

# Leaf Photosynthesis, Leaf Permeability, Crop Growth, and Yield of Short Spring Wheat Genotypes Under Irrigation<sup>1</sup>

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## ABSTRACT

Because of the expected importance of photosynthetic activity to yield, the relationships of leaf photosynthetic traits to crop growth rate and yield in 48 genotypes of spring wheat, were examined under irrigation in northwest Mexico. There were three tall and 33 short (Norin 10-derived) bread wheats (*Triticum aestivum* L.), eight short durum wheats (*T. turgidum* L.) and four triticales (X *Tritosecale* Wittmack). Photosynthetic activity (*A*) and leaf permeability to viscous air flow (*LP*) were measured weekly using <sup>14</sup>CO<sub>2</sub> uptake and an air flow porometer, respectively.

Genotypic effects on *A* (range 14.7 to 20.4 mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>) and *LP* (range 5.7 to 11.1 permeability units) were highly significant but species effects were small and nonsignificant. Looking now exclusively at the short bread wheat group, *A* was unrelated to specific leaf weight or to *LP*. *A* on the first sampling at 4 weeks before anthesis and preanthesis crop growth rate (g m<sup>-2</sup> day<sup>-1</sup>) were weakly correlated (phenotypic *r* = 0.42, significant at the 0.05 level), and both these traits were positively correlated with mature plant height (*r* = 0.56, significant at the 0.01 level, and 0.68, significant at the 0.05 level, respectively). *A* was also positively correlated with crop growth rate during grain filling (*r* = 0.46, significant at the 0.01 level) and with yield (*r* = 0.45, significant at the 0.01 level; yield range 516 to 860 g m<sup>-2</sup>). These correlations arose because of the positive influence of days to anthesis on all three traits and probably reflect an increase in sink size (more kernels m<sup>-2</sup>) with later anthesis. Yield was positively correlated with *LP* (*r* = 0.56, significant at the 0.01 level); the correlations remained significant (*r* = 0.46, significant at the 0.01 level) after allowance for the negative effect of plant height on both (*LP* was unrelated to anthesis date). While the cause of this correlation may be indirect, the testing of *LP* as an early generation selection criterion is suggested. Effects of major Norin 10 dwarfing genes on these relationships are discussed.

Additional index words: Norin 10 dwarfing genes, Leaf diffusive conductance, Air flow porometer, Plant height, Selection criteria, Durum wheat, Triticale.

UNDERSTANDING the physiological basis of genotypic variation in yield may facilitate further yield improvement through breeding. Amongst cultivars of bread wheat (*Triticum aestivum* L.) developed in the last 30 years for growth under irrigation at low and middle latitudes, increased yield is generally closely associated with increased harvest index (grain weight as a percentage of total above ground dry weight at maturity); total dry weight has tended to remain unchanged (1, 15). This avenue of yield improvement, in part associated with dwarfing genes and reduced stature, may be drawing to a

close, as stature and harvest index approach 80 cm and 50%, respectively. More attention to increasing dry matter production may now be appropriate.

It has been shown that the yield of irrigated spring wheat crops in northwest Mexico is sensitive to environmental factors (light, CO<sub>2</sub>) affecting crop photosynthesis and dry matter production in the period 50 to 130 days after sowing (anthesis at 90 days), with greatest sensitivity from 60 to 90 days (8, 9). These crops normally achieve full light interception throughout the former period, so that increased crop photosynthesis through genetic change must rely on improved canopy architecture and/or greater photosynthetic activity per unit leaf area, rather than on greater leaf area. This paper concentrates upon the question of variation in photosynthetic activity.

Genotypic variation in yield within crop species has generally not been related to variation in photosynthetic activity (e.g., 5). Although the situation with temperate cereals appears to be similar (e.g., 7, 18), there are exceptions (4, 16, 20, 22). In the most clear-cut case, Shimshi and Ephrat (22) showed positive correlations between yield and both leaf photosynthesis (<sup>14</sup>CO<sub>2</sub> uptake) and leaf permeability (air flow porometer) for eight irrigated spring wheats in each of two seasons.

The purpose of our study was to measure variation in leaf photosynthesis and leaf permeability in the field with a much larger set of spring wheat genotypes than that studied by Shimshi and Ephrat (22), using similar rapid techniques. In addition, we examined the relationship of this variation to other traits which may influence leaf photosynthetic rate (plant height, anthesis date, leaf morphology), or be influenced by it (crop growth rate, yield, and its components). Special emphasis is placed upon relationships amongst 33 Norin 10-derived short genotypes and upon possible new selection criteria for yield potential.

## MATERIALS AND METHODS

The experiment was conducted at the Centro de Investigaciones Agricolas del Noroeste (CIANO) near Ciudad Obregon in northwest Mexico during the 1974-1975 winter cropping season. It comprised 48 spring genotypes in four groups:

- (1) Tall (non-dwarf) bread wheat genotypes (*n* = 3)
- (2) Short bread wheat genotypes (*n* = 33), which (with one exception) contained Norin 10 major dwarfing genes (see Table 5 for many individual genotypes)

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- (3) Short durum wheat (*T. turgidum* L.) genotypes (n = 8) presumed to contain a Norin 10 major dwarfing gene  
 (4) Triticale (X *Tritosecale* Wittmack) genotypes (n = 4) of Mexican origin

Genotypes were seeded on 29 Nov. 1974 in plots 6 m long and 2 m wide (10 rows), arranged in a randomized block design with five replications. Seeding rate was 80 kg ha<sup>-1</sup>, and fertilizer (200 kg ha<sup>-1</sup> N and 26 kg ha<sup>-1</sup> P) was applied at seeding. The soil was of high clay content (50%), becoming slightly coarser with depth and cracking deeply upon drying. The experiment was flood irrigated at seeding and six times during the growing season, as recommended for highest yield (11). Portions of the plots of non-dwarf and taller semi-dwarf genotypes were protected against lodging by nets through which the plants grew. There were no weeds or diseases. Growth conditions therefore ensured maximum expression of yield potential in that environment. Reference is also made to the behavior of the above 48 genotypes in an adjacent replicated spaced planting (40 × 40 cm).

Photosynthetic activity and diffusive conductance were measured simultaneously on uppermost sunlit leaves chosen at random and without preconditioning from a pre-designated inner region of each plot. We used a ventilated diffusion porometer with the facility for simultaneous exposure of the leaf surface to <sup>14</sup>CO<sub>2</sub> (Cayuga Development Corporation, Ithaca, N.Y.) as described elsewhere (3). The cuvette exposed only the adaxial leaf surface to <sup>14</sup>CO<sub>2</sub> labelled dry air of known constant specific activity and total CO<sub>2</sub> content of 330 ppm; during the 30 sec exposure, which began immediately the cuvette was attached, the rate of humidity increase in the cuvette was recorded as well as the leaf and instrument temperatures. Throughout the leaf was held with the abaxial surface perpendicular to the sun's rays; having the abaxial surface illuminated is common for top leaves in the canopy because of the twisting of these leaves. Using appropriate temperature dependent calibration factors, the conductance of the adaxial leaf surface to water vapor, here termed leaf conductance (*g* in cm sec<sup>-1</sup>), could then be calculated. Immediately upon termination of the <sup>14</sup>CO<sub>2</sub> exposure, the exposed disc of leaf lamina (0.88 cm<sup>2</sup>) was punched from the leaf and frozen in liquid N<sub>2</sub> within 1 min, then stored in the frozen condition until assayed for <sup>14</sup>C activity (3). The net uptake of labelled CO<sub>2</sub>, hereafter termed photosynthetic activity (*A*, mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>), was assumed to estimate *A* max for the adaxial surface. A viscous airflow porometer was used to determine leaf porosity or permeability [*LP*, units of (10<sup>-3</sup> cm<sup>2</sup> sec g<sup>-1</sup>)<sup>1/2</sup>] as described elsewhere (13). Permeability was determined on similar leaves to those sampled for photosynthesis.

Leaf photosynthesis measurements began on 5 February, about 4 weeks before the mean date of anthesis, and leaf permeability on 19 February; last measurements were made on 21 April. Each week, one leaf was sampled for photosynthesis from each plot of the five replications. For leaf permeability, three leaves per plot were sampled weekly. Measurements were restricted to days without significant clouds and to the period 1000 to 1700 hours but were generally concentrated about noon. It took approximately 80 min and four persons to sample all 48 plots of one replicate for photosynthesis; another person made the leaf permeability determinations in this period.

Three harvests (22 January, 19 February, and 7 days after anthesis) were made during the season in order to determine rate of dry matter accumulation, leaf area index, etc. All above ground material was collected from a 0.42 m<sup>2</sup> quadrat of the central six rows in each plot on each occasion. Total photosynthetic or green area was determined on a subsample as described elsewhere (8). Stem sugar content (80% hot ethanol extraction), as a possible index of source/sink balance in the vegetative crop, was measured on subsamples from the 17 February harvest, and the specific leaf weight and N content were determined for flag leaf laminae obtained from subsamples of the harvest 7 days

after anthesis. At maturity, grain yield, yield components, and harvest index were determined from a 1.43 m<sup>2</sup> quadrat in each plot. All plant parts were dried at 80 C.

Nondestructive observations included a visual estimate of mean leaf angle of the canopy (angle to horizontal on nine dates over period 27 December to 15 March), canopy height on 12 February and mature plant height, and date of 50% anthesis and 50% maturity (= 50% spikes with zero green). Complete weather information was collected nearby (see 10); the 1974-1975 season was rainless as is common.

## RESULTS

### Time changes

Averaged across all genotypes, typical temporal patterns of total and grain dry matter accumulation and green area index change were obtained (Fig. 1, lower portion). The mean grain yield was 707 g m<sup>-2</sup> or about 8 t ha<sup>-1</sup> at field moisture content. Leaf photosynthesis (*A*), conductance (*g*) and permeability (*LP*) showed approximately parallel fluctuations superimposed on a general decline as maturity was approached (Fig. 1, upper portion). Environmental correlations between weekly means

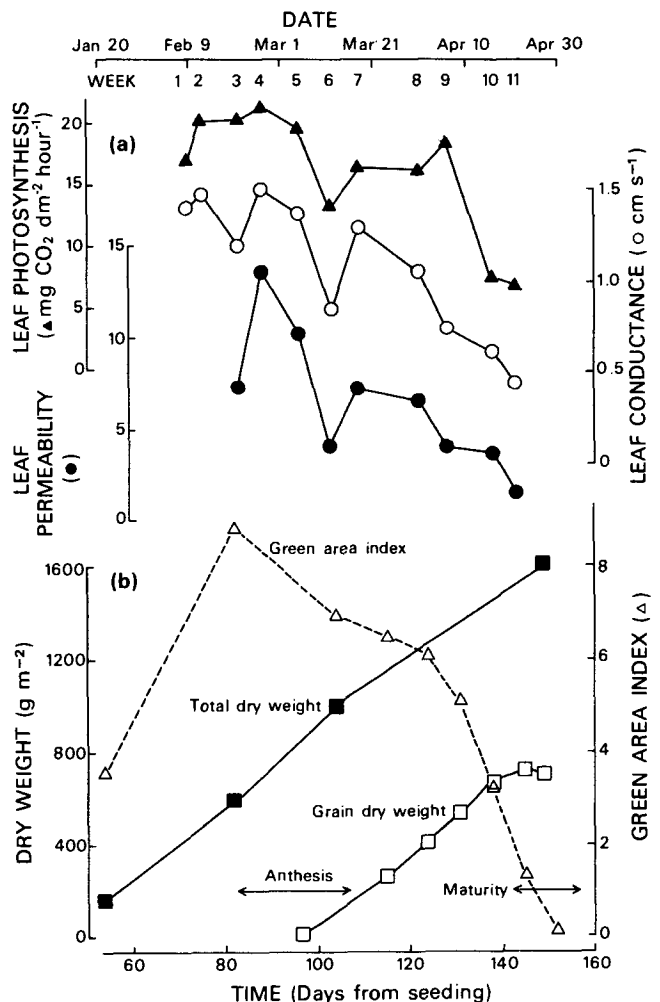


Fig. 1. Time changes in (a) leaf photosynthesis, conductance to water vapor and permeability and in (b) total dry weight, grain dry weight, green area index; mean of all genotypes, except for leaf traits on Week 10 and 11 when senesced genotypes excluded.

**Table 1. Analyses of variance for leaf photosynthesis (*A*, mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>), conductance to water vapor (*g*, cm sec<sup>-1</sup>) and permeability (*LP*).**

Source	df	<i>A</i> Mean square	<i>g</i> Mean square	df	<i>LP</i> Mean square
Weeks	8	307.03**	3.564**	6	548.2**
Genotype	47	13.58**	0.051**	47	9.27**
Weeks × genotype	376	4.10**	0.025*	282	1.32**
Error†	(1,692)	2.42	0.021	(1,316)	0.66

\*\*, \*\* Significantly ( $P < 0.05$ ) or highly significantly ( $P < 0.01$ ) different from error mean square (or interaction mean square in case of genotype effect).

† The analyses of variance used as an experimental unit the mean of the five replications for each week-genotype combination. The error mean square was estimated independently by pooling and adjusting (+5) error mean squares from separate analyses of variance of each week's genotype × replication data.

of Fig. 1 were as follows: *A* vs. *g*,  $r = 0.84^{**}$ ,  $n = 11$ ; *A* vs. *LP*,  $r = 0.78^*$ ,  $n = 9$ ; *g* vs. *LP*,  $r = 0.93^{**}$ ,  $n = 9$ . The depression in these traits around Day 104 probably reflects slight water stress immediately prior to the fifth irrigation (11).

### Genotypic Effects on Leaf Photosynthesis, Conductance and Permeability

Analyses of variance for the first 9 weeks (7 weeks for *LP*), when all genotypes were sampled, showed that the coefficient of variability for a single determination of *A* ranged from 13 to 26% across weeks; for *g* from 23 to 33%; and for *LP* (mean of three leaves per plot) from 16 to 31%. Nevertheless, genotypic effects were significant ( $P < 0.05$ ) or highly significant ( $P < 0.01$ ) in 8 of the 9 weeks for *A*, and in all 7 weeks for *LP*; effects on *g* were significant in only 2 weeks. Although the week by genotype interaction was significant for each trait, the genotype main effect was highly significant when tested against this interaction (Table 1).

Table 2 (upper portion) offers further evidence of the consistency of genotypic effects over the whole sampling period, and it is therefore assumed that the average of the first 9 weeks (7 for *LP*) for each genotype provided the best overall characterization of these effects. The means for *A* ranged from 14.7 to 20.4 mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>, for *g* from 1.06 to 1.43 cm sec<sup>-1</sup>, and for *LP* from 5.7 to 11.1 units. Genotype means of *A* in Week 1 (range 12.2 to 20.7 mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>) and for Weeks 1 to 3 (range 15.4 to 21.7 mg CO<sub>2</sub> dm<sup>-2</sup> hour<sup>-1</sup>) are also used later as more specific indices of preanthesis photosynthetic rate, since Table 2 indicates that genotypic effects on *A* then differed considerably from those on overall mean *A*.

Considering the genotype groups listed in Materials and Methods, group means for *A* and for *g* were not significantly different, the range in means being only 3 and 6% respectively. However the mean *LP* for tall bread wheats ( $6.21 \pm 0.46$  units) was significantly lower ( $P < 0.05$ ) than that for short bread wheats ( $7.73 \pm 0.48$  units). The *LP* means for durum wheats ( $7.39 \pm 0.54$  units) and triticales ( $7.84 \pm 0.61$  units) did not differ significantly from the bread wheat values.

Phenotypic correlations between genotype means (over all weeks) of *A*, *g*, and *LP* were not significant for *LP*, and weak but significant for *A* vs. *g* (Table 2, lower portion). This is surprising and is discussed later. For most individual weeks (2, 3, 5, 6, 8, and 9), the phenotypic

**Table 2. Phenotypic correlations within (upper portion) and between (lower portion) leaf photosynthesis (*A*), conductance to water vapor (*g*), and permeability (*LP*) determinations. †**

Weeks averaged	Correlation coefficient, <i>r</i>		
	Overall mean <i>A</i> (Weeks 1 to 9)	Overall mean <i>g</i> (Weeks 1 to 9)	Overall mean <i>LP</i> ‡ (Weeks 3 to 9)
1-9†	1.00	1.00	1.00
1-3§	0.40	0.66	0.84
4-5	0.79	0.77	0.91
6-7	0.78	0.59	0.85
8-9	0.78	0.42	0.76
Overall mean <i>A</i>	1.00	0.34	-0.06
Overall mean <i>g</i>		1.00	0.15
Overall mean <i>LP</i>			1.00

†  $n = 48$ ;  $r > 0.29$ ,  $P < 0.05$ ;  $r > 0.37$ ,  $P < 0.01$ .

‡ Average of Weeks 3 to 9 for *LP* since no determinations in Weeks 1 and 2.

§ Average of 3rd week for *LP*.

**Table 3. Phenotypic correlations between leaf photosynthesis (*A*) and permeability (*LP*), and various traits related to crop development, growth and morphology; short bread wheats only ( $n = 33$ ).**

Trait description	Range	$s_{\bar{x}}$	Correlation coefficient, <i>r</i>		
			<i>A</i> Weeks 1 to 3	<i>A</i> Weeks 1 to 9	<i>LP</i> Weeks 3 to 9
Anthesis date, days from seeding	83-104	0.8	-0.15	0.61**	0.27
Canopy ht. 12 Feb., cm	34-69	1.7	0.37*	0.08	-0.70**
Maturity ht., cm	50-112	2.7	0.37*	0.29	-0.65**
Green area index, 22 Jan.	2.6-5.3	0.3	0.30	0.35*	-0.33
Leaf angle, degrees	29-52	1.3	-0.33	-0.39*	0.09
Stem sugar on 19 Feb., % d.b.	4.0-11.6	0.7	0.08	-0.34	0.31
†Flag leaf area, cm <sup>2</sup>	22-54	2.1	-0.07	0.36*	0.34
†Flag specific leaf wt., mg cm <sup>-2</sup>	4.6-7.7	0.21	-0.26	-0.37*	-0.22
†Flag leaf N, % d.b.	3.5-4.5	0.15	0.31	-0.03	0.01
†Flag specific leaf N, mg × 100 cm <sup>-2</sup>	19-30	0.7	-0.11	-0.41*	-0.25
‡Crop growth rate, g m <sup>-2</sup> day <sup>-1</sup>	10.9-20.4	1.1	0.23	-0.24	-0.46**
§Total dry wt per day, g m <sup>-2</sup>	11.9-16.7	0.6	0.21	0.56**	0.10

† From sampling 1 week after 50% anthesis.

‡ Over period 22 January to 19 February. § Total dry weight at maturity divided by days sowing to maturity less 40 (to allow for period before full cover attained).

correlation between *A* and *g* was highly significant and greater than 0.5. The phenotypic correlation between the mean *LP* measured in plots and that measured over the same period and genotypes in the adjacent spaced planting was highly significant ( $r = 0.85^{**}$ ).

### Associations with Nonyield Traits

In the examination of associations amongst traits, here and for the remainder of the paper only correlations within the short bread wheat group ( $df = 31$ ) are presented since these are the most relevant. Correlations for the whole set of genotypes ( $df = 46$ ) were generally similar but weaker. Also there were too few genotypes within the durum and triticales groups to give meaningful within group correlations.

Table 3 shows phenotypic correlations of *A* and *LP* with nonyield traits, all of which showed significant and often substantial genotypic variation. The majority of the

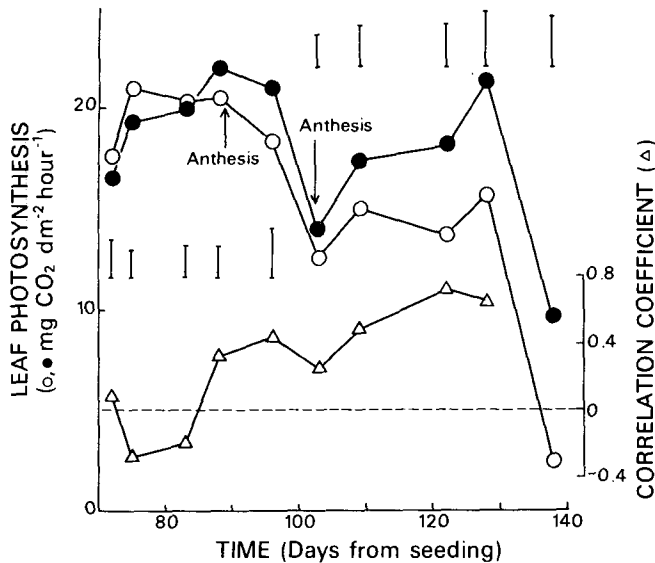


Fig. 2. Leaf photosynthesis averaged for nine early<sup>3</sup> (open circles) and nine late (closed circles) short bread wheat genotypes (see text), and the phenotypic correlation between leaf photosynthesis and days to anthesis for all genotypes (triangles) as affected by sampling date. Vertical lines show the least significant difference between early and late genotypes.

leaf photosynthesis measurements were made on flag leaves, yet phenotypic correlations between  $A$  and flag leaf characteristics were largely nonsignificant and tended to be in the opposite direction to expectation (e.g., negative correlations between  $A$  and specific leaf weight). Higher  $A$  was associated significantly with a lower leaf angle (more planophile canopy). The major effect on  $A$  however appeared to lie in the positive correlation between  $A$  and anthesis date. This arose during grain filling, since preanthesis  $A$  (average of Weeks 1 to 3) did not show this positive correlation. In fact, calculating phenotypic correlations between  $A$  values for each week and days to anthesis revealed a significant negative correlation for Week 2 and significant positive values for most weeks after Week 4 (Fig. 2, lower portion). This is further illustrated in Fig. 2 (upper portion) by the weekly mean  $A$  values for nine early (87 to 91 days to anthesis) compared to nine late (101 to 104 days) short bread wheat genotypes.

The period 22 January to 19 February was one of largely full light interception by the crop (see green area index in Fig. 1) and growth rate was not significantly correlated with green area index or leaf angle. Nor was it related to  $A$  (Table 3) although there were significant positive correlations with  $A$  determined in Week 1 (5 to 9 February) ( $r = 0.42^*$ ).  $A$  then showed highly significant positive correlations with canopy height ( $r = 0.56^{**}$ ) and mature plant height ( $r = 0.68^{**}$ ), as did crop growth rate ( $r = 0.68^{**}$ ). Thus the partial correlation, height held constant, for  $A$  in Week 1 vs. crop growth rate was close to zero. Also the strong positive correlation between  $A$  and total dry weight per day (Table 3) appears to be due

Table 4. Range of genotype means and standard error ( $s_{\bar{x}}$ ) for grain yield and some yield components, and phenotypic correlations with leaf photosynthesis ( $A$ ), leaf permeability ( $LP$ ), days to anthesis and mature plant height; short bread wheats only ( $n = 33$ ).

Trait	Grain yield $g m^{-2}$	Kernel number $m^{-2} \times 10^{-3}$	Harvest index %	Crop growth rate <sup>†</sup> $g m^{-2} d^{-1}$
Lowest mean	516	12.8	37.8	8.1
Highest mean	860	24.5	52.7	18.0
$s_{\bar{x}}$	20	0.6	1.1	0.6
Correlation coefficients				
A, Week 1 to 3	0.03	-0.11	-0.07	0.00
A, Week 1 to 9	0.45**	0.36*	-0.19	0.46**
Anthesis date	0.50**	0.43*	-0.23	0.62**
Partial A <sup>†</sup> , Week 1 to 9 (anthesis constant)	0.22	0.14	-	0.15
LP, Week 3 to 9	0.56**	0.47**	0.51**	0.43*
Height	-0.36*	-0.45**	-0.75**	-0.08
Partial LP <sup>†</sup> , Week 3 to 9 (height constant)	0.46**	0.25	0.04	-

<sup>†</sup> Partial correlations, anthesis date or height held constant.

<sup>‡</sup> Postanthesis crop growth rate, i.e., dry matter accumulation per day anthesis to maturity.

largely to the effect of anthesis date on both, since the partial correlation at constant anthesis date was barely significant ( $r = 0.31$ ).

The highly significant negative correlations between leaf permeability ( $LP$ ), and canopy height, mature plant height, and crop growth rate also appear to reflect inter-related phenomena. The partial correlation  $LP$  vs. crop growth rate, with canopy height constant, was close to zero. Similarly, the positive  $LP$  vs. stem sugar correlation (significant for the full set of genotypes) approaches zero when the negative relationship of stem sugar to plant height ( $r = -0.48^{**}$ ,  $n = 33$ ) is allowed for.  $LP$  was not significantly correlated with anthesis date.

#### Associations with Yield Traits

Genotypic effects on yield and yield components were highly significant and the range in genotype means was large (Table 4). Kernel weight, which ranged from 31 to 47 mg ( $s_{\bar{x}} = 0.9$  mg), was not significantly correlated with any of the photosynthetic traits examined.

Preanthesis  $A$  ( $A$  Week 1 to 3) was unrelated to yield or yield components (Table 4). Overall  $A$  was positively correlated with yield, postanthesis growth rate and kernel number, but the partial correlations (anthesis date constant) were all nonsignificant.  $LP$  was highly significantly correlated with yield and all yield components; the partial correlations (height constant) were not significant for harvest index or for kernel number but remained highly significant for yield (Table 4). The partial correlation (anthesis date constant) for  $LP$  vs. yield was also highly significant ( $r = 0.51^{**}$ ).

#### DISCUSSION

It is expected that the set of short bread wheats, which was representative of current cultivars of low latitude environments, is sufficiently large and unbiased for the correlations to have some general validity for spring wheats in similar environments. Notwithstanding the usual

<sup>3</sup> Completely senesced genotypes ( $n = 5$ ) are excluded from Day 138 (Week 10) average.

stability of the winter growing season climate in north-west Mexico, 1974-1975 was recognized as being more favorable to wheat than usual, because mean temperatures were 1 to 2 C less than average while solar radiation was normal. A reflection of this is the positive correlation between yield and anthesis date (Table 4); usually the correlation is close to zero in this environment. Calculation, where appropriate, of partial correlations, anthesis date held constant, attempts to allow for this effect. Also, 13 of the short genotypes had been compared in yield trials under similar conditions in three previous seasons (1970-1971, 1971-1972, 1973-1974, R. A. Fischer unpublished). Genotype mean yield ranged from 77 to 101% of the recurrent check cultivar Yecora 70 and correlated closely ( $r = 0.87^{**}$ ) with yield as a percent of this check in the 1974-1975 experiment (range 74 to 103%).

### Photosynthetic Activity

As an indicator of crop growth rate,  $A$  as determined in our study suffered from potential problems including neglect of photosynthetic tissue other than uppermost leaf lamina and measurement of  $\text{CO}_2$  uptake by only the adaxial side of the leaf. Adaxial photosynthesis usually exceeds abaxial (21). It is argued that our measure approximated the light saturated rate of photosynthesis,  $A_{max}$ , for that surface and that genotype interactions with leaf side, position, etc. are likely to be small. Nevertheless, the effect of variation in  $A_{max}$  on total canopy photosynthesis at full light interception is likely to be small, relative changes in the latter being only about one-third of those in the former according to model calculations for conditions similar to ours (5, 19). An added complication are genotypic differences in leaf display, acting in our case to cancel effects of variation in  $A_{max}$  which tended to fall with more erectophile display (Table 3).

In view of these considerations, it is perhaps surprising that early crop growth rate (22 January to 19 February) was correlated with  $A$  at that time (at least  $A$  in Week 1), and that later crop growth was also related to  $A$  ( $A$  Weeks 1 to 9, Table 4). The first-mentioned relationship, which amounted to a 0.3% increase in growth rate per 1% increase in  $A$ , was associated closely with genotypic differences in plant height. Increased crop growth rate after full cover with taller genotypes has been observed on other similar occasions (R. A. Fischer unpublished). Although it may be partly due to a less favorable leaf display in the compact canopies of extremely short wheats, our present results suggest it is also due to increasing  $A_{max}$  with taller genotypes. One possible cause of the latter effect is that in shorter cultivars,  $A$  is more limited by sink, i.e., the elongating stem (stem sugar concentration increased as height was reduced). It has been shown that under wet soil conditions, taller genotypes have lower daytime leaf water potentials (12, 17); apparently this does not reduce their photosynthetic activity.

In contrast to the situation with early crop growth, the correlation between  $A$  and postanthesis crop growth rate (Table 4) or total dry weight per day (Table 3) was attributed entirely to variation in anthesis date. The same applied to the correlation between  $A$ , and grain yield and

kernel number. Whilst ontogenetic effects on  $A$  (for example declining  $A$  with increasing flag leaf age), superimposed upon our system for sampling all genotypes on fixed calendar dates, could alone give rise to positive  $A$  vs. anthesis date correlations, this seems unlikely. Firstly,  $A$  showed no clear decline until after the last week of full sampling (Week 9, Fig. 1 and 2). Secondly, such an effect would not explain the covariance between  $A$ , crop growth rate, yield, and anthesis date. In this complex situation, we suggest that the underlying cause is a degree of sink control over photosynthesis (21), sink size during grain filling being greater with increased days to anthesis. Kernel number increased with later anthesis ( $r = 0.43^{*}$ ); also kernel number was 15,600  $\text{m}^{-2}$  for earlier cultivars cf. 19,700  $\text{m}^{-2}$  for the later cultivar (Fig. 2). This could have resulted from pre-anthesis events unrelated to  $A$  then, but through increased sink size after anthesis, it could have led to greater postanthesis photosynthesis, dry matter accumulation, and in turn yield. Yield was closely related to kernel number ( $r = 0.76^{**}$ ) and to postanthesis crop growth rate ( $r = 0.78^{**}$ ). The slopes of the relationship between yield and  $A$  (0.7% yield change per 1%  $A$  change), and postanthesis growth rate and  $A$  (1% per 1%  $A$  change) are also suggestive of sink control over  $A$ .

In conclusion, our results confirm the positive correlation between  $A$  and yield in spring wheat reported elsewhere (22), but our relationship was weaker. In addition, we conclude that this relationship reflected correlated responses to variation in days to anthesis, and probably sink strength during grain filling, rather than implying that increased photosynthetic activity was a primary cause of increased yield.

### Leaf Permeability

It was most surprising that despite a positive  $LP$ -yield correlation (confirming 22) and despite strong positive environmental correlations between  $LP$ , and  $A$  and  $g$ , the corresponding phenotypic correlations were close to zero (Table 2). In addition, plant height associations with  $LP$  and  $A$  tended to be opposite in sign (Table 3). Shimshi and Ephrat (22) found a close positive rank correlation between  $LP$  and  $A$ ; their  $A$  determination included both surfaces of the leaf. Also significant positive phenotypic correlations between  $LP$  and  $A$  measured by gas exchange on whole leaves have subsequently been found for wheat genotypes grown in a glasshouse (H. M. Rawson and R. A. Fischer unpublished).

$A$ , as measured in the present study, would have depended on adaxial stomatal conductance alone plus internal conductance to  $\text{CO}_2$ , while  $LP$  would have been controlled largely by the component of smallest permeability among the three components (adaxial stomata, intercellular air spaces, and abaxial stomata) through which the air flowed in the determination of permeability. This is likely to have been the abaxial stomata (23) and hence genotypic effects on the opening of abaxial stomata relative to adaxial ones, or relative to internal factors controlling photosynthesis, would lead to a poor phenotypic correlation between  $A$  and  $LP$ . It has been observed with a given wheat genotype that if the source to sink ratio was decreased artificially after an-

**Table 5. Mature plant height, leaf photosynthesis (A), leaf permeability (LP), crop growth rate, and grain yield ( $\pm$  standard error) as influenced by the presence of major dwarfing genes (see text); bread wheats only.**

Genes present	Genotypes	Height	A Week 1	A Weeks 1 to 9	LP Weeks 3 to 9	Crop growth rate $\ddagger$	Yield
(no. of genotypes)		cm	mg CO <sub>2</sub> , dm <sup>-2</sup>	hour <sup>-1</sup>	units	g m <sup>-2</sup> day <sup>-1</sup>	g m <sup>-2</sup>
Tall (3)	Mentana, Yaqui 50, Nainari 60	132 $\pm$ 5.3	18.4 $\pm$ .9	18.0 $\pm$ .5	6.2 $\pm$ .25	15.7 $\pm$ .5	552 $\pm$ 42
Rht 1 (8)	Tanori 71, Inia 66, WW15, Zaragoza 75, Pj-PI190982 $\ddagger$ , Jupateco 73, Siete Cerros 66, UQ105 $\ddagger$	102 $\pm$ 2.3	17.6 $\pm$ .7	18.4 $\pm$ .5	7.3 $\pm$ .37	15.8 $\pm$ .7	706 $\pm$ 29
Rht 2 (5)	Ciano 67, Tobarí 66, Jaral "S", Pitic 62, Cno-Gallo $\ddagger$	105 $\pm$ 1.4	18.3 $\pm$ .6	17.7 $\pm$ .4	6.8 $\pm$ .35	16.5 $\pm$ .3	625 $\pm$ 35
Rht 1 + Rht 2 (11)	Olesen, Yecora 70, Hira $\ddagger$ , E Yecora 70, Cajeme 71, Ferc 4A $\ddagger$ , Ferc 3 $\ddagger$ , Yaqui 50E $\ddagger$ , Vicam 71 $\ddagger$ , Kal-Bb $\ddagger$ , S948-A1 $\ddagger$	73 $\pm$ 3.4	15.4 $\pm$ .4	17.5 $\pm$ .4	8.7 $\pm$ .38	14.4 $\pm$ .3	767 $\pm$ 16
Rht 3 (1)	Tom Thumb (spring derivative)	65	14.5	19.7	8.9	10.9	729
Significance of group effect		**	**	NS	**	**	**

$\ddagger$  Classification deduced from pedigree and stature, the latter being used in some cases to distinguish between the possibility of one or two major dwarfing genes.

$\ddagger$  Over period 22 January to 19 February.

thesis, the conductance of the abaxial surface of the flag leaf, considerably lower than adaxial conductance in the control situation, increased markedly, while the adaxial conductance changed little (21). Measured leaf photosynthesis increased only slightly but permeability (not measured) would probably have increased more markedly since it would be governed by the surface of least conductance, the abaxial one. In other words, *LP* rather than *A*, especially *A* measured on the adaxial surface alone, could be the more sensitive indicator of source-sink balance during grain filling, and therefore of yield where higher yield is related to a larger sink. This may have been the case in our study explaining part of the positive *LP*-yield correlation. This does not exclude the possibility that such an effect is also related to that part of the *LP* vs. yield correlation which is associated with reduced stature. It suggests that the relationship between yield and *LP* is quite indirect.

### Breeding Implications

Given the consistency of genotypic differences in *LP* across time (Table 2) and between the spaced planting and plots, and the speed with which it can be determined (13), the positive *LP*-yield correlations in our study and that of Shimshi and Ephrat (22) suggest that *LP* determination may have value as an early generation selection criterion for yield. Subsequent testing of *LP* measurement on space-planted  $F_2$  populations has shown it is a useful predictor of  $F_4$  and  $F_5$  plot yields (6); further testing as a potential selection criterion appears warranted. On the other hand, *A* as measured by us appeared to have little value in this regard.

Also of significance to breeders are insights that our results throw upon the effect of the Norin 10 dwarfing genes. Recently, Gale and Marshall (14) reported on the identity of major Norin 10 dwarfing genes in many short spring wheat genotypes; other identities can be deduced from pedigrees. Table 5 was prepared to show the effect of the genes on key traits studied here. The gene nomenclature (Rht 1, 2, 3) is that used by these authors and includes Rht 3, the Tom Thumb dwarfing gene and not a Norin 10 gene. Rht 1 and 2 correspond to *Sd* 1 and 2 recognized earlier (2). If it is assumed that other genes

are at random with respect to the groups of Table 5, then the dwarfing genes are affecting height (reduction), *LP* (increase) and yield (increase) in a consistent manner: tall < Rht 2 < Rht 1 < Rht 1 + 2, although only some of the differences were statistically significant. The effects on *LP* and yield are closely associated with height change (between the five groups *LP* vs. height  $r = -0.982^{**}$ ; yield vs. height,  $r = -0.952^{**}$ ); within group correlations between these traits were not significant but the samples were small relative to error. On the other hand, dwarfing genes did not affect *A*, at least until Rht 1 and 2 were combined when *A* determined in Week 1 was clearly depressed, an effect paralleled by that on crop growth rate. Cultivars, in particular ones for irrigated conditions, are being sought in the height range of the Rht 1 + Rht 2 genotypes because of their high yield potential and lodging resistance. Our results suggest it is possible that their yield potential is being limited by reduced early photosynthesis and crop growth rate. The causes of these reductions should be elucidated.

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