

THE CONTRIBUTION OF STEM RESERVES TO GRAIN DEVELOPMENT IN A RANGE OF WHEAT CULTIVARS OF DIFFERENT HEIGHT

By H. M. RAWSON**† and L. T. EVANS*

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Abstract

Six wheat cultivars with more than a twofold range in stem height and weight were grown at 21/16°C in 16-hr days of high light intensity. Changes with time in photosynthesis, respiration, dry weight, and the distribution of ^{14}C fed to the flag leaf or ear of the main stem were followed in all cultivars. The effects on grain yields, stem weights, and ^{14}C distribution of prevention of photosynthesis by the ears or by the rest of the plant during grain filling were also examined.

Substantial losses of dry weight from the stem occurred during the most rapid period of grain filling, but stem weights then rose again in most cultivars. About one-third of the early loss in stem weight of control plants was due to stem respiration, the remainder to mobilization, but cultivars differed in these proportions, the respiration rate of stems per unit dry weight being higher in the shorter cultivars. The assimilates mobilized from the stems were equivalent to 2.7–12.2% of final grain weight in control ears. Mobilization increased when photosynthesis was reduced, particularly that from the lower internodes, which indicated that grain yields in the control plants were not limited by lack of assimilate. Balance sheets derived from gas analysis measurements supported this conclusion.

The amount of material lost from the stems of plants in all the conditions employed, measured as dry weight or as ^{14}C , was unrelated to stem height. Tall cultivars were no more dependent than short ones on stem reserves, and no more able to draw on reserves for grain filling in conditions limiting photosynthesis. Nor was there evidence that stem growth in tall cultivars was more likely to compete with grain growth.

The cultivars differed more than threefold in the rate of ear filling. High growth rate per ear was associated with high yield and grain number per ear and with slow initial growth of the grains.

I. INTRODUCTION

In view of the widespread success of semi-dwarf wheats (Reitz and Salmon 1968), and of the interest in specifying ideal crop types (Donald 1968), the possible advantages of the semi-dwarf habit require further analysis. In wheat these include greater resistance to lodging (particularly with high rates of nitrogen fertilizer application), reduced competition for assimilates between stem and grain, and other features associated with the dwarf habit, some of which may be pleiotropic effects of the dwarfing genes, such as increased spikelet or tiller numbers. Simpson (1968), for example, ascribed the yield advantage of short cultivars of wheat largely to their greater capacity for tillering.

* Division of Plant Industry, CSIRO, Canberra, A.C.T. 2601.

† Present address: Division of Land Research, CSIRO, Canberra, A.C.T. 2601.

The objectives of the experiments described below were to examine whether stem height influences the degree of competition between stem and grain on the one hand, and the contribution of stem reserves to grain development, particularly under stress, on the other. Carr and Wardlaw (1965) raised the possibility of competition between stem growth and early grain growth, and Birecka (1966) examined the question by using (2-chloroethyl)-trimethylammonium chloride (CCC). Treatment with CCC reduced both stem length and the amount of ^{14}C in the stems, but did not increase either grain yields or ^{14}C activity in the grains. Only the distribution of ^{14}C assimilated before anthesis, however, was examined.

Assimilates for grain growth in the temperate cereals are largely derived from photosynthesis during grain filling, material stored before anthesis contributing little to final grain yield. For example, in Gabo wheat under a sequence of conditions likely to enhance both initial storage and subsequent mobilization, Wardlaw and Porter (1967) found that reserves from the stem contributed at most only 5–10% of final grain weight. However, the role of stem reserves may be greater under conditions of severe stress during grain development, as indicated by the results of Asana and Basu (1963), Asana and Joseph (1964), and Yu *et al.* (1964). It might also be greater in cultivars adapted to short growing seasons, as Stoy (1963) has suggested.

II. MATERIALS AND METHODS

(a) Cultivars

Of the six cultivars used (Table 1), five were Mexican wheats which varied in their number of dwarf genes and because of their similar derivation were particularly suited to a study of the influence of stem height on yield. All had heavily awned ears. Nainari and Pitic 62 were chosen because of their high performance and yield stability in a wide range of environments, Sonora 64 and Mexico 120 as representing successful cultivars of short stature, and Mexico Triple Dwarf as an example of extreme dwarf habit. Sunset, a moderately tall, awnless Australian wheat developed by Farrer, was included in order that the patterns of ^{14}C distribution at various stages could be compared with those obtained by Rawson and Hofstra (1969).

(b) Growing Conditions

Imbibed seeds of all varieties were vernalized at 4°C for 3 weeks before being planted singly in 8 cm diameter pots containing a mixture of perlite and vermiculite. The pots were arranged in blocks by cultivar, at 10 cm centres, in a glasshouse of the Canberra phytotron CERIS held at 21°C for 8 hr each day, and at 16° for the remaining time. The natural day length of about 14 hr during the experiment was extended to 16 hr with light of 50 f.c. intensity from incandescent lamps. Average radiation for the period of grain filling was $697 \text{ cal/cm}^2/\text{day}$. All pots were saturated with a modified Hoagland nutrient solution, and with water, each day.

(c) Photosynthesis and Growth Measurements

Twice weekly, after ear emergence, lots of four to six plants were used to measure the rates of photosynthesis and respiration of main-stem ears and flag leaf blades, and

were then divided into grains, ear structures, main-stem internodes, leaves (including sheaths), and tillers for drying and weighing. Measurements were also made of photosynthesis and respiration by stems of two cultivars, Sonora and Mexico 120, both with and without the leaf sheaths, while still attached to the plants. In addition, respiration rates for the stems of all cultivars were measured between 15 and 17 days after anthesis.

Measurements of photosynthetic rate were made at 21°C under light of 3200 f.c. intensity from fluorescent and incandescent lamps ($8.7 \times 10^5 \mu\text{W cm}^{-2}$ of visible radiation), after the plants had been held at 21° in light of that intensity for about 2 hr. Two Grubb-Parsons infrared gas analysers, sensitive to at least 0.1 p.p.m. carbon dioxide, and calibrated with gas-mixing pumps were used. The cross-sectional dimensions of the Perspex assimilation chambers were 15 by 2 cm for flag leaves and 22 by 10 cm for ears. The air flow rate was 4 l/min.

(d) ^{14}C Distribution

Either the ears or the flag leaf blades of plants of all cultivars were exposed to $^{14}\text{CO}_2$ at two stages of development: at anthesis, when stem growth was still occurring, or 14 days later, when stem growth had ceased and grain growth was most rapid.

$^{14}\text{CO}_2$ was generated by the addition of 50% lactic acid to barium carbonate (1 mCi/mmole) used at the rate of 2 mg per plant, and the course of uptake under artificial light of 3200 f.c. intensity was followed with a gas flow scintillation cell (IDL 663).

Six plants of each cultivar were harvested 24 hr after the beginning of exposure to $^{14}\text{CO}_2$, to determine the initial pattern of ^{14}C distribution. Further lots of plants labelled at anthesis or 14 days later were harvested when the grain on the main ears was mature, to determine the patterns of mobilization. Plant parts were separated, dried, weighed, ground, and the relative specific activity of lots of 30 mg determined on the powders (O'Brien and Wardlaw 1961). ^{14}C distributions were also examined with a Geiger-Müller tube before drying.

(e) Treatments to Reduce Photosynthesis

These were applied to some of the plants whose flag leaves were exposed to $^{14}\text{CO}_2$ at anthesis or 14 days later. Six plants of each cultivar were used in each treatment group. The treatments were applied from 15 days after anthesis until grain maturity.

Two levels of stress on the assimilate supply to the main ears were imposed. In one, ear photosynthesis was inhibited without affecting the environment of the ear by dipping the main ear in $5 \times 10^{-5}\text{M}$ DCMU (3-(3,4-dichlorophenyl)-1,1-dimethyl-urea). The ears were dipped once, 15 days after anthesis, for 30 sec. The effectiveness of the treatment was checked with plants of cvv. Sonora and Nainari. Ear photosynthesis was completely inhibited for at least 14 days; flag leaf photosynthesis was not inhibited, and in fact rose in both cultivars, presumably in response to increased demand by the ear, as found by King, Wardlaw, and Evans (1967). The more severe stress treatment consisted of enclosing all except the main ear inside light-tight aluminium foil boxes 15 days after anthesis.

III. RESULTS

(a) Growth of Grains and Stems

Figure 1 indicates the marked differences between cultivars not only in final grain yield per ear, but also in the duration of growth, the maximum rates achieved,

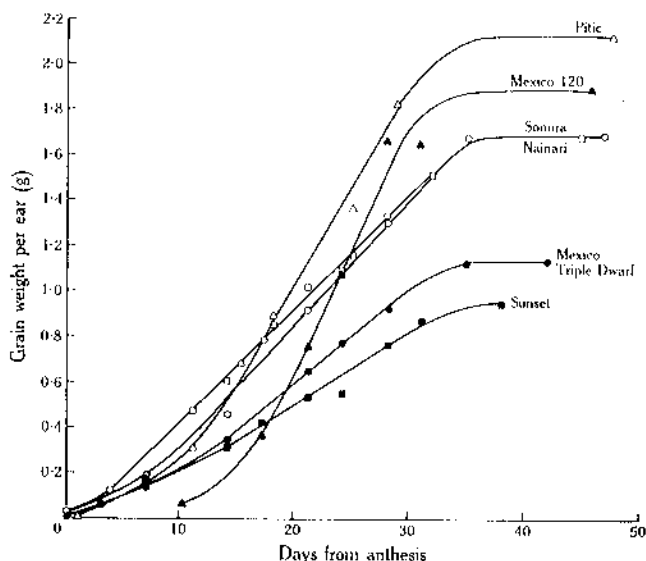


Fig. 1.—Changes in grain weight per main stem ear with time from anthesis in six wheat cultivars grown in 16 hr days of high light intensity at 21/16°C.

- △ Pitic.
- ▲ Mexico 120
- Sonora.
- Nainari.
- Mexico Triple Dwarf.
- Sunset.

and the length of the initial lag period. Further data on these differences are given in Table 1. Grain yield per ear varied more than twofold between cultivars. In

TABLE 1

SOME CHARACTERISTICS OF THE MAIN SHOOT OF SIX CULTIVARS OF WHEAT GROWN AT 21/16°C
Grain growth rates were computed from linear regressions for changes in grain weights with time over the period of most rapid grain filling

Class:	Medium Height			Semi-dwarf	Dwarf	
	Cultivar: Pitic 62	Sunset	Nainari	Sonora 64	Mexico 120	Mexico Triple Dwarf
Height (cm)	88	85	79	58	48	40
Maximum stem wt. (mg)	1085	999	1034	726	812	441
Final stem wt. in base-shaded plants (mg)	959	672	660	446	470	263
Spikelets per ear	19.3	15.7	17.0	15.7	27.2	14.7
Grains per ear	50	25	35	38	54	27
Grain wt. per ear (mg)	2122	954	1665	1667	1889	1127
Max. grain growth rate (mg/ear/day)	75	28	48	56	97	44

previous work cultivars have been similar in their rates of grain growth per ear (e.g. Asana and Williams 1965; Stoy 1965; Asana and Bagga 1966), differing mainly in

the duration of grain growth. In the present experiments, however, there was a more than threefold range in rates of grain growth per ear, determined from computed regressions for the linear part of each curve in Figure 1. Final yields were in the order of these rates, except in the case of Pitic compared with Mexico 120. Ear growth rate was generally higher the greater the number of spikelets or grains per ear (Table 1). More surprisingly, the cultivar with the most grains per ear (Mexico 120) also had the highest rate of growth per grain (1.79 mg/grain/day). It also showed the most marked lag in early grain growth, which was not due to an exceptionally long period of anthesis within the ear, since anthers appeared from the first florets only 5-6 days before those in the last florets.

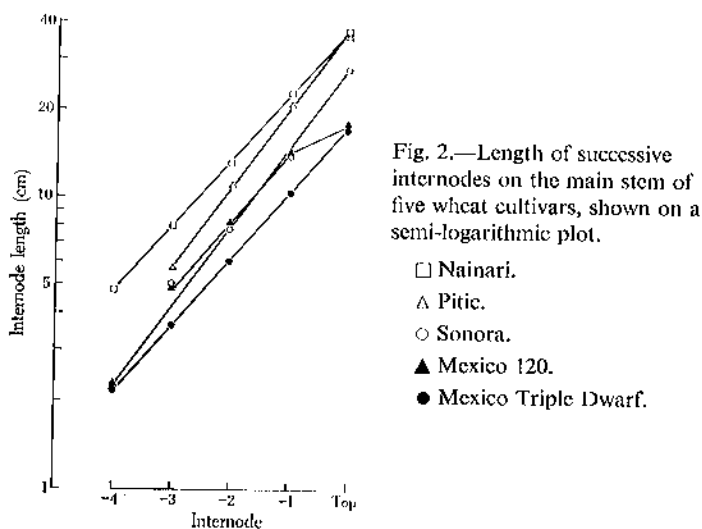


Fig. 2.—Length of successive internodes on the main stem of five wheat cultivars, shown on a semi-logarithmic plot.

- Nainari.
- △ Pitic.
- Sonora.
- ▲ Mexico 120.
- Mexico Triple Dwarf.

Among the wheats used in these experiments there was no relation between stem height and grain yield per ear. Increase in stem height ceased at anthesis in Sonora, 3 days later in Triple Dwarf and Nainari, and 1 week after anthesis in Mexico 120 and Pitic. Thus there was no consistent difference between dwarf and tall cultivars in this respect. Successive internodes increased in length by a constant proportion in all cultivars (Fig. 2), which indicated that the dwarfing genes did not have differential effects on the various internodes, except possibly in the case of the top internode of Mexico 120.

Stems of all cultivars continued to increase in weight after height growth ceased, attaining their maximum weights before peak grain growth rates were reached. All cultivars except Mexico 120 followed a course like that shown for Sonora in Figure 3 (see also Evans and Rawson 1970). Maximum stem weights were reached 3-15 days after anthesis (cf. Asana, Parvatikar, and Saxena 1969) and these then fell to a minimum over the next 6-14 days, at about the middle of the peak period of grain growth. They then rose again towards the end of this period and fell only slightly thereafter. In Mexico 120, maximum stem weight was not reached until 21 days after anthesis, when grain growth was approaching its peak rate, and stem weight then fell progressively.

During the period of increase in stem weight before peak grain growth set in, all internodes of the main stem increased in weight in all cultivars, and all contributed

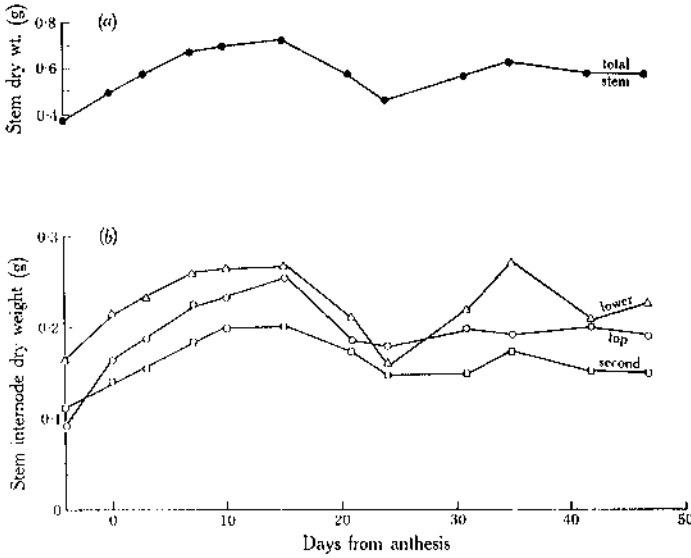


Fig. 3. Changes (a) in total stem weight, and (b) in the weight of the top (○), second (□), and lower (△) internodes of Sonora 64 wheat after anthesis.

to the subsequent fall in stem weight. In most cultivars the lowest internodes lost proportionally more weight than the top two at this stage, as shown for Sonora in

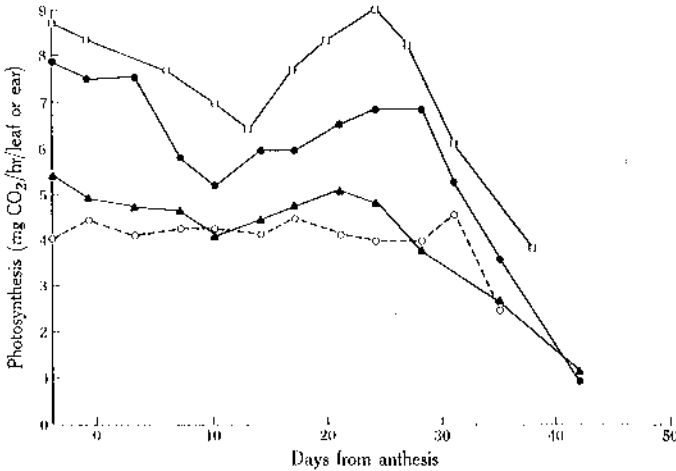


Fig. 4.—Changes in net photosynthesis by the flag leaf blade of Nainari (□), Sonora 64 (●), and Mexico Triple Dwarf (▲) and in gross photosynthesis by the ears in Sonora 64 wheat (○), with time from anthesis.

Figure 3. Similarly, when stem weights rose again towards the end of peak grain growth, it was the lowest internodes which increased most.

(b) *Photosynthesis and Respiration*

All wheats except Mexico 120 showed a similar trend in the rates of flag leaf photosynthesis, as illustrated for Sonora, Nainari, and Mexico Triple Dwarf in Figure 4, which also shows the gross rate of photosynthesis (i.e. net photosynthesis + dark respiration) by the ears of Sonora. The flag leaf blade rate was highest initially (34.5 mg CO₂/dm²/hr in Sonora) and fell to a minimum about 10 days after anthesis (22.5 mg/dm²/hr). It then rose throughout the period of peak grain growth (to 30.2 mg/dm²/hr) before falling rapidly as the grain reached maximum weight. A similar trend in flag leaf photosynthesis in relation to the demands for grain growth was found with Sonora plants grown under different conditions (Evans and Rawson 1970), and in all the other cultivars except Mexico 120, in which the fall in rate after anthesis was not evident, perhaps because of the continuing demands for stem growth and tillering.

TABLE 2

ASSIMILATE REQUIRED BY THE EAR AND PROVIDED BY PHOTOSYNTHESIS IN THE EAR AND FLAG LEAF BLADES DURING THE PERIOD OF MOST RAPID GRAIN GROWTH IN SIX WHEAT CULTIVARS

Grain increase was computed from regressions for changes in grain weight with time

Cultivar:	Mexico 120	Pitic	Sonora	Nainari	Triple Dwarf	Sunset
<i>Requirement</i>						
Grain increase (mg CO ₂ /ear/day)	155	120	90	77	70	45
<i>Supply</i>						
A. Ear photosynthesis						
(i) Net photosynthesis rate (mg CO ₂ /ear/hr)*	3.93±0.26	2.54±0.14	2.77±0.08	2.27±0.01	1.83±0.09	0.65±0.06
(ii) Respiration rate (mg CO ₂ /ear/hr)*	2.00±0.20	1.38±0.10	1.35±0.06	1.56±0.07	0.86±0.08	0.90±0.07
(iii) Net daily photosynthesis (mg CO ₂ /ear/day)	31.2	19.6	22.4	15.6	14.9	1.8
B. Flag leaf blade photosynthesis						
(i) mg CO ₂ /leaf/hr*	9.5±0.34	10.3±0.55	6.3±0.22	7.9±0.43	4.5±0.36	6.4±0.39
(ii) mg CO ₂ /leaf/day	104.6	113.3	69.6	86.9	49.8	70.8

* Mean ± standard error.

Rates of photosynthesis per unit flag leaf surface were similar in all cultivars. For example, the highest rates reached during peak grain growth were between 29.1 and 30.3 mg CO₂/dm²/hr for all cultivars except Sunset. However, rates of photosynthesis per flag leaf differed considerably between cultivars (see also Table 2) owing to differences in the size of the flag leaf blades.

In all cultivars the rate of gross ear photosynthesis remained fairly steady until about 30 days after anthesis, as in Sonora (Fig. 4). Ear respiration rose slowly to reach a maximum during the peak period of grain growth, and then slowly fell (cf. Evans and Rawson 1970). The results for the cultivars are not presented in detail, but the average rates of net ear photosynthesis and respiration during the peak period of grain filling are given in Table 2. Large differences between cultivars are evident in the rates of both photosynthesis and respiration. The differences in respiration rate are

probably due mainly to differences in grain number per ear, and those in gross photosynthesis to different spikelet numbers and the occurrence of awns. Gross photosynthesis was only 0.099 mg CO₂/spikelet/hr in the unawned Sunset, and varied between 0.183 and 0.262 mg/spikelet/hr in the awned Mexican cultivars.

Estimates of the extent to which net daily photosynthesis by the ears and flag leaf blades could meet the demands for grain growth in each cultivar were made from the gas analysis measurements (Table 2). The assumptions made for comparable estimations with other lines of wheat have been described elsewhere (Evans *et al.* 1970). The estimates suggest that Mexico 120 was the only cultivar that needed to draw substantially on sources of assimilate other than the flag leaf blade and ear to support grain growth, which was most rapid in this cultivar.

TABLE 3

LOSS OF DRY WEIGHT FROM THE STEM AND ESTIMATES OF ITS PARTITIONING BETWEEN STEM RESPIRATION AND MOBILIZATION IN FIVE MEXICAN WHEAT CULTIVARS DURING MOST RAPID GRAIN FILLING

Cultivar:	Pitic 62	Nainari	Sonora 64	Mexico 120	Triple Dwarf
Dry weight loss (mg) ± SE	91 ± 3.8	114 ± 3.4	238 ± 6.5	295 ± 11.0	98 ± 6.5
Days from full height to max. stem weight	2	4	15	14	3
Respiration rate* (mg/g/hr)	0.127	0.153	0.268	0.404	0.446
Duration of loss (days)	10	8	9	25	9
Respiratory loss (mg/stem)	33	30	34	119	48
Translocation loss:					
(i) mg/stem	58	84	204	176	50
(ii) % of grain weight	2.7	5.0	12.2	9.3	4.4

* Milligrams carbohydrate per gram dry weight per hour. Respiration rates were measured 15–17 days after anthesis.

mg CO₂/g/hr

Photosynthesis by the attached stems and sheaths of the two cultivars on which it was measured, Sonora and Mexico 120, was substantial. Net daily photosynthesis by the stems plus sheaths as measured in the crop was estimated to be about a quarter to a third of that by the flag leaf blades.

Stem respiration was measured on all cultivars between 15 and 17 days after anthesis, when losses of dry weight from the stems were marked (Table 3). The rates, ranging between 0.127 and 0.446 mg carbohydrate per gram dry weight per hour, were close to other estimates for wheat (0.24–0.29 mg/g/hr—Stoy 1965), and barley (0.45 mg/g/hr—Archbold 1945).

The rate of stem respiration throughout the period of grain filling was measured in Sonora and was relatively stable, as Stoy (1965) had found. The rates given in Table 3 were therefore used to estimate what proportion of the fall in stem weight during

mid grain filling could be due to respiratory loss. As may be seen from Table 3 this proportion apparently varied widely between cultivars, the average being about one-third. The remainder, presumably material translocated to other parts of the plant, likewise varied considerably between cultivars, being largest in Sonora and Mexico 120, in which it was equivalent to 12.2 and 9.3% respectively of final grain weight, while it was less than 5% in the other cultivars.

Although respiration per unit stem weight decreased progressively with increasing stem length, neither total stem losses nor the proportion of material translocated bore any simple relation to stem height. Both were, however, clearly related to the length of the period between the cessation of height growth and the attainment of maximum stem weight (see Table 3), this latter coinciding with the onset of rapid grain growth.

TABLE 4

EFFECT OF REDUCING PHOTOSYNTHESIS FROM 15 DAYS AFTER ANTHESIS UNTIL MATURITY ON GRAIN YIELDS AND ON THE LOSS OF DRY WEIGHT FROM MAIN STEM INTERNODES FROM THE BEGINNING OF STRESS UNTIL MATURITY

Averages for all Mexican cultivars (mg/culm)

	Treatment		
	Control	Ear with DCMU	Only ear in light
Grain weight (mg/ear):			
15 days after anthesis	503		
At maturity	1694	1639	1042
Loss per internode (mg):			
Top	49	50	57
Second	37	47	67
Remainder	23	29	102
Total	109	126	226
Loss from leaves (mg)	80	40	196

(c) *Effects of Reduced Photosynthesis*

Table 4 indicates the effect of reduced photosynthesis on grain yield and loss of weight from the stem. The results with the Mexican cultivars are averaged, as the pattern of effect was similar for all, though the magnitudes varied.

Inhibition of ear photosynthesis with DCMU reduced grain yield by only 3.3%. Calculations from values given in the preceding subsection suggest that the *minimum* contribution to grain growth by net ear photosynthesis, i.e. that during the period of fastest grain growth, varied from 16.3 to 24.9% for the Mexican wheats, averaging 17.8%. Since the reduction in yield by the ear DCMU treatment was far less than this, compensating mechanisms must have been called into play. One of these was probably the rise in the rate of flag leaf photosynthesis noted above (e.g. from 21 to 25 mg CO₂/dm²/hr in Nainari), another the increased mobilization from the second and lower internodes of the stem evident in Table 4.

The greater stress imposed by leaving only the ears in light reduced the average grain yield by 38.5% in the Mexican cultivars. Loss of weight from all internodes increased still further, particularly that from the basal internodes (Table 4). Under this severe stress the loss in stem weight increased from an average of 6.4% of final grain yield to 21.7%. Losses from the leaves and sheaths in this treatment were more than twice as high as those in control plants and, although respiratory losses must have been large, could have contributed substantially to grain filling.

Maximum stem weight and final stem weight in the heavily stressed, shaded treatment are given in Table 1 for each cultivar. Both increased with increase in height of cultivar, except that the stems of Mexico 120 were rather heavier than those of Sonora. The difference between the two stem weights for each cultivar can be taken as a measure of the mobilizable material in the stems, and this was not proportional to stem height, being least in Pitic, the tallest cultivar, greatest in Nainari, which was almost as tall, and almost as great in Mexico 120, one of the shortest. Mobilizable reserves are clearly not related in any simple way to stem height.

(d) ^{14}C Distribution

The average patterns of distribution of ^{14}C for all cultivars at different stages of exposure to $^{14}\text{CO}_2$ and harvest times, for both ear and flag leaf feeds, are presented in Table 5, and some differences between cultivars are shown in Table 6.

TABLE 5
DISTRIBUTION OF ^{14}C ACTIVITY IN CONTROL PLANTS, AS INFLUENCED BY STAGE OF EXPOSURE TO $^{14}\text{CO}_2$,
THE PART EXPOSED, AND TIME OF HARVEST
Figures are averages for all six cultivars

Stage of Exposure to $^{14}\text{CO}_2$	Part Exposed	Harvest	Percentage Distribution of ^{14}C Activity								
			Flag leaf	Ear	Internodes			Stem total	Roots	Lower leaves	Tillers
					Top	2nd	Lower				
Anthesis (A)	Flag leaf	After 1 day	24.8	10.0	19.2	22.6	8.5	50.3	4.3	0.7	9.7
Anthesis	Flag leaf	Maturity	7.3	32.9	24.9	16.8	4.2	45.9	2.8	0.2	10.8
Anthesis	Ear	Maturity	—	86.5	11.8	0.3	—	12.1	—	—	1.1
A + 14 days	Flag leaf	After 1 day	28.6	56.9	5.8	2.9	1.0	9.7	0.9	0.4	3.5
A + 14 days	Flag leaf	Maturity	8.4	82.7	1.2	1.0	0.7	2.9	0.6	0.2	5.1
A + 14 days	Ear	Maturity	—	99.3	—	—	—	—	—	—	—

The distribution of ^{14}C assimilated by the flag leaf blade at anthesis was similar to that found by Rawson and Hofstra (1969) except that a much higher proportion of activity was exported from the flag leaf in the present experiments, even in cv. Sunset. The growing stem was by far the major sink at this stage, receiving about half of the total assimilate, this proportion being greatest in the tall cultivars Nainari and Pitic and least in the shortest cultivars Mexico 120 and Triple Dwarf, both after 1 day and at maturity (Table 6). By contrast, the proportion going to the ear at this stage was rather higher in the dwarf cultivars than in the tall ones, both after 1 day and at maturity, when the proportion had risen considerably. The rise in the proportion of activity in the ear at maturity was largely at the expense of that in the flag

leaves, and of that in the basal and penultimate internodes as may be seen from Table 5. This was so for all cultivars.

TABLE 6

DISTRIBUTION OF ^{14}C ACTIVITY IN CONTROL PLANTS: SOME DIFFERENCES BETWEEN CULTIVARS

Stage of Exposure	Part Exposed	Harvest	Part Harvested	Percentage Distribution of ^{14}C Activity				
				Triple Dwarf	Mexico 120	Sonora	Nainari	Pite
Anthesis (A)	Flag leaf	After 1 day	Stem	43.2	41.7	50.7	68.2	56.6
Anthesis	Flag leaf	After 1 day	Ear	12.3	18.1	5.9	6.9	6.8
Anthesis	Flag leaf	Maturity	Stem	37.9	40.2	43.5	62.6	57.2
Anthesis	Flag leaf	Maturity	Ear	48.3	35.9	24.7	23.3	26.8
Anthesis	Ear	Maturity	Stem	6.0	15.9	10.5	15.1	18.4
A + 14 days	Flag leaf	After 1 day	Stem	5.8	11.1	6.2	9.5	8.5
A + 14 days	Flag leaf	Maturity	Stem	1.2	2.9	1.3	3.4	4.2

When ears were exposed to $^{14}\text{CO}_2$ at anthesis, 6–18% of the activity was found in the stem, most of this being at the base of the top internode, which was still growing at this stage. Thus bidirectional movement must have occurred, since the ears supplied assimilates to the stems while the flag leaf blades supplied them to the ears, as previously found by Carr and Wardlaw (1965). The proportion found in the stems differed among cultivars, being least in those (Sonora and Triple Dwarf) which were closest to their final height and most in those (Pite and Mexico 120) whose growth in height was most active. With exposures 14 days later virtually no activity was found outside the ears.

With flag leaf exposures 14 days after anthesis, most of the ^{14}C was translocated to the ear, and the stem was a minor sink in all cultivars (Table 6). Of the total activity found in the stem 1 day after feeding, 71.9% was lost by maturity in the control plants, 79.9% in the plants whose ears were treated with DCMU, and 92.4% in the base-shaded plants, whereas the loss in total activity by the whole plants over this period was only about 25%. Clearly, the material stored in the stems at this stage, after they had reached their final height, was highly mobilizable, the extent of mobilization increasing under stress but bearing no clear relation to stem height.

IV. DISCUSSION

The results given above suggest that stem height *per se* determines neither the extent to which there may be competition between the stem and the ear on the one hand, nor the extent to which assimilates stored in the stem are mobilized during grain filling, even under stress, on the other.

In taller cultivars a higher proportion of flag leaf assimilate at anthesis was found in the stems (Table 6), but this does not necessarily mean there was more active competition between the ear and the stem at this stage. Ears at anthesis may be largely self-supporting (Evans and Rawson 1970), and much of the material in the stems is mobilizable (Table 1) and not structural. Competition between stem and grain growth is most likely in cultivars whose stems continue to grow in height after

anthesis. Among those used in the present experiment, one of the shortest (Mexico 120) and one of the tallest (Pitic) were the latest to reach full height, whereas Sunset and Nainari were among the first. Thus, while there was considerable difference between cultivars in the time at which height growth ceased, this was not related to height *per se*.

Similarly, the extent to which stem reserves were mobilized was also unrelated to height, whether indicated by the fall in stem weight at the onset of rapid grain growth and allowing for stem respiration (Table 3), by the difference between maximum stem weight and final-stem weight in the severely stressed plants (Table 1), or by the change in ^{14}C distribution (Table 6).

The best relation we could discern with the extent of mobilization from the stem was the length of the period between the end of height growth and the onset of rapid grain growth (Table 3). This period was longest in two of the short-stemmed cultivars, in Sonora because it ceased height growth early, in Mexico 120 because there was a pronounced lag in its grain growth curve (Fig. 1). This initial lag period deserves further study, not only because it may influence the extent to which mobilizable reserves accumulate in the stem but also because, among the limited number of cultivars used in these experiments, those with the most pronounced lag (Mexico 120 and Pitic) set the most grains and reached the highest grain yield per ear (Table 1).

Two lines of evidence suggest that grain growth in the control plants was not limited by the supply of assimilates. One is that when photosynthesis by the ear or leaves and stems was prevented, mobilization from the stems increased, particularly that from the lower internodes (Table 4). The other is that estimates of available assimilates, from gas analysis measurements (Table 2) in relation to grain growth, indicated that the current supply of photosynthate was adequate at all stages, although there was less spare capacity in the high-yielding varieties. Under these conditions the mobilization of stem reserves could have contributed only a small proportion to grain filling (Table 3), less than 5% in three cultivars, and possibly up to 9.3% in Mexico 120 and 12.2% in Sonora. These estimates compare with those of Yu *et al.* (1964) and Wardlaw and Porter (1967) that stem reserves contributed 10% at the most.

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