

SOME PHYSIOLOGICAL ASPECTS OF EVOLUTION IN WHEAT

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Summary

Twenty-one lines representing wild progenitors and cultivated wheats at the diploid, tetraploid, and hexaploid levels were compared during growth under favourable conditions (21/16°C, 16-hr days of high intensity natural light, and non-limiting nutrient supply).

Grain weight, which varied 20-fold between lines, increased with increase in ploidy and with the shift from wild to cultivated forms, particularly at the diploid level. The area of individual leaves and the total leaf area of seedlings were proportional to the weight of the grains sown. In turn there was a close relation between the area of the largest leaf on the main stem and the weight of the ear and of the individual grains it supported. Evolution in wheat has thus involved a parallel increase in leaf and grain size, but this has been coupled with a progressive reduction in the rate of photosynthesis per unit leaf area. At low light intensities there was little difference between species in their rate of photosynthesis, but light saturation was approached at lower intensities in the more advanced forms. Photorespiration was also higher in the primitive wheats. Total photosynthesis per flag leaf blade was greatest in the wild and cultivated tetraploids and the cultivated hexaploids, due to their greater leaf size. All wild species showed a rapid fall in flag leaf photosynthesis during grain development, whereas in many of the cultivated wheats the flag leaf rate rose during most rapid grain development. The rate of ear photosynthesis depended on the presence of awns and the number of spikelets, and was highest in the *durum* wheats and in *Triticum dicoccoides*.

The duration and rate of grain growth has tended to increase during evolution in wheat. Ear photosynthesis was largely sufficient for grain needs in *Aegilops speltoides*, but the need to import carbohydrates from the leaves has increased in modern wheats, as shown by the increased movement of ¹⁴C-labelled assimilates to the ear from the flag leaf and from the leaf below it. The loss in dry weight from the stems is also greater in modern wheats. Movement of assimilates to the roots, stem, and tillers has been correspondingly reduced during evolution, and the proportion of the shoot weight in the grain at harvest has increased.

I. INTRODUCTION

Although much is known of the cytogenetics of the evolution of wheat and many other crop plants (e.g. Hutchinson 1965) the same cannot be said of the physiological changes that must have accompanied, and contributed to, this evolution. Some of these are examined here for wheat.

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Cultivated wheats at all three levels of ploidy and wild wheats at the diploid and tetraploid levels were grown under one set of favourable conditions in terms of temperature, light intensity, day length, mineral nutrition, and freedom from disease. Our objective in doing this was to expose the changes that have occurred during evolution of wheat in the capacity or potential of processes that may limit yield, which Vavilov (1951) suggested should be an early step in examining such "evolution directed by the will of man". In this paper we are primarily concerned with the changes during evolution in the growth rates and sizes of leaves and grain, in photosynthesis by leaves and ears, and in the partitioning of photosynthetic assimilates. Data on yield components, such as the numbers of spikelets, grains, or ears per plant are presented since comparative data for all species grown under one condition are difficult to find, but it must be emphasized at the outset that the absolute values, at least, are likely to be different under other conditions.

Wheat was chosen because its wild progenitors, and the main steps in its evolution, are known with some confidence (Bell 1965; Riley 1965), because the progenitors are available in a wide range of forms, and because comparisons can be made between three levels of ploidy and between wild and cultivated forms at two of these. The main steps in wheat evolution can be summarized as follows:

- (1) From wild diploid wheat, *Triticum boeoticum*, to cultivated einkorn, *T. monococcum*. Harlan and Zohary (1966) state that the most conspicuous difference between them is in the less fragile rachis of einkorn, the ear remaining intact until threshing.
- (2) Either *T. boeoticum* or *T. monococcum* hybridized with a species of *Aegilops*, probably *A. speltoides*, or possibly *A. bicornis*, to give rise to the wild species *T. dicoccoides*.
- (3) *T. dicoccoides* gave rise, under primitive selection, to emmer wheat, *T. dicoccum*, and
- (4) possibly by a single mutation, to the free-threshing *T. durum*.
- (5) *T. dicoccoides* hybridized with *A. squarrosa* to give rise to the cultivated hexaploid wheats. The evolutionary relation between forms with invested grains, such as *T. spelta*, and those with free-threshing ears, such as *T. aestivum*, is not clear (Helbaek 1960; Bell 1965).

II. MATERIALS AND METHODS

(a) Plant Materials

Twenty-one lines were used in the main experiment, to which we confine discussion, and these are listed in Table 1. Their geographic origin is known only for some. The lines were also compared in two exploratory experiments, together with many others and were chosen to represent the range of behaviour observed. With *T. boeoticum*, for example, five lines were used to cover the range from the small-seeded *aegilopoides* to the large-seeded *thaoudar* forms. Three of them behaved as spring forms in the preliminary experiments (T-6625 and T-6626 from Iran, and Kew C64.146), whereas the other two required vernalization. We were unable to obtain spring forms of the two *Aegilops* species, although some have been recorded (Kihara, Yamashita, and Tanaka 1965). The other lines requiring vernalization were *T. dicoccoides* (W1043) and Cappelle Desprez, while Late Mexico 120 had a marked vernalization response. Both lines of *T. dicoccoides* were of the robust Palestinian type which probably gave rise to *T. dicoccum* (Harlan and Zohary 1966).

The three cultivars of *T. aestivum* were chosen to represent a range of successful soft wheats: Gabo, an Australian spring variety with awnless ears; Late Mexico 120, a semi-dwarf variety with awned ears; and Cappelle Desprez, a high-yielding European winter wheat with awnless ears. Apart from Gabo and Cappelle Desprez, the only lines without well-developed awns were the two species of *Aegilops*. Of the two lines of *A. speltoides*, 6001 from Israel was of the *speltoides* morph, AS1 of the *ligustica* morph, with small awns on each spikelet.

We would have preferred to use more than two lines of all species, but the space available under one set of growing conditions, and the number of measurements to be made during the period of grain development, precluded more extensive comparisons. Replication within lines was sufficient to yield reliable estimates of the behaviour of individual lines. Indications of the errors for individual line data are given, where relevant. However, most of the data presented are means for each species, usually for two lines, and error estimates are not given because the lines were often chosen to expose the range of behaviour within a species. Thus, the mean values presented do not characterize the individual species, but taken together they indicate ways in which wheat has changed in the course of its evolution.

TABLE 1
SPECIES AND LINES USED IN THE MAIN EXPERIMENT

Group	Genome	Species	Line Code
Diploid			
Wild	A	<i>Triticum boeoticum</i> Boiss. emend Schiem.	Kew C64.146 T-6625 PBI C64.145 T-6626 TBI
	B	<i>Aegilops speltoides</i> Tausch	AS1 6001
	D	<i>Aegilops squarrosa</i> L.	G46 CHBS G90 CHBS
Cultivated	A	<i>T. monococcum</i> L.	W10 W292
Tetraploid			
Wild	AB	<i>T. dicoccoides</i> Korn.	W1043 T-6252
Cultivated	AB	<i>T. dicoccum</i> Schubl.	Khapli W12 W2698
	AB	<i>T. durum</i> Desf.	Kubanka W8 Acme W9
Hexaploid	ABD	<i>T. spelta</i> L.	H2
	ABD	<i>T. aestivum</i> L.	Gabo Late Mexico 120 Cappelle Desprez

(b) Growing Conditions

All seed sown in the main experiment was derived from plants grown in long days at 21/16°C. The seed samples were selected for uniformity, weighed, and set out for imbibition. More than 50 germinating seeds of each line were planted singly in small peat cups of perlite and vermiculite, and held in long days at 21/16°C for a few days. Because many of the lines required vernalization, all established seedlings were moved to 8-hr days at 7/4°C for 10 weeks. After vernalization they were transplanted to larger pots and moved to a phytotron glasshouse at 21/16°C. The natural summer days of about 14 hr were extended to a day length of 16 hr by

incandescent light of 50 f.c. intensity at plant height. During the period from anthesis to maturity the average irradiation was $614 \text{ cal cm}^{-2} \text{ day}^{-1}$. The plants were grouped by line in blocks which were rearranged weekly. They were given nutrient solution and water daily.

The main stems were identified by periodic leaf marking. Rates of tillering and of leaf area increase were measured over a period of about 3 weeks following vernalization. They were also measured on separate lots of 16 plants grown without vernalization in $21/16^\circ\text{C}$. With the vernalized plants, dissections 7 days after return to long days at $21/16^\circ\text{C}$ indicated that all lines had either initiated inflorescences or were close to doing so. Anthesis in all lines occurred within a period of about 2 weeks.

For each line, lots of seven or eight plants were harvested at ear emergence, at 5, 15, and 21 days after anthesis, and at maturity of the main stem ear. Prior to all harvests, except that at maturity, rates of photosynthesis and dark respiration were measured on the ear and flag leaf of the main stem, and the pattern of distribution of ^{14}C -labelled assimilates was examined in plants exposed to $^{14}\text{CO}_2$ 14 days after anthesis, and harvested the following day. At harvest all plants were divided into grains, ear structure, flag and other leaves (including sheaths), top, second and other internodes of the main stem, tillers, and roots, which were dried and weighed. At the end of the experiment, two plants representative of each line were dried and pressed to be held as type specimens.

(c) *Measurement of Photosynthesis and Respiration*

At all harvests measurements of photosynthesis and respiration by the ear and the flag leaf were made at 21°C in light of 3200 f.c. intensity from fluorescent and incandescent lamps, and at atmospheric CO_2 concentration. Plants were held under these conditions for at least 1 hr prior to the measurements, which were made during the morning on two lots of four leaves or ears of each line. Gas exchange was determined by two Grubb Parsons infrared gas analysers, calibrated with Wosthoff gas-mixing pumps. The Perspex assimilation chamber used for leaves had a cross-section of 2 by 15 cm, that for the ears of 10 by 22 cm. The flow rate was 4 litres/min. At ear emergence, rates of flag leaf photosynthesis were measured at 1000, 2000, 2500, 3200, and 7000 f.c. To obtain the highest light intensity, a high pressure mercury vapour lamp supplemented the fluorescent and incandescent lamps. Five days after anthesis the rate of flag leaf photosynthesis at 3200 f.c. was measured not only in air, but also in nitrogen containing 330 p.p.m. CO_2 , to obtain an estimate of photorespiration. The rate of photosynthesis by the penultimate leaf, that below the flag leaf, was also measured at that time.

(d) ^{14}C Distribution

Uptake of $^{14}\text{CO}_2$ was used to compare the patterns of assimilate distribution during the period of most rapid grain growth. This period varied to some extent between lines, but a standard time of exposure to $^{14}\text{CO}_2$ was used, namely 14 days after anthesis. In separate lots of eight plants either the flag or the penultimate leaf was exposed to $^{14}\text{CO}_2$, the plants being harvested 24 hr after the initial exposure.

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

At harvest the plant parts were separated, and a Geiger-Müller tube used to make a preliminary examination of the distribution of radioactivity. The parts were then dried, weighed, and ground and the relative specific activity determined on the powders by the method of O'Brien and Wardlaw (1961).

III. RESULTS

(a) *Growth Measurements*

(i) *Leaf Areas*

During early growth the total leaf area of unvernallized seedlings of the various lines was approximately proportional to the weight of the grains which were sown (see Fig. 1). Seedling establishment was slowest in the diploids with the smallest

grains, especially *A. speltoides*, and was most rapid in the tetraploids and the hexaploids. During early growth, there were only slight differences between lines in the rates of leaf appearance, and the differences in total leaf area in Figure 1 were due mainly to differences between lines in the size of individual leaves. Relative growth rates for leaf area between 11 and 27 days from sowing did not differ markedly between species (Table 2, column 5), and diagrams presented by Kranz (1966) support this conclusion.

Successive leaves were progressively larger in all lines except that the flag leaf blade was smaller than that of the penultimate leaf in *T. boeoticum*, *T. monococcum*, and *T. spelta*, being particularly reduced in *T. boeoticum* in which the area of the flag leaf was less than half that of the leaf below it.

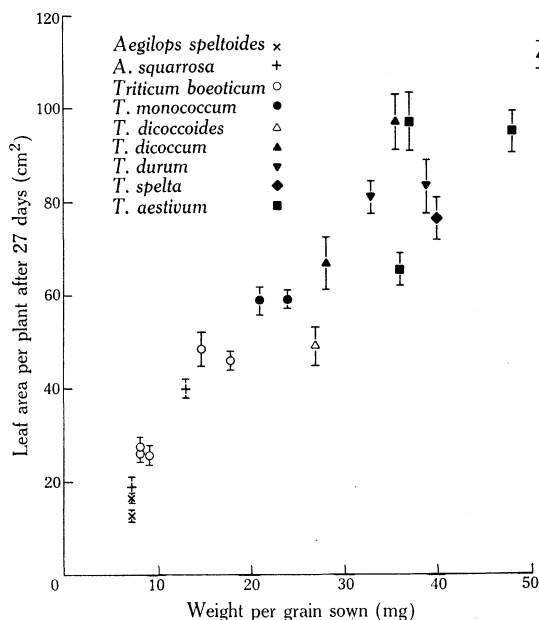


Fig. 1.—Relation between the average leaf area for seedlings of each line 27 days after germination and the average weight of the grains sown. The vertical line represents $2 \times \text{S.E.}$

(ii) Tillering

Lines differed to some extent in their early tillering rates, but after inflorescence initiation only a few additional tillers were formed in the tetraploid and hexaploid wheats whereas the diploids, especially *A. speltoides*, continued tillering at a high rate until maturity, resulting in very great differences in final number of tillers bearing ears (Table 2, column 8). The high tiller number in many of the diploids compensated for their smaller leaves and more slender stems. Dry weights at final harvest depended on the time to maturity of the main ear and on whether tillering continued, being highest in Cappelle Desprez, *T. monococcum* W292, and *A. speltoides* AS1. At maturity plants of Cappelle Desprez had 15.1 tillers, those of AS1 84.1.

TABLE 2
SOME CHARACTERISTICS OF WHEAT AND RELATED SPECIES

Each value is the average for all lines of the species. Further details in text

Species	(1) Spikelet Number per Ear	(2) Grain Number per Ear	(3) Weight per Grain (mg)	(4) Area of Largest Leaf (cm ²)	(5) Leaf Area Growth Rate (cm ² /cm ² /day)	(6) Maximum Grain Growth (mg/ear/day)	(7) Grain Weight as % of Main Stem Weight	(8) No. of Tillers with Ears at Final Harvest	(9) Stem Weight Loss (mg)	Photosynthetic Rate at 3200 f.c.		(12) Ear†
										(10)	(11)	
<i>T. boeoticum</i>	18.1	30.4	13.6	8.8	0.173	25.1	33.8	34.3	59	45.7	(18.8)	2.7
<i>T. monococcum</i>	22.1	21.4	32.0	19.1	0.184	31.8	39.6	46.4	69	34.9	(13.0)	1.8
<i>A. speltoides</i>	9.1	11.6	4.6	5.0	0.179	3.7	9.5	71.4	48	33.8	(9.6)	1.1
<i>A. squarrosa</i>	10.2	19.5	10.0	8.2	0.190	10.8	31.5	43.3	47	36.4	(13.1)	1.7
<i>T. dicoccoides</i>	14.3	26.8	32.9	34.5		40.2	36.3	19.6	80	34.6	(14.4)	6.4
<i>T. dicoccum</i>	20.0	37.1	35.8	29.2	0.161	44.3	39.0	18.5	210	29.5	(11.0)	4.1
<i>T. durum</i>	19.2	47.2	34.7	31.2	0.196	48.2	38.1	10.8	31	28.8	(12.9)	6.3
<i>T. spelta</i>	22.4	35.6	56.1	40.8	0.179	48.5	36.2	16.1	148	27.3	(10.8)	4.5
<i>T. aestivum</i>	17.9	36.0	49.0	28.6	0.176	57.1	49.3	14.1	198	31.4	(14.7)	3.3

* Photosynthetic rate for flag leaf in air expressed as mg CO₂/dm²/hr. Values in parenthesis show percentage increase in photosynthetic rate by flag leaf when oxygen is excluded.

† Gross photosynthetic rate expressed as mg CO₂/ear/hr.

(iii) *Stem Weight Losses*

The weight of the main stems varied greatly between lines depending mainly on their height. They were heaviest in *T. durum* and *T. spelta*, lightest in *A. squarrosa*. There was also considerable variation in the time at which stem weight reached its maximum, this being 5 days after anthesis in some lines (e.g. *T. dicoccum*, W12), 15 days after in many (e.g. Cappelle Desprez), 21 days after in several (e.g. *T. durum*, W9), and at maturity in *T. durum* (W8).

The average losses in stem weight between the maxima and the final harvests are given in Table 2, column 9. They were greatest in *T. dicoccum* and the hexaploid wheats, least in *T. durum* and the wild diploids.

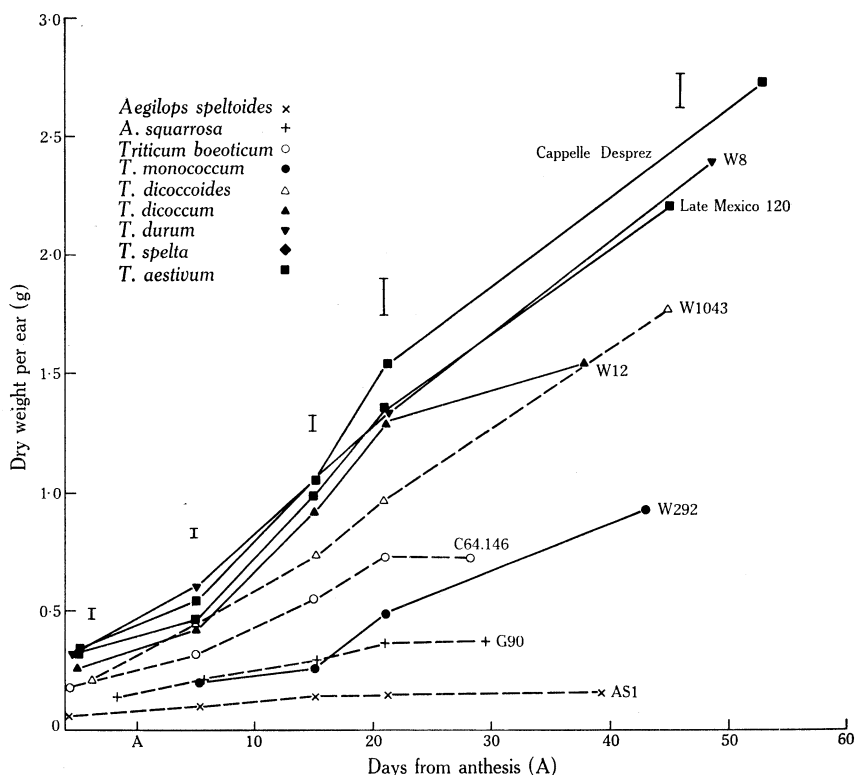


Fig. 2.—Changes in dry weight of main stem ears with time from anthesis, in some representative lines. The vertical lines represent $2 \times$ mean S.E. for each harvest.

(iv) *Ear Characteristics*

Changes in ear weight on the main stem with time after anthesis in some representative lines are shown in Figure 2. Grains were separated from the ears of all lines in the three last harvests, and grain weights increased in much the same way as ear weights. The weight of the ear structures (i.e. ear minus grains) remained fairly constant or increased to a small extent in some lines at the final harvest; they were smallest in *A. speltoides*, heaviest in *T. dicoccoides* and *T. spelta*. Figure 2 illustrates

the very great differences between lines in the course of ear growth. Final grain weight per ear was least in the wild diploids, and tended to increase with increase in ploidy, and with selection for cultivation. However, there were exceptions in that final grain weight in the wild *T. dicoccoides* (W1043) exceeded that in the cultivated *T. dicoccum* (W12), while the tetraploid *T. durum* (W8) exceeded the hexaploid Gabo and Late Mexico 120. The highest rate of grain growth measured increased with both ploidy and cultivation, as may be seen from Table 2, column 6. Grain growth began later but continued for longer in both lines of the cultivated *T. monococcum* compared

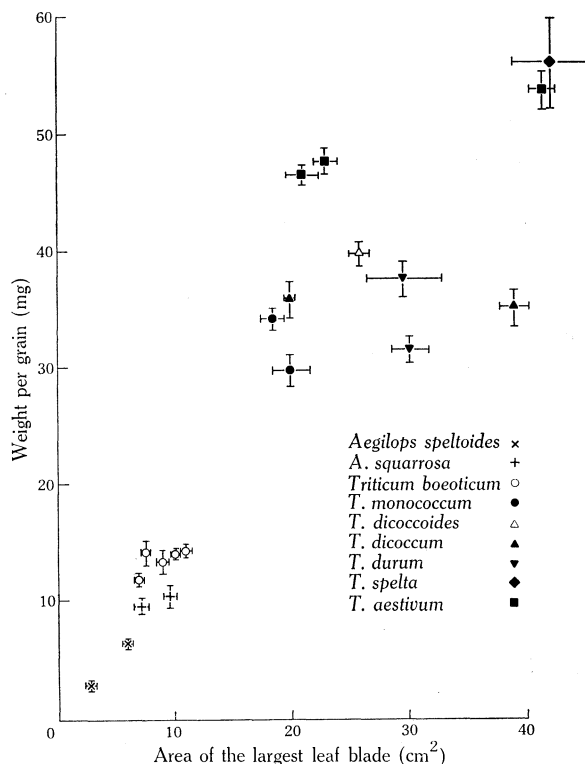


Fig. 3.—Relation between mean weight per grain in main stem ears and the area of the largest leaf blade. The vertical line represents $2 \times \text{S.E.}$ The horizontal line represents the range.

with that in all lines of the wild *T. boeoticum*. At the tetraploid level, however, grain growth continued for longer in the wild *T. dicoccoides* (W1043) than in the earlier-maturing *T. dicoccum* (W12).

Spikelet number per ear in *Aegilops* spp. was much lower than in *Triticum* spp. in which, under our conditions, there was no evidence of any increase with evolutionary level (Table 2, column 1). However, vernalization can reduce spikelet number in hexaploid wheat to a considerable extent (Rawson 1970) and may therefore have limited expression of the differences between the lines used in our experiment.

Grain number per ear (Table 2, column 2) was lowest in *A. speltoides*, which bore only about one grain per spikelet, and in *A. squarrosa* which bore about two. In the five lines of *T. boeoticum* grain number per spikelet ranged from 1.46 to 1.87, whereas in both lines of *T. monococcum* it was slightly less than one.

Individual grain weight varied greatly between species (Table 2, column 3) being lowest in *A. speltoides* and highest in the hexaploids. The values we obtained were similar to those given for a few of the species by Percival (1921) and Bell, Lupton, and Riley (1955). There was a 20-fold range between individual lines in mean weight per grain, which bore a close relation to the area of the largest leaf blade (Fig. 3). Differences in weight per grain accounted for most of the differences between lines in grain yield per ear, which was also closely related to the area of the largest leaf (Fig. 4). The smaller number of grains per ear in *T. monococcum* compared

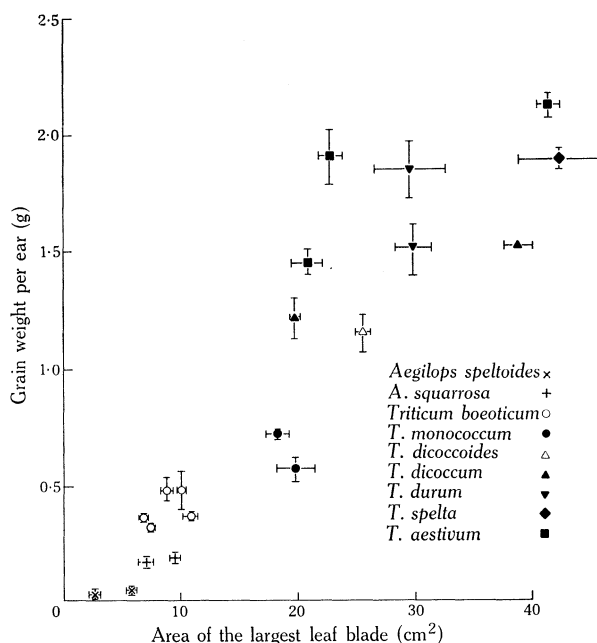


Fig. 4.—Relation between the average grain weight in the main stem ear of each line and the area of the largest leaf blade. The vertical line represents $2 \times \text{S.E.}$ The horizontal line represents the range.

with *T. boeoticum* was more than compensated by the 2.5-fold increase in mean grain size. Grain size in the tetraploids was greater than that in the diploids, but was greater in one genotype of the wild *T. dicoccoides*, W1043, than in the cultivated forms, particularly those of *T. durum*, in which there were many more grains per ear. Grain size was still greater in the hexaploids, being greatest in *T. spelta* and in Cappelle Desprez. The proportion of main shoot weight (including leaves) represented by the grain is given in Table 2, column 7. It was particularly low in both lines of *A. speltoides*, and highest (57.1%) in the semi-dwarf hexaploid Late Mexico 120.

(b) *Photosynthesis*

The rate of photosynthesis per unit flag leaf area, at high light intensity, has apparently fallen in the course of evolution of wheat (Fig. 5). The highest rates were found in *T. boeoticum*, and *A. squarrosa* (G46), the lowest, less than half those of *T. boeoticum*, in Cappelle Desprez. The rates were inversely related to the area of the flag leaf blade.

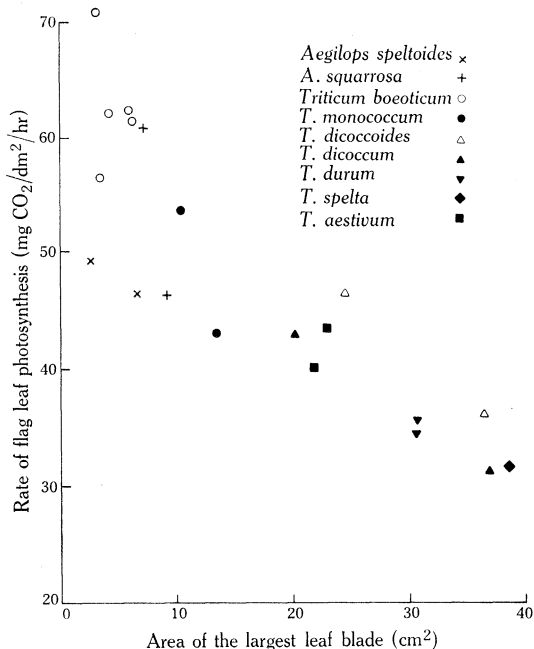


Fig. 5.—Relation between the rate of photosynthesis by flag leaf blades, at the time of ear emergence, in light of 7000 f.c. intensity at atmospheric CO₂ concentration, and the area of the flag leaf blades.

At lower light intensities the differences between species were less pronounced (Fig. 6), and gross photosynthesis (i.e. net photosynthesis plus dark respiration) at an intensity of 1000 f.c. ranged from only 16.4 mg CO₂ dm⁻² hr⁻¹ for *T. aestivum* to 19.1 for *T. boeoticum*. At an intensity of 3200 f.c. net photosynthesis by flag leaves of *T. aestivum*, *T. spelta*, and *T. durum* was approaching light saturation, whereas in *T. boeoticum* and *A. squarrosa* it increased by a further 50% with increase in light intensity to 7000 f.c. The average rates at 3200 f.c. are given in Table 2, column 10, together with the increase in photosynthetic rate at 3200 f.c. when oxygen is excluded (column 11). This estimate of the rate of photorespiration indicates that the high rates of net photosynthesis in the wild progenitors are not due to low rates of photorespiration. In fact these were also highest in *T. boeoticum*. The differences in flag leaf photosynthetic rates between species were also apparent between rates measured on the penultimate leaf.

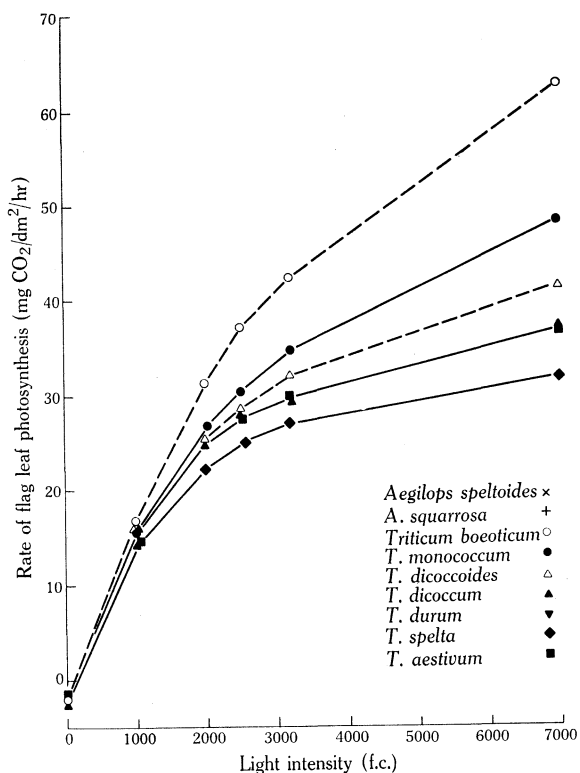


Fig. 6.—Relation between photosynthetic rate of flag leaf blades and light intensity in several species. Each curve is the average for all lines.

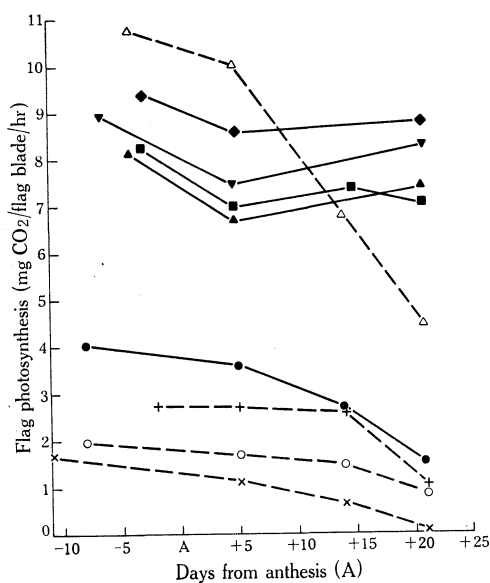


Fig. 7.—Changes with time from ear emergence in photosynthesis per flag leaf blade, at 21°C in light of 3200 f.c. intensity. Symbols as in Figure 6.

The larger area of the flag leaves of the more advanced wheats more than compensated for their lower rates of photosynthesis, as may be seen from Figure 7. Photosynthesis per flag leaf blade was initially greatest in the wild *T. dicoccoides*, and was about four times as great in the cultivated tetraploids and hexaploids as in *T. boeoticum*, which had the highest rate per unit leaf area. In addition to this major difference between the diploids and the other species, there was a further difference in the changes with time from ear emergence. In all the wild species, and in *T. monococcum*, flag leaf photosynthesis fell progressively throughout the period of grain development, whereas in all the cultivated tetraploids and hexaploids it

TABLE 3

PERCENTAGE DISTRIBUTION OF ^{14}C -LABELLED ASSIMILATES 1 DAY AFTER EXPOSURE TO $^{14}\text{CO}_2$
14 DAYS AFTER ANTHESIS

Species	Percentage ^{14}C in:						Tillers
	Fed Leaf	Ear	Top Stem Inter-node	Second Inter-node	Basal Inter-nodh	Roots	
Flag leaf exposed to $^{14}\text{CO}_2$							
<i>T. boeoticum</i>	21.4	40.3	5.1	9.8	4.2	2.1	16.9
<i>T. monococcum</i>	25.0	23.0	9.5	14.9	8.2	2.8	16.2
<i>A. speltooides</i>	22.0	3.7	4.1	14.6	9.1	14.5	31.9
<i>A. squarrosa</i>	30.1	39.9	6.4	7.2	2.8	2.3	11.6
<i>T. dicoccoides</i>	31.0	28.6	10.5	9.6	2.9	1.8	15.3
<i>T. dicoccum</i>	33.5	52.8	1.4	1.5	0.5	0.9	9.1
<i>T. durum</i>	22.5	44.9	12.2	6.0	1.7	0.9	11.3
<i>T. aestivum</i>	24.0	52.4	5.7	2.5	0.4	1.0	11.4
Penultimate leaf exposed to $^{14}\text{CO}_2$							
<i>T. boeoticum</i>	26.3	23.7	1.3	3.6	11.4	5.5	27.7
<i>T. monococcum</i>	33.0	3.7	1.5	5.7	28.3	6.7	20.6
<i>A. speltooides</i>	32.7	1.0	1.4	2.1	15.5	6.4	39.9
<i>A. squarrosa</i>	37.3	6.8	0.6	3.6	27.2	9.1	14.0
<i>T. dicoccoides</i>	36.1	5.7	0.6	2.6	11.5	4.1	38.6
<i>T. dicoccum</i>	41.3	19.4	0.5	2.2	9.4	3.2	22.5
<i>T. durum</i>	29.2	16.1	3.5	7.8	21.9	3.9	15.9
<i>T. aestivum</i>	25.5	23.9	2.7	11.1	17.0	3.1	14.2

remained high until at least 21 days after anthesis, in fact was higher than 5 days after anthesis. This rise in the rate of flag leaf photosynthesis during rapid grain growth has been examined in more detail elsewhere (Evans and Rawson 1970; Rawson and Evans, unpublished data) and is probably associated with increased demands for assimilates by the developing ears.

Rates of gross ear photosynthesis (Table 2, column 12) differed considerably between lines, being lowest in *A. speltooides* and highest in the heavily awned ears of *T. dicoccoides* and *T. durum*. The differences between species appeared to be determined mainly by ear size and awn length. Spikelet number was similar in Gabo and Late

Mexico 120 whereas gross ear photosynthesis was 2.1 mg CO₂ per ear per hour in the awnless Gabo and 5.2 mg in the awned Mexico.

(c) *Distribution of ¹⁴C-labelled Assimilates*

Of the ¹⁴C assimilated, the proportion exported within 24 hr was rather higher for flag leaves than for the penultimate leaves (see Table 3), and was differently distributed, much more flag leaf assimilate being found in the ear and less in the stems, roots, and tillers.

The species differed considerably in their partitioning of assimilates during ear development. Evolutionary changes are discernible but they are complicated by other factors, such as the relative size of the flag leaf, the magnitude of ear photosynthesis, and the time of exposure to ¹⁴CO₂ in relation to the course of grain growth. For example, it can be seen from Figure 2 that grain growth in *T. monococcum* (W292), as also in W10, was extremely slow at the time of exposure to ¹⁴CO₂, 14 days after anthesis, whereas that in *T. boeoticum* (C64.146), and also in the other lines, was much faster. This, and the relatively smaller flag leaves of *T. boeoticum*, probably account for the much higher proportion of labelled assimilates translocated to the ear in *T. boeoticum* compared with *T. monococcum*. Similarly, the rather high proportion of assimilates from the flag leaf, compared with that from the penultimate leaf, translocated to the ears of *A. squarrosa* may reflect the small size and early senescence of the flag leaves in that species.

With these effects in mind, the data of Table 3 suggest that evolution in wheat has been accompanied by an increase in the proportion of assimilates translocated to the grain. The ears of *A. speltoides* were largely self-supporting for assimilates; those of *T. monococcum* and *T. dicoccoides* imported about one-quarter of the flag leaf assimilate, but little from the leaf below; while those of *T. dicoccum* and *T. aestivum*, with faster grain growth and less ear photosynthesis to support it, imported more than half of the flag leaf assimilates, and almost a quarter of those of the penultimate leaf, within 24 hr.

The proportion of labelled assimilate translocated to the roots is low at this late stage of development of the plants, but was higher in the diploids (particularly the two species of *Aegilops*) than in the modern wheats. The proportion in the tillers was also lower in the modern wheats.

The partitioning of assimilates within the stem also appears to have changed progressively in the course of evolution. In the diploids most of the activity from the flag leaf was found in the penultimate and lower internodes, while that from the penultimate leaf was predominantly in the lowest internodes. In the tetraploids and hexaploids, on the other hand, very little activity from the flag leaf was found at the base of the stem, most being in the top internode, and a much higher proportion of that from the penultimate leaf was also found in the upper internodes. This change reflects the increased tendency towards upwards movement of assimilates in the more advanced wheats, which is coupled with a progressive reduction in the proportion distributed to the roots and tillers. It also suggests that the transport of assimilates from the flag leaf to the ear may follow a more direct route in the modern wheats, joining the upward flow at the uppermost node, whereas in the diploids it may, as Percival (1921) suggests, first move down to the penultimate node.

IV. DISCUSSION

Evolution in wheat has been accompanied by marked parallel increases in the size of leaves and grains, and by progressive changes in the pattern of distribution of plant substance, rather than by any increase in the efficiency of photosynthesis.

The great range in leaf and grain size, and the close relation between them, is illustrated in Figure 3. Grain size is likely to have been an important criterion for selection, at least during the early stages of wheat evolution. The much larger grains of *T. monococcum* compared with those of the wild *T. boeoticum* support this conjecture. Percival (1921) has noted that Neolithic grains of *T. monococcum* are smaller than present-day ones, and more closely resemble those of *T. boeoticum*. Several early writers on agriculture, such as Columella (*Res Rustica* 2, 9, 11), Varro (*Res Rusticae* 1, 52), and Virgil (*Georgics* 1, 197), emphasized the importance of selecting the largest grains of the harvest for the next sowing, a practice which may be as old as agriculture itself. Percival (1921) presents some striking data in support of it.

The larger the grain sown the faster was seedling establishment (Fig. 1) and the larger the individual leaves. In turn larger leaves were associated with larger grains in the ear. Whether these parallel changes reflect a common basis, such as increasing cell size, or whether changes in one determine the other, is not yet known. But the large increase in grain size appears to have played a major part in the evolution of yield potential in wheat. Matsushima (1966, p. 266) has shown that increase in the size of rice grains can be mechanically restricted by the lemma and palea. If the same was true of the primitive wheats, the gene conferring loose glumes would have been of advantage not only because of the greater ease of threshing, but also by permitting larger grains to develop. Boshnakian (1918) has discussed evidence for the mechanical restriction by the glumes of grain growth in wheat, such as the parallel marks of the glume veins along the mature grains. These are most evident in species with invested grains such as *T. monococcum* and *T. spelta*. However, the dimensions of glumes and of grains have probably changed in parallel (cf. Lamba 1949), with the result that glume size may not greatly limit grain size. In our experiments the invested grains of *T. spelta* were amongst the largest, in spite of their investing glumes.

The total dry weight at maturity of some of the wild progenitors was comparable to that of the modern wheats, but its distribution was very different. Evolution appears to have been accompanied by increased apical dominance following inflorescence initiation. Not only is the plant substance concentrated in fewer tillers, but more of that within each tiller is concentrated in the grain. The small, slow-growing ears of *A. speltoides* were largely self-supporting for photosynthate, as indicated by the small proportion of ¹⁴C-labelled photosynthate translocated to the ears from the flag leaf. In the other diploids this proportion was higher, particularly in *T. boeoticum* with its extremely small flag leaves. The proportion rose to still higher levels in the tetraploid and hexaploid wheats, whose ears also drew to a greater extent on assimilates from the leaves below the flag leaf to support their much higher rates of grain growth. Thus, the extent of import by the ears has increased progressively with evolution, and this has been accompanied by a proportional increase in the cross-sectional area of phloem tissue at the top of the stem (Evans *et al.* 1970). Similarly, the fall in stem weight from its maximum until maturity of the ear has tended to increase with increase in ploidy and with selection for cultivation. The great increase in the rate and extent of grain growth with evolution in wheat has thus

probably involved a greater mobilization of photosynthate from the stems and leaves, and an increase in the capacity of the culm phloem to transport it to the ear.

The rate of photosynthesis per unit flag leaf area was similar for all species at low light intensities, but at high intensities much higher rates were measured in the more primitive species (Figs. 5 and 6). At a light intensity of 7000 f.c. the photosynthetic rate in *T. boeoticum* (6625) was 2.6 times as high as that in Cappelle Desprez. The lower rates in the more advanced wheats were associated with larger flag leaves. A possible explanation of the fall in photosynthetic rate at high light intensities during evolution in wheat would be that chloroplast numbers per cell have not increased in proportion to cell size, but measurements by Kranz (1966) indicate that the number of chloroplasts per cell has increased in proportion to cell dimensions throughout wheat evolution as they have also in sugar beet (Butterfass 1964). A more likely explanation, therefore, is that the fall in photosynthetic rate is due to the reduced surface-volume ratio of the larger mesophyll cells of the more advanced wheats, resulting in an increase in mesophyll resistance to CO₂ exchange. Differences between lines of *Lolium perenne* in their photosynthetic rate at high light intensities have been found by Wilson and Cooper (1969) to be related to differences in mesophyll cell size.

Belikov, Motorina, and Kurkova (1961) found no difference in photosynthetic rate between *T. monococcum*, *T. dicoccum*, and *T. aestivum*, even at high light intensities. Their measurements were made only on the second leaf of young plants, with only one line of each species, but it is nevertheless surprising that the marked differences we found, in all our experiments, were not observed by them. Our rates for *Aegilops* spp. were similar to those obtained by Naaber (1964) under comparable conditions apart from a higher CO₂ concentration. The assimilation rates measured by Kranz (1964, 1966, 1967) are for whole plants and refer to unit ground (not leaf) surface; they are therefore not comparable with our data.

Since the fall during evolution in wheat in photosynthetic rate per unit leaf area has been more than compensated for by the increase in flag leaf area, photosynthesis per flag leaf has risen considerably, particularly in the advance from the diploid to the tetraploid level. Also, with the advance from the wild tetraploids to the cultivated tetraploids and hexaploids flag leaf senescence was delayed and photosynthesis at high rates continued for much longer, possibly in response to the continued demands for assimilates from more prolonged grain growth. A factor that may have contributed to the early senescence of flag leaves in *A. speltoides*, *T. boeoticum*, and *T. monococcum* was the long period between ear emergence and anthesis (8–12 days compared with 3–5 in the hexaploid wheats) during which the demand for assimilates by the ear would be small.

Our evidence thus suggests that increase in grain and leaf size, and in the proportion of dry weight mobilized to the grain, have been the dominant physiological changes in the evolution of yield in wheat. The fact that photosynthetic rate per unit leaf area has fallen markedly while grain and leaf size have increased more or less in parallel suggests that photosynthetic rate has not limited the evolution of yield in wheat up to the present, but it may well limit further evolution.

In terms of the physiological processes we have examined, the biggest evolutionary advance was in the step from diploid to tetraploid genomes. The wild tetraploid lines we used were both of the robust Palestine race which Harlan and

Zohary (1966) consider to be the likely progenitor of most modern wheats. In grain and leaf size and other features *T. dicoccoides* was much more advanced than *T. monococcum*. Our results support Bell's (1965) comment that cultivated wheat would not have progressed far at the diploid level. The greatest value of *T. monococcum* presumably lies in its resistance to frost, drought, rust, poor soils, and the depredations of birds (Percival 1921). On the other hand, grain yield per ear and many other features of the *durum* wheats were comparable to those of the hexaploids. Thus, in terms of the physiological processes determining productivity, the addition of the D genome may have had little effect, as Shebeski (1958) has already suggested, and its main contribution may have been to baking quality, the spectrum of disease resistance, and, as Zohary, Harlan, and Vardi (1969) suggest, to the adaptive range of wheat.

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