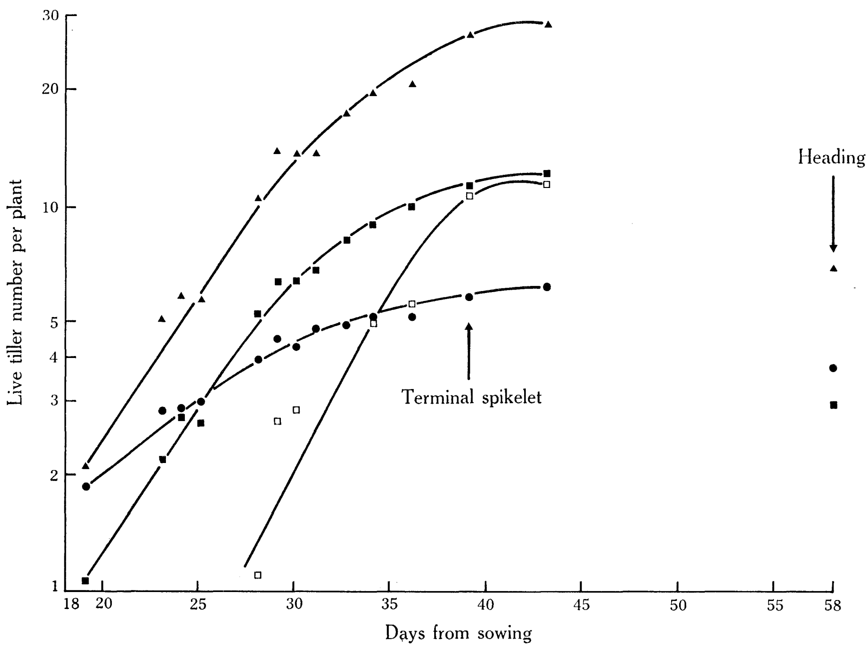


Fig. 5.—Total (▲) and live primary (●), secondary (■), and tertiary (□) tiller numbers for plants of Mexico 120 grown outside in nutrient solution. Each value is the mean for 36 plants.

Under these conditions of physiological drought, tillers differed in their persistence and although M, T1, and T2 all survived, the percentage survival for other major shoots was less: T1.1 78%, T3, T4 67%, T1P 55%, and T2P 45% survival. Age of a shoot and point of origin on the plant both apparently influenced persistence, with primary true-leaf tillers being advantageously positioned and secondary prophyll tillers being ill-placed (compare percentage survival here with that in Table 2 for

Mexico 120 when only 11 tillers were produced per plant, and with the order of production of tillers given in Table 5). T1.1 was more successful under these conditions than was found in the controlled-environment conditions of experiment 1.

IV. Discussion

Controlled-environment conditions and pot culture were used in these studies to isolate the effects of factors on tillering patterns in wheat in the absence of unwanted variables that are likely to occur in the field. Because field-planting densities and natural light were used in the variety $\times$ temperature experiment (1), it is felt that conclusions may be extrapolated, with some reservations, to the field situation. The wide-spacing studies (experiments 2 and 3) were done for the purpose of understanding plant behaviour in an environment of relatively non-limiting light and will be discussed only briefly.

Similarities between this work and that reported for barley (Thorne 1962; Cannell 1969*a*, 1969*b*) are marked and indicate that almost any finding regarding tillering patterns in either cereal may be applied to the other. Before making comparisons, it should be pointed out that the above two authors have used a slightly different system of naming tillers to that used here. In the present work the primary tiller at the coleoptile node is labelled P or prophyll tiller while the first true-leaf tiller is T1 (equivalent to the T2 of Thorne and Cannell). The reason for this change of nomenclature is that the prophyll tillers do not appear to accord with the pattern of growth for true-leaf tillers.

Tiller appearance follows a fairly well-defined pattern, being M, T1/P, T2, T1P, T3, T2P, with some variation in the timing of P which may arise before or after T1 depending on the cultivar and temperature. Thorne and Cannell differ a little in the placing of P in the sequence, either after T2 or before T1 respectively, but differences may be due somewhat to the criteria used for estimating presence. In these studies, at least 50% of plants had to bear a tiller before it was considered present, and as P is variable in its occurrence, the percentage value chosen introduces errors.

The grain yield of the main shoot is always superior to that of any tiller but its relative contribution varies depending on the conditions under which plants are grown. In field studies the main shoot of wheat supplied 50 and 70% towards total plant grain at planting densities of 151 and 303 plants per 1 m^2 respectively (Bremner 1969) while under the high fertility of experiment 1, the main shoot of Mexico 120 at 192 plants per 1 m^2 yielded 23% compared with only 13·6% at 10·6 plants per 1 m^2 (expt. 2). The latter value is very close to that of Thorne (1962), shown in Table 5, for which planting densities were not given. Therefore with better fertility and wider spacing, the relative contribution of the main shoot declines due to greater production and survival of the tillers.

Cannell (1969*b*) has drawn attention to the prophyll tiller as being a shoot which varies a great deal in its contribution to grain yield depending particularly on the temperature conditions during tillering and on soil fertility. He also pointed out that it yields better in the more modern barley varieties. It seems from the limited number of cultivars in these studies that there has been little or no selection for a greater yield contribution by P in wheat. Mexico 120, which is a representative of the semi-dwarf wheats, has no better survival and less yield from its prophyll tiller than Gabo which was released in 1948 (Tables 2 and 4). However, P does have much better survival and yield when the temperature is lower and, judging from its almost complete failure in Mexico 120 under relatively low nitrogen nutrition (cited in expt. 2) and success when nutrients are not limiting (expt. 1), it would appear that P is affected similarly in both wheat and barley. Spacing is unlikely to influence the time and order of production of P as light becomes limiting only later when further tillers have appeared.

Regarding the importance of P to grain yield, it seems that this tiller can account for differences in production between barley varieties even though it yields poorly in relation to the time of its occurrence on the plant. It usually appears before T1 but always yields less (Cannell 1969*a*) and may produce less grain than T3 (Thorne 1962; cf. Table 5). Similarly, in wheat it generally appears as second or third shoot but usually falls fourth or fifth in its contribution to grain yield together with T3 which may appear 2–3 weeks later. Even T1P may yield better in some varieties and conditions (Table 4). Apparently P is less advantageously placed on the plant than other shoots and particularly than the primary true-leaf tillers.

There was a simple relationship between the weight and age of primary true-leaf tillers at emergence of the main ear (Fig. 2) for different cultivars grown under different conditions. However, the dry weight of the prophyll tillers was much less than would be expected from their age, P being between 20 and 50% lighter than its more or less synchronous tiller T1. Only part of this poor performance was due to the lower survival of P. Because shoots produce grain in proportion to their total weight at the stage of heading (Fig. 3), P is by this time already at a disadvantage.

One point of interest is that Mexico 120 had the heaviest shoots at heading even though it had by far the shortest stature. This was due to its thick culms (cf. Evans *et al.* 1970 for details) and large leaves. The achievement of a heavy shoot by earing confers a distinct advantage, and this should be borne in mind by plant breeders.

Under conditions of wide spacing the prophyll tiller on T1 also yielded poorly; T1.1, a true-leaf tiller, yielded better although it appeared later (compare results in Table 4 with those in Table 5 for Mexico 120). The apparent advantage of the true-leaf tillers over prophyll tillers may be linked with the availability of assimilates during their early growth. Possibly leaves supply the tillers in their axils [although this would appear to be a wrong assumption judging from results with rice (Inosaka 1958)] and prophyll tillers have to depend largely on photosynthesis by their related prophyll (or coleoptile sheath in the case of P). Evidence in favour of this suggestion is that by terminal spikelet formation, T1 was already double the dry weight of P although the shoots appeared at approximately the same time. The better survival and yield of P at the lower temperature, where assimilates would be less limiting within the plant, also adds weight to this argument. A study with ^{14}C-labelled assimilates is required to provide information.

The poor survival of P may be partially related to the efficiency of its root system as has been suggested for other shoots which die between terminal spikelet formation and heading (Rawson and Donald 1969). This is unlikely to be the only factor influencing survival as separation of tillers from the main plant greatly increases their fertility. Miller in 1765 (quoted by Percival 1921) showed that by separating tillers and replanting them, one grain of wheat yielded over 21,000 ears and approximately 577,000 grains in one season. Similarly Tange (1961, 1963, 1965) working with rice and wheat and Rawson (1967) with wheat found that if tillers that were expected to die were excised and repotted individually, they survived to bear grain even if they had no roots at the time of separation.

Further studies are required to examine the grain yield of plants with and without prophyll tillers. It is proposed from the evidence at hand that a plant type which produces only true-leaf tillers in rapid succession would give a greater grain yield per unit area.

V. Acknowledgments

Financial support during the 1965 studies was provided by the Scientific Research Council of N.A.T.O. and for experiment 1 by the Australian Wheat Industry Research Council. Capable assistance for experiment 1 was provided by Mrs. A. Ashby.

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