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Effect of the D Genome and of Selection on Photosynthesis in Wheat

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Summary. Photosynthesis and transpiration in wheats and in their progenitors were analyzed in relation to their genome, ploidy and selection. The values of these parameters markedly depend on a specific effect of the D genome and on leaf enlargement in the course of evolution in wheats. Leaf enlargement has had a marked effect on photosynthesis in the genotypes that are devoid of the D genome; in addition, their photosynthetic capacity is greater in forms with lower leaf area. The increase in the mesophyll resistance r_m to CO_2 transfer is in relation to the increase in leaf area and is mainly responsible for the decrease in photosynthesis rate.

Owing to its stomatal regulation, *Triticum aestivum* L. is characterized by good water use efficiency in spite of its large leaves and of its low net photosynthesis. On the basis of the photosynthesis rate, the "large leaf" factor does not appear to be a good selection criterion for the *Triticum durum* genotypes that are devoid of the D genome.

Key words: *Triticum* – D genome – Photosynthesis – Transpiration – Water use efficiency – Wheat evolution

Introduction

Modern wheats (bread wheat and durum wheat) are allopolyploid species resulting from hybridizations between wild diploid species having A, B, or D genomes and from natural and man-made selections on the various genotypes. Hexaploid ABD genome bread wheat, a much improved species, is characterized by the highest productivity among the whole *Triticum* genus. The addition of the D genome has conferred on this species baking characteristics as well as a wide climatic adaptation which allows its cultivation from the sub-humid to the semi-arid areas (Zohary et al. 1969).

Evolution in wheats has resulted in the modification of various morphological and physiological characteristics. The increase in ploidy and the selection for cultivation, from the wild types to the improved types, brought about an increase in grain and leaf size and a decrease in net photosynthesis rate unter saturating irradiance (Khan and Tsunoda 1970; Evans and Dunstone 1970; Planchon 1974). The migration of the assimilates towards the ear has been markedly improved (Evans and Dunstone 1970), as well as the grain-filling duration in relation to the delayed senescence of the upper leaves (Welbank et al. 1966, 1968).

The numerous cytogenetical investigations on the genus *Triticum* have helped to determine the origin of the different genomes of wheat. *Triticum boeoticum*, a diploid species, is likely to be the donor of the A genome; through hybridization with a species closely related to *Aegilops speltoides*[1], it has given rise to the tetraploid AB types. *Aegilops squarrosa* provided the D genome, leading to the hexaploid ABD types. Most of the species underwent a natural or manmade selection, so that wild, primitive and cultivated types can be distinguished for each level of ploidy.

The evolution of bread wheat can be investigated at the physiological level by studying component processes such as photosynthesis and transpiration by the analysis of the different genotypes belonging to the genus *Triticum*. The investigation of the role of the various genomes (A, B, and D), of the ploidy level, and of the selection degree can be carried out on these two parameters.

1 The genotypes of the tetraploid and hexaploid *Triticum* species do not contain the genome of *Aegilops speltoides* under its present form (Vedel and Quetier 1978)

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Materials and Methods

Plant Culture

Two varieties representative of the different diploid (A, B and D) genomes, the tetraploid (AB) genome and the hexaploid (ABD) genome species for each evolutionary step (wild, primitive and cultivated types) were analysed. Table 1 lists the genotypes investigated. As the table is read along the lines, the data show the role of the various genomes and of ploidy level; the data listed in a same column show the effect of natural or man-made selection on the evolution of the characters investigated.

The cultures were grown under natural conditions in Mitscherlich pots containing 15 kg of soil; soil moisture was kept close to field capacity. The amounts of nitrogen fertilizer applied were relatively low (1.4 g NH_4NO_3/pot. i.e. 50 kg N_2/ha).

Gas Exchange

Photosynthesis measurements were carried out with a device including a CO_2 analyser, an assimilation chamber, and an air conditioning system. The CO_2 concentration in the airstream was measured by infra-red gas analysis (Schlumberger Analyzer Type Anir 12). The various water vapour and carbon dioxide transfer resistances as well as the transpiration were assessed by the thermal balance method (Impens 1966; Taylor and Gates 1970). The various thermal parameters were measured with copper-constantan thermocouples pinned to the leaves. The relative humidity was determined with a vapour air dewpoint hygrometer (Schlumberger Type HCP 2P). – The various measurements were performed in an assimilation chamber at 22 °C; the CO_2 concentration in air was 320 ppm and the relative humidity 75%. The determination of the water vapour diffusion resistance in air (Gaastra 1959) was achieved through evaporation from a sheet of green blotting-paper which had the shape and area of the actual leaf and was put under the same aerodynamic conditions. – The relationship of Cowan and Milthorpe (1968) was used to convert the boundary layer air diffusion resistance r'_a and the stomatal water vapour diffusion resistance r'_s to the corresponding carbon dioxide diffusion resistances r_a and r_s:

$r_a = 1.37\, r'_a$,
$r_s = 1.54\, r'_s$.

The mesophyll carbon dioxide transfer resistance r_m and the carboxylation resistance r_c were obtained by the method of Chartier (1969). – In order to obtain these measurements, a flow-through gas system was devised for an assimilation chamber with temperature control using water jackets. The chamber was illuminated by one Philips HPLR 400 W lamp. The measurements were performed at irradiance levels ranging from 0 to 240 $W \cdot m^{-2}$ (400–700 nm). The initial slope of the curve relating photosynthesis to irradiance gave the maximum efficiency of light energy conversion, α. – Chlorophylls were determined by the method of McKinney (Arnon 1949). The optical density values were obtained at 645 and 663 nm in 1 cm cells, using a blank containing a 8:2 acetone-water mixture. The chlorophyll a and chlorophyll b contents are given by:

chl a $= 12.7\, D_{663} - 2.67\, D_{645}$,
chl b $= 22.5\, D_{645} - 4.68\, D_{663}$.

Leaf areas were assessed by a planimetric method. – All the measurements were performed on the flag leaf blade of the various cultivars at the stage corresponding to the maximum net photosynthetic rate, between ear emergence and flowering.

Results

Net Photosynthesis (C.E.R.), Chlorophyll Content, and Leaf Surface Area (S)

The data obtained are listed in Table 2. The net photosynthesis values measured at saturating light and reported here are lower than those observed by other authors (Dunstone et al. 1973; Khan et Tsunoda 1970) as a result of the low nitrogen fertilization applied. The high irradiances used, as well as the low amounts of nitrogen fertilizer applied, during the flag leaf growth allowed the genetic differences to be emphasized. Diploid wild species are characterized by a higher photosynthesis rate under high irradiances (Dunstone et al. 1973), as a result of their good adaptability to irradiance Planchon 1974).

The cultivated AB and ABD genome wheats show the lowest net photosynthesis whereas the diploid species of genome A and B are the most efficient. The net photosynthetic rate per unit leaf area depends

Table 1. Species and lines used the experiments

Genomes	Related genera		Genus *Triticum*		
Species	D	B	A	AB	ABD
Wild species	*Aegilops squarrosa* n° 1 n° 9	*Aegilops speltoides* n° 1 n° 8	*T. aegilopoides* n° 1T n° 1039	*T. dicoccoides* n° 1T n° 2T	*T. macha* n° 1T n° 2T
Primitive species			*T. monococcum eredvianum hornemanni*	*T. dicoccum farrum pycnurum*	*T. spelta arduini coeruleum*
Cultivated species				*T. durum* Bidi 17 Dniepopetrovsk	*T. aestivum* Capitole Champlain

Table 2. CO_2 exchange rate, resistances to CO_2 transfer, total chlorophyll content, transpiration, leaf area and water efficiency of flag leaf of different lines

Species Lines	Genome	Type	C.E.R.	S	Chlt	α	r_s	r_m	r_c	r'_s	E	C.E.R./E
T. beoticum	A	Wild										
1T			652	0.123	2.50	6.4	139	770	40	90	343	188
1039			713	0.165	2.45	6.3	127	740	30	82	398	179
Aeg. speltoides	B	Wild										
n° 1			837	0.118	2.52	6.7	190	500	25	123	278	301
n° 8			653	0.101	2.28	6.0	194	760	40	125	285	227
Aeg. squarrosa	D	Wild										
n° 1			578	0.115	2.00	5.1	180	800	30	117	270	214
n° 9			618	0.085	1.75	4.9	210	870	35	136	265	233
T. dicoccoides	AB	Wild										
1T			577	0.293	3.24	5.6	142	830	55	92	403	143
2T			607	0.254	3.31	5.3	188	680	55	122	353	172
T. macha	ABD	Wild										
1T			558	0.281	2.54	5.2	155	930	65	100	382	146
2T			570	0.262	2.40	5.3	160	840	60	103	364	157
T. monococcum	A	Primitive										
hornemanii			688	0.203	2.84	6.4	259	600	40	164	253	272
eredvianum			752	0.141	2.82	5.8	258	580	20	167	258	292
T. dicoccum	AB	Primitive										
pycnurum			501	0.416	2.74	5.3	173	960	75	112	398	126
farrum			416	0.527	2.69	5.7	134	1 150	65	87	557	75
T. spelta	ABD	Primitive										
arduini			510	0.330	2.60	5.9	155	960	50	100	404	126
coeruleum			500	0.300	2.75	5.2	150	1 050	50	97	446	112
T. durum	AB	Cultivated										
Dniepopetrovsk			536	0.337	2.93	6.0	140	840	50	90	480	112
Bidi 17			400	0.494	2.69	5.0	150	1 150	100	100	483	89
T. aestivum	ABD	Cultivated										
Capitole			427	0.470	2.51	5.3	275	1 050	40	130	280	152
Champlein			440	0.442	2.60	5.5	250	1 000	50	160	319	138
L.S.D.			19	0.021	0.11	0.25	30	30	13	20	53	8

C.E.R.: CO_2 exchange rate 10^{-9} kg m^{-2}; s^{-1}; S: flag leaf area dm^2; Chlt: total chlorophyll content mg dm^{-2}; α: maximum efficiency of light energy conversion 10^{-9} kg J^{-1}; r'_s: stomatal water vapor diffusion resistance m^{-1} s; r_s: stomatal CO_2 diffusion resistance m^{-1} s; r_m : mesophyll CO_2 transfer resistance m^{-1} s; r_c: carboxylation resistance m^{-1} s; E: transpiration 10^{-7} kg m^{-2} s^{-1}

markedly on the leaf size and on the presence or absence of the D genome (Fig. 1). For the same leaf surface area (provided it is smaller than 0.4 dm^2), the genotypes that do not bear the D genome are more efficient than those which possess it. The difference between the genotypes of these two groups is significant at $P < 0.05$. However, in the genotypes devoid of the D genotypes display the same photosynthetic rate for a leaf surface area of 0.5 dm^2. The slope of the regression genotypes display the same photosynthetic rate for a leaf surface area of 0.5 dm^2. The slope of the regression lines C.E.R./S of the two groups of genotypes are significantly different at $P < 0.05$ (Fig. 1).

A marked increase in the flag leaf area from the diploid to the tetraploid level can also be observed. Selection for cultivation has had a marked effect as shown by the comparison between wild, primitive and cultivated species (Fig. 2).

The total chlorophyll content per unit leaf area is low in the small-leaf species. It increases with leaf size up to a maximum corresponding to a surface of circa 0.3 dm^2; the chlorophyll content is then decreasing as the surface reaches higher values. For a same leaf surface area, the genotypes possessing the D genome generally have a lower chlorophyll content than the species devoid of the D genome, with the possible ex-

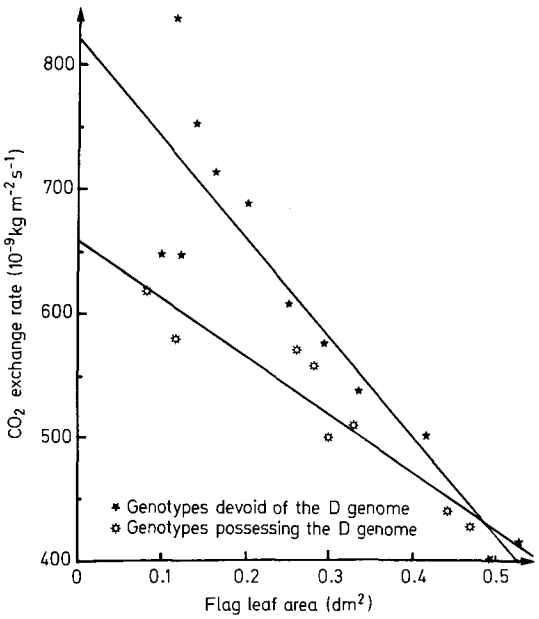

Fig. 1. Relationship between net photosynthesis per unit area and flag leaf size. The correlation coefficients. $r=-0.920$ for the genotypes devoid of the D genome and $r=0.945$ for the genotypes possessing the D genome are significant at $P<0.01$. The slopes of the regression lines of the two groups are significantly different at $P<0.05$

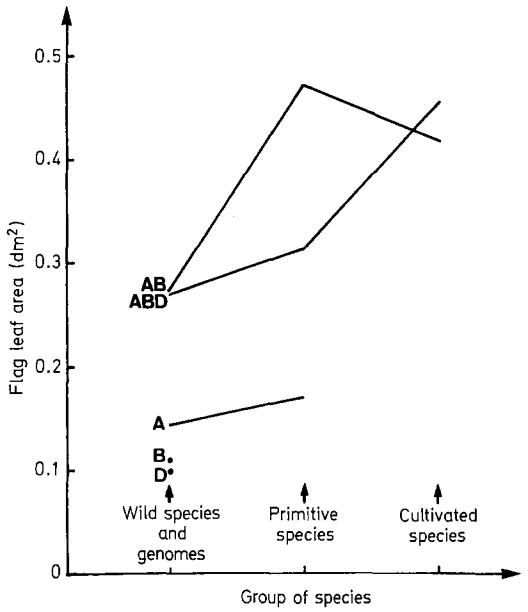

Fig. 2. Flag leaf area in the course of evolution in wheats

ception of the highest leaf area values, as a marked drop in the total chlorophyll content could be observed for the latter genotypes (Fig. 3).

Stomatal Resistance to Water Diffusion and Transpiration

The stomatal resistance at full opening (under saturating irradiance and non-limiting water supply conditions) ranges from 80 to 180 m^{-1} s, the highest values being observed for *Triticum moncoccum* and *Triticum aestivum* (Fig. 4). Under the same environmental conditions and for a given stomatal resistance, the transpiration per unit leaf area is higher for the broad leaf species, as a result of the lower air-leaf thermal exchanges (Fig. 5). Thus, in the course of evolution in wheats, an increase in transpiration per unit leaf area has paralleled the increase in leaf size. This can be clearly seen in the AB genotypes. However, the increase in the stomatal resistance in the ABD cultivated types has reversed this trend and *Triticum aestivum* L. has a lower transpiration rate than AB genome tetraploids (Fig. 6).

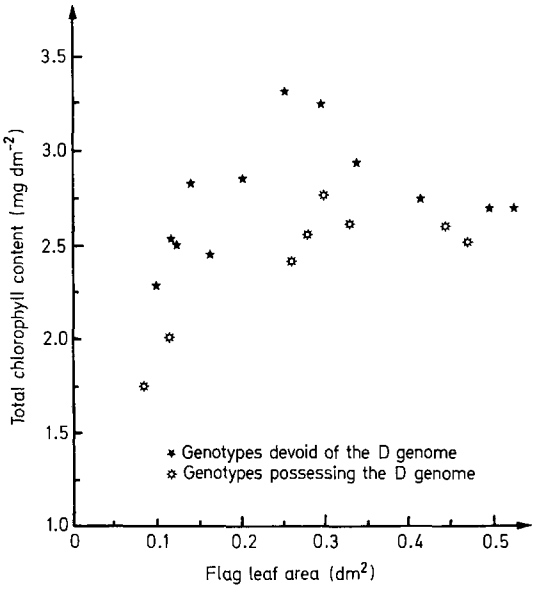

Fig. 3. Relationship between total chlorophyll content and flag leaf size

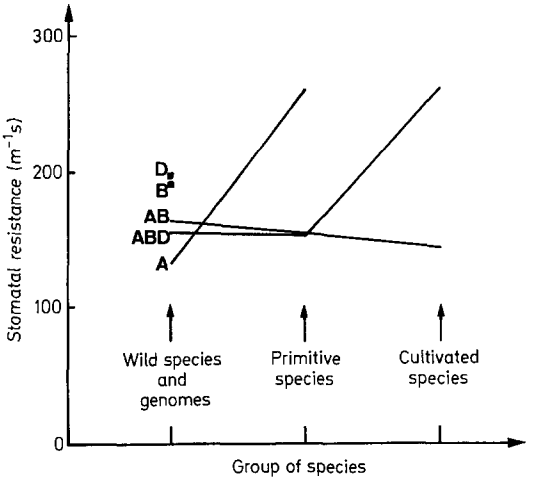

Fig. 4. Stomatal resistance in the course of evolution in wheats

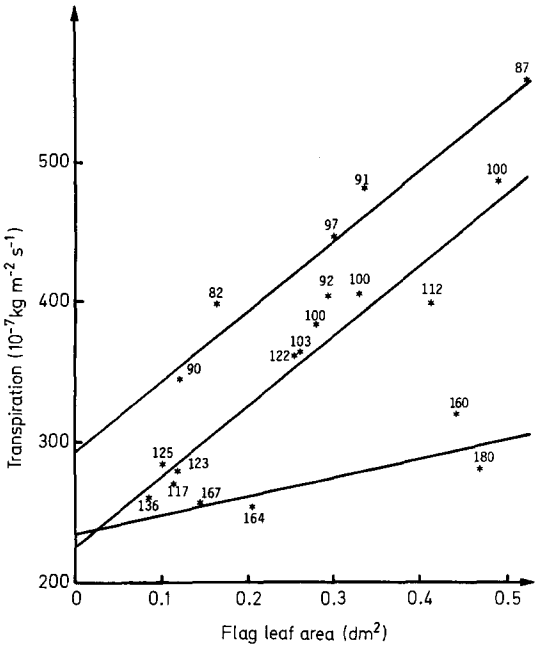

Fig. 5. Relationship between transpiration, stomatal resistance and flag leaf area

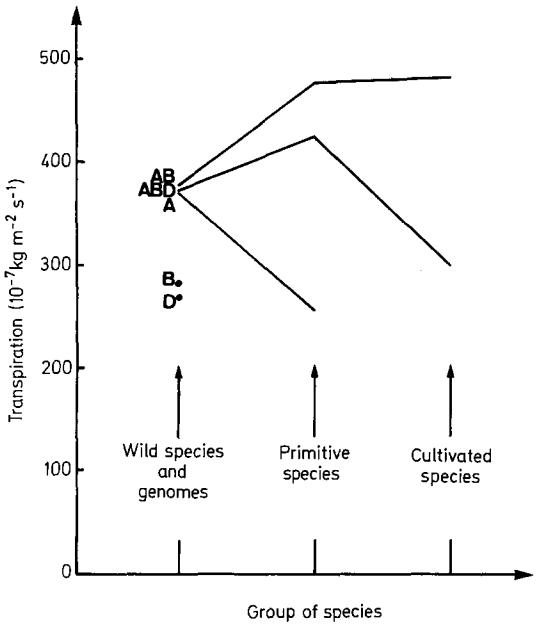

Fig. 6. Transpiration in the course of evolution in wheats

Resistance to CO_2 Diffusion

The mesophyll resistance r_m is the main obstacle to the penetration of carbon dioxide to the chloroplast; it is thus the limiting factor in photosynthesis in well-watered and well-illuminated plants. The value of this parameter depends on the leaf size as well as on the presence or absence of the D genome (Fig. 7). For the same leaf surface area, r_m is higher in the genotypes that bear the D genome. However, the increase in the parameter was slower in these genotypes as the leaf surface increased.

Water Use Efficiency

Water use efficiency can be expressed as the amount of carbon dioxide taken up per transpirated water unit. The data listed in Table 2 were obtained under non-limiting water supply conditions and under saturating irradiance at a temperature of 22–23 °C.

The small-leaf diploid types, particularly those of genome B, appeared to be the most efficient under these conditions. Water efficiency markedly depends on leaf surface area: net photosynthesis is decreasing whereas transpiration is increasing with increasing leaf surface area.

However, the cultivated ABD types, in spite of their high leaf area and of their low photosynthesis rate, display a fairly high efficiency owing to their limited stomatal opening. *Triticum monococcum* gives the best value as a result of a high photosynthesis rate and a high stomatal resistance (Fig. 8).

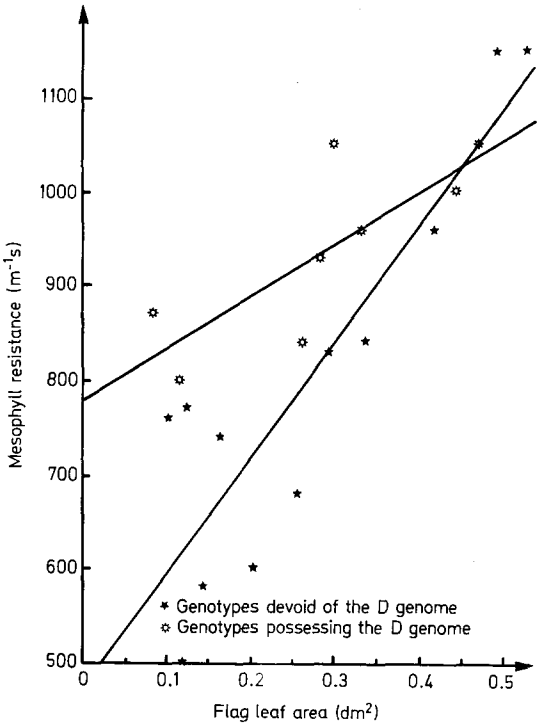

Fig. 7. Relationship between mesophyll resistance to CO_2 transfer (r_m) and flag leaf size. The correlation coefficients, $r = 0.872$ for the genotypes devoid of the D genome and $r = 0.801$ for the genotypes possessing the D genome are significant at $P < 0.05$

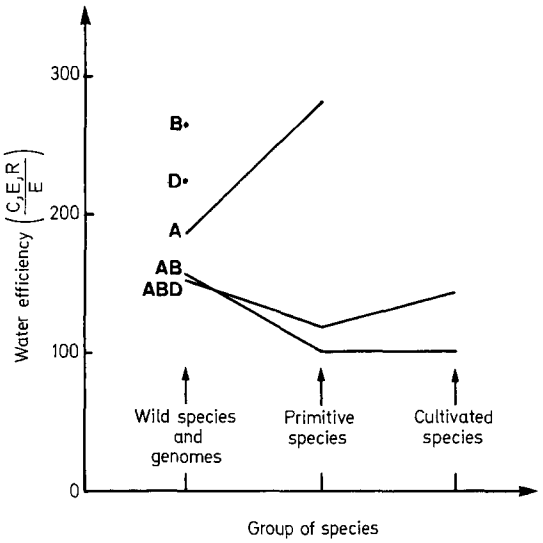

Fig. 8. Water efficiency in the course of evolution in wheats

Discussion

The main feature of evolution in wheats is the increase in the size of the chlorophyllous organs, particularly the leaves, which is paralleled by a decrease in the net photosynthesis rate per unit leaf area. This point is corroborated by the data reported here. Moreover, the D genome seems to play a particular role as it brings about a decrease in carbon dioxide exchange provided the leaf surface area is smaller than 0.4 dm^2. In spite of their lower chlorophyll content, the limiting factor of photosynthesis in the species bearing the D genome is the mesophyll resistance r_m to CO_2 transfer. This resistance increases with leaf size in every case. However, the quantum yield of CO_2 gross assimilation and photorespiration are not modified by the D genome and the ploidy level (Gaudillère 1979).

Phenotypic or genotypic variations of net photosynthesis rates are often assigned to the amount of assimilating material per unit area in relation to the thickness of the leaf (Charles-Edwards and Ludwig 1975, in tomato; Pearce et al. 1969, in lucerne; Dornhoff and Shibles, 1970, in soybean). In wheat, Singh and Tsunoda (1978) showed that *Triticum aegilopoides* has a better photosynthetic activity and thicker leaves that *Triticum aestivum* L., the cultivated type. The increase in thickness results in higher amounts of assimilates and in increased cellular surfaces, enhancing thus the penetration of CO_2 into the cell and decreasing therefore the mesophyll resistance to CO_2 transfer in the diploid types. Nobel et al. (1975) assumed that the phenotypical differences in the net photosynthesis rate per unit leaf area in *Plectanthrus parviflorus* H. were related to the ratio of the mesophyll cell membrane area to the leaf surface area.

Dunstone and Evans (1974) reported a relationship between mesophyll cell size and leaf size as well as between mesophyll cell size and net photosynthesis per unit leaf area, in wheat. Similar relationships between net photosynthesis per unit leaf area and mesophyll cell size were established by El-Sharkawy and Hesketh (1965) for 15 cultivated species and by Wilson and Cooper (1969) for various *Lolium perenne* genotypes. As the cell surface/volume ratio may be lower for the larger cells, the CO_2 penetration to the chloroplasts and the mesophyll conductance under the unit area could be decreased in the case of large leaves. Thus, the differences observed between genotypes for mesophyll resistance to CO_2 transfer and for net photosynthesis might depend on the foliar thickness and/or on the mesophyll cell size.

As far as net photosynthesis is concerned, a small flag leaf appears to be a very favourable character in the genotypes that are devoid of the D genome. The slow evolution of C.E.R. and r_m in relation to the leaf surface area might allow satisfactory values of these parameters to be maintained for large leaves in the genotypes possessing the D genome. The selection for the large leaf character in the cultivated AB genome species such as durum wheats seems to have reached a limit in terms of photosynthesis efficiency.

Moreover, a large flag leaf is characterized by an increased foliar transpiration rate as a result of lower air-leaf thermal exchanges. For an equivalent stomatal resistance, the lower transpiration rate of the wild diploid species, together with a higher photosynthetic rate, brings about a higher water use efficiency. The increase in the stomatal resistance in some ABD types (*Triticum aestivum* cultivars in the investigations reported here; *Triticum spelta* cultivars for Dunstone et al. (1973)) allowed the surface effect to be limited.

However the translocation rate of the photosynthesis products to the ear is known to be the major factor of productivity. In cultivated wheats, the flag leaf is the main source of assimilates for the development of the kernel (Stoy 1963; Planchon 1968; Wardlaw 1968; Rawson and Hofstra 1969). Evolution in wheats has resulted in a parallel increase of the productivity and of the flag leaf surface area. It would therefore be interesting to analyse the possible relationships between the flag leaf size and the translocation rate of the assimilates. An optimum flag leaf size might thus be determined, taking into account the different parameters involved in productivity: photosynthesis, transpiration and translocation.

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