Wheat Special Report No. 28

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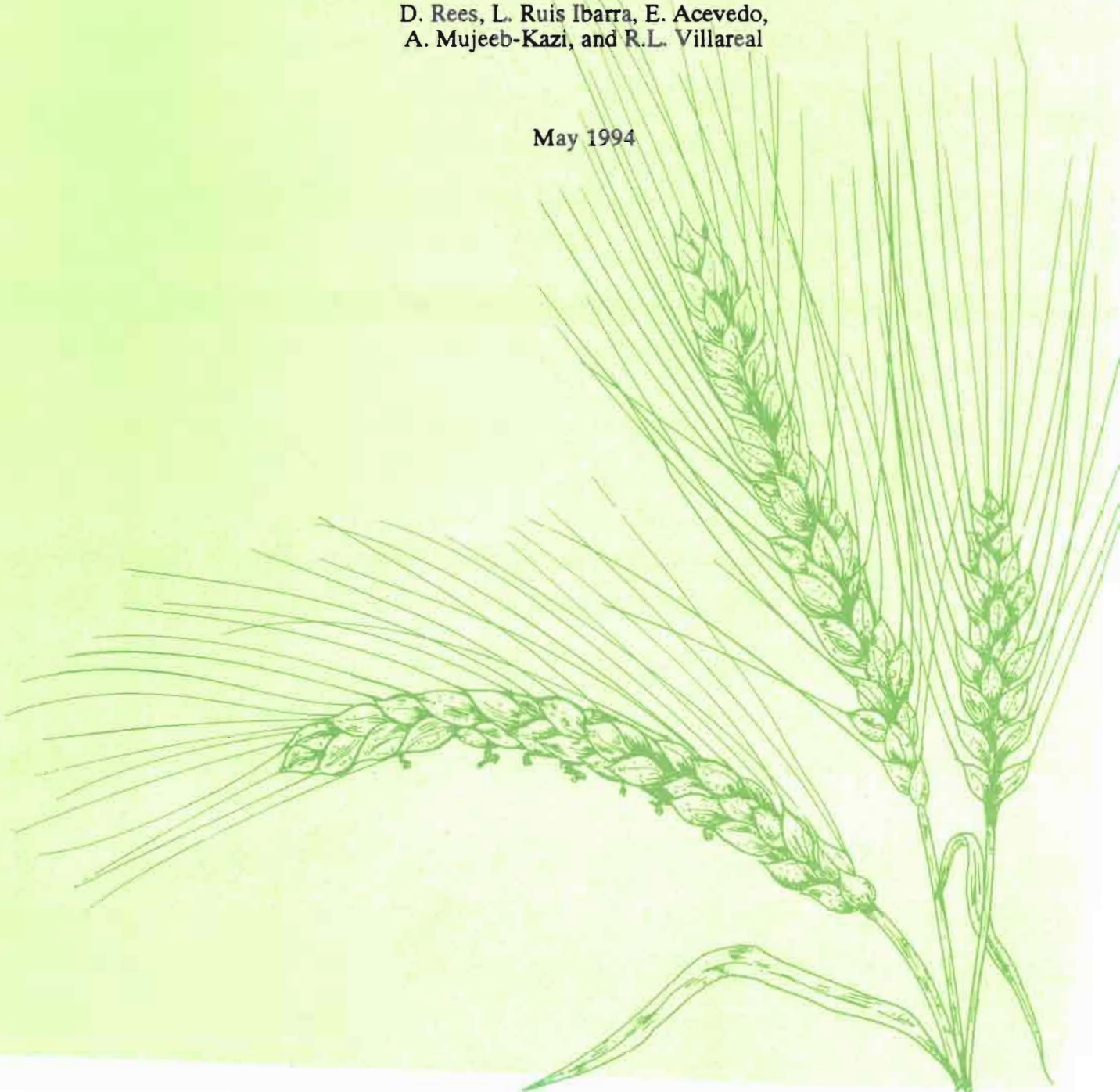

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Preface

In the process of genetic improvement of bread wheat, photosynthetic rate per unit leaf area has decreased significantly from the maximum photosynthetic rate (Pmax) of the crop's diploid ancestors (donors of the A, B, and D genomes that make up hexaploid bread wheat).

Much of the grain yield improvement of bread wheat accomplished by breeders can be traced to a change in the partitioning of assimilate to the grain, i.e., an increase in harvest index. It is the perception of wheat scientists that this avenue of grain yield improvement has pretty much run its course. However, it may be possible to increase harvest index (and subsequently grain yield) by increasing total biomass.

This Wheat Special Report presents the first efforts at CIMMYT to alter wheat biomass by increasing Pmax. It seems there is potential for using synthetic hexaploids, developed by our wide crosses laboratory, as a "bridge" to transfer the higher photosynthetic rate found in the diploid ancestor, *Triticum tauschii*, to bread wheat. The results are not definitive, but they are encouraging and certainly point to exploring this route further. The chlorophyll a/b ratio is discussed as a potential screening tool for Pmax.

E. Acevedo
Leader
Wheat Crop Management and Physiology

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Introduction

Significant advances in grain yield of both bread wheat and durum wheat have been made this century, especially since the introduction of dwarf and semidwarf varieties in the 1950s. Yield trials on a historical series of CIMMYT varieties, representative of yield increases since the 1960s, indicate that, although there has been some biomass yield increase in durum wheats, the 25% grain yield increase of bread wheats is due primarily to an increase in harvest index (K. Sayre, pers. comm.; see Rees et al. 1993). Similarly, Austin et al. (1980) showed that a 40% increase in grain yield achieved for winter wheats in England this century was not associated with a significant increase in biomass yield, and that a 59% increase in grain yield of modern varieties compared to those grown in the 19th century was associated with only a small increase in biomass yield (Austin et al., 1989).

As the rate of yield increase slows down, new strategies for wheat improvement are being sought. It seems likely that harvest index is now close to its maximum limit, as suggested by Austin et al. (1980) for winter wheat, and therefore methods for increasing total biomass yield should be investigated (Austin et al. 1980, Nelson 1988).

The process of photosynthesis is the initial step for biomass production, and therefore an important question is whether biomass production could be increased by increasing the total capacity of this process within the canopy. Austin et al. (1980) pointed out that the best strategy is to look for an increase in photosynthetic rate per unit leaf area, as most other strategies, such as increasing the area of photosynthesis by increasing leaf expansion rate, would tend to result in increased water requirement, and also would confer no advantage once full light interception was attained. Leaf photosynthesis can be described by two parameters: 1) quantum yield, which is the maximum efficiency of photosynthesis with respect to incident light, and can be measured by the initial slope of the photosynthesis vs. light intensity curve, and 2) maximum photosynthetic rate (Pmax) attained at saturating light intensities. Theoretically, increasing quantum yield would have a greater effect on leaf assimilation than increasing Pmax by the same proportion (Day and Chalabi 1988). However, except under stress conditions, little variation in quantum yield has been observed within or between plant species. On the other hand, significant variation of Pmax within C3 species has been observed (Austin 1989).

This report describes some initial results of a physiological study carried out to look at the potential for increasing biomass yield in bread wheats by raising Pmax through the introduction of genes from the diploid progenitors of wheat. The characteristics of the diploids will be described below, but first we will consider the evidence for and against the hypothesis that yield could be increased by increasing photosynthetic capacity.

It is interesting to note the paradox that, overall, the domestication of wheat has led to a decrease in maximum photosynthetic rates (Austin 1990, Evans 1993, Khan and Tsunoda 1970a), since modern bread wheats have a lower photosynthetic rate than their wild diploid ancestors. Many studies on a number of crops that have attempted to relate yield increases with an increase in photosynthetic rate have shown negative results (Nelson 1988). For example, Rawson et al. (1983) found no correlation between flag leaf Pmax and the grain yield of six spring wheats and 120 progeny. That study was carried out in the greenhouse. However, in a field study, Gent and Kiyomoto (1989) found no relationship between the yield increase of New York winter wheats and photosynthetic rate either of the flag leaf or of the whole canopy. Similarly, attempts to increase yield by selecting for increases in Pmax have so far been unsuccessful (Austin 1989, Nelson 1988). For example, by selecting specifically for high photosynthetic rates, Crosbie et al. (1981) were able to increase Pmax in maize by 1.5% per generation, but after 5

generations no grain yield increase was observed (Crosbie and Pearce 1982). Similar results have been observed in soybean (Ford et al. 1983) and in peas (Hobbs 1986).

There is, however, some evidence linking yield to photosynthetic rates. Increasing photosynthetic rates by environmental means, such as increasing CO_2 concentration or light intensity, has been shown to increase yield (Gifford 1977, Nelson 1988). Shimshi and Ephrat (1975) found correlations between grain yield and photosynthetic rate for eight spring wheat cultivars. Fischer et al. (1981) confirmed the relationship between photosynthesis and yield for a wider range of wheat varieties, but with weaker correlations, while studies by Khan and Tsunoda (1970b), and Sinha et al. (1981) both showed higher photosynthetic rates in new wheat varieties, compared with old. More recently, we have found a clear correlation between photosynthetic rate and grain yield in a historical series of CIMMYT bread wheats (Rees et al. 1993).

The failure to relate yield increases to photosynthetic rate in many studies could be explained partly by the fact that it is difficult to relate localized photosynthetic measurements to the whole canopy, and also that, until recently, the technology to make a large number of measurements in a short time span has not been available. In addition, there are many factors that need to be considered if an increase in photosynthetic efficiency is to result in an increase in yield (Austin 1989). First, high Pmax may be associated with undesirable characteristics, such as small or short-lived leaves, which would counteract any advantage (Austin 1989, Bhagsari and Brown 1986, Nelson 1988). Second, the increase in Pmax needs to be sufficient to infer a significant advantage. The magnitude of the advantage depends on the proportion of time for which the canopy is operating at or near saturating light conditions. Models suggest that, under average conditions, only 25-40% of the increase in Pmax would be expressed as an increase in canopy photosynthesis (Nelson 1988). However, this percentage would be greater under high light environments, such as during the spring season in Obregon, northwestern Mexico, where the present study was carried out. Third, since the evidence suggests that wheat yields are limited to a certain extent by both source and sink capacity (Gifford et al. 1973, Rawson et al. 1976, Aggarwal et al. 1990), higher photosynthetic rates may not be beneficial unless sink capacity is also increased. Fourth, both Austin (1989) and Nelson (1988) pointed out that the benefits of higher photosynthetic capacity would probably only be realized under higher nitrogen conditions.

We now turn to the characteristics of the diploid ancestors of wheat as possible sources of genetic material for improving the photosynthetic characteristics of modern bread wheats.

Photosynthetic characteristics of diploid species compared to modern bread wheat varieties

There are a number of reports in the literature that the flag leaves of several diploid ancestor species have a Pmax up to 40% greater, both per leaf area and per chlorophyll, than those of modern wheat varieties (Evans and Dunstone 1970, Austin et al. 1982; Austin et al. 1986, 1987; Austin 1990; Kaminski et al. 1990). In some of these reports, it is also suggested that tetraploid species have higher rates than the hexaploid species (Austin 1990, Kaminski et al. 1990). Some of the diploid species that have been included in the studies are listed in **Table 1**, together with the percentage increase in Pmax over that of *Triticum aestivum*.

One interesting and important observation made by Dunstone et al. (1973) was that the difference between the diploids and hexaploids is greater when the plants are grown at high light intensities. It seems that diploids can adapt to higher light intensities by increasing maximum photosynthetic capacity, while hexaploids have lost this ability.

Table 1. Pmax of diploid species compared to that of *Triticum aestivum*.

Species	Pmax/Pmax of *T. aestivum*	Conditions
Evans and Dunstone (1970)		
Aegilops squarrosa (*T. tauschii*)	116%	Pot experiment
Aegilops speltoides	108%	614 cal/cm^2/day
Triticum boeoticum	146%	
Triticum monococcum	111%	Meas int. 3200 fc Atmospheric CO_2
Kaminski et al. (1990)		
Aegilops squarrosa	116%	Field expt, UK
Triticum boeoticum	107%	Meas int. 2200 $\mu E.m_{-2}.s^{-1}$
Triticum monococcum	104%	Atmospheric CO_2
Triticum urartu	112%	
Triticum thaoudar	137%	
Triticum aegilopoides	110%	
Austin (1986)		
Triticum urartu	141%	Field experiment, UK
Triticum thaoudar	129%	Meas inten., 2000 $\mu E.m^{-2}.s^{-1}$
Triticum aegilopoides	128%	Atmospheric CO_2
Austin (1990)		
Triticum urartu	149%	Field experiment, UK Sat measurement intensity Atmospheric CO_2

Pmax is compared on a leaf area basis. When more than one genotype of any species was given in the original references, the mean value Pmax was used.

Several possible explanations for the higher Pmax of diploids have been considered. Diploids tend to have smaller leaves and smaller mesophyll cells. Thus, one initial suggestion was that diploids could be more efficient due to a shorter diffusion distance for CO_2 and O_2 to and from the chloroplasts within the mesophyll. However, the fact that photosynthetic differences persist even with saturated CO_2 concentrations, argues against this possibility (Austin et al. 1987). Higher photosynthetic rates could arise due to a higher capacity of the Calvin cycle. Attention has been concentrated on the enzyme Rubisco (ribulose bisphosphate carboxylase-oxigemase). This is the enzyme that fixes CO_2 by catalyzing the carboxylation of ribulose bisphosphate to form two molecules of phosphoglycerate. However, it is not completely specific for CO_2, such that a proportion of photosynthetic energy is lost when Rubisco catalyzes a reaction between ribulose bisphosphate and oxygen. The products of this reaction are recycled by the process of photorespiration. The Calvin cycle would be a more efficient process if Rubisco had a higher specificity for CO_2 and in various laboratories around the world, attempts are being made to achieve this by engineering the enzyme. However, a comparison of the relative rates of photosynthesis and photorespiration in diploids and hexaploids indicates that the characteristics of the enzyme are identical (Austin et al. 1987). It has also been

shown, that, if anything, the concentration of Rubisco with respect to chlorophyll in diploids is slightly lower than in hexaploids (Austin et al. 1987).

There is, however, evidence that the light reactions of photosynthesis are faster in diploids than in hexaploids. For example, higher rates of electron flow to artificial acceptors have been measured in chloroplasts isolated from diploids (Zelenski et al. 1978, Miginiac-Maslow et al. 1979). It has been observed that diploids grown at high light intensity have a higher ratio of chlorophyll a to chlorophyll b than hexaploid wheats, indicating a higher concentration of photosystems per chlorophyll (Austin et al. 1987). This would infer an advantage at high-incident light intensities when light absorption is not limiting, and therefore the total size of the light-harvesting apparatus associated with each reaction center is not critical. A higher concentration of photosystems would probably be associated with a higher concentration of the other components of the electron transfer chain.

Despite higher photosynthetic rates, diploids tend to have the same or lower biomass yields than modern varieties (Austin et al. 1982, 1986). This may be accounted for, at least to some extent, by the facts that the flag leaves of diploids tend to lose chlorophyll and to senesce earlier (Austin et al. 1982, Kaminski et al. 1990), and also that all the leaves tend to be smaller. It is a general observation that varieties with higher photosynthetic rates tend to compensate for this with smaller leaves, presumably because factors other than photosynthetic capacity limit productivity (Austin et al. 1982, 1986). The same behavior has been observed in a number of other plant species (Bhagsari and Brown 1986). The small sink size in diploids may also limit their growth. All these points demonstrate the important fact that higher photosynthetic rates *per se* do not necessarily lead to higher biomass yield.

In England, Austin (1990) attempted to increase wheat yields by means of Pmax, using genetic material from diploids. He has also made a detailed study of the genetics of the system. Amphiploids were produced by crossing durum wheats with the A genome diploid, *T. urartu*, and doubling the chromosome number with colchicine. The resulting lines (6x AAAABB) had higher Pmax than *T. aestivum*, from which it was deduced that nuclear genes were responsible, as both parents had B-type cytoplasm. This was confirmed by cytoplasm substitution lines. Most of the lines produced in this way were not agronomically acceptable, but of those that were, a few showed significantly higher biomass yield than bread wheats. A larger study was carried out looking at lines produced by crossing *T. urartu* with bread wheat as the female parent, and then backcrossing to the bread wheat. As it was impossible to measure Pmax directly in such a large number of lines, selection was carried out on the basis of visual assessment for high biomass. Most of these lines were found to have 42 chromosomes, and analysis of the endosperm storage proteins indicated that most contained proteins from *T. urartu* (Austin 1990). Following selection in this way, a subset was found to have significantly higher Pmax than bread wheat, however, disappointingly, in further yield trials, they did not have significantly higher biomass (R.B. Austin, pers. comm.).

In this report, we describe a study with similar aims. It was carried out in northwestern Mexico in a high radiation (but short day) environment where we would expect the crop to be acting near to Pmax for more of the time than a crop growing in the relatively low light environment of England, such that the benefits of high Pmax may be more apparent. We consider synthetic hexaploid lines produced by crossing durum wheats with the D genome diploid, *Aegilops squarrosa* (*Triticum tauschii*), and doubling the chromosome number with colchicine, and also progeny obtained when these synthetics are crossed to bread wheats. We compare characteristics of these two groups of lines with a selection of bread wheats and durum wheats. To measure Pmax, we used a relatively new technique

(described below) by which it is possible to calculate photosynthetic rate from chlorophyll fluorescence yield. In this way, measurements can generally be obtained more rapidly than by using more traditional methods of gas exchange measurement such as infrared gas analysis. However, we still do not regard this as a practical selection technique when large numbers of lines are to be considered. We, therefore, investigate the validity and practicality of using analysis of the ratio of chlorophyll a to chlorophyll b, as an indirect indication of the Pmax differences that might arise due to photosystem concentration differences.

Using chlorophyll fluorescence to measure rates of photosynthesis

The technique used to measure photosynthetic rates in this study was based on measurements of fluorescence yield from chlorophyll complexes of wheat leaves. The process of photosynthesis is never 100% efficient, and a fixed proportion of the absorbed light energy that is not used for photosynthesis is re-emitted as fluorescence. Thus, if a leaf is photosynthesizing very efficiently, for example, under low light intensity, the proportion of energy re-emitted is very low, whereas, if the leaf is photosynthesizing with low efficiency, as, for example, under high light conditions, the proportion is higher. Thus, there is an inverse correlation between fluorescence yield and photosynthetic efficiency. Photosynthetic rates (rates of photosynthetic electron transfer) are given by the product of efficiency and incident light intensity.

The technology for measuring chlorophyll fluorescence has advanced significantly in the last few years. The introduction of modulated systems allows, for the first time, the measurement of fluorescence in the presence of external light, such as sunlight. In modulated systems, a low-intensity modulated light source is used, and only the modulated fluorescence, excited by this source, is recorded. Thus, a direct measure of fluorescence yield (i.e., the proportion of absorbed light re-emitted as fluorescence) is given that does not need to be corrected for incident light intensity.

For the calculation of photosynthetic efficiency, steady-state fluorescence yield, Ft, needs to be related to maximum fluorescence yield, Fm, i.e., when photosynthetic efficiency is zero. Fm is approximated by measuring the fluorescence yield during the application of a saturating pulse of light, which effectively overloads the photosynthetic process, so that only a negligible proportion of the light can be used for photosynthetic processes.

Seaton and Walker (1990) have shown that, for a wide range of plant species, a fixed relationship exists between photosynthetic efficiency and (Fm - Ft)/Fm, that at all but low light intensities: Efficiency = 0.0722 x (Fm - Ft)/Fm [μmol $O_2.\mu E^{-1}$]. See also Genty et al. (1989).

Chlorophyll fluorescence does not give an equivalent measurement to gas exchange measurements. Gas exchange systems measure the uptake of CO_2, and, as such, give a measurement of photosynthesis minus respiration and photorespiration. On the other hand, fluorescence measures the efficiency with which absorbed light is used for the light reactions of photosynthesis (including associated with photorespiration) with no account of respiration.

Another difference between the two methodologies is that gas exchange systems tend to measure assimilation across the whole thickness of the leaf, while fluorescence measurements are specific to the upper surface.

A comparison of varieties by fluorescence techniques assumes that light absorption per leaf area is identical. This may be a reasonable assumption, as light absorption does not seem to be significantly affected by leaf chlorophyll concentration or leaf thickness

(Austin 1989, Seaton and Walker 1990), however, possible errors should be borne in mind.

Materials and Methods

The 64 wheat lines used in this study (**Table 2**) were of four groups: bread wheats (13 lines), durum wheats (13 lines), synthetic hexaploids produced by crossing *Aegilops squarrosa* (*T. tauschii*) with durum wheats (19 lines), and hexaploids selected from progeny of simple crosses between the synthetics and bread wheats (19 lines) in F6. Throughout this report, these four groups will be referred to as: bread, durum, synthetic, and crosses, respectively. See **Appendix 1** for a description of how the synthetics were selected for this study.

The trial was run under basin (melga) irrigation in field 810, block C9, at the experimental station of CIANO (Centro de Investigaciones Agricolas de Noroeste), Ciudad Obregon, Sonora, Mexico (27^{o} 20'N, 109^{o} 54'W, at an elevation of 38 masl) during the 1993 spring season.

Following a germination test in the laboratory of 100 seeds for each line, seeds were sown on 28 November at a rate of 200 viable seeds/m^2 in rows 20 cm apart in plots consisting of 6 rows of 4.5 m (5.4 m^2). Within each melga, the plots were arranged in two rows of eight, with additional border plots at each end of each row. The plots were placed 40 cm apart in order to decrease interplot interference between lines that often differed significantly in height. There were three replications. The trial was analyzed as a randomized complete block.

Biomass cuts of 0.4 m^2 (4 rows x 0.5 m) were taken from each plot on 4 and 25 February to measure the rate of biomass accumulation.

The soil type is a clay loam, mixed montmorillonitic typic calciorthid, low in organic matter and slightly alkaline (pH 7.7). Before planting 150 kg N ha^{-1} and 46 kg P_2O_5 ha^{-1} were applied. Irrigations were carried out at 50% depletion of available water measured gravametrically in a 60-cm profile.

Photosynthesis measurements
The maximum rate of photosynthesis (Pmax) of flag leaves was calculated from chlorophyll fluorescence yield parameters measured using a PAM-2000 Portable Modulated Chlorophyll Fluorometer (Walz, Effeltrich, Germany). A modulated light emitting diode (LED) (intensity < 10 $\mu E.m^{-2}.s^{-1}$) is used to excite chlorophyll fluorescence, and the resulting modulated fluorescence is measured to indicate fluorescence yield. The efficiency of photosynthetic reactions with respect to incident light is calculated as:

$$\text{Efficiency} = C \times (Fm - Ft)/Fm \ [\mu\text{mol } O_2.\mu E]$$

where Ft is the chlorophyll fluorescence yield under ambient light conditions, and Fm is the maximum fluorescence yield attained when the photosynthetic process is saturated by the application of a bright pulse of light (Intensity > 6000 $\mu E.m^{-2}.s^{-1}$, duration 0.8 s).

The constant C (= 0.0722) was derived empirically by Seaton and Walker (1990). Photosynthetic rate is calculated as:

$$\text{Photosynthesis} = \text{Efficiency} \times \text{Incident Light Intensity.}$$
$$[\mu\text{mol } O_2.m^{-2}.s^{-1}]$$

Table 2. Wheat lines used in this study.

Group		Origin
Bread wheats		
B113	Pfau	Obregon 92
B114	Hahn*2/PRL (Weaver)	Obregon 92
B119	Opata M 85	Obregon 92
B120	Seri M 82 Obregon 92	
B1	Rayon Multivars S-14	Hermosillo 90-91
B2	Oasis Multivars S-1	Hermosillo 90-91
B3	Papago, PMI Bur S-9	Hermosillo 89-90
B4	Bacanora, CHRWYT Bur S-5	Hermosillo 90-91
B5	Pavon PMI Bul Pavon 76 S-2	Hermosillo 89-90
B6	Star Sur, M 7215-2Y-2Y-OY-2Y-OY-SOM-OY	
B7	Kauz'S', WP 133	BV-92
B8	Yaco'S', WP-46	BV-92
B9	Tody, CM67394-11Y-1M-2Y-1M-3Y-OB-14M-OY, Orig C15ESWYT#16	Hermosillo 91-92
Durum wheats		
D2	Stilts'S'	
D3	Unknown, probably Laru	
D8	Unknown	
D74	Altar 84	Obregon 92
D75	Decoy 1	Obregon 92
D77	SB A8/CRU'S'//CIT'S'/3/CHIS/4/PAL'S'	Obregon 92
D78	CPT/GEDIZ'S'/3/GOO'S'//JO'S'/CR'S'	Obregon 92
D79	Chen'S'	Obregon 92
D81	Duergand	Obregon 92
D82	Rokel'S'/Kalam'S'	Obregon 92
D89	68111/RGB/WARD RESEL/3/STIL'S'	Obregon 92
D92	Gan'S'	Obregon 92
D93	Yar'S'	Obregon 92
Synthetic hexaploid wheats (from F709)		**El Batan 91 (row #)**
S7	SBA81/CR'S'//CIT'S'/3/CHI'S'/4/PAL'S'/5/*Ae. squarrosa* (192)	W177
S13	Altar 84/*Ae. squarrosa* (205)	W31
S16	SBA81/CR'S'//CIT'S'/3/CHI'S'/4/PAL'S'/5/*Ae. squarrosa* (208)	W85
S17	Altar 84/*Ae. squarrosa* (211)	W32
S21	Duergand/*Ae. squarrosa* (214)	W15
S22	ROK'S'/KMLI'S'//*Ae. squarrosa* (214)	W18
S33	Duergand/*Ae. squarrosa* (221)	W14
S40	CPT/GEDIZ'S'/3/GOO'S'//JO'S'/CR'S'/4/*Ae. squarrosa* (223)	W95
S43	Altar 84/*Ae. squarrosa* (224)	W20
S49	68111/RGB//WARD RESEL/3/STIL'S'/4/*Ae. squarrosa* (332)	W113

Table 2. Continued.

Group		Origin
S51	68111/RGB//WARD RESEL/3/STIL'S'/4/ *Ae. squarrosa* (368)	W115
S54	Sterna'S'/*Ae. squarrosa* (446)	W119
S55	Decoy 1/*Ae. squarrosa* (446)	W120
S56	Gan'S'/*Ae. squarrosa* (446)	W21 N
S57	Yar'S'/*Ae. squarrosa* (?)	W118
S60	Altar 84/Araos'S'//*Ae. squarrosa* (?)	W193
S65	Yar'S'/*Ae. squarrosa* (783)	W31 N
S72	Altar 84/*Ae. squarrosa* (J Bangor)	W21
S91	Altar 84/*Ae. squarrosa* (191)	W143
Crosses between synthetics and bread wheats		**El Batan 92 (row #)**
SB1	Chen/*Ae. squarrosa* (213)//Papago	672
SB2	Chen/*Ae. squarrosa* (213)//Papago	673
SB3	Chen/*Ae. squarrosa* (213)//Papago	675
SB4	Papago//Chen'S'/*Ae. squarrosa* (210)	682
SB5	Chen/*Ae. squarrosa* (205)//Kauz	710
SB6	Chen/*Ae. squarrosa* (205)//Kauz	711
SB7	Chen/*Ae. squarrosa* (205)//Kauz	714
SB8	Chen/*Ae. squarrosa* (205)//Kauz	720
SB9	Chen/*Ae. squarrosa* (205)//Kauz	723
SB10	Chen/*Ae. squarrosa* (205)//Kauz	741
SB11	Chen/*Ae. squarrosa* (205)//Hahn*2/Parula	767
SB12	Chen/*Ae. squarrosa* (205)//Hahn*2/Parula	770
SB13	Chen/*Ae. squarrosa* (224)//Yaco	809
SB14	Chen/*Ae. squarrosa* (224)//Yaco	822
SB15	Chen/*Ae. squarrosa* (224)//Yaco	825
SB16	Chen/*Ae. squarrosa* (224)//Opata	948
SB17	Chen/*Ae. squarrosa* (224)//Opata	963
SB18	Altar 84/*Ae. squarrosa* (191)//Opata	992
SB19	Altar 84/*Ae. squarrosa* (191)//Opata	998

In order to carry out the measurement of Pmax, a flag leaf was placed in the leaf clip holder of the fluorometer, such that the measurement would be carried out on a circular portion (diameter 1 cm) of the leaf that had previously been exposed perpendicular to full sunlight. The leaf clip was positioned such that this part of the leaf was exposed to 1800-2000 $\mu E.m^{-2}.s^{-1}$ during the measurement. In most cases, this was possible using sunlight, but on cloudy days an artificial light source (see below) was used. In order to measure Ft and Fm, a saturating pulse was applied every 10 sec. The pulses were repeated until 6-7 constant readings had been recorded, such that each measurement took 90-120 sec. The Leaf Clip monitored leaf temperature and incident light intensity continuously.

The artificial light source consisted of a 12 V 250 W projector bulb powered by a 12-V car battery. To minimize the heat incident on the leaf, a filter was constructed using two pieces of glass spaced by plastic tubing and filled with water. A small quantity of milk

was added to the water to scatter the light and make the intensity more uniform at the leaf surface.

A subset of 16 lines was measured: 4 bread wheats--B113, B119, B3, B6; 5 durum wheats--D2, D74, D75, D79, D82; 3 synthetics--S13, S22, S43; and 4 crosses--SB2, SB5, SB17, SB18 (D2 was originally identified as a synthetic but was later found to be a durum). Only lines with good germination were used. The lines were chosen to include as much as possible the durum and bread wheat parents of the synthetics and crosses being measured. All measurements were made early in the day (between 9:30 and 13:30) in order to measure maximum photosynthetic rates in the absence of any inhibition by build-up of assimilates in the leaves. Five sets of measurements were made between 2 February and 22 March. A set of measurements generally consisted of 3 days of readings, completing one repetition each day. For each plot, four leaves were measured from its center; thus 16x4 = 64 leaves were measured in the 4-hour period.

The Pmax of representatives of three diploid species; *Ae. squarrosa* (D genome), *T. urartu* (A genome), and *T. boeoticum* (A genome) were also measured. They were grown as individual plants in a separate part of the field station, which was equipped with lights to increase the day length perceived by the plants and promote flowering. As the plants were grown for crossing purposes only, they were not managed optimally for water and nitrogen. Measurements were made on 17, 25, and 29 March at which time most plants were at the pre-anthesis stage.

Analysis of chlorophyll a/chlorophyll b
Four flag leaves were sampled from each plot on 25 February (near to anthesis) and were stored, wrapped in aluminium foil, at -10 to -20^{o}C until the time of the analysis (4-6 weeks).

For the analysis, a central portion of each leaf was cut and the four portions were ground together with a total of 15 ml 80% acetone in a stone pestle and mortar kept on ice until all color was extracted from the leaf material. The extract and leaf material were centrifuged at 3000 rpm for 6 minutes in a bench top centrifuge. The absorption of the supernatant at 645 nm and 663 nm was measured using a Milton Roy 620 Spectrophotometer (Milton Roy Co., Rochester, New York, USA). The ratio of chlorophyll a to chlorophyll b was calculated from the following equation (Arnon 49):

$$\text{Chlorophyll a/Chlorophyll b} = [(12.7 \times A663) - (2.69 \times A645)]/[(22.9 \times A645) - (4.68 \times A663)]$$

Regular measurements of control samples were carried out to check the consistency of stored samples. No time-dependent changes in the results of the analysis were observed.

Chlorophyll concentration
Flag leaf chlorophyll concentration was measured on 26 February (mean date of anthesis was 24 February) using a chlorophyll meter (SPAD 502, Minolta, Spectrum Technologies Inc., Plainfield IL, USA). Each value is the mean of four leaves, for each of which four readings were taken.

Leaf area and specific weight
Fifteen flag leaves were sampled at random from the central rows of each plot after flag leaf ligule emergence (19-25 February). Leaf area of fresh leaves was measured using a Li-Cor Portable Area Meter (LI-3000, Li-Cor Inc., Lincoln, Nebraska, USA) fixed to a Transparent Belt Conveyor Accessory (LI-3050 A/4). The leaves were then dried in an oven at 65^{o}C for 48 hours for determination of specific weight.

Staygreen determination
Flag leaf staygreen was determined by estimating visually the date when flag leaves of each plot had 50% chlorophyll remaining, and comparing this with the date of physiological maturity when peduncle and head had lost all their green color.

Harvest components
At harvest, measurements were made of grain yield, biomass yield, and harvest components as described by Meisner et al. (1992). Plots were harvested between 13 April and 11 May, 1 to 2 weeks following physiological maturity (considered as complete loss of chlorophyll from the spike and peduncle), between 13 April and 11 May.

Results

A number of physiological characteristics were measured for all 64 lines in the trial. In order to compare the characteristics of the groups, the average values by group are shown in **Table 3**, where significant differences between the groups, calculated by orthogonal contrast analysis, are also indicated. **Table 4** shows the results of the contrast analysis in more detail.

The highest grain yields were obtained by the bread wheats, followed by the durum wheats and crosses, while the synthetics showed the lowest grain yield. These differences were due primarily to differences in harvest index.

With respect to biomass yield, which is the main focus of this study, the synthetics were significantly higher than the other three groups. However, the duration of active assimilation varied between lines, and this should be corrected for when comparing rates of biomass accumulation.

We also measured rate of biomass accumulation by taking biomass samples on two dates chosen to cover, on average, the three weeks immediately prior to anthesis (4 and 25 February). However, we observed that for many of the synthetics, for an unknown reason, there was poor germination in the field compared to the laboratory tests. Thus, at the time of the first biomass sampling, there was a wide range of biomass density with the synthetics generally low due to low plant number. Due to high variability, no significant differences between groups were observed for biomass accumulation (i.e., 2nd biomass cuts - 1st biomass cuts). For the rate of biomass accumulation calculated as percentage increase in biomass between the two sampling dates, the synthetics showed a higher rate than the other groups. However, there was a strong negative correlation between first biomass sample weight and rate of biomass accumulation, from which we deduce that the results were influenced by development. For this reason, we did not have complete confidence in this as a method for comparing biomass accumulation rate.

To back up the above data, we calculated an alternative biomass accumulation rate by dividing biomass yield by the duration of active assimilation (emergence until 50% chlorophyll in the flag leaf). The synthetics showed a rate of biomass accumulation higher than the other groups (significantly to 5% for bread and durum wheats, and to 6% for crosses).

The harvest components give some indication as to which factors were responsible for the low grain yield of the synthetics compared to the other groups. Despite high grain

Table 3. Mean values of measured parameters for each group of varieties.

Parameter	Bread n=13	Durum n=13	Synthetic n=19	Cross n=19
Grain yield ($t.ha^{-1}$)	6.48a	6.02b	3.96d	5.79c
Biomass yield ($t.ha^{-1}$)	12.46b	13.12b	17.10a	12.76b
Harvest index	0.53a	0.48b	0.24c	0.47b
Biomass 1 ($t.ha^{-1}$)	8.18b	7.45d	5.88c	9.38a
Biomass 2 ($t.ha^{-1}$)	13.42ab	12.68b	10.90c	14.28a
Biomass (2-1)	5.15a	5.50a	5.10a	4.92a
% increase	70%b	78%b	101%a	55%c
Duration of crop (days)	117a	118a	118a	115a
Biomass accum. rate ($t.ha^{-1}.day^{-1}$)	0.096c	0.101c	0.114ab	0.103bc
Grains per spike	38.3a	36.2a	25.1c	32.1b
Spikes/m^2	470a	365b	365b	472a
Grains/m^2	17400a	12600c	9000d	14900b
1000-grain weight (g)	37.6c	49.1a	44.4b	39.4c
Flag leaf area (cm^2)	40.4c	43.0b	45.9a	31.8d
Flag leaf weight (g)	0.201c	0.214b	0.241a	0.158d
Spec. weight ($mg.cm^{-2}$)	5.0b	5.3a	5.2b	5.0b
Chlorophyll a/b	2.69c	2.74b	2.81a	2.70c
Chlorophyll conc. (Spad units)*	45.1a	46.1a	41.8b	45.3a

Duration of crop was measured from 50% seedling emergence until 50% chlorophyll remained in the flag leaf. Biomass accumulation rate was calculated using this value.

* Spad units are arbitrary units set by the manufacturer of the chlorophyll meter.

The letters indicate significant differences at a confidence level of 5% between the groups calculated by contrast analysis (see Table 4).

Table 4. Contrast analysis by group of measured parameters. Numbers refer to the probability that the two groups are the same.

Parameter	BvD	BvS	BvX	DvS	DvX	SvX	SvB+D
Grain yield	0.029	0.0001	0.0006	0.0001	0.256	0.0001	0.0001
Biomass yield	0.337	0.0001	0.637	0.0001	0.564	0.0001	0.0001
Harvest index	0.007	0.0001	0.0006	0.0001	0.563	0.0001	0.0001
Biomass 1	0.032	0.0001	0.0002	0.0001	0.0001	0.0001	0.0001
Biomass 2	0.219	0.0001	0.120	0.0014	0.0042	0.0001	0.0001
Biomass (2-1)	0.992	0.711	0.581	0.720	0.589	0.840	0.664
% growth	0.552	0.0067	0.152	0.037	0.038	0.0001	0.0044
Duration	0.739	0.814	0.734	0.900	0.484	0.525	0.948
Bio. Rate	0.472	0.005	0.247	0.042	0.710	0.063	0.004
Grains/spike	0.154	0.0001	0.0001	0.0001	0.003	0.0001	0.0001
Spikes/m^2	0.0001	0.0001	0.907	0.990	0.0001	0.0001	0.0004
Grains/m^2	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
1000-grain w.	0.0001	0.0001	0.135	0.0001	0.0001	0.0001	0.272
Flag leaf area	0.002	0.0001	0.0001	0.0004	0.0001	0.0001	0.0001
Flag leaf wt.	0.010	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Spec. wt.	0.518	0.0009	0.626	0.0001	0.815	0.0001	0.0001
Chlorphyll a/b	0.028	0.0001	0.609	0.0001	0.059	0.0001	0.0001
(Chlorphyll)	0.068	0.0001	0.577	0.0001	0.151	0.0001	0.0001

B = bread wheat, D = durum wheat, S = synthetics (diploid x durum), X = crosses (synthetics x bread wheat). The parameters are the same as those shown in Table 3.

weight, second only to durums, the synthetics had a low number of grains/m^2, due both to low grains per spike, and low spikes/m^2.

As expected, durums had a lower number of grains/m^2 than bread wheats, but this was compensated for by a higher grain weight. The bread wheats and crosses had similar

values for spikes/m^2 and grain weight, but the crosses had lower yield partly due to fewer grains per spike.

We now turn to characteristics of the flag leaf, which may help explain why synthetics can have a higher rate of biomass accumulation. Synthetics clearly have a larger flag leaf area than the other groups, although specific weight is very similar. With respect to the possible photosynthetic advantage of a high photosystem concentration, it is very important to note that the synthetics have a higher ratio of chlorophyll a to chlorophyll b, which indicates a higher photosystem concentration per unit chlorophyll, since although antenna have both chlorophyll a and b, photosystems have only chlorophyll a. On the other hand, the synthetics showed a lower total chlorophyll concentration.

Light interception is obviously also central to biomass accumulation. We have no direct measurement of leaf area index, but visually there was near complete light interception in almost all plots by anthesis.

Photosynthetic rates
Maximum photosynthetic rates of 16 selected lines were measured over 5 weeks between the beginning of February and the end of March. The results of individual lines are given in **Table 5**, and the analysis in **Table 6**. The mean values for each group are plotted by week in **Figure 1**. From this, it can be seen that there is variation in Pmax with time which is consistent between groups. This is probably due to variation in the environmental conditions, rather than stage of development, as the latter varies between the groups. Mean anthesis date was 24 February, 1 March, 2 March, and 18 February for bread wheats, durum wheats, synthetics, and crosses, respectively.

The mean Pmax for each group averaged over all dates is given in Table 6b. The synthetics show a higher rate than the other groups. By LSD analysis, this is only significantly higher than the rate for durums. From the results of a contrast analysis (Table 6c), it can be seen that the Pmax of synthetics is significantly higher (significant to 5%) than the bread and durum wheats considered together, but only to 10% when compared to bread wheats alone and 24% when compared to crosses alone.

Characteristics associated with Pmax or biomass yield
One of the aims of this project was to determine whether the chlorophyll a/b ratio is correlated with Pmax, such that it could be used as a screening technique for lines with higher photosynthetic rate. **Table 7** shows the results of correlation analyses between Pmax values of the 16 lines measured over 4 weeks and seven parameters that logically could be associated with photosynthetic rates (the first week was not included, since for many lines only one day of data was obtained). All correlations significant to within 15% are shown. The most consistent parameter is chlorophyll a/b ratio, which has a significant positive correlation on 3 of the 4 weeks tested. Surprisingly, in the first 2 weeks, biomass accumulation per day was significantly negatively correlated with Pmax.

The ultimate aim of selecting for high Pmax is to achieve high biomass. From Table 3, two characteristics that could be related to the high biomass yield of the synthetics are the chlorophyll a/b ratio and flag leaf area. Considering the 64 lines used in this trial, the correlations between biomass yield parameters and chlorophyll a/b ratio and leaf area are shown in **Table 8** (D8 was omitted from the analysis due to missing Chl a/b values).

For any characteristic to be used as a selection criterion, there must be variation within the population for selection. The results of an ANOVA analysis for the characteristics measured within each group are shown in **Table 9**. Most variation overall is seen within the synthetics. Interestingly, this is not apparent for the chlorophyll characteristics of the

Table 5. Maximum photosynthetic rates (Pmax) measured from selected lines.

Date	Pmax [μmol $O_2.m^{-2}.s^{-1}$]					
Bread wheats						
	B3	B6	B119	B113	Mean ±SE	
Week 1						
Feb 2		38.12		39.00		
Feb 3		42.70		40.02		
Feb 5	46.93	39.88	52.54	39.50		
Mean	46.93	40.23	52.54	39.51	44.73 ±3.40	
Week 2						
Feb 18	41.35	48.04	50.25	45.69		
Feb 19	32.29	42.41	32.98	56.77		
Mean	36.82	45.22	41.62	51.23	43.43 ±3.51	
Week 3						
Feb 22	40.20	45.57	44.12	47.49		
Feb 23	37.32	39.45	34.63	43.92		
Feb 25	44.12	46.20	44.83	37.79		
Mean	40.55	43.74	41.19	43.07	41.04 ±4.17	
Week 4						
Mar 1	37.21	31.46	36.60	47.48		
Mar 2	39.53	39.77	40.27	32.22		
Mar 3	38.04	44.09	41.85	33.78		
Mean	38.26	38.44	39.57	37.83	38.53 ±4.70	
Week 5						
Mar 16	44.17	43.59	50.83	37.09		
Mar 20	39.56	39.73	46.81	39.08		
Mar 22	34.03	32.95	43.02	31.43		
Mean	39.25	38.76	46.89	35.87	41.19 ±2.27	
Anthesis date	Feb 22	Feb 26	Feb 19	Feb 22		
Durum wheats						
	D2	D74	D75	D79	D82	Mean ±SE
Week 1						
Feb 2	32.34				37.78	
Feb 3	34.84				41.01	
Feb 5	43.15	36.90	50.71	49.61	47.15	
Mean	36.78	36.90	50.71	49.61	41.98	43.62 ±2.45

Table 5. Continued.

Date		Pmax [μmol $O_2.m^{-2}.s^{-1}$]			
Durum wheats					
	D2	D74	D75	D79	D82	Mean ±SE
Week 2						
Feb 18	40.09	39.96	48.62	39.89	47.59	
Feb 19	40.04	47.71	43.32	43.58	46.12	
Mean	40.06	43.84	45.97	41.74	46.86	45.00 ±4.01
Week 3						
Feb 22	34.61	43.62	41.61	45.59		
Feb 23	23.22	39.40		42.02	43.37	
Feb 25	34.11	27.15	44.25	40.31	55.93	
Mean	30.65	36.72	42.93	42.64	49.65	39.40 ±2.94
Week 4						
Mar 1	21.00	28.47		26.49	37.18	
Mar 2	26.14	46.84	37.96	40.65	40.50	
Mar 3	29.66	46.00	42.40	36.47	40.14	
Mean	25.60	40.44	40.18	34.54	39.27	38.54 ±3.33
Week 5						
Mar 16	36.19	35.42	42.40	37.37		
Mar 20	36.25	36.71	37.61	45.20		
Mar 22	37.08	45.26	49.86	41.02		
Mean	36.51	39.13	43.29	41.20		39.15 ±3.15
Anthesis date	Mar 3	Feb 27	Mar 1	Feb 26	Feb 23	
Synthetics (*Ae. squarrosa* x durum)					
	S13	S43	S22	Mean ±SE
Week 1				
Feb 2	37.42	37.02		
Feb 3	34.64	39.82		
Feb 5	45.28	48.29	48.43	
Mean	39.11	41.71	48.43	44.75 ±2.49
Week 2				
Feb 18	42.86	43.68	46.37	
Feb 19	41.29	35.05	43.14	
Mean	42.08	39.36	44.76	42.33 ±1.88

Table 5. Continued.

Date	Pmax [μmol $O_2.m^{-2}.s^{-1}$]				
Synthetics (*Ae. squarrosa* x durum)					
	S13	S43	S22	Mean ±SE	
Week 3					
Feb 22	41.66	45.34	41.56		
Feb 23	31.40	48.35	33.84		
Feb 25	47.73	38.63	48.75		
Mean	40.26	44.11	41.38	41.44 ±3.61	
Week 4					
Mar 1	39.51	34.53	38.32		
Mar 2	42.96	40.23	32.83		
Mar 3	43.83	45.85	39.40		
Mean	42.10	40.20	36.85	39.72 ±2.04	
Week 5					
Mar 16	45.21	51.81	53.53		
Mar 20	42.97	41.06	49.66		
Mar 22	46.50	41.14	48.32		
Mean	44.89	44.67	50.50	46.99 ±3.50	
Anthesis date	Feb 28	Mar 12	Feb 22		
Crosses (synthetic x bread)					
	SB2	SB5	SB17	SB18	Mean ±SE
Week 1					
Feb 2	44.65	38.27	34.02	46.55	
Feb 3	34.42	40.27	35.08	40.96	
Feb 5	37.39	45.06	44.82	50.56	
Mean	38.82	41.20	37.97	46.02	41.35 ±3.40
Week 2					
Feb 18	44.57	49.61	49.20	45.81	
Feb 19	40.97	45.36	36.28	46.26	
Mean	42.77	47.48	42.74	46.04	44.49 ±3.23
Week 3					
Feb 22	44.83	50.14	46.19	40.66	
Feb 23	35.35	43.14	42.57	41.07	
Feb 25	35.95	47.94	36.29	41.62	
Mean	38.71	47.07	41.68	41.12	40.49 ±4.15

Table 5. Continued.

Date	Pmax [μmol $O_2.m^{-2}.s^{-1}$]				
Crosses (synthetic x bread)					
	SB2	SB5	SB17	SB18	Mean ±SE
Week 4					
Mar 1	36.09	40.86	45.28	41.71	
Mar 2	30.17	43.11	45.10	39.71	
Mar 3	29.78	46.22	39.84	32.68	
Mean	32.01	43.40	43.41	38.03	39.20 ±2.98
Week 5					
Mar 16	34.45	45.52	46.07	33.47	
Mar 20	34.85	50.06	44.35	34.57	
Mar 22	29.89	42.79	49.76	44.90	
Mean	33.06	46.12	46.73	37.47	42.78 ±3.52
Anthesis date	Feb 18	Feb 19	Feb 20	Feb 15	

Table 6. Analysis of Pmax data.

a) ANOVA

Source	**DF**	**Sum of squares**	**Mean square**
Week	3	903.25	301.08 **
Group	3	214.97	71.66 *
Variety	12	1554.45	129.54 **
Error	167	4412.97	26.42

The data for Feb 2 and 3 were omitted, and Feb 5 was considered together with Feb 18 and 19. * indicates significant to 5% and ** to 0.01%

b) Mean Pmax values by group

Group	**Mean Pmax**
Bread	41.23 ab
Durum	40.38 b
Synthetic	43.04 a
Cross	41.73 ab

Different letters indicate differences at a confidence level of 5% by LSD analysis.

c) Orthogonal contrast analysis

	Prob
Synthetic *v* Bread + Durum	0.023
Synthetic *v* Bread	0.104
Synthetic *v* Cross	0.238
Cross *v* Bread	0.626

Prob is the probability that the two specified groups have no difference in P max.

flag leaf. Only the crosses group shows variation of chlorophyll a/b ratio. Significant variation in biomass yield is seen only within the synthetics. There is significant variation in flag leaf area for all groups.

Tables 10 and **11** show the lines of the synthetics and of the crosses ranked by biomass yield, and also by biomass accumulation per day. The ranking of the two parameters differs in only a few cases. The range of biomass yield within the synthetics is very large. Within this group, correlations with chlorophyll a/b ratio and flag leaf area were -0.279 and 0.295, respectively (neither was significant). The range of biomass yield within the crosses was much smaller, but in this case correlations with leaf area and chlorophyll a/b ratio were -0.508* and 0.392, respectively.

Stability of chlorophyll a/b over time

Figure 2 shows the chlorophyll a/b ratio measured from flag leaves removed from four individual plots, of one line from each group, on four different dates. This shows that during the life of the flag leaf the chlorophyll a/b ratio was decreasing. We have no evidence to distinguish between the two possibilities that this is due to changing external environment, or flag leaf age. However, it appears to be important to sample flag leaves at the same time if different lines are to be compared.

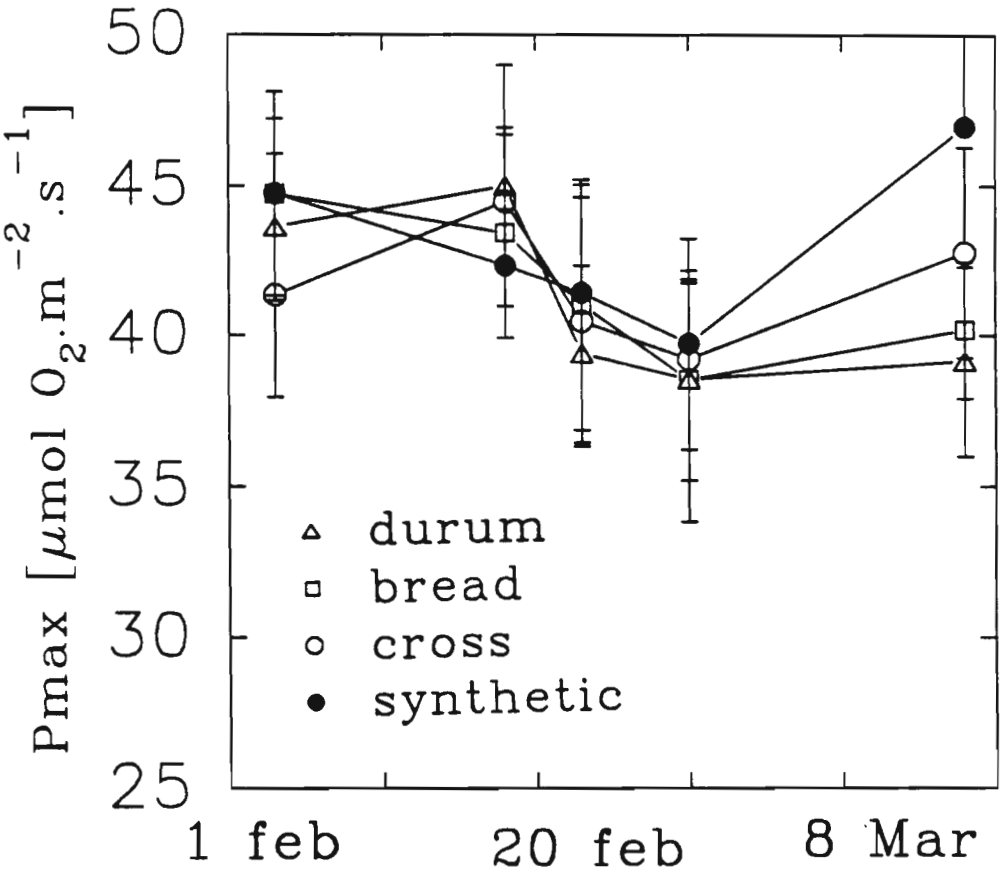

Figure 1. Plotting the mean values for each group shows that there is variation in Pmax with time, which is consistent between groups.

Staygreen characteristics
One characteristic that should be favorable for wheat yields is that the flag leaf should remain photosynthetically active until as close to the end of grain-fill as possible. In this trial, we gauged this characteristic by measuring the interval between the date when the flag leaf retains 50% of the chlorophyll and that of physiological maturity of the spike (complete loss of chlorophyll from spike and peduncle). If flag leaf chlorophyll was retained almost until physiological maturity, we considered this as a good attribute. Thus, we arbitrarily set a delay of 2 days or less between 50% chlorophyll retention and maturity as "good", and a delay of 6 or more days as "poor". The results in **Table 12** show it is quite clear the crosses generally are good compared to the other groups.

Screening diploid species
Table 13 shows the results of an initial screening of three diploid species; *Aegilops squarrosa*, *Triticum urartu*, and *Triticum boeoticum*, for Pmax and also chlorophyll a/b ratio. Of the three species considered, *T. boeoticum* gave a Pmax significantly higher than the other two species. However, in this case, it was *T. urartu* that gave the highest chlorophyll a/b ratio. The chlorophyll a/b ratios are generally higher than those measured in the main trial, except for the synthetics.

The Pmax values for the diploids are lower than those generally measured in the main trial. We attribute this to the fact that, although the main trial was conducted under near optimal management, the diploids were not grown under optimal conditions. The level of nitrogen was probably not sufficient for maximum photosynthetic potential to be realized, and at times the plants suffered from water stress.

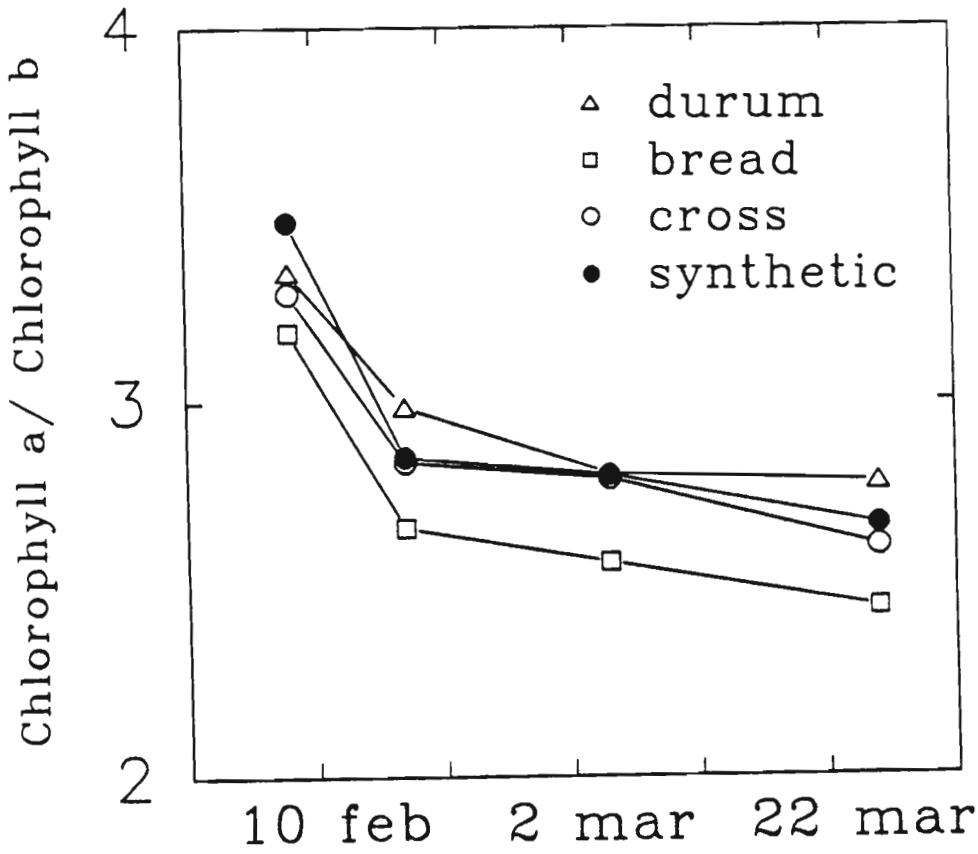

Figure 2. Chlorophyll a/b ratio measured from flag leaves removed from four individual plots, of one line from each group, on four different dates.

Table 7. Results of correlation analysis between Pmax and other measured parameters for 16 selected lines.

Parameter	Correlation with Pmax			
	Week 2	Week 3	Week 4	Week 5
Biomass yield	-0.531 5%	n.s.	n.s.	n.s.
Biomass/day	-0.396 15%	-0.468 10%	n.s.	n.s.
Grains/spike	n.s.	n.s.	n.s.	n.s.
1000-grain weight	n.s.	n.s.	-0.515 5%	n.s.
Flag leaf area	-0.484 10%	n.s.	n.s.	n.s.
Flag leaf weight	-0.582 5%	n.s.	n.s.	n.s.
Flag leaf spec weight	-0.477 10%	n.s.	n.s.	n.s.
Chlorophyll a/b	n.s.	0.401 15%	0.388 15%	0.455 10%
[Chlorophyll]	n.s.	n.s.	n.s.	n.s.

Only correlations significant to 15% are shown. The significance level is given below the correlation coefficient (r) in each case.

Table 8. Correlations for all lines used in the trial.[a]

	Chlorophyll a/b	Flag leaf area
Biomass yield	0.190	0.332**
Biomass/day	0.097	0.208
Growth rate	0.377**	0.337**

[a] D8 was omitted from the analysis due to missing Chl a/b values.
** indicates significant to 1%.

Table 9. Results of ANOVA analyses within groups for measured parameters.

Parameter	Bread	Durum	Synthetic	Cross
Grain yield	n.s.	n.s.	**	**
Biomass yield	n.s.	n.s.	***	n.s.
Harvest index	n.s.	n.s.	***	*
Duration of crop	n.s.	n.s.	***	n.s.
Biomass accum. rate	n.s.	n.s.	***	n.s.
Grains/spike	n.s.	n.s.	***	*
Spikes/m^2	**	n.s.	**	n.s.
Grains/m^2	*	n.s.	***	***
1000-grain weight	***	n.s.	***	***
Flag leaf area	***	***	***	***
Flag leaf weight	***	***	***	***
Spec. weight	n.s.	**	*	*
Chlorophyll a/b	n.s.	n.s.	n.s.	***
Chlorophyll conc.	***	***	n.s.	***

Discussion

One aim of this project was to determine whether it is possible to introduce photosynthetic characteristics of diploid species into bread wheat lines. The synthetics as a group have a high chlorophyll a/b ratio, a characteristic which they almost certainly retained from their *Ae. squarrosa* parents. The low harvest index is an undesirable characteristic, which is presumably also obtained from the diploid parent. Characteristics that appear to have been inherited from their durum parents are large grain size and large flag leaf size.

For the subsection of lines measured, we found that the Pmax of the synthetics was slightly but significantly greater than that of the other groups. Unlike previous studies (R.B. Austin, pers. comm.), we also found that the biomass yield and the rate of biomass accumulation were significantly higher in the synthetics than other groups. Within the synthetics, there is a very wide range in the biomass yield, but there is no obvious parental connection between lines with high biomass yield.

Table 10. Synthetics ranked by biomass yield.

Line	Biomass yield ($t.ha^{-1}$)	Biomass/d ranking
S21	25.78 A	1
S7	23.17 AB	2
S72	20.83 BC	3
S56	20.31 BCD	5
S22	19.45 BCDE	4
S40	18.63 CDEF	6
S57	18.27 CDEFG	7
S65	18.16 CDEFG	8
S55	17.11 CDEFGH	9
S60	16.61 CDEFGHI	10
S49	15.91 DEFGHIJ	11
S91	15.77 EFGHIJ	14
S33	15.50 EFGHIJ	12
S13	14.67 FGHIJ	13
S51	13.82 GHIJ	15
S17	13.55 HIJ	15
S54	13.36 HIJ	15
S16	12.23 IJ	16
S43	11.69 J	17

Different letters indicate significantly different to 5% confidence level.

Table 11. Crosses ranked by biomass yield.

Line	Biomass yield ($t.ha^{-1}$)	Biomass/d ranking
SB12	15.45 A	1
SB1	15.23 AB	2
SB2	14.91 ABC	3
SB15	14.11 ABC	4
SB8	13.99 ABC	5
SB18	13.71 ABC	6
SB11	13.45 ABC	7
SB13	12.90 ABC	9
SB19	12.84 ABC	8
SB14	12.32 ABC	10
SB17	12.31 ABC	11
SB4	11.56 ABC	14
SB3	11.53 ABC	12

Table 11. Continued.

Line	Biomass yield [t.ha^{-1}]	Biomass/d ranking
SB6	11.52 ABC	15
SB7	11.43 ABC	13
SB16	11.41 ABC	17
SB5	10.64 ABC	18
SB10	10.42 BC	16
SB9	10.10 C	19

Different letters indicate significantly different to 5% confidence level.

Table 12. Staygreen characteristics of the four groups.

Bread	Durum	Synthetic	Cross
B113	D74	S7	SB1 +
B114 -	D75 -	S91	SB2 +
B119	D77	S13 -	SB3 +
B120 +	D78	S16 -	SB4 +
B1	D79 -	S17	SB5 +
B2	D81 -	S21	SB6
B3	D82	S22 -	SB7 +
B4	D89	S33	SB8 +
B5	D92	S40 -	SB9 +
B6	D93	S43	SB10
B7	D2	S49 -	SB11 +
B8	D3 -	S51 -	SB12 +
B9	D8	S54	SB13 +
		S55	SB14 +
		S56	SB15 +
		S57	SB16
		S60 -	SB17 +
		S65	SB18 +
		S72	SB19 +

Staygreen was assessed by the interval between 50% chlorophyll remaining in the flag leaf and physiological maturity; + = good staygreen (<2 days) and - = poor staygreen (> 6 days).

Table 13. Maximum photosynthetic rates of diploid varieties.

Diploid species	Accession number	Pmax (μmol $O_2.m^{-2}.s^{-1}$)	Mean	Chl a/b	Mean
Ae. squarrosa (D genome)	189	32.98		2.805	
	191	25.77		3.065	
	213	27.91	28.05 b	2.828	2.805 b
	214	25.95		2.914	
	224	27.64		2.954	
T. urartu (A genome)	556	27.20		2.876	
	562	28.59		2.600	
	542	33.78	30.08 b	2.670	2.913 a
	544	33.57		2.793	
	549	27.28		2.793	
T. boeoticum (A genome)	91	29.21		2.721	
	36	36.69		2.937	
	75	35.27	34.09 a	2.697	2.746 b
	89	35.05		2.950	
	44	34.21		2.715	

The P max value given for each accession is the mean of 4 measurements on each of 3 days. The chlorophyll a/b ratios are the mean of 4 repeat measurements on a sample consisting of 4 flag leaves.

The letters after the mean values indicate significant differences to 5% confidence level calculated by a contrast analysis.

The characteristics described above are not apparent in the crosses. It should be pointed out that the synthetic parents of the crosses are not generally included in this trial. The crosses are agronomically much better lines than the synthetics, in that, for example, they have a higher harvest index. The chlorophyll a/b ratio, Pmax, biomass yield, and grain size are all indistinguishable from the bread wheats. However, it is noticeable that the crosses have a flag leaf size that is significantly smaller than that of the bread wheats. The selection of the crosses was primarily on the basis of disease resistance. It is possible that this favoured small leaves, which would tend to give a more open canopy that could dry more quickly, and is less suitable for propagating disease. This emphasizes the point that, in order to determine whether favorable photosynthetic characteristics can be passed onto crosses, it is important to identify and to use relevant selection criteria. Otherwise, visual selection of other traits deemed important could lead to the discarding of lines carrying high Pmax.

Our results do not give strong support for the use of chlorophyll a/b ratio as a selection criterion. The positive evidence depends on the observations that, as a group, the synthetics have a high chlorophyll a/b ratio, and high Pmax and biomass yield, and that chlorophyll a/b ratio has a more consistent correlation with Pmax than other characteristics. Contrary to this, however, considering the groups separately, there are

negative correlations between chlorophyll a/b ratio and biomass yield for synthetics and crosses, which in the latter case is significant to 5%.

Another possible selection criterion that has emerged from this trial is flag leaf area, which is significantly greater in the synthetics than for other groups. In this case, the correlation with biomass within the synthetics is positive, although insignificant, and within the crosses negative, but insignificant.

Suggestions for future work

The results obtained so far in this study give few definite answers. However, they suggest that there may be potential to increase biomass yield by introducing genes from diploid ancestors of bread wheats, and point to future studies that should be done to advance this work:

- High biomass-producing synthetics could be selected (Table 10) to be used to make a random population of crosses. This population of crosses could then be used to test the inheritance of high Pmax and high biomass yield, and selection criteria. Thus, within this population, measurements of biomass yield, chlorophyll a/b ratio, and flag leaf area should be made. The duration of each line would also need to be measured for the comparison of rate of biomass accumulation. (One possible criticism of the trial reported here, is that duration was measured from emergence until loss of chlorophyll from the flag leaf, and took no account of the contribution of head photosynthesis, which could have been significant for the synthetics.)

- A wider screening of diploid species for high Pmax (or high chlorophyll a/b) should be carried out (under high nitrogen conditions), for the future production of a wider range of synthetics.

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Appendix 1. Selection of the Synthetics.

The synthetics used in this study were chosen from a trial run the previous year (F709). In a single repetition trial, with checks, 73 synthetic lines were grown. From these, 18 synthetics were chosen, on the basis of biomass yield and resistance to lodging. The data of the lines chosen are shown below, together with the mean values for the 73 lines. It is clear that the yield of the selected lines is higher than the whole population, but no other consistent differences are seen.

Line	Biomass yield ($t.ha^{-1}$)	Grain yield ($t.ha^{-1}$)	Date of anthesis	Height of plant (cm)	Flag leaf area (cm^2)
S7	18.679	1.847	14 Mar	135	44.1
S13	19.403	2.983	8 Mar	105	68.3
S16	15.824	2.570	11 Mar	100	57.0
S17	19.500	3.194		102	44.6
S21	20.101	3.828	9 Mar	132	64.5
S22	23.775	4.332	2 Mar	105	53.7
S33	19.948	3.396	7 Mar	110	62.0
S40	17.102	1.865	2 Mar	105	48.3
S43	14.761	2.688	11 Mar	95	56.6
S49	21.377	3.671	13 Mar	133	33.8
S51	16.171	2.621	10 Mar	135	38.3
S54	17.498	2.305	11 Mar	105	21.3
S55	17.184	3.086	11 Mar	122	37.6
S56	20.216	3.771	9 Mar	123	32.9
S57	19.556	2.654	14 Mar	115	50.8
S60	18.834	2.434	28 Feb	110	41.6
S65	16.819	3.371	12 Mar	120	56.1
S72	15.812	3.376	10 Mar	130	39.6
Mean	18.476	3.000	9 Mar	116	47.3
S.D.	2.21	0.665	4 days	13	12.1
Data for 73 synthetics included in F709					
Mean	15.936	2.228	10 Mar	116	46.0
S.D.	3.162	0.882	6 days	12	16.4

Appendix 2. Mean Data Across Three Reps.

YIELD DATA

VARIETY	GROUP	BIOMASS	GRAIN	H.I.
B113	1	11057.3	6540.3	0.59
B114	1	12249.0	6355.0	0.52
B119	1	8654.7	6836.3	0.35
B120	1	14113.0	5815.3	0.45
B1	1	10708.3	6653.3	0.62
B2	1	7687.0	6595.3	0.38
B3	1	13401.0	6324.3	0.48
B4	1	13096.7	7047.7	0.54
B5	1	11100.0	6661.3	0.60
B6	1	11489.0	6665.0	0.58
B7	1	16040.3	6169.3	0.38
B8	1	9515.7	5453.0	0.57
B9	1	14656.7	7158.7	0.49
D74	2	15354.3	6575.7	0.47
D75	2	11931.3	6573.7	0.55
D77	2	8601.7	7011.3	0.36
D78	2	10940.0	6382.0	0.60
D79	2	10855.3	5202.3	0.48
D81	2	14270.0	6608.3	0.50
D82	2	11087.0	5644.0	0.51
D89	2	13031.0	6094.0	0.47
D92	2	12369.3	6011.0	0.49
D93	2	13673.3	5447.3	0.41
D2	2	13651.3	5497.7	0.44
D3	2	13498.3	5787.3	0.47
D8	2	17150.7	5360.7	0.31
S7	3	23170.3	3737.3	0.16
S91	3	15766.7	3630.3	0.23
S13	3	14669.7	3906.0	0.27
S16	3	12227.3	3303.7	0.27
S17	3	13550.7	4555.3	0.34
S21	3	25781.0	4862.7	0.19
S22	3	19454.0	5123.3	0.26
S33	3	15501.3	3614.3	0.24
S40	3	18630.0	4697.7	0.25
S43	3	11692.3	3034.3	0.27
S49	3	15908.0	2750.7	0.17
S51	3	13818.3	2654.7	0.19
S54	3	13362.0	5424.3	0.41
S55	3	17106.7	3524.0	0.20
S56	3	20308.3	4532.0	0.23
S57	3	18274.3	2899.3	0.15
S60	3	16614.3	5272.0	0.32
S65	3	18160.0	3683.7	0.20
S72	3	20827.0	4068.3	0.20
SB1	4	15228.3	4909.0	0.32
SB2	4	14909.0	5368.3	0.36
SB3	4	11525.0	4426.0	0.40
SB4	4	11556.3	5701.3	0.51

YIELD DATA

VARIETY	GROUP	BIOMASS	GRAIN	H.I.
SB5	4	10643.0	4427.0	0.41
SB6	4	11516.3	6538.3	0.57
SB7	4	11431.7	7092.0	0.62
SB8	4	13991.7	7873.3	0.58
SB9	4	10101.0	4694.3	0.47
SB10	4	10417.7	4402.0	0.44
SB11	4	13449.7	7039.3	0.55
SB12	4	15453.7	6418.3	0.42
SB13	4	12895.7	6004.0	0.51
SB14	4	9240.0	5634.0	0.31
SB15	4	14105.3	5653.7	0.40
SB16	4	8557.0	5475.3	0.30
SB17	4	12313.7	6678.0	0.54
SB18	4	13712.0	5692.0	0.43
SB19	4	12839.3	6036.7	0.48

Biomass: Biomass yield [Kg_1Ha^{-1}]
Grain: Grain yield [$Kg.Ha^{-1}$]

DATA FROM BIOMASS CUTS

VARIETY	GROUP	Biom.1	Biom.2	% growth
B113	1	386.7	513.3	33.7
B114	1	295.8	465.0	57.5
B119	1	328.3	641.4	99.9
B120	1	299.2	554.2	86.8
B1	1	312.5	520.0	68.9
B2	1	255.0	500.0	103.2
B3	1	240.0	504.2	129.9
B4	1	345.0	479.2	39.7
B5	1	320.0	495.0	58.2
B6	1	334.2	506.7	57.0
B7	1	421.4	664.4	57.2
B8	1	391.7	599.4	54.1
B9	1	325.8	537.5	69.1
D74	2	205.0	435.8	120.0
D75	2	291.7	506.7	76.4
D77	2	279.2	566.7	103.6
D78	2	285.8	466.7	81.3
D79	2	253.3	346.7	35.7
D81	2	341.9	433.9	27.3
D82	2	350.0	684.2	94.5
D89	2	375.8	600.8	63.4
D92	2	369.2	629.2	74.3
D93	2	297.5	576.7	97.8
D2	2	322.5	572.5	87.8

DATA FROM BIOMASS CUTS

VARIETY	GROUP	Biom.1	Biom.2	% growth
D3	2	232.5	423.3	115.1
D8	2	270.0	352.5	30.3
S7	3	216.7	391.7	89.7
S91	3	121.7	295.0	167.4
S13	3	292.5	598.3	110.6
S16	3	137.5	253.3	95.7
S17	3	193.3	367.5	89.9
S21	3	326.4	525.0	71.9
S22	3	210.8	565.8	187.9
S33	3	279.2	619.2	133.7
S40	3	255.0	324.2	44.4
S43	3	338.9	590.0	74.4
S49	3	131.7	358.3	182.9
S51	3	228.3	321.7	73.7
S54	3	283.3	505.8	74.4
S55	3	230.8	377.5	61.1
S56	3	231.7	492.5	140.6
S57	3	242.5	392.5	63.5
S60	3	257.5	475.0	100.6
S65	3	269.2	358.3	32.8
S72	3	215.0	466.7	113.5
SB1	4	456.4	646.9	42.9
SB2	4	427.5	535.8	24.9
SB3	4	376.7	636.7	69.3
SB4	4	390.8	604.2	55.2
SB5	4	389.7	571.7	46.6
SB6	4	329.2	590.8	85.5
SB7	4	372.5	558.3	49.6
SB8	4	389.2	505.0	30.4
SB9	4	346.7	507.5	49.2
SB10	4	300.8	535.0	78.9
SB11	4	294.2	430.8	50.4
SB12	4	386.7	550.0	43.5
SB13	4	390.8	583.3	48.7
SB14	4	364.7	565.6	57.0
SB15	4	370.0	615.8	68.3
SB16	4	301.7	511.7	69.6
SB17	4	386.7	618.1	61.9
SB18	4	441.7	665.8	52.6
SB19	4	405.0	622.5	54.2

Biom.1: 1st biomass cut [Kg from cut of 0.4 m^2]
Biom.2: 2nd biomass cut [Kg from cut of 0.4 m^2]
% growth: (Biom.2 - Biom.1)/Biom.1 * 100%

RATE OF BIOMASS ACCUMULATION

VARIETY	GROUP	Bio Yld	Duration	Bio/Day
B113	1	11057	120.3	91.88
B114	1	12249	132.3	92.50
B119	1	8655	118.3	73.35
B120	1	14113	122.0	115.19
B1	1	10708	121.3	88.30
B2	1	7687	120.0	64.39
B3	1	13401	127.7	104.74
B4	1	13097	119.0	110.16
B5	1	11100	121.3	91.65
B6	1	11489	124.0	92.63
B7	1	16040	117.0	137.15
B8	1	9516	117.7	80.92
B9	1	14657	127.7	114.71
D74	2	15354	128.7	119.26
D75	2	11931	123.7	96.50
D77	2	8602	125.0	67.44
D78	2	10940	119.7	92.16
D79	2	10855	126.0	85.50
D81	2	14270	123.0	116.24
D82	2	11087	80.3	59.50
D89	2	13031	117.7	110.74
D92	2	12369	117.7	105.07
D93	2	13673	126.0	108.49
D2	2	13651	119.7	114.40
D3	2	13498	126.7	106.52
D8	2	17151	134.0	127.99
S7	3	23170	136.0	170.39
S91	3	15767	137.0	115.30
S13	3	14670	123.0	118.90
S16	3	12227	120.0	101.69
S17	3	13551	0.0	0.00
S21	3	25781	133.3	193.34
S22	3	19454	127.3	151.81
S33	3	15501	129.7	119.19
S40	3	18630	128.3	145.92
S43	3	11692	132.0	88.40
S49	3	15908	130.0	122.27
S51	3	13818	134.7	102.70
S54	3	13362	0.0	0.00
S55	3	17107	134.3	127.28
S56	3	20308	135.0	150.61
S57	3	18274	136.0	134.20
S60	3	16614	131.0	126.70
S65	3	18160	137.3	132.20
S72	3	20827	135.3	154.35
SB1	4	15228	117.0	130.19
SB2	4	14909	116.0	128.55
SB3	4	11525	117.3	98.31
SB4	4	11556	120.7	95.35

RATE OF BIOMASS ACCUMULATION

VARIETY	GROUP	Bio Yld	Duration	Bio/Day
SB5	4	10643	120.7	88.24
SB6	4	11516	121.0	94.85
SB7	4	11432	118.3	96.61
SB8	4	13992	119.7	117.04
SB9	4	10101	118.7	85.15
SB10	4	10418	115.0	90.59
SB11	4	13450	119.0	113.46
SB12	4	15454	120.3	128.43
SB13	4	12896	119.7	107.74
SB14	4	9240	117.3	79.69
SB15	4	14105	117.7	119.92
SB16	4	8557	127.0	67.87
SB17	4	12314	119.0	103.55
SB18	4	13712	118.7	115.50
SB19	4	12839	118.7	108.42

Bio Yld: Biomass yield [$Kg.Ha^{-1}$]
Duration: Days from 50% seedling emergence until 50% staygreen of the flag leaves.
Bio/Day: Bio Yld/Duration

HARVEST COMPONENTS

VARIETY	GROUP	GrWt1000	Sp/m2	Grns/m2	Grns/Sp
B113	1	35.7	408.7	18346.3	44.5
B114	1	40.8	456.7	15575.7	34.2
B119	1	33.2	731.0	20655.7	29.3
B120	1	38.7	475.7	15019.0	35.2
B1	1	37.7	474.7	17746.0	37.6
B2	1	38.8	569.3	16994.7	29.8
B3	1	38.4	426.3	16477.0	39.4
B4	1	34.4	504.7	20469.3	41.6
B5	1	38.3	437.3	17376.0	39.7
B6	1	42.1	411.3	15804.7	38.5
B7	1	32.5	479.3	18909.0	39.4
B8	1	38.9	321.0	14010.7	43.8
B9	1	38.9	415.0	18380.7	45.2
D74	2	45.3	375.3	14519.0	41.4
D75	2	43.2	316.7	15305.7	48.3
D77	2	49.2	439.0	14246.3	35.2
D78	2	47.9	298.0	13504.0	45.4
D79	2	50.7	310.7	10268.0	32.5
D81	2	49.3	450.7	13450.7	30.8
D82	2	44.0	430.0	12831.0	29.9

HARVEST COMPONENTS

VARIETY	GROUP	GrWt1000	Sp/m2	Grns/m2	Grns/Sp
D89	2	43.6	354.0	14000.7	40.2
D92	2	78.7	287.0	8667.0	30.9
D93	2	42.3	383.0	12833.0	33.5
D2	2	33.5	417.3	6786.7	17.2
D3	2	51.5	403.7	11272.0	30.3
D8	2	42.9	278.7	12450.3	45.5
S7	3	46.5	411.0	8060.3	19.6
S91	3	47.3	324.3	7626.7	23.4
S13	3	40.8	373.3	9564.0	26.3
S16	3	46.0	240.3	7224.3	29.7
S17	3	37.5	366.7	12394.7	34.6
S21	3	52.5	455.3	9227.7	20.2
S22	3	49.5	399.3	10369.7	26.2
S33	3	43.1	297.0	8579.0	29.2
S40	3	48.7	407.3	9649.0	23.9
S43	3	39.7	442.3	7654.7	17.9
S49	3	48.8	292.7	5636.3	19.2
S51	3	45.5	277.7	5840.7	21.0
S54	3	37.1	403.3	14596.3	36.2
S55	3	46.7	312.7	7592.0	24.3
S56	3	41.6	456.0	10926.3	24.0
S57	3	34.9	359.3	8140.7	22.7
S60	3	43.1	366.3	12229.3	33.7
S65	3	43.5	334.3	8520.3	25.3
S72	3	51.7	418.3	7899.3	18.6
SB1	4	42.5	496.0	11580.7	23.3
SB2	4	43.1	460.7	12454.3	27.0
SB3	4	44.7	375.0	9900.3	27.5
SB4	4	44.9	419.3	12724.0	31.1
SB5	4	37.6	454.3	11813.7	25.6
SB6	4	32.8	485.3	19958.7	42.3
SB7	4	37.5	476.7	19041.7	40.2
SB8	4	35.2	562.7	22343.3	40.3
SB9	4	34.9	409.3	13426.7	33.6
SB10	4	31.7	349.3	13905.0	39.6
SB11	4	46.5	494.3	15074.3	31.0
SB12	4	45.1	484.3	14238.0	29.6
SB13	4	38.1	514.3	15684.3	32.8
SB14	4	33.3	519.3	16861.7	32.9
SB15	4	36.0	440.7	15702.0	35.8
SB16	4	36.8	544.0	14874.0	27.4
SB17	4	43.3	505.0	15634.0	30.7
SB18	4	40.9	487.3	13909.0	28.6
SB19	4	42.5	491.7	14205.0	29.0

GrWt1000: Thousand grain weight [g]
Sp/m2: Spikes per m^2
Grns/m2: Grains per m^2
Grns/Sp: Grains per spike

CHLOROPHYLL CHARACTERISTICS OF FLAG LEAVES

VARIETY	GROUP	Chl a/b	[Chl]
B113	1	2.744	46.367
B114	1	2.674	43.925
B119	1	2.747	46.075
B120	1	2.813	44.967
B1	1	2.661	41.892
B2	1	2.813	47.333
B3	1	2.572	48.308
B4	1	2.628	43.325
B5	1	2.589	45.675
B6	1	2.634	48.150
B7	1	2.672	43.525
B8	1	2.710	45.050
B9	1	2.700	41.725
D74	2	2.664	50.517
D75	2	2.923	41.858
D77	2	2.752	46.892
D78	2	2.788	47.533
D79	2	2.739	44.075
D81	2	2.634	45.283
D82	2	2.744	47.708
D89	2	2.673	45.975
D92	2	2.707	44.983
D93	2	2.692	45.200
D2	2	2.646	50.175
D3	2	2.705	49.433
D8	2	1.941	39.442
S7	3	2.798	41.492
S91	3	2.814	39.892
S13	3	2.769	41.275
S16	3	2.854	36.517
S17	3	2.856	42.158
S21	3	2.786	42.492
S22	3	2.778	44.592
S33	3	2.827	39.842
S40	3	2.788	43.433
S43	3	2.827	42.750
S49	3	2.940	41.958
S51	3	2.824	41.500
S54	3	2.805	43.742
S55	3	2.810	38.542
S56	3	2.822	40.758
S57	3	2.709	43.233
S60	3	2.739	43.892
S65	3	2.893	42.808
S72	3	2.802	42.433
SB1	4	2.595	44.175
SB2	4	2.621	42.667
SB3	4	2.738	44.367
SB4	4	2.632	46.250

CHLOROPHYLL CHARACTERISTICS OF FLAG LEAVES

VARIETY	GROUP	Chl a/b	[Chl]
SB5	4	2.782	46.950
SB6	4	2.819	46.317
SB7	4	2.786	44.050
SB8	4	2.804	44.325
SB9	4	2.744	40.708
SB10	4	2.716	40.275
SB11	4	2.725	48.192
SB12	4	2.632	47.683
SB13	4	2.641	44.008
SB14	4	2.664	44.875
SB15	4	2.655	44.733
SB16	4	2.756	45.500
SB17	4	2.700	48.083
SB18	4	2.622	49.925
SB19	4	2.645	49.050

Chl a/b: chlorophyll a / chlorophyll b of flag leaves
[Chl]: Chlorophyll concentration of flag leaves measured by SPAD meter [SPAD units]

FLAG LEAF CHARACTERISTICS

VARIETY	GROUP	Lf area	Lf Wt	Wt/area
B113	1	42.21	0.200	0.0047
B114	1	51.73	0.247	0.0048
B119	1	43.01	0.200	0.0046
B120	1	38.79	0.180	0.0046
B1	1	33.31	0.175	0.0053
B2	1	31.15	0.147	0.0047
B3	1	52.47	0.271	0.0052
B4	1	30.66	0.167	0.0055
B5	1	44.74	0.225	0.0050
B6	1	37.10	0.187	0.0050
B7	1	26.56	0.142	0.0054
B8	1	37.25	0.186	0.0050
B9	1	55.89	0.293	0.0052
D74	2	46.54	0.251	0.0054
D75	2	39.24	0.187	0.0048
D77	2	38.05	0.209	0.0055
D78	2	46.75	0.225	0.0048
D79	2	51.79	0.167	0.0032
D81	2	48.04	0.231	0.0048
D82	2	44.00	0.200	0.0046
D89	2	38.29	0.189	0.0049
D92	2	35.05	0.191	0.0054
D93	2	44.62	0.229	0.0051
S2	2	37.60	0.189	0.0050
S3	2	53.58	0.276	0.0051

FLAG LEAF CHARACTERISTICS

VARIETY	GROUP	Lf area	Lf Wt	Wt/area
S8	2	12.17	0.053	0.0014
S7	3	51.93	0.258	0.0050
D91	3	50.05	0.273	0.0054
S13	3	47.23	0.256	0.0054
S16	3	40.41	0.160	0.0042
S17	3	37.36	0.198	0.0053
S21	3	54.64	0.198	0.0036
S22	3	50.26	0.271	0.0054
S33	3	60.14	0.307	0.0051
S40	3	45.70	0.251	0.0055
S43	3	52.67	0.243	0.0046
S49	3	36.52	0.186	0.0051
S51	3	32.17	0.176	0.0055
S54	3	45.65	0.233	0.0051
S55	3	37.39	0.193	0.0052
S56	3	30.08	0.173	0.0058
S57	3	50.76	0.160	0.0032
S60	3	40.53	0.227	0.0056
S65	3	53.28	0.248	0.0047
S72	3	54.82	0.286	0.0052
SB1	4	28.99	0.133	0.0046
SB2	4	28.24	0.138	0.0049
SB3	4	33.34	0.153	0.0046
SB4	4	32.96	0.158	0.0048
SB5	4	33.63	0.107	0.0033
SB6	4	28.87	0.144	0.0050
SB7	4	29.59	0.149	0.0050
SB8	4	31.25	0.158	0.0051
SB9	4	31.86	0.151	0.0047
SB10	4	29.40	0.147	0.0050
SB11	4	21.29	0.118	0.0055
SB12	4	21.17	0.111	0.0052
SB13	4	30.52	0.165	0.0054
SB14	4	27.27	0.138	0.0050
SB15	4	38.09	0.189	0.0050
SB16	4	46.73	0.216	0.0046
SB17	4	40.89	0.211	0.0052
SB18	4	33.06	0.169	0.0051
SB19	4	37.97	0.191	0.0050

Lf area: Flag leaf area [cm^2]
Lf Wt: Dry weight of flag leaf [g]
Wt/area: Specific weight of flag leaf.

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(As of May 16, 1994)

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International Maize and Wheat Improvement Center
Centro Internacional de Mejoramiento de Maíz y Trigo
Lisboa 27, Apartado Postal 6-641, 06600 México, D.F., México