

ACCUMULATION OF DRY MATTER AND NITROGEN BY GRAINS IN DIFFERENT POSITIONS OF THE WHEAT EAR AS INFLUENCED BY SHADING AND DEFOLIATION

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Abstract

The order of priority for supply of assimilate and nitrogen between individual grains of the wheat ear was studied by determining their accumulation of dry matter and nitrogen when the supply was varied by shading and defoliation, alone and combined, from 2 weeks after anthesis.

The production of assimilates by untreated plants was surplus to the requirements of grain filling. Treatments influenced the distribution of dry matter so as to minimize effects on grain.

In one cultivar, there was no well-defined pattern of individual grain responses to treatments. In another, the data were consistent with the predominance of an effective parallel linkage of spikelets to sources, although a series-type linkage assumed some importance when there was severe shortage of assimilate (60% reduction in grain growth); upper spikelets were then more seriously affected. Within spikelets, a series effect was more evident, grains being increasingly affected by severe shortage with progression from base to apex of the spikelets; when the overall grain growth reduction was about 60%, growth of first, second, and third grains in a central spikelet was reduced by about 50, 60, and 70% respectively. There were differences between shading and defoliation in their effects on distribution of assimilate, and these differences were consistent with preferential distribution of shoot assimilate to second grains and central spikelets.

The third grain of three-grain spikelets was characteristically lower in nitrogen than the others, and this difference was increased by even moderate levels of shortage.

It is suggested that the fast growth rate of the second grain in central spikelets is due to its capacity for growth rather than to a favourable position *vis-à-vis* the vascular system.

I. INTRODUCTION

Following a period in which much of the research into the physiology of grain yield in cereals was focused upon the productive capacity of the photosynthetic system during grain filling, in the belief that this primarily limited yield (see Watson 1956; Thorne 1966), there has been a shift towards a greater awareness of sink-source relations. Particular interest has centred around the capacity of the ear to use assimilate. It is considered that in optimal conditions at least, this may limit yield more often than does the supply of assimilate, which may exceed the demands of grain filling (e.g. Asana 1968; Evans and Rawson 1970).

Two attributes, possibly interrelated, which might influence the capacity of the ear to use assimilate are the number of grains it contains and the size and efficiency of its vascular system. Although valuable anatomical studies of the latter have been

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made (Zee and O'Brien 1971), little is known of its quantitative functioning—whether, for example, the spikelets and florets within them are connected with the main sources effectively in parallel or in series. This paper describes an indirect approach to this problem; treatments varied the level of assimilate available for grain filling, and the resulting effects on the accumulation of dry matter and nitrogen by individual grains were examined with a view to estimating the order of priorities, hence the general nature of the vascular connections, within the ear.

II. METHODS

Two cultivars, WW 15 (Mexican) and Timgalen (Australian), were used, and treatments applied 2 weeks after anthesis, so that they would not affect grain numbers.

The plants were grown in a glasshouse of the Canberra phytotron in pots (8 in. deep, 3 in. diameter; one plant per pot) containing a mixture of perlite and vermiculite which was soaked with nutrient solution each morning and with water each afternoon. The temperature was 21°C from 8.30 a.m. until 4.30 p.m. and 16°C for the remaining 16 hr, and natural light was supplemented with low-intensity incandescent lamps to give a 16-hr day. Tillers were removed periodically and the experimental material selected from the resulting population of single-culm plants. Selection was made at anthesis (10 days earlier in WW 15 than in Timgalen) on the basis of the date of anthesis, general uniformity, and the probable possession of 13 fertile spikelets. All leaves but the youngest three were removed. Two weeks after anthesis, all remaining tillers were removed and the following treatments imposed: untreated control (C); whole-plant shading with black Sarlon, which reduced light intensity by 45% (S); all leaf laminae removed (D); and a combination of S and D (SD).

TABLE 1
FREQUENCY OF OCCURRENCE OF GRAINS IN VARIOUS POSITIONS IN WW 15 AND TIMGALLEN CULTIVARS
Spikelets numbered from the apex of the ear and grains from the base of the spikelet

Spikelet	WW 15			Timgalen		
	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>
3	0.99*	0.99*	0.10	0.93	0.65	0.10
5	0.96*	0.95*	0.61	0.92*	0.90*	0.15
7	0.99*	0.96*	0.87*	0.99*	0.94*	0.65
9	0.99*	0.95*	0.87*	1.00*	0.93*	0.83*
11	0.92*	0.87*	0.87*	0.93*	0.88*	0.78*
13	0.91*	0.86*	0.45	0.94*	0.88*	0.60

* Grains on which the analyses of the data were based.

At anthesis and again a week later, six plants were harvested from each cultivar, so that the early stages of grain growth could be described. A further harvest of 10 plants per cultivar was made the day treatments were imposed, and at weekly intervals over the next 4 weeks four plants per treatment were taken. These were separated into leaves, stems, ears, roots, and tillers, all of which were dried and weighed. Grains were dissected from all positions on one side of the ear—counting from the apex, spikelets 3, 5, 7, 9, 11, and 13; the frequency of occurrence of grains in the various positions is given in Table 1—and individually dried and weighed. Their nitrogen content was determined by a microKjeldahl method, grains from the four replicates being bulked for this purpose. The nitrogen content of stems and leaves was similarly determined on bulked samples.

The statistical treatment of the individual grain data was based on those grains marked with an asterisk in Table 1. For between-spikelet comparisons, the first two grains (*a* and *b*)

in all the recorded spikelets of WW 15 and in 5, 7, 9, 11, and 13 of Timgalen were used, and for those within spikelets grains *a*, *b*, and *c* in spikelets 7, 9, and 11 of WW 15 and 9 and 11 of Timgalen. When a grain was absent from a position marked with an asterisk, a missing value was estimated in the usual way. A necessary condition for the validity of this treatment of the grain is that the grains behaved as independent units. That is, that the presence or absence of any grain had no effect on the other grains in the spikelet: if *c* were missing, *a* and *b* should not, thereby, be larger; nor should *b* and *c* if *a* were absent. Although Rawson and Evans (1970) found such independence not to operate during the grain set phase, it did in this experiment, which covered the period from 14 days after anthesis until near maturity. For example, in WW 15 *5c* was present rather more often than it was absent; on the last two harvest occasions and averaged over all treatments, *5a* and *5b* weighed 26.6 and 25.9 mg respectively when *5c* was absent and 30.4 and 32.0 mg when it was present. Thus, there is no evidence here that the absence of *5c* increased the size of *5a* and *5b*. However, the test is unsatisfactory in that the presence or absence of *5c* is confounded with spikelet vigour—*5c* is present in more vigorous spikelets in which *5a* and *5b* tend to be larger. A better test is comparison of the ratio $(5a + 5b)/(7a + 7b + 9a + 9b + 11a + 11b)$ in the presence and absence of *5c*. This was done for a dozen pairs of ears from the last two harvests, and the ratios were almost identical, with a pooled standard error of less than 2% of the mean. Similar tests for the effects of absence of *a* or *b* on remaining grains gave similar results. The same pattern was evident in Timgalen. Thus, it seemed that grains within a spikelet were no more closely related to each other than to grains in other spikelets. Presumably the apparent conflict with Rawson and Evans' results stems from differing requirements at different stages of growth; during grain set, grains compete for some factor in short supply, whilst in rapid grain growth, the main factor involved—carbohydrate supply—is often not limiting.

III. RESULTS

The mean daily radiation over the experimental period was 380 cal cm⁻². Because the cultivars were out of phase, there was some difference in the radiation they received at comparable stages of growth, but *in toto* this amounted to only 4%. Senescence was more rapid in Timgalen, being almost complete by the end of the experiment, at which time there was only some 5% leaf senescence in WW 15.

(a) Dry Matter Production and Distribution

The data for Timgalen are suspect because the final harvest was variable, particularly in respect of plants subject to shading alone, where it was at variance with the trend of previous harvests to a degree that the effects of this treatment on the cultivar are uncertain Fig. 1(a).

In WW 15, shading and defoliation had similar effects on total dry weight and these were less than additive in the combined treatment (SD). Shading had a smaller effect on grain yield than did defoliation [Fig. 1(b)], and the effects of the two were more than additive. If we consider treatment effects on the relative increments in dry weight and grain weight over the experimental period (taking as final values the means of harvests 3 and 4 to improve the stability of the data), we have for WW 15:

	Relative increments			
	C	S	D	SD
Dry weight	100	53	46	17
Grain weight	100	85	73	38

The increment in grain weight was 63, 100, 130, and 141% of that in total dry weight in C, S, D, and SD respectively. Thus, during grain filling, control plants produced

dry matter over one-third in surplus of the needs of grain filling, this surplus being used or stored in stems and roots or for tiller growth (Table 2). At the other extreme, only the grain increased in weight in the main culms of plants which were both shaded and defoliated, although there was some tiller growth. Similar general trends were apparent in Timgalen although treatment effects on total dry weight were smaller.

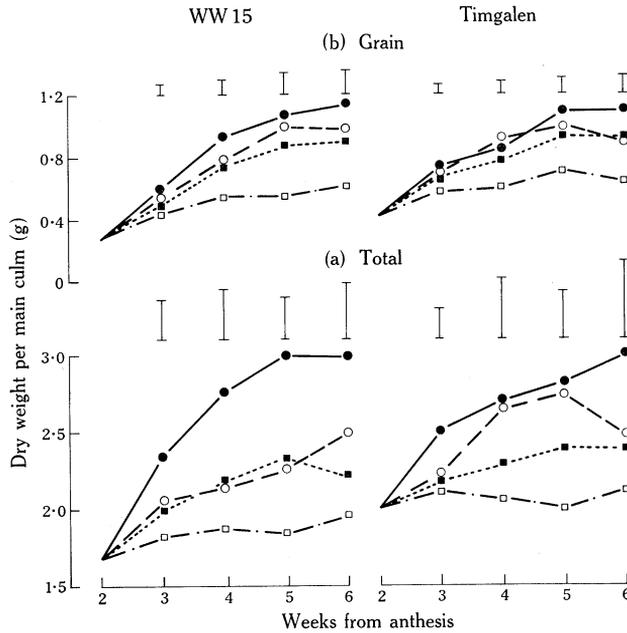


Fig. 1.—Effect of treatments on the change with time in (a) main shoot total dry weight (minus leaf laminae) and (b) grain dry weight. Vertical bars represent least significant differences at $P = 0.05$. ● Control. ○ Shaded. ■ Defoliated. □ Shaded and defoliated.

TABLE 2
EFFECT OF TREATMENT ON THE NUMBER AND WEIGHT OF TILLERS PER PLANT AT THE END OF THE EXPERIMENT

All plants de-tillered at beginning of experiment

	WW 15				Timgalen			
	C	S	D	SD	C	S	D	SD
No. of tillers per plant	11.00	4.50	2.75	0.75	1.00	1.00	2.00	0.50
Weight of tillers per plant (mg)	2508	603	341	77	178	129	96	49

(b) Growth of Individual Grains

As the data for WW 15 were less variable, we shall concentrate on these, and except where otherwise stated, what follows in this section refers to this cultivar.

Also, the bases of between- and within-spikelet comparisons should be recalled: the former is grains *a* and *b* in all recorded spikelets (except the third in Timgalen) and the latter grains *a*, *b*, and *c* in spikelets 7, 9, and 11 (9 and 11 in Timgalen).

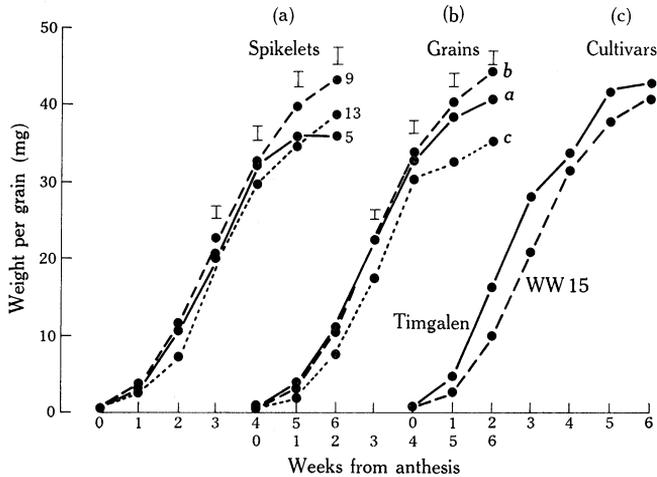


Fig. 2.—Change with time in weight per grain at various positions in the ear of control plants: (a) upper, middle, and lower spikelets of WW 15 based on the means of grains *a* and *b*; (b) grains *a*, *b*, and *c* of WW 15 based on the means of spikelets 7, 9, and 11; (c) a comparison of the two cultivars based on the means of *a*, *b*, and *c* in spikelets 9 and 11. Vertical bars represent least significant differences at $P = 0.05$.

The growth of grains in control plants was similar to that observed by Rawson and Evans (1970) and will not be described in detail here. Grains in middle spikelets were larger than those in upper or lower spikelets at anthesis (0.50, 0.40, and 0.35 mg respectively) and they maintained this advantage; those in lower spikelets, although

TABLE 3
MEAN DRY WEIGHTS (MG) OF GRAINS IN THE VARIOUS POSITIONS OF THE EARS OF CONTROL PLANTS AT THE END OF THE EXPERIMENT

Spikelet	WW 15			Timgalen		
	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>
3	32.9	31.5	—	38.2	—	—
5	35.2	36.4	—	42.0	40.2	—
7	38.3	42.6	32.5	43.0	44.4	—
9	41.8	44.2	35.0	44.3	46.8	39.6
11	41.3	45.3	37.6	43.7	47.4	34.4
13	35.7	36.8	—	43.1	41.4	—

smaller than grains in upper ones at anthesis, overtook the latter which ceased growth earlier [Fig. 2(a)]. Within spikelets, grain *a* was the largest at anthesis (0.58 mg), but *b* (0.41 mg) grew faster, so that by the end of the experiment it was either of a similar size to *a* or larger, depending on the position of the spikelet [Fig. 2(b); Table 3].

Grain *c* (0.22 mg) was smaller than either *a* or *b* and the difference increased towards maturity. These data and those for Timgalen, which were essentially similar, do not support the conclusion of Walpole and Morgan (1970) that grains do not differ in relative growth rate in the month after anthesis. Grains of Timgalen were larger than those of WW 15 at anthesis (0.48 and 0.40 mg respectively) and grew relatively faster for the next 2 weeks (to 16.8 and 9.5 mg); even though their relative growth rate was subsequently slower, Timgalen grains were still larger at the end of the experiment [Fig. 2(c); Table 3].

The significance of the relevant interactions encountered in the analyses of variance of the grain weights of the two cultivars is shown in Table 4; the increments in grain dry weight over the experimental period, treatments relative to control plants, are given in Table 5.

TABLE 4
SIGNIFICANCE OF THE VARIOUS INTERACTIONS ENCOUNTERED IN THE ANALYSES OF VARIANCE OF THE GRAIN WEIGHT DATA

Cultivar	Harvest	Significance of interactions:			
		Between spikelets†		Within spikelets‡	
		Treatment × spikelet	Treatment × grain	Treatment × spikelet	Treatment × grain
WW 15	1				
	2			*	**
	3		***		**
	4	*	***		***
Timgalen	1				
	2				
	3	**			**
	4				

* $P = 0.05$. ** $P = 0.01$. *** $P = 0.001$.

† Grains *a* and *b* in spikelets 3, 5, 7, 9, 11, and 13 of WW 15, and 5, 7, 9, 11, and 13 of Timgalen.

‡ Grains *a*, *b*, and *c* in spikelets 7, 9, 11 of WW 15, and 9 and 11 of Timgalen.

Considering first the comparison between spikelets (Table 4), and again directing our attention at the data for WW 15, the treatment × spikelet interaction was significant, and then comparatively weakly so, on only one of four occasions. Thus, when the supply of assimilate was severely reduced (SD), upper spikelets were more affected than others; the smaller reduction occasioned by shading or defoliation alone had little effect on distribution between spikelets (Table 5). In Timgalen, neither large nor small reduction in assimilate supply had any perceptible effect on distribution between spikelets; even when the treatment × spikelet interaction was significant (Table 4) the distribution of more seriously affected spikelets did not conform to any well-defined pattern (data not presented).

Within spikelets, the effects of severe shortage (SD) increased progressively from base to apex of the spikelet (Tables 4 and 5): the increments were about 50, 40, and 30% of controls in *a*, *b*, and *c* respectively. A greater effect on *c* than on other grains was apparent in treatments S and D as well, and S had a greater effect on *b* than on *a*.

TABLE 5

EFFECT OF TREATMENTS ON THE INCREMENT IN DRY WEIGHT PER GRAIN

Values given in *italic* font represent the increments (mg) for control plants; the remainder are treatment values expressed as a percentage of the controls

Spikelet	Treatment	WW 15			Mean <i>a+b</i>	Timgalen			Mean <i>a+b</i>
		Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>		Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>	
3	C	<i>23.3</i>	<i>23.1</i>	—		—	—	—	
	S	83.7	74.9	—	79.3	—	—	—	
	D	73.0	67.5	—	70.3	—	—	—	
	SD	33.9	20.4	—	27.2	—	—	—	
5	C	<i>24.5</i>	<i>26.4</i>	—		<i>24.6</i>	<i>25.4</i>	—	
	S	89.4	85.2	—	87.3	52.9	62.2	—	57.6
	D	74.7	72.4	—	73.6	66.3	74.8	—	70.6
	SD	43.3	31.0	—	37.2	29.7	33.9	—	31.8
7	C	<i>26.2</i>	<i>32.0</i>	<i>24.8</i>		<i>25.1</i>	<i>29.4</i>	—	
	S	93.9	82.5	71.0	88.2	61.8	67.7	—	64.8
	D	66.4	71.6	60.5	69.0	75.3	79.9	—	77.6
	SD	48.5	37.8	29.8	43.2	35.5	35.0	—	35.3
9	C	<i>30.4</i>	<i>33.7</i>	<i>26.4</i>		<i>25.9</i>	<i>29.3</i>	<i>23.6</i>	
	S	82.9	81.0	71.6	82.0	68.7	68.9	67.8	68.8
	D	64.1	69.1	60.6	66.6	82.6	67.6	66.1	75.1
	SD	51.3	44.5	22.7	47.9	27.4	30.0	23.3	28.7
11	C	<i>29.9</i>	<i>34.8</i>	<i>31.1</i>		<i>26.4</i>	<i>30.4</i>	<i>22.0</i>	
	S	87.0	81.9	64.6	84.5	81.1	73.0	99.6	77.1
	D	72.2	68.4	64.3	70.3	79.2	71.7	96.4	75.5
	SD	55.9	40.8	28.3	48.4	33.3	33.2	38.6	33.3
13	C	<i>27.4</i>	<i>29.3</i>	—		<i>29.4</i>	<i>28.5</i>	—	
	S	82.1	84.6	—	83.4	75.2	82.8	—	79.0
	D	84.7	79.2	—	82.0	72.5	76.1	—	74.3
	SD	48.5	23.1	—	40.3	34.0	43.2	—	38.6

In Timgalen, the responses of spikelets 9 and 11 present a confusing picture, so it is worth while to consider, on the basis of Table 5, the following less variable data of harvest 3, in which the treatment \times grain interaction was significant (see Table 4):

Spikelet	Treatment	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>
9	C	<i>24.7</i>	<i>28.6</i>	<i>23.2</i>
	S	85.4	83.2	92.2
	D	81.0	77.3	65.5
	SD	41.3	47.6	23.7
11	C	<i>21.6</i>	<i>25.9</i>	<i>27.5</i>
	S	107.0	89.2	86.6
	D	97.7	86.5	59.3
	SD	61.6	50.6	25.1

These confirm that grain *c* is most likely to be affected by severe shortage, but little else can be said about the responses of this cultivar.

(c) *Accumulation and Distribution of Nitrogen*

Treatment effects on the nitrogen content of stem and leaves combined and of the grain are shown in Figure 3 and the percentage of nitrogen in grains from various positions is given in Table 6.

Nitrogen uptake continued throughout the experiment. Total uptake (i.e. stems, leaves, and grain) was greater in Timgalen; this was a reflection of its longer growth period, as the cultivars did not differ in rate of uptake over the experimental period. The grain of Timgalen contained much more nitrogen than that of WW 15, but the nitrogen content of its stem and leaves was less, as was the concentration of nitrogen: in untreated plants at the last harvest this was 2.30% for WW 15 and

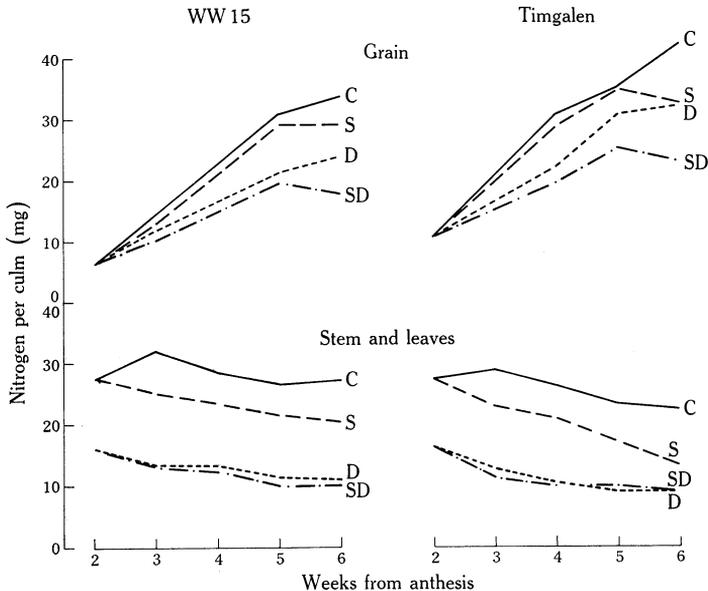


Fig. 3.—Effect of treatments on the change with time in the amount of nitrogen per main shoot. C, control; S, shaded; D, defoliated; SD, shaded and defoliated.

only 1.60% for Timgalen. Responses to treatments were similar in the two cultivars: if allowance is made for the removal of nitrogen by defoliation (by adding 12.5 and 10.9 mg to the appropriate values for WW 15 and Timgalen respectively) total uptake by final harvest was 61.5, 49.9, 47.5, and 40.7 mg nitrogen per culm for C, S, D, and SD treatments in WW 15, and 65.6, 46.5, 52.7, and 43.3 mg nitrogen per culm in Timgalen. Thus in WW 15, shading and defoliation were similar in their effects on nitrogen uptake and these effects were less than additive in the combined treatment. The same may be true of Timgalen if account is taken of the atypical final harvest of treatment S; uptakes at the penultimate harvest—59.3, 51.9, 51.5, and 45.7 mg nitrogen per culm—suggest that this was so.

Defoliation alone reduced the percentage of nitrogen in the grain—i.e. compared with control plants relatively more carbohydrate than nitrogen entered the grain. Grain *c* invariably had a lower percentage nitrogen than *a* and *b* and this difference

was greater in treated than in control plants; treatments may have restricted movement of nitrogen into grain *c* more than they did that of carbohydrate. Percentage nitrogen in grains *a* and *b* did not differ much between spikelets, and as treatments affected all spikelets equally, only the means of *a*+*b* over all treatments are given in Table 6.

TABLE 6
EFFECT OF TREATMENTS ON THE PERCENTAGE OF NITROGEN IN SPIKELETS (MEAN OF GRAINS *a* AND *b* OVER ALL TREATMENTS AND HARVESTS 3 AND 4) AND WITHIN SPIKELETS (MEAN OF SPIKELETS 7, 9, AND 11 IN WW 15, AND OF 9 AND 11 IN TIMGALLEN)

Spikelet No.	3	5	7	9	11	13
WW 15	2.79	2.89	2.92	2.96	2.92	2.89
Timgalen	—	3.49	3.59	3.70	3.75	3.81

Treatment	WW 15			Timgalen			Mean (±0.05)
	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>	Grain <i>a</i>	Grain <i>b</i>	Grain <i>c</i>	
C	3.04	3.03	2.83	3.80	3.86	3.51	3.34
S	3.11	3.03	2.75	3.63	3.61	3.43	3.26
D	2.69	2.71	2.37	3.60	3.55	3.17	3.02
SD	2.90	2.95	2.58	3.87	3.86	3.34	3.25
	S.E. ±0.122						
Mean (±0.025)	2.93	2.93	3.63	3.73	3.72	3.36	

IV. DISCUSSION

(a) Whole-plant Responses

During the experimental period, the rate of senescence was much faster in Timgalen—perhaps because of the greater movement of nitrogen into the grain (Fig. 3)—and its rate of dry matter production was slower. This was reflected in lower stem and root weights and in the production of fewer smaller tillers (Table 2), but not in smaller grain production [Fig. 1(b)]. In control plants, the appreciably smaller photosynthetic system of Timgalen apparently sufficed to sustain a grain growth rate not much slower than that in WW 15; this was so even in the last week when leaf senescence was complete in Timgalen, yet had hardly begun in WW 15. WW 15 control plants used only 63% of the net dry matter produced during the experimental period for grain filling (this estimate ignores any contribution by main shoots to tillers). In these plants, at least, the supply of assimilate during grain filling did not limit grain yield.

When dry matter production was reduced by shading, defoliation, or both, plants responded with a compensatory distribution so that grain was less seriously affected than other parts: in WW 15, shading reduced the total dry weight increment by 47%, but the grain dry weight increment by only 15%. Combined shading and defoliation was less than additive in its effects on total dry weight because when plants were defoliated there was less tissue to be affected by shading; it was more

than additive as regards grain yield because there was a limit to the extent of compensatory distribution, and this limit was exceeded by either shading or defoliation alone.

(b) Grain Growth

The difference between the cultivars in early grain growth [Fig. 2(c)] may be of significance in connection with grain set. Rawson and Evans (1970) concluded that grain set in upper florets might be inhibited by rapid growth of grains in lower ones. The more rapid early growth of grains in Timgalen and its poorer grain set (Table 1)—at 7% the difference was smaller than usually occurs between these cultivars (Bremner and Davidson, unpublished data)—are in line with this hypothesis.

In WW 15, dry weight responses to treatments by individual grains were consistent with the predominance of a parallel linkage of spikelets with sources, although the greater effect on upper spikelets when shortage of assimilates was acute (treatment SD) indicates an element of series linkage too (Table 5). Series linkage was more evident within spikelets: there was a progressive increase in severity of effect from base to apex of the spikelet, most marked in treatment SD, also present in S, but absent from D in so far as *b* was less affected than *a*. However, there is no question of the growth of upper grains being dependent on complete fulfilment of the growth needs of lower ones, for all grains were affected by shortage, which indicates an appreciable degree of effective parallel linkage within spikelets. The data for Timgalen confirm the likelihood of grain *c* being the most seriously affected, but little else.

Shading and defoliation might well be expected to have different effects on distribution at any given level of effect on assimilate supply: when plants are defoliated, the ear structure becomes the main source, and this assimilate is uniformly distributed (Rawson and Evans 1970), whereas with shading, all the sources operate. The effects of shading should therefore give a better indication of the linkages existing between the *main* sources and the grains, because in the defoliated treatment what are normally the main sources—the leaves, especially the flag—were removed. Considering the data of Table 5 in this light, it may be seen that shading had a greater effect than defoliation on grain *b*; and that the effects of shading relative to those of defoliation were least severe in central spikelets. This is in agreement with Rawson and Evans' finding that ¹⁴C-labelled flag leaf assimilates were preferentially distributed to lower central spikelets and grain *b*.

Treatment effects on nitrogen distribution between and within spikelets conformed to the same general pattern observed with dry weight, except that grains *a* and *b* seemed always to be equally affected. Neales, Anderson, and Wardlaw (1963) found a constant relation between grain dry matter per ear and grain nitrogen for a number of cultivars, ear shading, and defoliation treatments. Here, Timgalen had an appreciably higher grain nitrogen content at any given grain dry weight, and the relative amounts of nitrogen and carbohydrate in the grain were also influenced by one treatment (D) and by grain position (Table 6). The uppermost grains of three-grain spikelets were poorer in nitrogen than the others, and it may be that their survival and growth is more limited by nitrogen than by the supply of carbohydrate.

An interesting and perhaps illuminating feature of grain growth from the point of view of possible vascular linkages is the behaviour of the second grain. Its faster growth rate than the first is a commonly observed phenomenon (Rawson and Evans 1970; Rawson and Ruwali 1972) for which there is no ready explanation. Walpole and Morgan's (1970) claim that grains do not differ in their relative growth rates in the month after anthesis, and the concomitant implication that they do not differ in their potential for growth, is due to an error in their method: they assumed that a was always larger than b and distinguished between them on this basis. In fact, this would be true in the first 2 weeks, but probably not thereafter, and if this is so, their growth curve for a is derived from a data in the first 2 weeks and b data subsequently. Their curve for b is similarly wrong.

If we designate grain growth rate G , and, as before, the first, second, and third grains a , b , and c , then in WW 15 when assimilate supply was plentiful (control plants) $G_a < G_b > G_c$; when it was short (treatment SD) $G_a > G_b > G_c$. In addition, G would be affected by the grain's capacity for growth (S) and the resistance within the spikelet (R). Neither S nor R is likely to have been affected by treatments applied 2 weeks after anthesis when cell division in the grain would be substantially complete (Wardlaw 1970; Evers 1970), as presumably was vascular differentiation. Probably $R_c > R_a$ or R_b , because c was considerably further from the base of the rachilla than a or b which were both close to the base; and $R_b > R_a$ because a grew faster when assimilate was short. If this is so, the second grain commonly grows faster because it has a greater capacity for growth—sufficiently greater, apparently, than that of a to enable it to overcome a rather larger resistance—and not because it is especially well-served by the vascular system (cf. Zee and O'Brien 1971). It is of passing interest that insofar as a was some 40% heavier than b at anthesis, capacity for growth is not related to grain weight at this time.

In conclusion, reduction in the supply of assimilate affects its distribution among the various grains, but the effect is not generally dramatic and may differ between cultivars. Apparently the resultants of the attractive forces of the grains and the resistances of movement of assimilate to them are such as to prevent effects being confined to particular grains, although some are more affected than others.

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