PHOTOSYNTHETIC CHARACTERISTICS OF MODERN AND PRIMITIVE WHEAT SPECIES IN RELATION TO ONTOGENY AND ADAPTATION TO LIGHT

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Abstract

Some characteristics of photosynthesis in seven species of *Triticum* and two of *Aegilops* were examined. Differences between species in the rate of net photosynthesis per unit area were more pronounced in later formed leaves than in earlier ones, flag leaves showing the greatest range of photosynthesis rates. The range in flag leaf net photosynthetic rates was greatest for plants grown under high light intensity. Net photosynthetic rates of flag leaves of diploid species of *Triticum*, measured under high light intensity, increased progressively with increase in light intensity during growth, whereas the rates for the *Aegilops* species and the tetraploid and hexaploid lines of *Triticum* reached their maxima at intermediate light intensity during growth.

Under one set of environmental conditions during growth, a diffusion resistance study of flag leaf photosynthesis revealed that both the gas phase resistance and "residual" ("mesophyll" or "intracellular") resistance contribute to the observed differences in photosynthetic rate. When the average values of residual resistance for each genotype were plotted against the corresponding gas phase resistance a positive correlation, to which all but three of the lines adhered, was found, an increase of $0 \cdot 5$ s cm^{-1} in gas phase resistance being associated with an increase of $1 \cdot 0$ s cm^{-1} in residual resistance.

When adaptation to different light intensities occurred over a prolonged period, the stomatal density on the flag leaf of two diploid lines and of a hexaploid (*T. spelta*) line adapted upwards to high light but did not do so for *T. aestivum*. However, the adaptation was small and of minor significance to the overall photosynthetic adaptation. Variation in stomatal density was not a major determinant of variation in stomatal resistance.

Specific leaf weight bore no consistent relation with either photosynthetic rate or residual resistance.

I. INTRODUCTION

Previous work (Evans and Dunstone 1970; Khan and Tsunoda 1970) has shown the net photosynthetic rate (i.e. net CO_2 exchange rate per unit area) of flag leaves of the diploid and tetraploid species of *Triticum* and *Aegilops* to be higher than those of the modern hexaploid wheats. Belikov *et al.* (1961) had earlier found no differences between diploid, tetraploid, and hexaploid cultivated wheats when they measured, under both high and low light intensities, the photosynthesis rates of the second leaf to develop.

These different results may be due to earlier formed leaves not exhibiting the differences which become apparent later in ontogeny, or to differences in photosynthetic rate being dependent upon the environmental conditions under which the plants

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are grown. It is known that light intensity during growth can affect subsequent rates of photosynthesis in grasses and cereals (Hesketh 1968; Downes 1971; Woledge 1971), and that the magnitude of adaptation to prior light conditions can vary between ecotypes of some species (Björkman and Holmgren 1963).

In the first experiment described here the possibility that differences between species in photosynthetic rate are less pronounced in earlier formed leaves was examined. Data for the flag leaves in this experiment are then combined with data from two other experiments and from the previously published work (Evans and Dunstone 1970) to examine whether the species differ in the response of their net photosynthetic rate to seasonal variations in the intensity of daylight. The effect of light intensity during growth was also examined with four selected lines grown under artificial light at two intensities.

In all these experiments ancillary studies were made on parameters associated with photosynthetic rate in an attempt to elucidate the mechanism behind the phenomena observed.

II. Materials and Methods

(*a*) *Genetic Materials and Cultural Conditions*

Twenty-one lines representing nine species of the genera *Triticum* and *Aegilops* were used in the series of experiments. These lines, which are listed below, are described more fully in Evans and Dunstone (1970):

Group	Genome	Species	Line code
Diploid			
Wild	A	*Triticum boeoticum* Boiss. emend. Schiem.	Kew C64.146
			T.6625
			PBI C64.145
			T.6626
			TBI
			G31
	B	*Aegilops speltoides* Tausch	AS1
			G19
	D	*A. squarrosa* L.	G46 CHBS
			G90 CHBS
Cultivated	A	*T. monococcum* L.	W10
			W292
Tetraploid			
Wild	AB	*T. dicoccoides* Korn.	W1043
Cultivated	AB	*T. dicoccum* Schubl.	Khapli W12
			W2698
	AB	*T. durum* Desf.	Kubanka W8
			Acme W9
Hexaploid	ABD	*T. spelta* L.	H2
	ABD	*T. aestivum* L.	Gabo
			Late Mexico 120
			Cappelle Desprez

The plants for all experiments were grown from seeds which had been vernalized for 7½ weeks at 2°C on wet filter paper in Petri dishes in the dark. The germinated seeds were planted singly in a 1 : 1 perlite–vermiculite mixture in 13-cm pots and grown under a 21°C day (8.30 a.m.–4.30 p.m.) and 16°C night (4.30 p.m.–8.30 a.m.) temperature regime in a phytotron glasshouse with natural day length extended to 16 hr using low-intensity incandescent lamps. The

plants for experiment 1 were grown under winter light conditions, and plants for experiments 2 and 3 were grown at times of year which gave radiation levels intermediate between those in experiment 1 and in the earlier experiments under very bright light (Evans and Dunstone 1970). For experiment 4 the plants were grown in an LB-type artificially lit cabinet (Morse and Evans 1962) containing, as well as the standard 28 140 W VHO warm white fluorescent lamps, two Philips HPLR 1000 W mercury vapour lamps. One-half of the cabinet was shaded with Sarlon shade-cloth to reduce the light intensity at plant level from 175 to 84 W m^{-2} (400–700 nm) measured with an Eppley pyranometer. This provided high light and low light pretreatments.

Plants were watered each morning with Hoagland's No. 2 nutrient solution and each afternoon with demineralized water. Main stems were tagged and the plants staked to prevent lodging. The total radiant energy received above the glasshouse roof each day was measured by means of a Kipp solarimeter connected to a CSIRO solar integrator.

(*b*) *Measurement of Net Photosynthetic Rate*

Measurements of photosynthesis were carried out on groups of 2–4 attached leaves in order to keep the total leaf area in the leaf chamber about the same each time. In experiment 1, the measurements were made when the appropriate leaves had first reached full expansion. In the other experiments, the photosynthetic rate of the flag leaves was determined at ear emergence. In experiment 3, single leaves from the groups measured by the method described in this section were also studied in the diffusion resistance analyser described in Section II(*d*).

The Perspex leaf chamber used had a cross-section of 15 by 1 cm. Atmospheric air was drawn from a source on the roof of the building, passed through a mixing tank of 170 litres capacity, and then through the assimilation chamber at the rate of 6 litres per minute. The CO_2 differential across the leaf chamber was measured with a Grubb Parsons' SB2 infrared gas analyser which had been calibrated with Wösthoff gas-mixing pumps. The temperature of the assimilation chamber was controlled by placing it in an LB-type artificially lit cabinet set at 21°C. The temperature inside the chamber stabilized at 25 ± 1°C as measured underneath the leaf with a thermocouple.

The chamber was illuminated by the fluorescent lamps of the cabinet augmented by a Philips HPLR 1000 W high-pressure mercury vapour lamp. The net photosynthetic rate was measured at 266 W m^{-2} (visible) within the chamber for experiments 1–3, and 326 W m^{-2} (visible) for experiment 4. In experiment 4 a range of low light intensities was obtained by placing layers of white organdie fabric across the top of the assimilation chamber. The photosynthetic rate was also measured in an atmosphere consisting of 300 p.p.m. CO_2 in nitrogen with 1% oxygen; the extent of enhancement when the oxygen content was lowered was taken as one estimate of the rate of photorespiration (Hesketh 1967).

Leaf areas were determined by weighing cut-out blueprint images of the leaves and the specific leaf weight was calculated as dry weight per unit leaf area.

(*c*) *Stomatal Frequencies and Lengths*

Impressions were made of the upper and lower surfaces of the leaves with silicone rubber (Sampson 1961). Replicas of the rubber impressions were made using clear nail polish and mounted on a microscope slide. In all cases the impression was made of the centre section of the leaf where stomatal frequency is at about the mean value for the whole leaf (Pazourek 1969).

The number of stomata falling within six microscope fields for the upper and six fields for the lower surface of each of nine leaves of each line were counted and a mean calculated. Twenty-four measurements of pore length were taken for each line of each species using $\times 1000$ magnification and an eyepiece micrometer.

(*d*) *Diffusion Resistance Measurements*

A double leaf chamber 10 cm long, 0·8 cm wide, and 1 cm deep on each side of the leaf, with air recirculation over cooling coils producing leaf temperatures of 25 ± 1°C and a wind speed of 350 cm s^{-1}, was used in an open gas-exchange system. For species with leaves 1 cm or more wide gas exchange was determined separately for the two sides of the leaves, since they acted as a septum

between the two sides of the double chamber. For species with narrower leaves the two sides were measured together as in a normal leaf chamber. The air supply to the chamber had controlled CO_2 concentration and humidity, producing conditions of 490 ± 15 ng cm^{-3} (284 p.p.m.) CO_2 and $74 \pm 7\%$ R.H. in the chamber. The leaf was illuminated from above by a mixture of VHO fluorescent and Philips HPLR mercury vapour lamps, filtered through Perspex and glass to remove some of the heat and ultraviolet radiation, giving a light intensity on the upper leaf surface of 200 W m^{-2} (400–700 nm).

Carbon dioxide concentration was determined with a Grubb–Parsons' SB2 infrared gas analyser. Humidity was determined with a wet-bulb psychrometer using thermocouples as the temperature sensors (Slatyer and Bierhuizen 1964). Stomatal resistance plus boundary layer resistance to CO_2 diffusion was calculated for the narrow leaves from the relation

$$(r_a/1{\cdot}46 + r_s/1{\cdot}56) = (e_l - e_a)/E, \tag{1}$$

where e_l is the saturation vapour pressure of water at leaf temperature (g cm^{-3}), e_a is the water concentration in the leaf chamber air (g cm^{-3}), E the transpiration rate (g cm^{-2} s^{-1}), and the factors 1·46 and 1·56 are to convert the resistances to water vapour diffusion to the equivalent terms for CO_2.

Substomatal CO_2 concentration (C_s) was calculated from

$$C_s = C_a - P(r_a + r_s), \tag{2}$$

where C_a is the ambient CO_2 concentration in the leaf chamber, and P is the net CO_2 exchange per unit leaf area.

Residual resistance (r_r) to CO_2 uptake was calculated from

$$r_r = (C_s - C_p)/P, \tag{3}$$

where C_p is the CO_2 compensation point. This was determined immediately after the measurement of P at 284 p.p.m. CO_2 by reducing C_a to a value very close to the assumed value of C_p and measuring the small uptake or release of CO_2 in the open system. Graphical extrapolation to $P = 0$ yielded a close estimate of C_p.

For broad leaves, values of $(r_a + r_s)$, C_s, and r_r were calculated separately for the upper (u) and lower (l) sides of the leaf $(r_a + r_s)_u$; $(r_a + r_s)_l$, etc. To obtain terms analagous to $(r_a + r_s)$ and r_r for the narrow leaves, resistances for the two sides of the wide leaves were added in parallel, thus:

$$\|(r_a + r_s) = [(r_a + r_s)_u . (r_a + r_s)_l]/[(r_a + r_s)_u + (r_a + r_s)_l],$$
$$\|r_r = (r_{r,u}).(r_r)/(r_{r,u} + r_{r,l})$$

Hereafter, the stomatal plus boundary layer resistance will be referred to as the "gas phase resistance".

III. Results

(a) *Net Photosynthetic Rate of Successive Leaves up the Main Stem*

The mean net photosynthetic rate for each leaf of the species in the winter study (expt. 1) is shown in Figure 1. The single line of *T. spelta* (cv. H2) is omitted from the figure and the observations below because it behaved differently from all other lines in a number of respects including its photosynthetic behaviour; for the flag leaf and the third leaf below it, net photosynthetic rate for cv. H2 was very significantly lower ($P < 0{\cdot}001$) than the overall mean of all other lines. Excluding the anomalous *T. spelta*, the range of species mean net photosynthetic rates increased with each successive leaf. The between-line variance increased sixfold ($P < 0{\cdot}05$) from leaf F—3 to the flag (F). Since none of the between-species comparisons for leaf (F—3) is significant, whereas there are many significant differences between

species for the flag leaf net photosynthetic rates, these data do not contradict the findings of Belikov *et al.* (1961) that there was no difference, between cultivated species at the three levels of ploidy, in net photosynthetic rate of the early leaves to develop on the young vegetative plants. It seems that photosynthetic differences between species emerge as the plant develops.

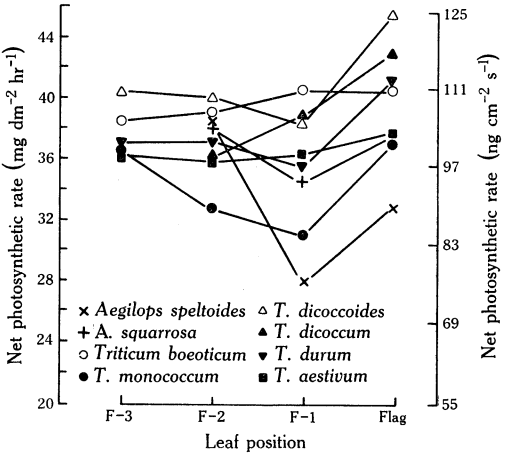


Fig. 1.— Net photosynthetic rate at 266 W m^{-2} and atmospheric CO_2 concentration for successive attached leaves from the third below the flag (F−3) to the flag leaf. Each point is the mean for the species, calculated from the measurement of two groups of four leaves of each line of that species.

The range of flag leaf net photosynthetic rates in experiment 1 was less than that found in the earlier experiments of Evans and Dunstone (1970), and did not display the strong negative correlation with leaf blade area which was observed earlier. The breakdown of this relationship was associated with a marked reduction in the photosynthetic rates of diploid species, but not in the tetraploid and hexaploid species. In order to study the behaviour of flag leaves grown under a wide range of light conditions, two further experiments (2 and 3) were carried out in the phytotron glasshouses and photosynthetic measurements were made on the flag leaves at ear emergence.

(*b*) *Photosynthetic Adaptation under Natural Light*

The data for rates of flag leaf photosynthesis in each line for each of the experiments with glasshouse grown plants (expts. 1–3 plus the original experiment) were plotted against the mean incident radiation for 3 days prior to measurement (referred to below as the prior radiation environment) (Fig. 2). It was decided to use the short period of 3 days before measurement in view of the observation by Pearce *et al.* (1969) that the most recent light regime under which the plants are grown has the greatest effect on the photosynthetic response of leaves. Each point in Figure 2 is the mean of 8 or 9 leaves of one line.

Figure 2 indicates that the various species responded differently to the effect of prior radiation environment on their light-saturated photosynthetic rate. With the diploid *Triticum* species, both wild and cultivated, the light-saturated photosynthetic rate of the flag leaves increased progressively with increase in prior radiation environment over the full range from less than 200 to over 800 cal cm^{-2} day^{-1}. The light-

saturated photosynthetic rates of the *Aegilops* species and the tetraploid and hexaploid *Triticum* species showed no evidence of increasing responses to prior radiation environment above about 400 cal cm^{-2} day^{-1}. Of the hexaploids, the winter lines (Cappelle Desprez and H2) tended to exhibit lower rates than did the spring lines (Late Mexico 120 and Gabo).

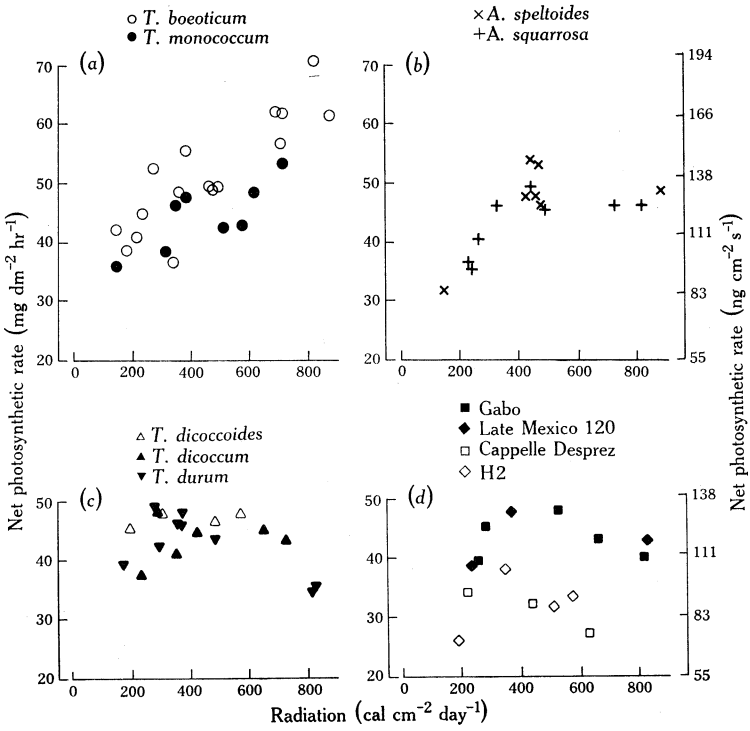


Fig. 2.—Photosynthetic adaptation to prior radiation environment. Net photosynthetic rate was measured under 266 W m^{-2} visible radiation and atmospheric levels of oxygen and CO_2. Radiation is the mean total radiation per day received on the glasshouse roof during the 3 days prior to the day of measurement. (*a*) Diploid *Triticum* species. (*b*) Diploid *Aegilops* species. (*c*) Tetraploid *Triticum* species. (*d*) Hexaploid *Triticum* cultivars.

(*c*) *Photosynthetic Adaptation to Artificial Light Intensity*

Two diploid lines (both *T. boeoticum*) and two hexaploid cultivars (*T. spelta* cv. H2, and *T. aestivum* cv. Cappelle Desprez) were chosen to study the effect of light intensity during growth on the photosynthetic response of the flag leaf, using artificially lit growth cabinets (expt. 4). The net photosynthetic rate of the flag leaf at the stage of ear emergence was determined over a range of leaf chamber light intensities.

Light response curves are shown for each pretreatment of each line in Figure 3. The diploid lines T.6625 and C64.146 had maximum net photosynthetic rates for the high light pretreatment which were 50–60% higher than the rates for the corresponding

low light pretreatment, whereas the hexaploid lines exhibited only a slight, statistically non-significant, adaptation of net photosynthetic rate to the light pretreatments.

These data confirm the conclusions drawn from the results compiled in Figure 2, namely, that the net photosynthetic rate of the diploid species had a marked response to preceding light intensity which is not evident in the hexaploid species.

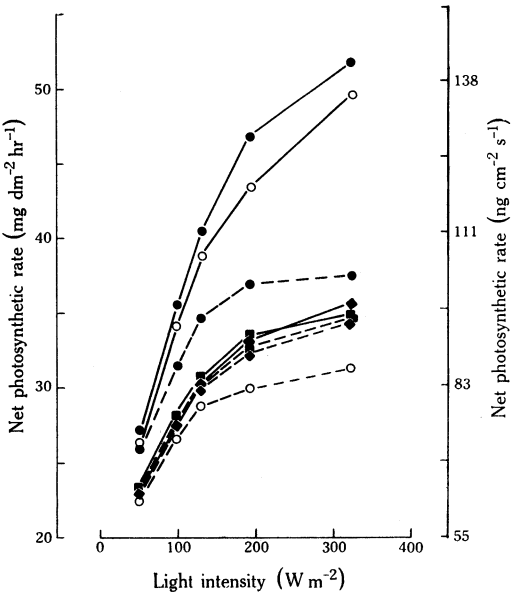


Fig. 3.—Response of net photosynthetic rate of the flag leaves to leaf chamber light intensity for the high light (HL) (———) and low light (LL) (– – –) pretreatments (experiment 4). The L.S.D. for difference between pretreatments is 28 ng cm^{-2} s^{-1}.
● *T. boeoticum* Kew C64.146.
○ *T. boeoticum* T.6625.
♦ *T. spelta* cv. H2.
■ *T. aestivum* cv. Cappelle Desprez.

(*d*) *Determinants of Net Photosynthetic Rates*

In each of the experiments described above a range of leaf parameters (discussed below) was studied in order to gain some insight into the factors determining photosynthesis in these species, but not all the parameters could be investigated in every experiment.

A diffusion resistance analysis was performed on the material grown for experiment 3. The values of the parameters of the analysis are indicated in Table 1 as an average for each species. The gas phase resistance to CO_2 diffusion, (r_s+r_a), is about one-third of the residual resistance (r_r) in nearly all species. Both gas phase and residual resistances contribute to the variation of photosynthetic rate between species.

A plot of the mean for each line of residual resistance against gas phase resistance (Fig. 4), reveals that the two are linked for all except three lines (*T. spelta*, H2; *T. boeoticum*, C64.145; and *T. monococcum*, W10). For all except these three lines a difference between lines of 0·5 s cm^{-1} in gas phase resistance is associated with a difference in residual resistance of about 1 s cm^{-1}. Thus, residual resistance appears as the more dominant of the two resistance variables determining photosynthetic rate in these species. It is tempting to postulate that the value of stomatal resistance may be linked causally to residual resistance via the CO_2 concentration in the sub-

stomatal cavity. However, on plotting gas phase resistance against substomatal CO_2 concentration for the lines which adhere to the correlation in Figure 4 we find that gas phase resistance is not positively correlated with substomatal CO_2 concentration (Fig. 5); a positive correlation would be expected if stomatal resistance were largely determined by substomatal CO_2 concentration.

The ranking of mean stomatal density per square centimetre ($\bar{n}$) in experiment 3 was in the sequence diploid > tetraploid > hexaploid. However, the regression of gas phase resistance on $\bar{n}$ for the mean values of all 18 lines studied was not significant, indicating that stomatal density is not a major determinant of the variation in stomatal resistance. Data obtained in experiment 1 also indicate that stomatal density was greatest in the diploids and least in the hexaploids (Fig. 6).

TABLE 1

RESULTS OF THE DIFFUSION RESISTANCE ANALYSIS (EXPT. 3)

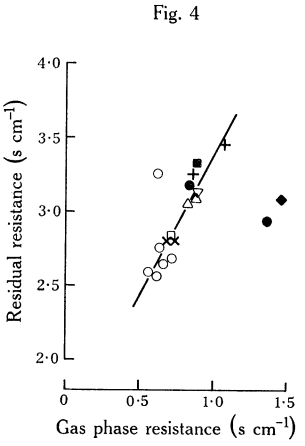
Symbols as defined in Section II(*d*)

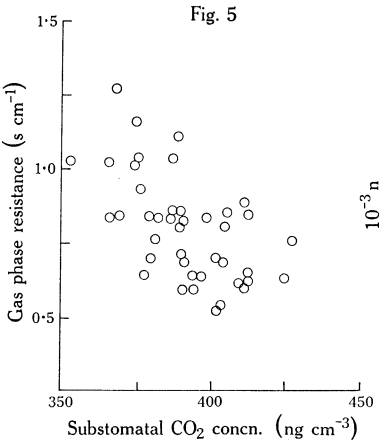
Species	No. of lines	Net photosynthetic rate (ng cm^{-2} s^{-1})	r_a+r_s (s cm^{-1})	r_r (s cm^{-1})	C_p (ng cm^{-3})	C_s (ng cm^{-3})
Diploid						
Triticum boeoticum	6	122	0·66	2·71	85	405
T. monococcum	2	103	1·12	3·06	68	382
Aegilops speltoides	2	122	0·75	2·78	71	405
A. squarrosa	2	93	0·99	3·36	71	386
Tetraploid						
T. dicoccum	1	102	0·85	3·06	70	380
T. dicoccoides	1	101	0·91	3·11	63	377
T. durum	1	99	0·91	3·13	80	388
Hexaploid						
T. aestivum	2	102	0·81	3·07	73	385
T. spelta	1	93	1·47	3·09	76	364
Average		105	0·96	3·02	74	387

Stomatal counts on the leaves exposed throughout their development to high or low light environments in experiment 4, show that there were significant increases ($P<0·05$) in the stomatal density in the high light environment for the two lines of *T. boeoticum* (mean increase of 13% above low light) and for *T. spelta* (H2) (increase of 27%), but no effect in *T. aestivum* cv. Cappelle Desprez. Since gas phase resistance is only about one-third of residual resistance, this adaptation is of only slight significance to the overall adaptation of photosynthetic rate. Measurements on the stomatal pore lengths of the same leaves indicated that in none of the four species was there an upward adaptation of pore length to the high light environment.

A number of workers has found good relationships between specific leaf weight (SLW) and net photosynthetic rate (Pearce *et al.* 1969; Beuerlein and Pendleton 1971). Such a correlation could imply that there is a larger quantity of photosynthetic apparatus per unit leaf area at higher SLW. On that basis SLW and residual resistance should be negatively correlated. In experiment 3, however, we found no correlation between residual resistance and SLW, despite a range of SLW between 1·8 and 4·9

mg cm^{-2}. Similarly there was no detectable relation between net photosynthetic rate and SLW in experiments 2 or 3. In experiment 1 a positive relation was observed between net photosynthetic rate and SLW for the diploid *Triticum* species and for the tetraploids, but not for the species of *Aegilops* or for the hexaploids (Fig. 7). It must be concluded for this wide range of species that SLW is not an adequate indicator of photosynthetic capability.





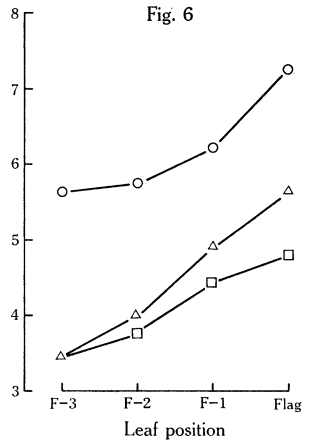


Fig. 4.—Relationship between residual resistance and gas phase resistance. Each point is a mean value for the line (expt. 3). Symbols as in Figure 2.

Fig. 5.—Correlation between gas phase resistance (r_a+r_s) and substomatal CO_2 concentration (C_s) for those lines which fall on the straight line in Figure 4 (expt. 3). Each point is for an individual leaf.

Fig. 6.—Mean stomatal frequency per square centimetre ($\bar{n}$) for the last four successive leaves of the plant at the three levels of ploidy (expt. 1). The 5% minimum significant difference is 728 cm^{-2} for the flag leaf. ○ Diploid. △ Tetraploid. □ Hexaploid.

A component of net photosynthetic rate which is reflected in the residual resistance is photorespiration. This was estimated, on the one hand, by determining the difference between net photosynthetic rate in oxygen-free and normal air, and on the other hand by extrapolating the curve of net photosynthetic rate versus C_s (the substomatal CO_2 concentration of the leaf) to $C_s = 0$. The data are presented in Figure 8. Gross photosynthesis for each point in Figure 8 was obtained from the estimated photorespiration added to net photosynthetic rate in normal air. A number of points emerge from Figure 8. First the estimates of photosynthesis using the simple apparatus are higher than those using the diffusion resistance analyser. This difference has been consistent throughout our work, and we suspect that it is due to effects of the very differently shaped and constructed leaf chambers. Second, photorespiration is a positive function of gross photosynthesis for both estimates, which fall on the same curve. The oxygen-free method should overestimate photorespiration, because of probable oxygen inhibition of true photosynthesis (Forrester *et al.* 1966; Bowes *et al.* 1971) and the CO_2 extrapolation method should underestimate it because of intracellular recycling of respired CO_2.

The percentage inhibition of net photosynthetic rate by atmosphere oxygen was about 20%. This agrees with the value found by Jolliffe and Tregunna (1968) for detached *T. aestivum* leaves exposed to 0·03% CO_2 and 25°C. The consistent relationship between photorespiration and photosynthesis for the whole range of *Triticum* and *Aegilops* species suggests that differences between them in their photosynthetic rates are not due to qualitative differences in the magnitude of photorespiration.

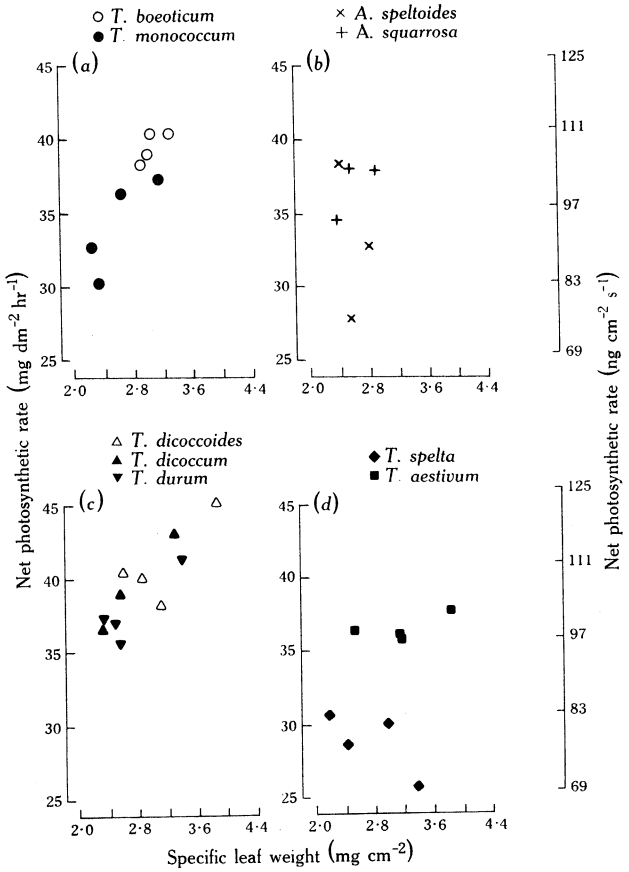


Fig. 7.—Correlation of net photosynthetic rate and specific leaf weight. The data cover all leaf positions used in experiment 1.

IV. Discussion

The pattern illustrated in Figure 1 of an increasing range and variance in net photosynthetic rate between the various lines over the last four successive leaves fits in with the earlier results that differences in photosynthetic rate did exist between species for the flag leaf (Evans and Dunstone 1970) but not for the second leaf to emerge (Belikov *et al.* 1961). This dependence of the expression of differences on plant age suggests that there are no qualitative differences in the photosynthetic

mechanism of the various species at the three levels of ploidy. This conclusion is supported by the continuity across most of the lines of the relation between the gas phase resistance and intracellular resistance to CO_2 uptake (Fig. 4), the continuity across all lines of the photorespiration versus gross photosynthesis relation (Fig. 8), and the high and similar values of the CO_2 compensation point for all species examined (Table 1). Dvorak and Natr (1971) also found similarly high values of compensation point for a wide range of *Triticum* and *Aegilops* species.

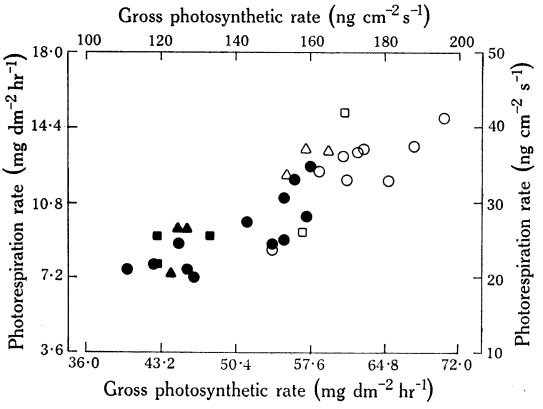


Fig. 8.—Photorespiration as a function of gross photosynthesis. Photorespiration estimated (*a*) by enhancement of net photosynthesis in oxygen-free air (open symbols) and (*b*) by extrapolation of the net photosynthesis versus substomatal CO_2 concentration (C_s) to $C_s = 0$ (solid symbols) (expt. 3).
○● Diploid.
△▲ Tetraploid.
□■ Hexaploid.

It is difficult to envisage evolutionary reasons why the leaves of wheat-like species at the three levels of ploidy should exhibit differential adaptive responses to the prior radiation environment (Fig. 2). The ontogenetic pattern of increasing difference between species in their photosynthetic rate with each new leaf suggests that the differential adaptation of flag leaf photosynthesis may be a secondary phenomenon, perhaps associated with the balances between sink size and available leaf area. The relative sink size can have an effect on photosynthetic rate of flag leaves (King *et al.* 1967). Tillering patterns of the different species may be important in this connection. The diploid *Triticum* and *Aegilops* species tiller profusely compared with tetraploids and the hexaploids. After the main shoot has become floral, the tetraploids and hexaploids produce only a few more tillers whereas diploids continue to tiller rapidly until maturity (Evans and Dunstone 1970). Thus, the diploid species are continually generating large numbers of new sinks at the time of ear emergence, when the flag leaf photosynthesis rate was measured, whereas the tetraploids and hexaploids are not. Moreover, tillering in grasses, including cereals such as wheat (Khalil 1961; Friend 1965), is enhanced by high light intensity. Thus continued tillering especially at high light intensities, could stimulate photosynthesis in the mature leaves of the diploids grown under favourable light conditions. Mitchell (1953) stresses that in *Lolium* spp. tillering rate can adjust rapidly to changes in the light conditions.

The diffusion resistance study indicates that there was no one characteristic with an overwhelming influence on the variation in photosynthetic rate between species. The two major resistances, stomatal and residual, both contributed to variation of photosynthetic rate and seemed to vary in parallel across the majority of lines,

as they do in leaves of Italian ryegrass grown under a range of light intensities (Prioul 1971) and in leaves of orange (Kriedemann 1971) and other species (H. D. Barrs, personal communication) which are undergoing cyclical oscillations of stomatal resistance.

One possible explanation of this parallel variation in leaf resistances is that the primary source of variation is the residual resistance, stomatal aperture varying in response to the induced variation of the substomatal CO_2 concentration. However, the absence of a positive correlation between gas phase resistance and substomatal CO_2 concentration (Fig. 5) does not support this explanation if we accept the widely held view that stomatal aperture is inversely related to substomatal cavity CO_2 concentration (Heath 1959; Meidner and Mansfield 1968). Alternatively, the primary variable may be stomatal resistance, residual resistance being linked to it by some unknown mechanism. The negative slope in Figure 5 is consistent with, but by no means proves, this explanation. It is also possible that some other factor may be the source of variation influencing both gas phase resistance and residual resistance directly.

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VI. References

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