

AN ABSTRACT OF THE THESIS OF

Isabel Alicia del Blanco for the degree of Doctor of Philosophy in Crop Science presented on February 17, 1999.

Title: Agronomic Potential and Physiological Performance of Synthetic Hexaploid Wheat-Derived Populations.

Abstract approved

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Sanjaya Rajaram

Synthetic hexaploid wheats, obtained by crossing durum wheat [*Triticum turgidum* L. ssp. *durum* (Desf.) Husn.] and goatgrass (*Aegilops tauschii* Coss.), have proven to be very useful as a source of resistance to biotic and abiotic stresses. Studies were conducted to investigate synthetic hexaploids as a source of variability for agronomic and physiological traits. Six different synthetic hexaploid-derived populations were evaluated for grain yield and the components of grain yield in two-year experiments (1995-96 and 1996-97) at the Agricultural Research Center for the Northwest (CIANO), Sonora, Mexico. Three different populations were evaluated for physiological traits, during the 1996-97 crop season at the same site.

For all agronomic traits there were synthetic-derived lines significantly superior to their respective bread wheat recurrent parent. Kernel weight was the

trait that showed the greatest gain in crosses with synthetic hexaploids. Overall population means were 12% to 20%, superior to bread wheat recurrent parental means, for the first and second year experiments respectively. For other traits, outstanding lines were observed in most populations. Some synthetic lines had 14% higher yield than their respective recurrent parent. Grains per m<sup>2</sup> and biomass were the traits with strongest association with yield. Path coefficient analysis showed a strong direct effect of biomass and harvest index on grain yield.

Differences in maximum photosynthetic rate were detected among genotypes. Most of the synthetic-derived lines showed higher photosynthesis compared to their recurrent parent. Senescence was not substantially premature in synthetic-derived lines compared to their bread wheat recurrent parents. Maximum photosynthetic rate was negatively associated with leaf area and leaf specific weight and positively associated with stomatal and mesophyll conductances, leaf temperature depression, grain yield, and above ground biomass. Differences in conductance in the diffusion pathway of CO<sub>2</sub> were the main reasons for the differences in photosynthesis.

Results indicate that synthetic-hexaploid wheats can be a very useful source of genetic diversity for agronomic and physiological traits if conveniently directed by breeding and selection.

Agronomic Potential and Physiological Performance of  
Synthetic Hexaploid Wheat-Derived Populations

By

Isabel Alicia del Blanco

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Dr. Sanjaya Rajaram proposed to investigate synthetic wheats. He organized the preparation of nurseries and the field operations at CIANO, Ciudad Obregon, Sonora, Mexico. He also advised me throughout the research process.

Dr. Warren E. Kronstad advised me throughout the research process and edited the manuscripts extensively.

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*To the memory of my grandmother*

*Beatriz Alejo*

# AGRONOMIC POTENTIAL AND PHYSIOLOGICAL PERFORMANCE OF SYNTHETIC HEXAPLOID WHEAT-DERIVED POPULATIONS

## I GENERAL INTRODUCTION

As the rate of increases in grain yield per hectare has declined, new strategies for wheat improvement are being addressed. Conventional wheat improvement programs have focused on genetic variability resulting from intraspecific hybridization. Reduced genetic variability within cultivated crop species is a common phenomenon of contemporary agricultural systems. The introgression of exotic germplasm from wild and cultivated relatives, to enhance genetic diversity, might be a suitable approach to enhance grain yield. In oat breeding programs, bursts in improved yield are associated with introductions of germplasm from other species or ecotypes into the cultivated oat (*Avena sativa* L). During the 1940's, the introgression of germplasm from *Avena byzantina* C. Koch (Langer et al., 1978; Rodgers et al., 1983) resulted in an abrupt increase in yield of cultivated oats. More recently, crosses between cultivated oat and *Avena sterilis* L. produced large increments of positive and negative transgressive segregants for yield (Lawrence and Frey, 1975). Agronomically acceptable backcrossed lines, with 20-30 % higher grain yield than the recurrent cultivated oat parent, have been obtained (Frey, 1976).

The two major components of grain yield are biomass and harvest index (Slafer et al., 1994). Harvest index (HI) is the ratio between grain yield and

aboveground biomass. It is widely known that previous increases in grain yield, with semidwarf cultivars, were associated with increased HI. This increased HI has been mainly due to a higher number of grains per area unit or kernel number (KN) rather than to an increase in grain or kernel weight. Many authors have found a close association between increase in grain yield and increase in KN (Waddington et al., 1986; Cox et al., 1988; Ledent and Stoy, 1988; Austin et al., 1989; Perry et al., 1989; Siddique et al., 1989; Slafer and Andrade, 1989; Slafer et al., 1990; Slafer and Andrade, 1993). There are also many references reporting new wheat cultivars with significantly higher KN (20% to 75%), when compared to older cultivars. Contrary to the progress achieved in KN, kernel weight has not been substantially changed and in a few instances declined (Slafer and Andrade, 1989; Siddique et al., 1989).

Kernel weight is determined by the accumulation of carbohydrates produced during post-anthesis with temperature influencing all the processes of kernel growth and development. Starch is the largest constituent of kernels and its accumulation determines their final weight. Kernel weight is considered to be a fairly stable yield component. It has been observed that synthetic hexaploid-derived populations appear to possess larger and heavier kernels than common bread wheat (S. Rajaram, personal communication). Therefore, it might be possible to further expand sink capacity with this new source of genetic diversity by increasing kernel weight while maintaining KN.

Since HI of modern wheat cultivars has reached 50%, i.e., near the theoretical potential ceiling of 60% (Austin et al., 1980), it appears that further increases in HI could be difficult to achieve. Consequently, obtaining genotypes with increased biomass, while maintaining current levels of HI, might be a feasible way of increasing grain yield (Austin et al., 1980; Slafer et al., 1994). Takeda and Frey (1976) found, in oat lines derived from the *A. sterilis* L. introgression program, that improvement in grain yield resulted from an increase in vegetative growth. Several of these lines outyielded their cultivated oat parents by up to 30 %, but had essentially the same maturity and harvest index values (Frey, 1976).

Potentially useful alien genetic variation exists in wild relatives of wheat. This genetic variation has been primarily exploited as a source of resistance to diseases and insects. *Aegilops tauschii* Coss, commonly known as goatgrass and donor of the D genome to common bread wheat, carries alleles for resistance to 1) leaf rust, *Puccinia recondita* f. sp. *tritici* (Dyck and Kerber, 1970; Rowland and Kerber, 1974; Kerber, 1987; Gill et al., 1986; Holubec et al., 1993; Cox et al., 1994); 2) stem rust, *Puccinia graminis* f. sp. *tritici* (Rowland and Kerber, 1974; Kerber and Dick, 1978); 3) stripe rust, *Puccinia striiformis* Westend. (Holubec et al., 1993; Ma et al., 1995); 4) powdery mildew, *Erysiphe graminis* f. sp. *tritici* (Gill et al., 1986; Tosa and Sakai, 1991; Cox et al., 1992; Holubec et al., 1993; Lutz et al., 1994; 1995; Shi et al., 1998); 5) karnal bunt, *Tilletia indica*, (Warham et al., 1986; Multani et al., 1988; Villarreal et al., 1994a); 6) Septoria tritici blotch, *Mycosphaerella graminicola* (Fuckel) Schroeter (McKendry and Henke, 1994); 7)

spot blotch, *Cochliobolus sativum* Ito et Kuribay (Mujeeb-Kazi et al., 1996; Mujeeb-Kazi and Delgado, 1998); **8**) tan spot, *Pyrenophora tritici-repentis* (Died.) Drechs. (Siedler et al., 1994; Riede et al., 1996); **9**) Hessian fly, *Mayetiola destructor* Say (Hatchett and Gill, 1983; Raupp et al., 1993; Cox and Hatchett, 1994); **10**) greenbug, *Schizaphis graminum* Rondani (Harvey et al., 1980; Joppa and Williams, 1982; Gill et al., 1986); **11**) Russian wheat aphid, *Diuraphis noxia* Mordvilko (Nkongolo et al., 1990; 1991); **12**) root-lesion nematode, *Pratylenchus thornei* Sher & Allen (Thompson and Haak, 1997); and it is also a potential source of stress resistance to drought (Zohary, 1969; Reddy, 1998); cold (Limin and Fowler, 1981); and salt (Gorham, 1990a; 1990b; Mujeeb-Kazi et al., 1993). A high number of *A. tauschii* that have been screened are resistant to at least one disease or insect pest of wheat (Gill et al., 1983; 1986; Hatchett et al., 1981; Pasquini, 1980).

Crop growth depends on photosynthesis. Some authors (Austin et al., 1989; Carver and Nevo, 1990) proposed the utilization of genes for higher photosynthetic rate, present in wild relatives, to increase wheat yield. Together with domestication and breeding of wheat, a decrease in photosynthetic rate through time has been the common path (Evans and Dunstone, 1970). Wild relatives of wheat reportedly have higher photosynthetic rates than modern cultivars (Carver et al., 1989; Johnson et al., 1987; Austin et al., 1982). Evans and Dunstone (1970) studying nine species of *Aegilops* and *Triticum*, from diploid to hexaploid, wild and cultivated, found that *A. tauschii* and *Triticum boeoticum* were the two species with the highest rate of

photosynthesis. A higher photosynthetic rate might be beneficial when sink capacity (kernel number, kernel weight) is increased.

Synthetic wheats are artificially-made hexaploids obtained from the hybridization between durum wheat, *Triticum turgidum* L. ssp. *durum* (Desf.) Husn. ( $2n=4x=28$ , AABB), and goatgrass, *Aegilops tauschii* Coss. ( $2n=14$ , DD), [Syn. *Triticum tauschii* (Coss.) Schmal]. Durum wheat, used primarily for pasta products, is widely grown around the world. The D genome of *A. tauschii* is completely homologous to the D genome of hexaploid wheat (Riley and Chapman, 1960), therefore the total genetic variation in *A. tauschii* is readily accessible. Furthermore, there is evidence that *A. tauschii* has greater useful genetic variability than the other progenitors of wheat (Gill et al., 1986). Thus, *A. tauschii* may be the most suitable progenitor species to introgress new favorable alleles into bread wheat.

Synthetic hexaploids (SH) are increasingly used as sources of resistance to diseases and pests as well as for abiotic stress, therefore, an investigation as to their agronomic potential and physiology is necessary to identify factors contributing to productivity as well as to detect possible detrimental genes.

## II MANUSCRIPT 1

### AGRONOMIC POTENTIAL OF SYNTHETIC HEXAPLOID WHEAT-DERIVED POPULATIONS

Isabel Alicia del Blanco, Sanjaya Rajaram, and Warren E. Kronstad

#### II.1. Abstract

Wild relatives of wheat (*Triticum aestivum* L.) have been primarily used as a source of genetic factors for biotic and abiotic resistance or tolerance. As the rate of increase in grain yield per hectare has declined, more attention is directed to exotic germplasm to enhance genetic diversity to avoid potential yield plateaus. To assess the usefulness of such germplasm for contributing genetic variability to further improve the yield of wheat, experiments were conducted at the Agricultural Research Center for the Northwest (CIANO) Experimental Station, Yaqui Valley, Sonora, Mexico. Two-hundred and eighty-two BC<sub>2</sub>F<sub>2:6</sub>-derived lines, representing six different populations of synthetic hexaploids from crosses between tetraploid wheat and *Aegilops tauschii* Coss., were evaluated for grain yield and the components of grain yield. These derived lines were compared to their bread wheat recurrent parent. There were synthetic lines that excelled their respective recurrent parent for all measured traits. For kernel weight, 67% to 85% of the synthetic lines for the first and second year experiment, respectively, were significantly superior to their bread wheat recurrent parent. For other traits, superiority was not as obvious;

however, the presence of outstanding lines within populations provides the basis for further selection. Grain yield of some synthetic lines was 14% higher compared to their respective recurrent parent. Lines with outstanding yield also exceeded their respective bread wheat parent for kernel weight, biomass, height, and for the rates of grain and biomass production. These lines had similar phenological cycles, spikes per unit area, kernels per spike, and harvest index compared to their respective recurrent parents. A strong association of grains per m<sup>2</sup> and biomass with grain yield was observed in most populations. Path coefficient analyses revealed a strong direct effect of biomass and harvest index on grain yield.

## II.2. Introduction

Modern bread wheat (*Triticum aestivum* L.) has a very narrow genetic basis. Its origin was the result of series of natural hybridizations between wild diploids possessing A, B, and D genomes. The addition of the D genome, contributed by *Aegilops tauschii* Coss., had a major impact during domestication on environmental adaptation and utilization of wheat (Zohary et al., 1969). Indeed, *A. tauschii* appears to have wider geographical distribution than the proposed donors of the A and B genomes: *Triticum urartu* Thum. ex Gandil., and a species closely related to *Aegilops speltoides* Tausch.

Although the series of steps by which common hexaploid wheat was domesticated are not accurately known, first domestications of diploid (einkorn)

and tetraploid (emmer) species date from about 10,000 years ago. Since that time, selection by humans resulted in a gradual loss of allelic variations of genes. Following domestication, wheat breeding stressed the depletion of variability to produce the wheat cultivars with high-yield potential, on which contemporary wheat farming is based. Crosses with unproductive wild relatives or primitive ancestors are not usual in a wheat improvement program because they will not immediately result in highly productive agronomic types

In the 1930's, Vavilov first pointed out the potential of wild relatives as a valuable source of genes for improving crops. Wheat's narrowing genetic base has become an ever more prevalent threat coping with disease and insect epidemics, as well as when facing different environmental stresses. For this reason, distantly related germplasm has been considered almost exclusively as donors of favorable alleles to improve resistance and/or tolerance to diseases, insects, and environmental stresses.

Synthetic hexaploid wheat, produced by crossing durum wheat (*Triticum turgidum* L. ssp. *durum* (Desf.) Husn., AB genomes) with goatgrass (*Aegilops tauschii* Coss., D genome), was mainly used during the last decade as an intermediary for transferring biotic and abiotic resistances and/or tolerance from the wild ancestor to cultivated bread wheat.

Synthetic hexaploids have been reported as having resistance to diseases such as **1)** karnal bunt (Multani et al., 1988; Villareal et al., 1994a; 1996), **2)** leaf rust (Kerber and Dick, 1969; Kerber, 1987), **3)** tan spot (Siedler et al., 1994; Riede

et al., 1996), 4) spot blotch, *Cochliobolus sativum* Ito et Kuribay (Mujeeb-Kazi et al., 1996; Mujeeb-Kazi and Delgado, 1998), 5) stripe rust (Ma et al., 1995). They have also been found tolerant to abiotic stresses such as cold and salt (Limin and Fowler, 1993; Gorham, 1990).

An important and still lacking dimension when considering these resources from the wild is the possibility of using beneficial alleles for increased yield potential over the long term. Considering that yield is a very complex trait, contemporary wheat varieties doubtfully have the best alleles for all yield-related loci. Bottlenecks imposed by domestication and breeding may have left many positive yield alleles behind.

A few investigations have been conducted into the impact of the introgression of *A. tauschii* on important agronomic traits of bread wheat, usually following the direct cross of bread wheat with *A. tauschii* (Cox et al., 1995a; 1995b; Murphy et al., 1997). Investigations on the effects of introgression of both durum wheat and *A. tauschii*, as synthetic hexaploids, into bread wheat are even scarcer. In those studies, substantial variability was observed in the synthetic and synthetic-derived germplasm tested (Villareal et al., 1994b; 1994c).

The objective of this study was to investigate twelve agronomic traits in BC<sub>2</sub>F<sub>2:6</sub> derived-lines, from six synthetic hexaploid x (spring bread wheat)\*<sup>2</sup> derived populations, and to determine their potential utility in wheat breeding programs.

### II.3. Materials and Methods

A two-years study was conducted at the Agricultural Research Center for the Northwest (CIANO) Experimental Station, Yaqui Valley, Sonora, Mexico. The Yaqui Valley is 40 meters above sea level and between 26° 45' and 27° 33' Latitude North and 109° 30' and 110° 37' Longitude West. The climate of this region is semiarid with an average of 60 mm of rain per year distributed mainly during the winter months. Meteorological records for the two crop-cycles (1995/96 and 1996/97) are provided in Appendix 1.

#### II.3.1. Plant material

Six populations derived from crosses between synthetic hexaploids and spring bread wheat cultivars were obtained from Dr. Reynaldo Villarreal, CIMMYT (International Maize and Wheat Improvement Center). The populations were:

*Population 1:* Altar 84/*A. tauschii* (219)//2\*Esmeralda

*Population 2:* Altar 84/*A. tauschii* (223)//2\*Flycatcher

*Population 3:* Duergand 2/*A. tauschii* (214)//2\*Seri

*Population 4:* Duergand 2/*A. tauschii* (214)//2\*Opata

*Population 5:* Duergand 2/*A. tauschii* (214)//2\*Esmeralda

*Population 6:* Croc 1/*A. tauschii* (205)//2\*Opata

Forty-seven lines from each population were included in the experiments. Details of crosses and pedigrees for the two hundred and eighty-two derived lines are provided in Appendix 2.

### **II.3.2. Experimental design and growing conditions**

All of the six populations were evaluated in six adjacent randomized complete block designs with three replications. Populations were considered fixed effects, lines within populations were randomly assigned. The bread wheat recurrent parent was entered as a check in each respective population. The experiments were sown during the optimum seeding period for the Yaqui Valley, which extends from the middle of November to the middle of December. The two cycles, 1995-96 and 1996-97, will be referred as Experiment I and Experiment II, respectively. Experiment I was sown on 26 November 1995, and harvested on 15 May 1996. Experiment II was sown on 28 November 1996, and harvested on 9 May 1997. The soil for both experiments was a coarse sandy clay, mixed montmorillonitic, typic Calciorthid (USDA-Soil Taxonomy, 1975) low in organic matter and pH of 7.7. Plots were 3m long and 1.6m wide, and consisted of six rows. Plot area planted was 4.8m<sup>2</sup>. The plots were fertilized with 150 kg ha<sup>-1</sup> N and 40 kg ha<sup>-1</sup> P before planting. Frequent irrigation, following the general management for that environment, ensured adequate water availability. Six irrigations from late November to early April covered the normal crop cycle. Preventive chemical control of weeds, diseases, and insects was applied as required. Herbicides used to

control weeds were Topik (250 ml ha<sup>-1</sup>), and Brominal (1.5 l ha<sup>-1</sup>) plus Starane (1 l ha<sup>-1</sup>). To control diseases, Folicur and Tilt (0.5 l ha<sup>-1</sup> each) were applied twice during the crop cycle. Insecticides used were Monitor and Lorsban (1 l ha<sup>-1</sup> each). Neither biotic nor abiotic factors had obvious effects on yield in either trial.

### **II.3.3. Collection of data**

Several traits were directly measured from the field plots while values of other traits were derived by calculations from a random sample of 50 tillers taken from the plots. The measured traits were:

Days to heading (HD): Number of days from sowing to the date when 50% of the spikes had emerged from the flag leaf.

Days to physiological maturity (M): Number of days from sowing to the date when 50% of the peduncles turned yellow.

Plant height (H): Distance (cm) from soil surface to the tip of the tallest spikes, excluding awns.

Grain yield (Y): Weight in kg of the grain harvested in a 4.8m<sup>2</sup> plot area multiplied by 2.08 to report it as kg ha<sup>-1</sup>. After weighing, a grain sample of approximately 100g was taken from all plots, weighed, oven-dried at 70°C for 48 hours and weighed again to determine grain moisture content. These data were used to adjust all reported grain yields to a 12% moisture level.

Thousand kernel weight (TKW): An additional sample of 250 random kernels (from the dried sample mentioned before), was weighed and multiplied by 4.

The various yield components (spikes per m<sup>2</sup>, grains per m<sup>2</sup>, grains per spike), as well as biomass per unit of area (or biological yield) and harvest index, were derived from the data obtained for aerial biomass and grain weight of 50 tillers. These 50 tillers were sampled at random during physiological maturity and oven dried for 48 hours at 70°C. The dry sample was weighed, threshed, and the resulting grain weight recorded.

The production rates (for grain and biomass) were calculated as the ratio between yield values of grain and biomass, respectively, and the relevant growth periods.

#### **II.3.4. Statistical analysis**

Separate analyses for all traits and six populations were performed. A Fisher's protected least significant difference (FPLSD) was computed for separating means. The distribution of the means from BC<sub>2</sub>F<sub>2:6</sub>-derived lines around their respective recurrent parental mean was estimated in LSD units for each trait, based on a score (Cox et al., 1995a, 1995b):

$$\text{Score} = (\text{mean line} - \text{mean recurrent parent}) * \text{LSD}^{-1}$$

A line with a score greater than 1 or less than -1 was significantly different from its recurrent parent.

#### **II.3.4.1. Associations among traits:**

Phenotypic and genotypic correlations were calculated using the Statistical Analysis System for Windows, version 6.12 (SAS Institute Inc., North Carolina, 1993). The 'CORR' procedure was used to estimate phenotypic correlations (Pearson). The 'VARCOMP' procedure was used to estimate genetic correlations.

#### **II.3.4.2. Path coefficient analysis:**

Correlation coefficients between yield and each one of six primary yield components were partitioned into direct and indirect effects by path-analysis. The traits included in this analysis were kernel weight, harvest index, biomass, spikes per m<sup>2</sup>, grains per m<sup>2</sup>, and grains per spike. The path coefficient analyses were conducted as described by Dewey and Lu (1959), and Singh and Chaudhary (1977).

## II.4. Experimental Results

Given the significant genotype\*year interaction obtained in the combined (two-year) analysis, separate analyses of variance were conducted for each year. Observed mean-square values for five measured traits and seven derived traits are presented in Tables II-1 and II-2 (Experiment I and Experiment II, respectively). Significant differences ( $P < 0.01$ ) among genotypes were detected for all traits and populations. Therefore, the introgression of synthetic-hexaploid germplasm, i.e. durum wheat and goatgrass, into common hexaploid wheat did modify the overall yielding ability of the derived lines. Performance for other traits was also modified in all populations. Significant differences were, in general, detected among replications, indicating that replications accounted for part of the total variation. The lower coefficients of variation observed in Experiment II were due to the superior stand of plants achieved in all plots.

### II.4.1. Distribution of $BC_2F_{2:6}$ lines

Line means and ranges, as well as recurrent-parent mean values, and Fisher's Protected LSD's values for all measured and derived traits for all six synthetic-hexaploid-derived populations are presented in Table II-3 (Experiment I) and Table II-4 (Experiment II).

Table II-1. Observed mean squares and coefficient of variation (C.V.%) for grain yield, thousand kernel weight (TKW), harvest index (HI), biomass, spikes per square meter, grains per square meter, grains per spike, heading, physiological maturity, plant height, grain production rate (G.P.R.), and biomass production rate (B.P.R.) for genotypes in six advanced populations grown at CIANO. Experiment I, 1995-96.

Source of Variation	df	Yield (Kg/ha)	TKW (gr.)	HI %	Biomass (Ton/ha)	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading (days)	Maturity	Height (cm)	G.P.R. (Kg/ha/day)	B.P.R.
<b>POPULATION 1</b>													
Replication	2	8,703,973**	3.49	2.12**	9,169**	7,029**	40,611,283**	180*	360**	822**	1,125**	1,296**	2,776**
Genotypes	47	4,316,845**	74.30**	1.16**	1,017**	3,564**	19,975,018**	193**	277**	156**	584**	1,990**	741**
Error	94	236,623	9.87	0.11	155	961	2,083,955	53	2	4	14	104	80
C.V. %		8.1	7.7	7.6	9.7	11.5	10.9	14.7	1.7	1.4	3.9	8.2	9.4
<b>POPULATION 2</b>													
Replication	2	8,349,131**	48.33**	0.63**	5,090**	860	24,165,243**	349**	236**	634**	817**	1,038**	1,449**
Genotypes	47	1,794,982**	39.64**	0.32**	505**	7,769**	14,639,333**	83**	50**	42**	334**	775**	316**
Error	94	282,165	1.61	0.04	130	1,088	1,559,074	17	2	3	10	150	77
C.V. %		8.1	3.2	4.1	9.1	10.7	8.4	8.5	1.5	1.4	3.3	8.5	9.1
<b>POPULATION 3</b>													
Replication	2	3,773,895**	5.77**	0.23**	2,159**	2,156*	10,391,084**	126**	86**	233**	435**	607**	631**
Genotypes	47	1,129,550**	19.33**	0.32**	267**	2,855**	7,901,076**	76**	56**	38**	137**	780**	132**
Error	94	132,946	0.67	0.03	75	567	503,327	11	1	3	7	85	42
C.V. %		5.8	1.9	3.7	7.1	8.7	5.5	6.9	1.4	1.3	2.6	6.2	6.8
<b>POPULATION 4</b>													
Replication	2	24,428,486**	18.60**	0.10	10,679**	670	67,077,006**	876**	37**	339**	903**	5,575**	4,253**
Genotypes	47	3,495,737**	93.88**	1.40**	338**	6,701**	19,351,481**	109**	298**	185**	89**	1,684**	306**
Error	94	220,164	3.40	0.08	170	1,506	2,577,812	23	1	3	14	123	87
C.V. %		8.2	4.8	6.7	10.3	11.9	12.1	11.6	1.3	1.2	3.6	8.0	9.8
<b>POPULATION 5</b>													
Replication	2	14,647,153**	7.12	0.05	5,340**	1,244	61,028,947**	472**	128**	518**	1,234**	1,868**	1,480**
Genotypes	47	2,220,812**	65.78**	0.49**	450**	5,444**	8,388,853**	79**	147**	95**	166**	1,069**	342**
Error	94	212,674	3.17	0.08	153	1,201	919,439	30	8	4	10	110	82
C.V. %		7.4	4.3	6.4	9.5	11.6	7.1	12.0	3.3	1.6	3.1	7.8	9.2
<b>POPULATION 6</b>													
Replication	2	5,404,029**	28.11**	0.96**	4,850**	5,594*	15,371,318**	202**	39**	120**	132**	1,320**	2,078**
Genotypes	47	1,256,556**	48.59**	0.11**	432**	5,464**	9,988,644**	52**	54**	41**	181**	687**	307**
Error	94	204,815	1.29	0.04	90	1,418	1,081,336	27	1	3	9	110	52
C.V. %		6.8	3.0	3.9	7.3	11.7	6.5	10.2	1.2	1.4	3.0	6.8	7.1

\*, \*\*, significant at the 0.05 and 0.01 probability level.

Table II-2. Observed mean squares and coefficient of variation (C.V.%) for grain yield, thousand kernel weight (TKW), harvest index (HI), biomass, spikes per square meter, grains per square meter, grains per spike, heading, physiological maturity, plant height, grain production rate (G.P.R.), and biomass production rate (B.P.R.) for genotypes in six advanced populations grown at CIANO. Experiment II, 1996-97.

Source of Variation	df	Yield (Kg/ha)	TKW (gr.)	HI %	Biomass (Ton/ha)	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading (days)	Maturity (days)	Height (cm)	G.P.R. (Kg/ha/day)	B.P.R.
<b>POPULATION 1</b>													
Replication	2	816,504**	0.62	0.08	889**	4,460**	3,906,354**	93**	8*	116**	7	931**	795**
Genotypes	47	4,257,208**	84.04**	0.53**	1,488**	6,059**	27,703,654**	142**	420**	176**	665**	1,533**	1,083**
Error	94	142,359	1.33	0.03	115	856	536,827	14	2	5	8	107	71
C.V. %		5.4	2.8	5.1	6.8	8.7	4.6	8.0	1.8	1.6	2.7	7.5	7.2
<b>POPULATION 2</b>													
Replication	2	374,205	21.58**	0.07	315*	3,591	6,070,873**	0	21**	68**	5	419*	76
Genotypes	47	1,405,536**	38.42**	0.20**	586**	9,688**	9,556,689**	80**	75**	35**	326**	620**	391**
Error	94	150,073	1.43	0.04	96	1,520	856,609	17	2	4	10	87	63
C.V. %		5.4	3.0	4.8	6.5	10.3	5.6	9.1	1.8	1.6	3.0	6.1	6.8
<b>POPULATION 3</b>													
Replication	2	445,476*	66.30**	0.05	79	163	2,470,868*	11	30**	101**	24*	25	31
Genotypes	47	991,487**	20.07**	0.26**	325**	4,178**	7,927,134**	76**	126**	25**	81**	1,393**	146**
Error	94	121,500	1.59	0.02	93	608	606,407	13	1	2	7	84	56
C.V. %		4.7	2.8	3.4	6.3	7.2	5.1	8.0	1.4	1.0	2.4	5.4	6.3
<b>POPULATION 4</b>													
Replication	2	37,398	37.47**	0.01	15	437	6,205,147**	77**	1	16**	33*	370**	39
Genotypes	47	3,264,246**	80.13**	0.43**	739**	6,725**	25,722,498**	105**	401**	229**	64**	1,439**	694**
Error	94	85,983	1.92	0.02	77	901	847,838	11	1	2	10	62	42
C.V. %		4.4	3.5	3.5	5.7	8.3	5.9	7.9	1.2	1.0	2.8	4.9	5.7
<b>POPULATION 5</b>													
Replication	2	798,959**	9.56**	0.01	417	1,790	5,211,628**	10	17**	176**	54**	341*	32
Genotypes	47	1,886,716**	65.13**	0.18**	631**	6,389**	10,285,061**	78**	240**	105**	157**	743**	532**
Error	94	125,789	1.05	0.03	143	891	632,871	9	2	6	8	96	72
C.V. %		4.8	2.4	4.6	7.3	7.7	5.0	7.0	1.7	1.9	2.7	6.5	6.9
<b>POPULATION 6</b>													
Replication	2	1,165,361**	23.65**	0.04	608**	524	21,563,812**	108**	49**	31**	2	727**	266**
Genotypes	47	914,536**	50.33**	0.06**	414**	6,726**	12,744,087**	65**	124**	58**	134**	893**	304**
Error	94	89,692	1.41	0.02	57	1,225	802,066	17	7	4	7	81	37
C.V. %		4.3	3.2	3.6	5.1	9.1	5.2	9.1	3.0	1.5	2.5	5.6	5.4

\*, \*\*, significant at the 0.05 and 0.01 probability level.

Table II-3. Agronomic trait performance of BC<sub>2</sub>F<sub>2,6</sub> synthetic-hexaploid-derived lines in six populations and their respective recurrent parents (Rec. Par.) grown at CIANO. Experiment I, 1995-96.

GENOTYPE	Yield (Kg ha <sup>-1</sup> )	TKW (gr)	HI	Biomass (Ton ha <sup>-1</sup> )	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading Maturity ------(days)-----	Height (cm)	G.P.R. ---( Kg ha <sup>-1</sup> day <sup>-1</sup> )---	B.P.R.	
POPULATION 1												
Line mean	5,988	40.71	0.44	12.8	268	13,255	50	87	135	96	123	95
Line range	2451-7492	29.21-49.80	0.28-0.53	7.4-16.3	187-352	6,940-17,442	35-66	78-118	128-156	61-117	65-169	48-120
Rec. Par. (Esmeralda)	6,961	37.44	0.49	13.3	308	16,625	54	83	131	96	144	101
Fisher's LSD (0.05)	789	5.09	0.05	2.0	50	2,340	12	2	3	6	17	15
POPULATION 2												
Line mean	6,582	40.15	0.49	12.5	308	14,796	49	84	129	98	144	97
Line range	3580-7712	31.31-47.84	0.39-0.55	8.7-15.7	199-396	7,718-18,952	38-61	77-93	121-138	69-126	86-178	68-126
Rec. Par. (Ocoroni)	6,760	36.82	0.50	12.6	311	16,437	53	83	129	96	148	98
Fisher's LSD (0.05)	861	2.06	0.03	1.9	53	2,024	7	2	3	5	20	14
POPULATION 3												
Line mean	6,338	44.05	0.49	12.2	273	12,928	48	85	128	100	149	95
Line range	4941-7658	38.79-49.73	0.38-0.53	10.4-13.9	209-339	9,954-16,554	36-59	75-94	120-138	86-120	117-175	81-108
Rec. Par. (Seri)	7,010	39.51	0.53	12.4	290	15,863	55	89	132	91	163	94
Fisher's LSD (0.05)	591	1.32	0.03	1.4	39	1,150	5	2	3	4	15	11
POPULATION 4												
Line mean	5,750	38.77	0.42	12.6	325	13,215	41	91	133	101	138	95
Line range	2233-6918	26.58-50.00	0.20-0.49	10.4-14.3	214-447	7,123-18,742	27-57	79-119	121-156	91-114	58-169	67-108
Rec. Par. (Opata)	6,768	32.18	0.47	13.4	447	18,742	43	88	129	97	165	103
Fisher's LSD (0.05)	761	2.99	0.05	2.1	63	2,603	8	2	2	6	18	15
POPULATION 5												
Line mean	6,278	41.90	0.45	13.1	299	13,463	46	86	133	100	135	99
Line range	3853-7545	25.73-49.99	0.29-0.50	9.5-15.4	232-401	10,619-17,824	33-58	76-114	123-150	70-113	80-169	70-116
Rec. Par. (Esmeralda)	7,400	38.36	0.47	14.5	337	17,238	52	84	133	97	151	109
Fisher's LSD (0.05)	748	2.89	0.05	2.0	56	1,555	9	5	3	5	17	15
POPULATION 6												
Line mean	6,708	37.50	0.48	13.1	321	16,113	51	87	130	103	155	100
Line range	4956-8135	28.17-45.45	0.43-0.52	9.7-15.6	217-427	12,017-20,763	39-57	79-98	123-137	84-117	116-186	72-122
Rec. Par. (Opata)	7,710	33.20	0.49	14.6	389	20,763	54	89	132	101	180	111
Fisher's LSD (0.05)	734	1.84	0.03	1.5	61	1,686	8	2	3	5	17	12

Table II-4. Agronomic trait performance of BC<sub>2</sub>F<sub>2.6</sub> synthetic-hexaploid-derived lines in six populations and their respective recurrent parents (Rec. Par.) grown at CIANO. Experiment II, 1996-97.

GENOTYPE	Yield (Kg ha <sup>-1</sup> )	TKW (gr)	HI	Biomass (Ton ha <sup>-1</sup> )	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading Maturity ------(days)-----	Height (cm)	G.P.R. ---(Kg ha <sup>-1</sup> day <sup>-1</sup> )--	B.P.R.	
POPULATION 1												
Line mean	7,036	41.62	0.41	15.8	336	15,778	47	84	135	102	138	118
Line range	2850-8672	30.43-53.03	0.32-0.49	8.4-19.8	185-469	7571-22137	34-62	73-119	126-160	67-118	70-188	53-150
Rec. Par. (Esmeralda)	7,752	36.77	0.42	17.0	387	19,379	50	82	133	102	150	127
Fisher's LSD (0.05)	612	1.87	0.03	1.7	47	1,188	6	2	3	5	17	14
POPULATION 2												
Line mean	7,179	40.09	0.44	15.1	378	16,589	45	83	130	105	152	116
Line range	5123-8287	31.70-47.27	0.38-0.49	10.8-17.6	222-478	11345-19715	32-55	75-96	124-140	68-130	118-178	81-141
Rec. Par. (Ocoroni)	7,297	37.87	0.44	15.4	399	17,711	45	82	128	105	156	120
Fisher's LSD (0.05)	628	1.94	0.03	1.6	63	1,500	7	2	3	5	15	13
POPULATION 3												
Line mean	7,361	45.02	0.45	15.3	342	15,174	45	84	128	107	170	119
Line range	6182-8551	40.87-50.37	0.35-0.49	13.0-17.6	275-443	12083-18582	33-57	70-96	122-136	97-122	131-219	103-136
Rec. Par. (Seri)	7,977	37.77	0.48	15.3	360	19,447	54	92	133	97	195	114
Fisher's LSD (0.05)	565	2.04	0.02	1.6	40	1,262	6	2	2	4	15	12
POPULATION 4												
Line mean	6,640	40.05	0.40	15.3	362	15,493	43	94	136	110	159	113
Line range	3134-7786	30.93-50.70	0.26-0.46	9.9-17.4	211-428	8841-21574	29-56	78-125	124-160	102-120	82-188	62-133
Rec. Par. (Opata)	7,421	29.27	0.43	15.9	415	23,283	56	91	132	105	181	121
Fisher's LSD (0.05)	475	2.25	0.02	1.4	49	1,493	5	2	2	5	13	11
POPULATION 5												
Line mean	7,347	42.43	0.41	16.3	386	16,039	42	85	134	106	152	122
Line range	5386-8708	28.10-52.70	0.35-0.46	13.1-19.6	270-477	12811-20235	34-52	71-116	126-155	79-118	111-182	92-151
Rec. Par. (Esmeralda)	7,749	35.03	0.44	16.4	372	20,401	56	83	133	101	154	123
Fisher's LSD (0.05)	575	1.66	0.03	1.9	48	1,290	5	2	4	5	16	14
POPULATION 6												
Line mean	6,970	37.29	0.43	14.7	386	17,384	45	87	131	106	160	112
Line range	5414-8097	30.03-46.20	0.41-0.47	12.1-17.1	298-506	13492-20716	35-55	74-99	123-143	91-118	126-199	90-130
Rec. Par. (Opata)	7,386	29.70	0.45	15.0	428	22,820	54	91	132	102	180	114
Fisher's LSD (0.05)	485	1.93	0.03	1.2	57	1,452	7	4	3	4	15	10

Kernel weight (TKW) was the only trait in synthetic populations where mean values were superior to the recurrent-parent mean values: Overall population means were 12 % and 20 %, in Experiment I and II respectively, greater than recurrent parental means. The two populations having the recurrent parent with lower kernel weight showed the highest increase in weight in the synthetic derived lines as compared with their recurrent parent (Opata), in both experiments.

Backcross population means for yield were about 12% and 7% lower, in Experiment I and II respectively, than recurrent-parent means. Considering that Experiment II had a higher overall yield, it can be inferred that improved experimental conditions reduced the differences between backcross population means and the corresponding bread wheat parental means. For harvest index and biomass, population means were also lower than recurrent parental means (6%, 5% in Experiment I; 4%, 3% in Experiment II, respectively). Population means for spikes per unit area, grains per unit area, and grains per spike were also lower than corresponding recurrent parental means in both years (13%, 20%, 8% respectively in Experiment I; 7%, 21%, 15% in Experiment II). Population means for days to heading and to physiological maturity were similar to recurrent-parent means in both years. Population means for height were 4% higher than recurrent-parental means in both experiments. Paradoxically, increased height did not translate to a greater aboveground biomass yield. Most population means for biomass were lower than recurrent-parent means. Possible explanations to this paradox might be an

inferior foliar area, given by fewer leaves or/and smaller leaves, or a lower specific weight of leaves or/and stem in synthetic-derived lines.

Growth rate population means were lower than recurrent-parent means, 11% for grain production rate and 5% for biomass production rate in Experiment I, and 8% and 3%, respectively, in Experiment II. These lower growth rates were expected from populations having lower grain and biomass yields and similar phenological phases than their corresponding bread wheat recurrent parents.

Although kernel weight was the only yield component that showed population means superior to recurrent parental means, for most traits and within all populations there were individual lines that exceeded their recurrent parents as illustrated by the line ranges. Classification of lines based on mean score (Table II-5, Experiment I; Table II-6, Experiment II) shows the number of lines falling within plus or minus 0, 1, 2, and 3 LSD's values of their recurrent parental mean. When averaged across all measured and derived traits, the distributions of BC<sub>2</sub>F<sub>2.6</sub> lines relative to their recurrent parents indicated that 50% of the lines in Experiment I and 44% of the lines in Experiment II fell within one LSD of their recurrent parents. Individual-trait score was positively skewed for kernel weight with 67% to 86% of the lines (Experiments I and II, respectively) superior to their respective recurrent parent. For other agronomic yield components and yield per se, the distribution was negatively skewed, although for all traits some lines were significantly superior to their respective recurrent parent in both years. Three lines from two different populations (Experiment I) and ten lines from five different

Table II-5. Distribution of BC<sub>2</sub>F<sub>2.6</sub>-derived line means relative to their recurrent parents for measured and derived traits in six synthetic hexaploid backcross populations. Experiment I, 1995-96.

Trait	Population	Number of entries with mean score†						
		Less than -2.99	-2.99 to -2.00	-1.99 to -1.00	-0.99 to 0.99	1.00 to 1.99	2.00 to 2.99	Greater than 2.99
Grain Yield	1	7	4	9	27	0	0	0
	2	1	2	2	40	2	0	0
	3	1	11	13	21	1	0	0
	4	5	7	11	24	0	0	0
	5	6	2	23	16	0	0	0
	6	3	6	26	12	0	0	0
Kernel Weight	1	0	0	3	26	13	5	0
	2	0	2	2	14	10	10	9
	3	0	0	0	4	5	9	29
	4	0	0	2	9	12	7	17
	5	2	0	2	13	14	11	5
	6	0	1	0	13	6	12	15
Harvest Index	1	5	4	17	21	0	0	0
	2	1	3	7	31	5	0	0
	3	2	14	15	16	0	0	0
	4	4	2	9	32	0	0	0
	5	1	3	2	41	0	0	0
	6	0	1	8	38	0	0	0
Biomass	1	0	3	6	36	2	0	0
	2	0	1	3	42	1	0	0
	3	0	0	5	39	3	0	0
	4	0	0	7	40	0	0	0
	5	0	1	11	35	0	0	0
	6	1	4	17	25	0	0	0
Spikes per m <sup>2</sup>	1	0	3	15	29	0	0	0
	2	0	3	4	32	8	0	0
	3	0	1	11	33	2	0	0
	4	3	20	20	4	0	0	0
	5	0	0	19	26	2	0	0
	6	0	4	23	20	0	0	0
Grains per m <sup>2</sup>	1	6	7	15	19	0	0	0
	2	3	2	10	31	1	0	0
	3	20	9	14	4	0	0	0
	4	8	19	14	6	0	0	0
	5	16	15	11	5	0	0	0
	6	18	19	9	1	0	0	0

Score is the difference between an entry mean and its recurrent parent's mean, expressed in LSD units.

† Score = (backcross line mean - recurrent parent) x LSD<sup>-1</sup>

Table II-5. (Continued)

Trait	Population	Number of entries with mean score†						
		Less than -2.99	-2.99 to -2.00	-1.99 to -1.00	-0.99 to 0.99	1.00 to 1.99	2.00 to 2.99	Greater than 2.99
Grains per Spike	1	0	0	10	36	1	0	0
	2	0	3	11	32	1	0	0
	3	3	9	21	14	0	0	0
	4	1	6	21	16	3	0	0
	5	0	1	14	32	0	0	0
	6	0	0	7	40	0	0	0
Days to Heading	1	0	1	7	22	5	6	6
	2	1	9	6	13	8	7	3
	3	19	4	10	10	3	1	0
	4	4	6	7	9	8	3	10
	5	0	0	5	31	6	3	2
	6	11	10	6	11	6	2	1
Days to Maturity	1	0	0	0	28	5	7	7
	2	0	2	10	22	9	3	1
	3	5	14	13	14	0	1	0
	4	1	2	5	17	10	3	9
	5	1	3	8	27	4	0	4
	6	2	7	11	24	3	0	0
Height	1	10	0	0	18	12	6	1
	2	2	0	8	21	11	1	4
	3	0	0	1	9	9	10	18
	4	0	0	0	26	17	4	0
	5	2	0	2	21	15	6	1
	6	2	2	6	19	11	5	2
G.P.R.	1	8	7	7	24	1	0	0
	2	1	1	3	40	2	0	0
	3	1	12	10	24	0	0	0
	4	5	5	19	18	0	0	0
	5	2	5	13	26	1	0	0
	6	3	8	24	12	0	0	0
B.P.R.	1	1	4	7	33	2	0	0
	2	0	1	3	41	2	0	0
	3	0	0	2	39	6	0	0
	4	0	1	12	34	0	0	0
	5	0	3	11	33	0	0	0
	6	1	6	13	26	1	0	0

Score is the difference between an entry mean and its recurrent parent's mean, expressed in LSD units.

† Score = (backcross line mean - recurrent parent) x LSD<sup>-1</sup>

Table II-6. Distribution of BC<sub>2</sub>F<sub>2,6</sub>-derived line means relative to their recurrent parents for measured and derived traits in six synthetic hexaploid backcross populations. Experiment II, 1996-97.

Trait	Population	Number of entries with mean score†						
		Less than -2.99	-2.99 to -2.00	-1.99 to -1.00	-0.99 to 0.99	1.00 to 1.99	2.00 to 2.99	Greater than 2.99
Grain Yield	1	8	2	10	24	3	0	0
	2	2	3	2	37	3	0	0
	3	2	8	16	20	1	0	0
	4	8	6	10	23	0	0	0
	5	4	4	4	33	2	0	0
	6	2	6	12	26	1	0	0
Kernel Weight	1	2	0	1	10	6	9	19
	2	2	0	3	16	11	8	7
	3	0	0	0	0	3	11	33
	4	0	0	0	1	5	8	33
	5	1	0	0	3	5	3	35
	6	0	0	0	2	5	10	30
Harvest Index	1	3	3	11	23	5	2	0
	2	0	1	8	33	5	0	0
	3	8	8	19	12	0	0	0
	4	7	6	14	18	2	0	0
	5	0	3	15	29	0	0	0
	6	0	0	10	37	0	0	0
Biomass	1	2	1	9	33	2	0	0
	2	0	2	5	35	5	0	0
	3	0	0	4	40	3	0	0
	4	1	3	10	32	1	0	0
	5	0	0	6	39	2	0	0
	6	0	1	12	32	2	0	0
Spikes per m <sup>2</sup>	1	1	2	19	24	1	0	0
	2	0	2	7	36	2	0	0
	3	0	1	13	29	3	1	0
	4	3	3	20	21	0	0	0
	5	0	0	4	33	10	0	0
	6	0	3	17	25	2	0	0
Grains per m <sup>2</sup>	1	24	7	5	9	1	1	0
	2	3	4	8	30	2	0	0
	3	29	11	6	1	0	0	0
	4	43	2	2	0	0	0	0
	5	29	9	8	1	0	0	0
	6	36	7	4	0	0	0	0

Score is the difference between an entry mean and its recurrent parent's mean, expressed in LSD units.

† Score = (backcross line mean - recurrent parent) x LSD<sup>-1</sup>

Table II-6. (Continued)

Trait	Population	Number of entries with mean score†						
		Less than -2.99	-2.99 to -2.00	-1.99 to -1.00	-0.99 to 0.99	1.00 to 1.99	2.00 to 2.99	Greater than 2.99
Grains per Spike	1	0	4	15	22	6	0	0
	2	0	0	4	37	6	0	0
	3	2	12	25	8	0	0	0
	4	16	17	12	2	0	0	0
	5	23	13	10	1	0	0	0
	6	0	8	25	14	0	0	0
Days to Heading	1	5	4	10	14	2	2	10
	2	0	4	11	17	5	4	6
	3	31	2	1	10	3	0	0
	4	9	7	0	6	3	5	17
	5	3	4	4	20	5	2	9
	6	2	10	12	16	7	0	0
Days to Maturity	1	0	0	14	17	9	1	6
	2	0	0	2	30	11	3	1
	3	19	14	7	6	1	0	0
	4	1	4	5	15	2	7	13
	5	0	0	6	34	3	1	3
	6	0	4	10	25	6	1	1
Height	1	0	0	10	11	10	11	5
	2	2	0	8	26	5	3	3
	3	0	0	0	7	12	13	15
	4	0	0	0	25	14	7	1
	5	2	0	0	19	15	7	4
	6	0	2	3	16	15	4	7
G.P.R.	1	2	7	9	25	3	1	0
	2	0	4	5	34	4	0	0
	3	7	16	10	11	3	0	0
	4	8	11	12	16	0	0	0
	5	0	3	6	33	5	0	0
	6	4	11	15	16	1	0	0
B.P.R.	1	2	6	6	31	2	0	0
	2	1	2	4	37	3	0	0
	3	0	0	0	42	5	0	0
	4	3	4	8	31	1	0	0
	5	0	3	5	35	3	1	0
	6	0	2	10	30	5	0	0

Score is the difference between an entry mean and its recurrent parent's mean, expressed in LSD units.

† Score = (backcross line mean - recurrent parent) x LSD<sup>-1</sup>

populations (Experiment II) had higher grain yield than their respective wheat recurrent parent. Mean scores for phenological traits, days to heading and maturity, were symmetrically distributed, with most individual lines within a LSD of their recurrent parent. Height was positively skewed, indicating that synthetic-derived lines were, on average, taller than their recurrent parent, although most of the lines fell within one LSD. The production rates were negatively skewed. Approximately 50% of the lines had a similar grain production rate as their recurrent parent, but only 2% (Experiment I) and 6% (Experiment II) surpassed it. For biomass production rate, 73% of the lines were close to their recurrent parent; only 4% and 7%, for Experiment I and II, respectively, were superior.

#### **II.4.2. Outstanding BC<sub>2</sub>F<sub>2:6</sub> lines**

Synthetic-derived lines with higher yield than their bread wheat parent occurred in both experiments (Tables II-7 and II-8). In Experiment I, superior lines were observed in two populations, while five different populations produced higher yielding lines in Experiment II. Only one line (entry 136, Population 3) outyielded its recurrent parent in both experiments. Superior lines exceeded their respective recurrent parent in kernel weight, biomass, height, grain production rate, and biomass production rate. In most instances grains per m<sup>2</sup> and grains per spike were similar or lower compared to the recurrent parent. The best line of Population 3 had a shorter phenological cycle compared to its recurrent parent (Seri). In other

Table II-7. Agronomic traits and number of lines with grain yield at least one Fisher's LSD higher than recurrent parent (Rec. Par.). Experiment I, 1995-96.

Population	Number of outstanding lines	Yield (Kg ha <sup>-1</sup> )	TKW (gr)	HI %	Biomass (Ton ha <sup>-1</sup> )	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading -----(days)-----	Maturity	Height (cm)	G.P.R. --- (Kg ha <sup>-1</sup> day <sup>-1</sup> ) ---	B.P.R.
2	2	7,712	39	0.50	14.27	389	17,750	46	84	132	100	160	108
		7,649	39	0.45	15.74	375	17,520	46	82	125	118	178	126
---Rec. Par. (Ocoroni)---		6,760	37	0.50	12.60	311	16,437	53	83	129	96	148	98
3	1	7,658	41	0.53	13.41	284	16,554	59	83	128	105	170	105
---Rec. Par. (Seri)---		7,010	39	0.53	12.41	290	15,862	55	89	132	91	163	94

Table II-8. Agronomic traits and number of lines with grain yield at least one Fisher's LSD higher than recurrent parent (Rec. Par.). Experiment II, 1996-97.

Population	Number of outstanding lines	Yield (Kg ha <sup>-1</sup> )	TKW (gr)	HI %	Biomass (Ton ha <sup>-1</sup> )	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading -----(days)-----	Maturity	Height (cm)	G.P.R. ---(Kg ha <sup>-1</sup> day <sup>-1</sup> )---	B.P.R.
1	3	8672	41	0.44	17.89	380	19,630	52	77	131	107	161	136
		8,503	42	0.46	17.22	336	18,848	57	80	130	103	172	133
		8,421	46	0.45	17.09	309	17,031	55	78	132	104	155	130
		---Rec. Par. (Esmeralda)---	7,752	37	0.42	16.96	387	19,379	50	82	133	102	150
2	3	8,287	43	0.44	17.37	463	17,723	38	83	130	113	178	134
		8,260	45	0.43	17.64	306	16,863	55	81	134	108	158	132
		7,937	37	0.47	15.52	395	19,715	51	82	131	99	162	119
		----Rec. Par. (Ocoroni)----	7,297	38	0.44	15.36	399	17,711	45	82	128	105	156
3	1	8,551	42	0.49	16.00	357	18,582	53	83	128	108	190	126
		----Rec. Par. (Seri)----	7,977	38	0.48	15.25	360	19,447	54	92	133	97	195
5	2	8,708	44	0.44	18.01	388	18,276	47	85	134	107	177	134
		8,425	45	0.43	17.84	468	16,945	36	82	132	108	167	135
		---Rec. Par. (Esmeralda)---	7,749	35	0.44	16.37	372	20,401	56	83	133	101	154
6	1	8,097	45	0.43	17.05	366	16,655	46	87	131	115	184	130
		----Rec. Par. (Opata)----	7,386	30	0.45	14.99	428	22,820	54	91	132	102	180

populations, phenological cycles of the outstanding lines were similar to their respective recurrent parent. The harvest index of superior lines was similar to that of the bread wheat parent, suggesting that it was possible for the lines to maintain the grain yield-biological yield ratio in spite of the increased biomass and height. Spikes per m<sup>2</sup> varied, being higher, lower, or similar when compared to the respective recurrent parent, depending on the population.

The two growth rates for grain and biomass were higher in the outstanding lines than in the bread wheat parent, indicating that these lines were more efficient at producing grain and vegetative growth than their respective recurrent parent.

#### **II.4.3. Effect of bread wheat parent**

Populations 3, 4, and 5 were derived from crosses between the same synthetic hexaploid, Duergand/*A. tauschii* (214), and different bread wheats (Seri, Opata, and Esmeralda respectively).

The influence of the bread wheat parent on those three populations was very important. In general, bread wheat parental performance corresponded with mean performance of the population, i.e., the best parent for a trait has the best derived population for that trait (Tables II-3 and II-4, Experiment I and II respectively). Population 3, derived from Seri, had the best mean grain yield, kernel weight, harvest index, grains per spike, and grain production rate in both experiments. Population 5, derived from Esmeralda, had the highest mean biomass production, grains per m<sup>2</sup>, and biomass production rate. Population 4, derived from Opata, was

inferior to the other two populations for most traits. The best line for each trait was also commonly found in the population with the highest mean for that trait. Some exceptions were grain yield, with the best line from Population 5 (Experiment II); kernel weight, with the best performing line in Population 4 (Experiment I), and Population 5 (Experiment II); and grains per m<sup>2</sup> with the best lines from Population 4 for both experiments.

It is interesting that Population 3 had both the highest kernel weight and the highest number of grains per spike, compared to Populations 4 and 5, suggesting that competition between those two yield components was not a determinant of the magnitude of their difference. Furthermore, this population was intermediate in biomass production, indicating that the increased sink did not require an increased source.

#### **II.4.4. Associations among traits**

Phenotypic correlations for yield, yield components, harvest index, biomass, heading, maturity, height, and growth rates are presented in Table II-9 for Experiment I, and in Table II-10 for Experiment II. Genotypic correlations for the same traits are presented in Table II-11 and II-12, respectively.

Phenotypic and genotypic coefficients were similar in most instances. This similarity in part reflects the low error obtained in both experiments, which was probably due to the large number of entries and to the low environmental variation.

Table II-9. Pearson correlations among measured and derived traits. Experiment I, 1995-96.

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Yield	0.36**	0.57**	0.72**	0.49**	0.79**	0.48**	-0.59**	-0.58**	0.38**	0.91**	0.82**
	-0.03	0.29**	0.87**	0.53**	0.82**	0.34**	-0.10	0.14	-0.06	0.91**	0.87**
	-0.16	0.40**	0.74**	0.59**	0.90**	0.32**	0.12	0.23**	0.23*	0.86**	0.76**
	0.46**	0.69**	0.68**	0.41**	0.70**	0.47**	-0.62**	-0.50**	0.51**	0.93**	0.83**
	0.46**	0.51**	0.80**	0.41**	0.72**	0.23**	-0.35**	-0.25**	0.39**	0.88**	0.85**
	0.38**	0.04	0.90**	0.42**	0.58**	0.00	-0.21*	-0.08	0.29**	0.89**	0.90**
TKW		0.10	0.36**	-0.02	-0.26**	-0.31**	-0.47**	-0.50**	0.42**	0.32**	0.47**
		-0.29**	0.13	-0.52**	-0.58**	0.00	0.06	0.07	0.59**	-0.05	0.12
		-0.33**	0.09	-0.17*	-0.56**	-0.42**	0.10	0.04	0.13	-0.09	0.08
		0.37**	0.30**	-0.11	-0.16	-0.07	-0.56**	-0.48**	0.21*	0.36**	0.46**
		0.49**	0.21*	-0.11	-0.27**	-0.18*	-0.57**	-0.58**	0.13	0.40**	0.38**
		0.20*	0.28**	-0.30**	-0.52**	-0.14	-0.45**	-0.30**	0.19*	0.24**	0.35**
HI			-0.15	-0.06	0.52**	0.61**	-0.66**	-0.68**	-0.28**	0.49**	0.04
			-0.21*	0.08	0.39**	0.41**	-0.44**	-0.32**	-0.59**	0.26**	-0.14
			-0.31**	0.15	0.47**	0.36**	-0.36**	-0.37**	-0.21*	0.35**	-0.22**
			-0.04	0.08	0.48**	0.58**	-0.81**	-0.77**	0.22**	0.65**	0.22**
			-0.11	-0.17*	0.18*	0.32**	-0.52**	-0.53**	-0.14	0.44**	0.05
			-0.39**	-0.33**	-0.14	0.31**	-0.22**	-0.23**	-0.29**	0.04	-0.32**
Biomass				0.64**	0.51**	0.06	-0.17*	-0.13	0.71**	0.68**	0.96**
				0.48**	0.63**	0.17*	0.13	0.31**	0.24**	0.80**	0.96**
				0.49**	0.58**	0.09	0.38**	0.50**	0.40**	0.62**	0.95**
				0.46**	0.47**	0.09	-0.06	0.08	0.47**	0.61**	0.93**
				0.57**	0.69**	0.05	-0.04	0.09	0.55**	0.71**	0.95**
				0.50**	0.58**	-0.11	-0.10	0.03	0.41**	0.80**	0.97**
Spikes m <sup>-2</sup>					0.50**	-0.21*	-0.03	-0.10	0.31**	0.56**	0.62**
					0.73**	-0.44**	0.03	0.06	-0.30**	0.56**	0.48**
					0.57**	-0.46**	0.17*	0.09	-0.03	0.65**	0.52**
					0.52**	-0.35**	-0.11	-0.18*	0.08	0.51**	0.50**
					0.52**	-0.56**	-0.11	-0.09	0.02	0.40**	0.58**
					0.66**	-0.65**	0.07	0.04	0.02	0.46**	0.48**

\*, \*\* Significant at the 0.05 and 0.01 levels of probability

Table II-9. (Continued)

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Grains m <sup>-2</sup>						0.73**	-0.37**	-0.31**	0.15	0.70**	0.55**
						0.28**	-0.10	0.10	-0.39**	0.76**	0.64**
						0.46**	0.06	0.18*	0.14	0.76**	0.60**
						0.50**	-0.32**	-0.26**	0.35**	0.70**	0.54**
						0.40**	0.06	0.16	0.33**	0.66*	0.62**
						0.12**	0.21*	0.20*	0.10	0.61**	0.52**
Grains/Spike							-0.38**	-0.25**	-0.06	0.34**	0.12
							-0.18*	0.02	-0.08	0.23**	0.17*
							-0.11	0.10	0.17*	0.11	0.08
							-0.30**	-0.15	0.32**	0.37**	0.13
							0.20*	0.29**	0.30**	0.18*	-0.05
						0.14	0.15	0.05	-0.00	-0.14	

\*, \*\* Significant at the 0.05 and 0.01 levels of probability

Table II-10. Pearson correlations among measured and derived traits. Experiment II, 1996-97.

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Yield	0.23**	0.56**	0.81**	0.56**	0.78**	0.46**	-0.64**	-0.64**	0.40**	0.78**	0.86**
	0.23**	0.25**	0.79**	0.39**	0.67**	0.03	-0.29**	-0.13	0.03	0.80**	0.79**
	-0.16*	0.42**	0.63**	0.45**	0.82**	0.29**	0.09	0.16	0.07	0.67**	0.65**
	0.24**	0.75**	0.84**	0.69**	0.72**	0.25**	-0.69**	-0.68**	0.36**	0.85**	0.89**
	0.43**	0.45**	0.81**	0.48**	0.54**	-0.01	-0.55**	-0.47**	0.15	0.63**	0.83**
	0.17*	0.16	0.88**	0.40**	0.52**	0.11	0.00	-0.08	0.22**	0.75**	0.83**
TKW		-0.13	0.39**	-0.13	-0.42**	-0.38**	-0.41**	-0.46**	0.61**	0.12	0.47**
		-0.09	0.29**	-0.41**	-0.56**	0.04	-0.25**	-0.27**	0.59**	0.20*	0.34**
		-0.18*	0.00	-0.17*	-0.69**	-0.45**	0.13	0.07	0.16*	0.01	-0.02
		0.01	0.39**	0.04	-0.48**	-0.60**	-0.41**	-0.34**	0.30**	0.00	0.43**
		0.23**	0.36**	-0.06	-0.52**	-0.42**	-0.43**	-0.43**	0.32**	0.23**	0.44**
		0.01	0.17*	-0.35**	-0.74**	-0.35**	-0.44**	-0.49**	0.42**	-0.02	0.33**
HI			-0.01	0.20*	0.60**	0.55**	-0.57**	-0.52**	-0.29**	0.28**	0.12
			-0.38**	-0.08	0.29**	0.32**	-0.24**	-0.13	-0.40**	0.10	-0.33
			-0.43**	-0.07	0.43**	0.44**	-0.37**	-0.32**	-0.19*	0.05	-0.36**
			0.29**	0.35**	0.66**	0.50**	-0.66**	-0.68**	0.25**	0.64**	0.46**
			-0.16	0.10	0.21*	0.09	-0.47**	-0.44**	-0.23**	0.19*	-0.00
			-0.32**	-0.10	0.12	0.23**	-0.04	0.00	-0.24**	0.04	-0.29**
Biomass				0.54**	0.51**	0.15	-0.39**	-0.42**	0.70**	0.76**	0.96**
				0.40**	0.44**	-0.15	-0.13	-0.05	0.28**	0.70**	0.96**
				0.49**	0.45**	-0.07	0.41**	0.44**	0.23**	0.61**	0.95**
				0.71**	0.49**	-0.07	-0.49**	-0.46**	0.33**	0.71**	0.93**
				0.42**	0.43**	-0.06	-0.33**	-0.26**	0.32**	0.55**	0.94**
				0.41**	0.44**	0.02	0.02	-0.08	0.33**	0.70**	0.94**
Spikes m <sup>-2</sup>					0.61**	-0.16*	-0.18*	-0.20*	0.08	0.56**	0.49**
					0.62**	-0.75**	0.10	0.12	-0.40**	0.40**	0.35**
					0.39**	-0.58**	0.27**	0.18*	-0.18*	0.51**	0.48**
					0.59**	-0.21*	-0.36**	-0.40**	0.08	0.71**	0.68**
					0.48**	-0.59**	-0.23**	-0.23**	-0.19*	0.36**	0.43**
					0.55**	-0.52**	0.22**	0.17*	-0.17*	0.42**	0.31**

\*, \*\* Significant at the 0.05 and 0.01 levels of probability

Table II-10. (Continued)

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Grains m <sup>-2</sup>					0.67**		-0.35**	-0.32**	-0.01	0.64**	0.50**
					0.03		-0.07	0.10	-0.42**	0.51**	0.39**
					0.51**		-0.00	0.10	-0.05	0.48**	0.47**
					0.65**		-0.36**	-0.40**	0.11	0.76**	0.51**
					0.41**		-0.13	-0.05	-0.14	0.39**	0.38**
					0.41**		0.37**	0.36**	-0.20*	0.52**	0.27**
Grains Spike <sup>-1</sup>							-0.28**	-0.22**	-0.06	0.28**	0.19*
							-0.15	-0.06	0.21*	-0.09	-0.13
							-0.26**	-0.09	0.12	-0.05	-0.04
							-0.11	-0.13	0.08	0.27**	-0.01
							0.13	0.19*	0.04	-0.03	-0.12
							0.13	0.19*	-0.01	0.07	-0.04

\*, \*\* Significant at the 0.05 and 0.01 levels of probability

Table II-11. Genetic correlations among measured and derived traits. Experiment I, 1995-96.

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Yield	0.40	0.78	0.74	0.58	0.87	0.74	-0.74	-0.87	0.37	0.92	0.85
	-0.15	0.59	0.83	0.59	0.78	0.33	-0.30	-0.09	-0.29	0.93	0.83
	-0.31	0.69	0.65	0.66	0.90	0.42	0.04	0.05	0.14	0.88	0.73
	0.48	0.94	0.65	0.51	0.74	0.53	-0.82	-0.83	0.51	0.94	0.88
	0.55	0.80	0.83	0.40	0.63	0.23	-0.60	-0.69	0.32	0.92	0.93
	0.42	0.31	0.92	0.39	0.42	-0.08	-0.38	-0.39	0.36	0.91	0.92
TKW		0.12	0.50	-0.09	-0.10	-0.08	-0.59	-0.66	0.53	0.34	0.60
		-0.34	0.07	-0.65	-0.73	-0.03	-0.04	-0.10	0.62	-0.12	0.10
		-0.40	-0.01	-0.22	-0.69	-0.62	0.07	-0.07	0.10	-0.15	0.01
		0.42	0.45	-0.23	-0.22	-0.06	-0.60	-0.58	0.33	0.35	0.62
		0.67	0.27	-0.22	-0.30	-0.14	-0.64	-0.75	0.23	0.49	0.50
		0.45	0.29	-0.49	-0.64	-0.24	-0.52	-0.43	0.20	0.24	0.38
HI			0.17	0.30	0.77	0.80	-0.73	-0.77	-0.28	0.63	0.35
			0.05	0.34	0.63	0.44	-0.47	-0.26	-0.70	0.46	0.12
			-0.10	0.41	0.70	0.42	-0.41	-0.43	-0.22	0.54	0.09
			0.36	0.32	0.70	0.71	-0.88	-0.88	0.37	0.84	0.71
			0.34	0.15	0.29	0.06	-0.71	-0.83	-0.23	0.71	0.58
			-0.06	-0.14	-0.21	-0.10	-0.35	-0.29	-0.34	0.20	0.02
Biomass				0.62	0.56	0.31	-0.40	-0.54	0.85	0.77	0.96
				0.47	0.52	0.16	-0.05	0.06	0.12	0.85	0.95
				0.47	0.50	0.14	0.44	0.50	0.42	0.63	0.92
				0.59	0.42	-0.10	-0.29	-0.33	0.55	0.69	0.84
				0.45	0.69	0.32	-0.30	-0.32	0.77	0.78	0.93
				0.42	0.50	-0.01	-0.26	-0.29	0.55	0.88	0.96
Spikes m <sup>-2</sup>					0.67	0.18	-0.08	-0.28	0.38	0.71	0.58
					0.81	-0.35	0.07	0.19	-0.43	0.56	0.39
					0.59	-0.27	0.24	0.17	-0.06	0.71	0.47
					0.80	-0.02	-0.15	-0.22	0.26	0.60	0.50
					0.66	-0.44	-0.17	-0.16	-0.01	0.35	0.44
					0.83	-0.42	0.18	0.09	-0.03	0.50	0.34

Table II-11. (Continued)

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Grains m <sup>-2</sup>						0.85	-0.50	-0.56	0.13	0.79	0.61
						0.25	-0.17	0.02	-0.61	0.72	0.50
						0.61	0.00	0.09	0.05	0.73	0.55
						0.59	-0.44	-0.47	0.27	0.76	0.51
						0.38	-0.08	-0.09	0.15	0.60	0.59
						0.16	0.21	0.12	0.09	0.52	0.40
Grains/Spike							-0.60	-0.53	-0.09	0.55	0.40
							-0.38	-0.27	-0.21	0.26	0.22
							-0.24	-0.05	0.11	0.18	0.20
							-0.50	-0.45	0.07	0.45	0.16
							0.20	0.19	0.21	0.27	0.18
							0.04	0.05	0.24	-0.08	-0.02

Table II-12. Genetic correlations among measured and derived traits. Experiment II, 1996-97.

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Yield	0.21	0.64	0.84	0.60	0.78	0.59	-0.67	-0.68	0.43	0.79	0.89
	0.26	0.39	0.82	0.30	0.62	0.13	-0.34	-0.18	0.09	0.80	0.81
	-0.30	0.64	0.51	0.49	0.85	0.36	0.09	0.12	0.00	0.65	0.59
	0.26	0.85	0.88	0.76	0.73	0.32	-0.72	-0.72	0.43	0.87	0.91
	0.47	0.71	0.88	0.47	0.47	-0.03	-0.64	-0.67	0.12	0.66	0.90
	0.23	0.20	0.94	0.40	0.44	0.11	-0.02	-0.11	0.26	0.79	0.87
TKW		-0.17	0.42	-0.19	-0.44	-0.42	-0.42	-0.48	0.64	0.09	0.51
		-0.20	0.40	-0.56	-0.59	0.14	-0.25	-0.29	0.66	0.21	0.45
		-0.29	-0.08	-0.22	-0.75	-0.53	0.14	0.02	0.17	-0.02	-0.08
		0.01	0.46	0.05	-0.45	-0.64	-0.44	-0.37	0.44	0.00	0.49
		0.29	0.48	-0.07	-0.55	-0.48	-0.45	-0.50	0.36	0.27	0.54
		-0.03	0.26	-0.47	-0.77	-0.42	-0.47	-0.53	0.48	-0.02	0.43
HI			0.13	0.35	0.69	0.66	-0.63	-0.60	-0.31	0.34	0.27
			-0.21	0.15	0.50	0.20	-0.28	-0.18	-0.49	0.21	-0.15
			-0.34	0.00	0.60	0.59	-0.44	-0.47	-0.21	0.11	-0.18
			0.50	0.52	0.76	0.58	-0.71	-0.74	0.32	0.75	0.64
			0.29	0.35	0.36	0.02	-0.61	-0.63	-0.26	0.36	0.43
			-0.14	-0.05	0.18	0.28	-0.17	0.04	-0.48	-0.08	-0.13
Biomass				0.55	0.50	0.26	-0.44	-0.47	0.79	0.79	0.96
				0.21	0.34	0.02	-0.19	-0.08	0.37	0.72	0.96
				0.59	0.37	-0.19	0.60	0.66	0.23	0.67	0.94
				0.78	0.49	-0.04	-0.58	-0.55	0.43	0.74	0.93
				0.38	0.36	-0.07	-0.50	-0.52	0.34	0.63	0.95
				0.40	0.37	0.02	0.02	-0.14	0.44	0.83	0.93
Spikes m <sup>-2</sup>					0.70	0.11	-0.20	-0.25	0.10	0.65	0.50
					0.68	-0.71	0.19	0.25	-0.49	0.37	0.14
					0.43	-0.49	0.36	0.35	-0.25	0.57	0.56
					0.67	0.01	-0.43	-0.50	0.09	0.82	0.74
					0.48	-0.53	-0.29	-0.34	-0.24	0.37	0.40
					0.67	-0.33	0.37	0.30	-0.23	0.52	0.23

Table II-12. (Continued)

Character	TKW	HI	Biomass	Spikes m <sup>-2</sup>	Grains m <sup>-2</sup>	Grains Spike <sup>-1</sup>	Heading	Maturity	Height	G.P.R.	B.P.R.
Grains m <sup>-2</sup>						0.79	-0.37	-0.33	-0.02	0.65	0.50
						0.02	-0.10	0.08	-0.47	0.47	0.30
						0.57	-0.00	0.09	-0.10	0.46	0.43
						0.74	-0.37	-0.43	0.08	0.79	0.51
						0.49	-0.16	-0.13	-0.22	0.36	0.32
						0.49	0.40	0.41	-0.26	0.52	0.17
Grains Spike <sup>-1</sup>							-0.34	-0.26	-0.08	0.37	0.29
							-0.29	-0.22	0.28	-0.06	0.07
							-0.37	-0.27	0.14	-0.09	-0.10
							-0.14	-0.15	0.05	0.34	0.03
							0.15	0.22	-0.00	-0.04	-0.13
						0.04	0.15	-0.06	0.04	-0.03	

#### II.4.4.1. Grain yield

Biomass, grains per  $m^2$ , and both growth rates (biomass and grain production) had the highest correlations with yield, in all six populations and both years. Thus, yield was strongly influenced by both source (biomass) and sink (grains per  $m^2$ ), and also by the efficiency of production for these two traits. A significant correlation of harvest index with yield was also observed in five populations, the exception being Population 6. The explanation for this lack of association might be due to this population having the highest association between biomass and yield (about 0.90). Therefore, the higher the denominator in the harvest index ratio, the higher the yield. Spikes per  $m^2$  were also significantly correlated with yield for all populations and both experiments. In general, the associations between yield and kernel weight were positive and significant, although correlation coefficients were intermediate to low. A negative correlation between kernel weight and yield was observed for Population 3. This population had the highest association between yield and grains per  $m^2$ . Since grains per  $m^2$  and kernel weight are competing sinks, a negative association could be expected, in that instance, between kernel weight and yield. Grains per spike were also, positively correlated with yield, in most populations. For Population 6, grains per spike and grain yield were not correlated. As previously mentioned, Population 6 had the highest correlation between yield and biomass; thus, grains per spike were probably compensated by the number of tillers bearing spikes and by kernel weight.

For those traits, Populations 2 and 5 had a positive association in Experiment 1 and no association in Experiment II. Heading and maturity dates were usually found to be negatively associated with yield, therefore longer cycle genotypes resulted in lower grain yield. In that environment, temperatures were increasing to very high at the end of the wheat crop season; hence, very long-cycle lines did not have time for adequate grain-filling. Height had no, or low, association with yield.

#### II.4.4.2. Associations among other traits

The correlation between kernel weight and harvest index depended upon population and year. A negative association between these two traits was noted in Experiment I for Populations 2 and 3, while Populations 4, 5, and 6 had a positive association. Correlation coefficients were moderate to low in all cases, except in Population 1, where no association was found. No substantial association was observed between kernel weight and harvest index in Experiment II. Only Population 3 and Population 5 showed some low negative and positive associations, respectively. Significant associations between kernel weight and biomass were observed for four populations in Experiment I and five populations in Experiment II. No association between kernel weight and biomass was found for Population 3 in either experiment. A consistent negative association was observed for kernel weight and grains per  $m^2$ . This was expected, since these traits represent two competitive sinks. For the same reason, kernel weight had a negative or no association with spikes per  $m^2$  and grains per spike, even though not as strong and

consistent as between kernel weight and grains per  $m^2$ . Kernel weight was lower in longer cycle genotypes that, as already explained, did not have adequate grain-filling. This situation was reflected in the frequent negative correlation between kernel weight and phenological traits (days to heading and to maturity). Grain production rate had low, or no association with kernel weight. A positive association was found between biomass production rate and kernel weight.

Harvest index and biomass associations were negative or not significant, in most instances. The negative association between harvest index and biomass would be expected, as biomass is the denominator of the harvest index ratio. Harvest index was positively associated with sink-traits such as grains per spike and grain per  $m^2$ . The only exception was Population 6, where no association between grains per  $m^2$  and harvest index was observed in either year. Harvest index was negatively associated with days to heading, maturity, and height. Delayed heading and maturity had an adverse effect on grain filling and, consequently, on harvest index. Height was also negatively associated with harvest index. While harvest index was positively associated with grain production rate, the association with biomass production rate was more erratic, depending on population and year.

Consistent, positive associations between biomass and spikes per  $m^2$ , and biomass and grains per  $m^2$ , were observed for all crosses and years. No association between biomass and grains per spike was noted. The association between biomass and days to heading or maturity varied. In Experiment II, these associations were often negative. A strong positive relationship was observed between biomass and

height, and between biomass and the two production rates. The highest correlation coefficient values were, as would be expected, for biomass-biomass production rate.

Spikes per  $m^2$  showed a strong positive association with grains per  $m^2$ . This association was consistent for populations and years. Due to compensation between yield components, a negative correlation for all populations and experiments was found between spikes per  $m^2$  and grains per spike. There was no consistent association between spikes per  $m^2$  and days to heading or maturity, and height. The correlation coefficients were variable, depending on experiment and population, but in general they were low or not significant. There was a strong, positive association between spikes per  $m^2$  and the two production rates, grain and biomass.

Grains per  $m^2$  were positively associated with grains per spike. Correlations between these two yield components were intermediate to high. The association between grain per  $m^2$  and heading, maturity, and height was erratic, depending on population and year. In Experiment II, this association was usually negative. Strong positive correlations between grain per  $m^2$  and the two production rates, grain and biomass, were observed.

Grains per spike had negative, no, or positive associations with days to heading and to maturity. There was no substantial association of grains per spike with height, nor with the rates of grain and biomass production.

#### II.4.5. Path-coefficient analysis

To provide a better understanding of direct and indirect effects of the studied traits, a path coefficient analysis was performed. Direct and indirect contributions on grain yield of kernel weight, harvest index, biomass, spikes per  $m^2$ , grains per  $m^2$ , and grains per spike are presented in Table II-13 and Table II-14 for Experiment I and II, respectively.

Though kernel weight and grain yield were, in most cases, positively associated, kernel weight had no direct effect on yield in Experiment I and a low to intermediate effect in Experiment II. Major indirect effects of kernel weight were via positive contributions with biomass and negative contributions to grains per  $m^2$ . Negative indirect effects of kernel weight through grains per  $m^2$  were observed when kernel weight had direct, positive effects on yield. The exception was Population 3, which had a negative association between kernel weight and grain yield. In this population, the direct effect of kernel weight on yield was positive (larger in Experiment II), but its indirect negative effect via grains per  $m^2$  was greater. No indirect effects of kernel weight via biomass were detected in Population 3.

Harvest index had a substantial, positive direct effect on grain yield. In some populations, there was a positive indirect effect of harvest index via grains per  $m^2$  and a negative indirect effect via biomass.

Biomass, the trait with the highest correlation with grain yield, also had the greatest direct effect on yield. Biomass also influenced grain yield via positive, but

Table II-13. Direct and indirect effects of six agronomic yield components on grain yield.  
Experiment I, 1995-96.

<i>Character</i>	<i>Pop. 1</i>	<i>Pop. 2</i>	<i>Pop. 3</i>	<i>Pop.4</i>	<i>Pop. 5</i>	<i>Pop. 6</i>
<b>YIELD vs KERNEL WEIGHT</b>						
Direct effect	0.09	0.07	0.07	-0.03	-0.10	0.14
Indirect effect via Harvest Index	0.06	-0.14	-0.19	0.28	0.34	0.08
Indirect effect via Biomass	0.25	0.12	0.07	0.22	0.20	0.25
Indirect effect via Spikes m <sup>-2</sup>	-0.00	0.29	0.19	0.00	0.00	-0.00
Indirect effect via Grains m <sup>-2</sup>	-0.04	-0.37	-0.75	-0.01	0.02	-0.09
Indirect effect via Grains Spike <sup>-1</sup>	-0.00	0.00	0.45	0.00	0.00	0.00
Phenotypic Correlation	0.36**	-0.03	-0.16	0.46**	0.46**	0.38**
<b>YIELD vs HARVEST INDEX</b>						
Direct effect	0.58	0.47	0.60	0.75	0.69	0.40
Indirect effect via Kernel Weight	0.01	-0.02	-0.02	-0.01	-0.05	0.03
Indirect effect via Biomass	-0.10	-0.19	-0.25	-0.03	-0.11	-0.35
Indirect effect via Spikes m <sup>-2</sup>	-0.00	-0.04	-0.17	-0.00	0.00	-0.00
Indirect effect via Grains m <sup>-2</sup>	0.08	0.25	0.63	0.02	-0.01	-0.03
Indirect effect via Grains Spike <sup>-1</sup>	0.00	-0.18	-0.39	-0.04	-0.01	-0.01
Phenotypic Correlation	0.57**	0.29**	0.40**	0.69**	0.51**	0.04
<b>YIELD vs BIOMASS</b>						
Direct effect	0.69	0.89	0.79	0.72	0.95	0.90
Indirect effect via Kernel Weight	0.03	0.01	0.01	-0.01	-0.02	0.04
Indirect effect via Harvest Index	-0.09	-0.10	-0.18	-0.03	-0.08	-0.15
Indirect effect via Spikes m <sup>-2</sup>	0.01	-0.27	-0.56	-0.01	-0.00	0.00
Indirect effect via Grains m <sup>-2</sup>	0.08	0.41	0.78	0.02	-0.05	0.11
Indirect effect via Grains Spike <sup>-1</sup>	0.00	-0.07	-0.10	-0.01	-0.00	0.00
Phenotypic Correlation	0.72**	0.87**	0.74**	0.68**	0.80**	0.90**
<b>YIELD vs SPIKES PER m<sup>2</sup></b>						
Direct effect	0.01	-0.56	-1.13	-0.03	-0.00	0.01
Indirect effect via Kernel Weight	-0.00	-0.04	-0.01	0.00	0.01	-0.04
Indirect effect via Harvest Index	-0.04	0.04	0.09	0.06	-0.12	-0.13
Indirect effect via Biomass	0.44	0.43	0.39	0.33	0.54	0.45
Indirect effect via Grains m <sup>-2</sup>	0.08	0.47	0.76	0.02	-0.04	0.12
Indirect effect via Grains Spike <sup>-1</sup>	-0.00	0.19	0.49	0.03	0.02	0.01
Phenotypic Correlation	0.49**	0.53**	0.59**	0.41**	0.41**	0.42**
<b>YIELD vs GRAINS PER m<sup>2</sup></b>						
Direct effect	0.15	0.65	1.34	0.05	-0.08	0.18
Indirect effect via Kernel Weight	-0.02	-0.04	-0.04	0.00	0.03	-0.07
Indirect effect via Harvest Index	0.30	0.18	0.28	0.36	0.12	-0.06
Indirect effect via Biomass	0.35	0.56	0.46	0.34	0.66	0.52
Indirect effect via Spikes m <sup>-2</sup>	0.01	-0.41	-0.65	-0.02	-0.00	0.01
Indirect effect via Grains Spike <sup>-1</sup>	0.00	-0.12	-0.49	-0.03	-0.01	-0.00
Phenotypic Correlation	0.79**	0.82**	0.90**	0.70**	0.72**	0.58**
<b>YIELD vs GRAINS PER SPIKE</b>						
Direct effect	0.00	-0.43	-1.07	-0.07	-0.03	-0.02
Indirect effect via Kernel Weight	-0.03	0.00	-0.03	0.00	0.02	-0.02
Indirect effect via Harvest Index	0.36	0.19	0.21	0.44	0.22	0.12
Indirect effect via Biomass	0.04	0.15	0.07	0.07	0.05	-0.10
Indirect effect via Spikes m <sup>-2</sup>	-0.00	0.25	0.52	0.01	0.00	-0.00
Indirect effect via Grains m <sup>-2</sup>	0.11	0.18	0.62	0.02	-0.03	0.02
Phenotypic Correlation	0.48**	0.34**	0.32**	0.47**	0.23**	0.00

\* \*\* Significant at the 0.05 and 0.01 levels of probability.

R<sup>2</sup> for all populations were ≥ 0.98

Table II-14. Direct and indirect effects of six agronomic yield components on grain yield.  
Experiment II, 1996-97.

<i>Character</i>	<i>Pop. 1</i>	<i>Pop. 2</i>	<i>Pop. 3</i>	<i>Pop. 4</i>	<i>Pop. 5</i>	<i>Pop. 6</i>
<b>YIELD vs KERNEL WEIGHT</b>						
Direct effect	0.21	0.46	0.38	0.09	0.43	0.27
Indirect effect via Harvest Index	-0.05	-0.03	-0.08	0.00	0.07	0.00
Indirect effect via Biomass	0.22	0.15	0.00	0.23	0.17	0.14
Indirect effect via Spikes m <sup>-2</sup>	0.01	-0.02	-0.00	-0.00	-0.00	-0.02
Indirect effect via Grains m <sup>-2</sup>	-0.18	-0.33	-0.47	-0.14	-0.26	-0.22
Indirect effect via Grains Spike <sup>-1</sup>	0.02	0.00	0.01	0.06	0.02	-0.00
Phenotypic Correlation	0.23**	0.23**	-0.16*	0.24**	0.43**	0.17*
<b>YIELD vs HARVEST INDEX</b>						
Direct effect	0.39	0.31	0.42	0.47	0.34	0.38
Indirect effect via Kernel Weight	-0.03	-0.04	-0.07	0.00	0.09	0.00
Indirect effect via Biomass	-0.04	-0.19	-0.21	0.17	-0.12	-0.26
Indirect effect via Spikes m <sup>-2</sup>	-0.01	-0.00	-0.00	-0.03	0.00	-0.00
Indirect effect via Grains m <sup>-2</sup>	0.25	0.17	0.29	0.19	0.10	0.04
Indirect effect via Grains Spike <sup>-1</sup>	-0.03	0.00	-0.01	-0.05	-0.01	0.00
Phenotypic Correlation	0.53**	0.25**	0.42**	0.75**	0.40**	0.16
<b>YIELD vs BIOMASS</b>						
Direct effect	0.58	0.50	0.49	0.59	0.50	0.81
Indirect effect via Kernel Weight	0.08	0.14	0.00	0.03	0.15	0.04
Indirect effect via Harvest Index	-0.03	-0.12	-0.18	0.14	-0.07	-0.12
Indirect effect via Spikes m <sup>-2</sup>	-0.04	0.02	0.01	-0.07	0.00	0.02
Indirect effect via Grains m <sup>-2</sup>	0.22	0.25	0.31	0.14	0.21	0.13
Indirect effect via Grains Spike <sup>-1</sup>	-0.01	-0.00	0.00	0.01	0.00	0.00
Phenotypic Correlation	0.80**	0.79**	0.63**	0.84**	0.79**	0.88**
<b>YIELD vs SPIKES PER m<sup>2</sup></b>						
Direct effect	-0.07	0.05	0.02	-0.09	0.00	0.04
Indirect effect via Kernel Weight	-0.02	-0.19	-0.06	0.00	-0.02	-0.10
Indirect effect via Harvest Index	0.06	-0.03	-0.03	0.17	0.01	-0.04
Indirect effect via Biomass	0.33	0.20	0.24	0.42	0.22	0.33
Indirect effect via Grains m <sup>-2</sup>	0.26	0.36	0.27	0.17	0.24	0.17
Indirect effect via Grains Spike <sup>-1</sup>	0.01	-0.00	0.01	0.02	0.02	-0.00
Phenotypic Correlation	0.57**	0.39**	0.45**	0.69**	0.47**	0.40**
<b>YIELD vs GRAINS PER m<sup>2</sup></b>						
Direct effect	0.43	0.58	0.68	0.28	0.50	0.30
Indirect effect via Kernel Weight	-0.09	-0.26	-0.26	-0.04	-0.22	-0.20
Indirect effect via Harvest Index	0.23	0.09	0.18	0.32	0.07	0.05
Indirect effect via Biomass	0.29	0.22	0.22	0.29	0.21	0.35
Indirect effect via Spikes m <sup>-2</sup>	-0.04	0.03	0.01	-0.06	0.00	0.02
Indirect effect via Grains Spike <sup>-1</sup>	-0.04	0.00	-0.01	-0.07	-0.02	0.00
Phenotypic Correlation	0.78**	0.66**	0.82**	0.72**	0.54**	0.52**
<b>YIELD vs GRAINS PER SPIKE</b>						
Direct effect	-0.06	0.01	-0.02	-0.10	-0.04	0.01
Indirect effect via Kernel Weight	-0.08	0.02	-0.17	-0.05	-0.18	-0.10
Indirect effect via Harvest Index	0.22	0.10	0.18	0.24	0.06	0.09
Indirect effect via Biomass	0.07	-0.08	-0.03	-0.04	-0.05	0.01
Indirect effect via Spikes m <sup>-2</sup>	0.01	-0.04	-0.01	0.02	-0.00	-0.02
Indirect effect via Grains m <sup>-2</sup>	0.28	0.02	0.34	0.18	0.20	0.12
Phenotypic Correlation	0.44**	0.03	0.29**	0.25**	-0.01	0.11

\* \*\* Significant at the 0.05 and 0.01 levels of probability.

R<sup>2</sup> for all populations were = 0.99

low, indirect effects on grains per  $m^2$  and through low negative, indirect effects on harvest index.

The correlation between spikes per  $m^2$  and grain yield was positive and significant in all populations and years. However, this trait had no or a negative direct effect on yield. Main effects of spikes per  $m^2$  were through indirect associations as positive indirect effects on yield via biomass was observed for all populations and years. Indirect positive effects on yield via grains per  $m^2$  were relevant in two populations of Experiment I and in most populations of Experiment II. Indirect positive effects on yield via grains per spike were important only during the first experiment for Population 3, which had the largest negative direct effect of spikes per  $m^2$  on grain yield.

Grains per  $m^2$  had a substantial, positive association with yield in all populations and experiments. Nevertheless, the direct effects on yield by grains per  $m^2$  were not as consistent as those of biomass on grain yield. Direct contributions to yield by grain per  $m^2$  varied depending on year and/or population. In Experiment I, only two populations had important direct effects of grains per  $m^2$  on yield (Population 2 = 0.65, Population 3 = 1.34), other populations had no, or very low, direct effects on yield. In Experiment II, direct effects on grain yield were more consistent in all populations. Grains per  $m^2$  influenced yield via positive indirect effects on biomass. In Experiment I, grains per  $m^2$  had a positive indirect effect through harvest index; however, in Populations 2 and 3, some negative indirect effects via spikes per  $m^2$  and grains per spike were observed. In Experiment II,

there were negative indirect effects via kernel weight and some positive indirect effects via harvest index detected with grains per m<sup>2</sup> on yield.

Depending on the population, grains per spike had no or a negative direct effect on yield, with the main positive indirect effects being via harvest index. Populations 2 and 3 in Experiment I had strong negative direct effect of grains per spike on yield. In these two populations, grains per spike had an important positive indirect influence on grain yield through spikes per m<sup>2</sup> and grains per m<sup>2</sup>.

## II.5. Discussion

There have been indications during the last decade that grain yield of wheat is leveling off. The utilization of wild relatives of wheat for increasing genetic variability to enhance grain yield potential has not been considered in the past and may constitute a new and challenging insight in this primitive germplasm routinely used as a source of resistance to biotic and abiotic stresses. Considering that yield is a very complex trait, modern wheat varieties doubtfully have the best alleles for all yield-related loci, bottlenecks imposed by domestication and breeding may have left many yield-positive alleles behind. In the present study, several synthetic-derived lines had significant higher yield than their bread wheat recurrent parents. This proves that introgression of synthetic germplasm in common bread wheat can result in positive transgressive segregation for yield. Some outstanding lines yielded up to 14% more than their recurrent parent.

Studies of historical sets of wheat cultivars released at different eras indicated that most of the genetic gains in grain yield during the last century have mainly been due to increases in HI (Richards, 1996). The increase in wheat HI was the consequence of both the shortening of the stem with the introduction of semidwarf varieties and the increase in number of grains per m<sup>2</sup>. Kernel weight has not been positively changed, and in some cases decreased, during that period (Slafer and Andrade, 1989; Siddique et al., 1989; Sayre et al., 1997).

It has been accepted that grain number is negatively associated with grain weight. However, the phasic development of these two yield components overlap minimally (Slafer et al., 1996). Thus, the common explanation that a higher number of grains per m<sup>2</sup> may reduce the availability of assimilates for each individual grain may become true if there are source limitations during grain filling. Yet, wheat, particularly under optimum conditions, has repeatedly been reported as sink-limited (Borojevic, 1978; Thorne et al., 1979; Borghi et al., 1986; Bindraban, 1997). A possible explanation to this sink limitation proposed by Bindraban (1997) is that, under a wide range of crop conditions, wheat plants are "in balance", producing determined grain number with a standard weight. Sink demand is completely fulfilled by post-anthesis assimilation plus translocation of reserves. However, under optimum conditions, synthesis of assimilates may overwhelm the limited capacity of the sink, resulting in an underutilization of the source capacity. If this is the case, the possibility is open to further increase the grain yield of wheat by enlarging sink capacity.

Genetic gains in yield potential may be achieved in the future by increasing kernel weight while maintaining (or, if possible, augmenting) kernel number. In the case of barley, kernel weight is higher than in wheat even when grain per m<sup>2</sup> is the same and the duration of grain-filling is shorter (Richards, 1996). Several reasons may account for this difference, the first and obvious one being that rate of grain-filling in barley is faster than in wheat (Lopez Castañeda and Richards, 1994). It is not known why the rate of grain-filling in barley is greater than in wheat, but some possible explanations could be differences in spike structure or vascular limitations between the two species.

Dwarfing genes (*Rht1* and *Rht2*) have been reported to be associated with smaller cell size (Keyes et al., 1989). If these genes also limit the elongation and growth of the kernels, then germplasm carrying those factors may have some genetic limitations for producing larger caryopses. Miralles and Slafer (1995), studying the effects of *Rht* alleles in isogenic lines of a spring wheat, found that reduction in average grain weight produced by *Rht* alleles was due to a combination of both reduction in potential size of each grain and contribution of grains from distal positions in the spike.

Results from two years experiments with six different synthetic hexaploid wheat populations indicated that synthetic-derived lines have heavier kernels than their bread wheats parents. Overall population means were 12% to 20% (Experiment I and II, respectively) higher than recurrent parental means. Sixty-seven percent of the lines in Experiment 1, to eighty-five percent of the lines in

Experiment II, had significantly heavier kernels compared to their bread wheat recurrent parents. Hence, synthetic wheat is a promising source to improve this important yield component that has been postponed for so many years of wheat breeding. Association between kernel weight and grains per  $m^2$  was always negative; however correlation coefficients values went from high to low, depending on the population. Furthermore, outstanding lines for yield had superior kernel weight and, in several cases, also had higher number of grains per  $m^2$ .

Synthetic-derived lines, contrary to expectations, did not have higher mean biomass production than their bread wheat parents, even when the mean height of the lines was higher than their bread wheat parent mean height. However, outstanding lines for yield did have higher biomass and biomass production rate than their bread wheat recurrent parents. Therefore, biomass is a target trait for selection in these synthetic-derived populations.

The effect of the bread wheat parent was observed in Populations 3, 4, and 5, which have the same synthetic parent and different bread wheats in combination. As a general rule, the best performing bread wheat parent gave rise to the best synthetic-derived population. The best line for each trait was, in most cases, also found in the best population.

## II.6. Conclusions

- Degree of variability among BC<sub>2</sub>F<sub>2.6</sub> synthetic-derived lines for yield and yield-related traits indicated that the introgression of alleles from *A. tauschii* Coss. and durum wheat did modify the performance of quantitative traits such as grain yield and its components.
- Kernel weight was the trait that showed the highest gain as a result of the introgression of synthetic hexaploid germplasm.
- Some synthetic-derived lines were 14% higher for grain yield than their bread wheat recurrent parent, suggesting the possibility of finding transgressive segregation for enhanced grain yield.
- Superior yielding, synthetic-derived lines had increased kernel weight and biomass, while maintaining their grain number per m<sup>2</sup> and harvest index. Therefore, a simultaneous increase in source and sink was observed in higher yielding genotypes.
- Grain yield showed a strong association with biomass and grains per m<sup>2</sup>, as well as for the production rates for grain and biomass.

- Path coefficient analysis revealed a strong direct effect of biomass and harvest index on grain yield.

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### III. MANUSCRIPT 2

## PHYSIOLOGICAL PERFORMANCE OF SYNTHETIC HEXAPLOID WHEAT-DERIVED POPULATIONS

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### III.1. Abstract

Wild ancestors of common bread wheat (*Triticum aestivum* L.) have repeatedly been reported as having higher photosynthetic rates than modern cultivated wheats. Synthetic hexaploid wheats, obtained by crossing tetraploid wheat and goatgrass (*Aegilops tauschii* L.), have proven to be very useful as a source of resistance or tolerance to biotic and abiotic stresses. Three different populations of BC<sub>2</sub> F<sub>2:6</sub> synthetic-derived lines were evaluated in this study. The objective was to assess genetic variability among genotypes for physiological traits, and to establish associations between those physiological traits and selected agronomic traits. Differences in maximum photosynthetic rate were detected among genotypes. Several synthetic-derived lines showed higher photosynthetic rate than their bread wheat recurrent parent. Senescence of upper leaves was not substantially premature in synthetic-derived lines compared to their recurrent bread wheat parents. Maximum photosynthetic rate was negatively associated with leaf area and leaf specific weight and positively associated with stomatal and mesophyll conductances, leaf temperature depression, grain yield and aboveground biomass.

Differences in conductances, in the diffusion pathway of CO<sub>2</sub>, accounted for most of the differences in photosynthesis. These results suggest that synthetic-derived wheats can be also a source of genetic diversity for important physiological traits such as enhanced photosynthetic rate, which can be conveniently manipulated by means of selection.

### III.2. Introduction

Common bread wheat (*Triticum aestivum* L.) is an allopolyploid species originated from hybridization between wild diploids having A, B, and D genomes. Evolution and artificial selection have modified morphological and physiological traits, leading to a substantially improved hexaploid bread wheat, which is further characterized by being the highest in grain yield among the whole *Triticum* genus. Evolution, higher level of ploidy, and selection from the wild ancestors to the modern wheat have resulted in increased grain and leaf size, grain filling duration (related to delayed senescence of upper leaves), and decreased net photosynthetic rate under saturating irradiance (Welbank et al., 1966, 1968; Evans and Dunstone, 1970; Khan and Tsunoda, 1970). Expansions in grain and leaf dimensions were the consequence of increases in endosperm and mesophyll cell number and also size. The D genome, originated from *Aegilops tauschii* Coss. (commonly known as goatgrass), is the carrier of many baking quality traits. This genome also supports

the wide adaptation that allows wheat cultivation even in low rainfall areas (Zohary et al., 1969).

Synthetic hexaploid wheat is a relatively new germplasm obtained by artificially crossing durum wheat, *Triticum turgidum* L. ssp. *durum* (Desf.) Husn. ( $2n=4x=28$ , AABB), and *Aegilops tauschii* Coss. ( $2n=14$ , DD), [Syn. *Triticum tauschii* (Coss.) Schmal]. This germplasm has proven to be very useful as a source of resistance to diseases and pests, as well as for tolerance to environmental stresses such as drought and salinity. Synthetic hexaploids are routinely crossed and backcrossed with common bread wheat ( $2n=6x=42$ , AABBDD) to achieve acceptable agronomic types.

Net assimilation of CO<sub>2</sub> through the process of photosynthesis is the initial step for biomass production. Some authors (Austin et al., 1989; Carver and Nevo, 1990) proposed the utilization of genes for higher photosynthetic rate, commonly present in wild relatives, to increase grain yield of wheat. Indeed, domestication and breeding of wheat, over many years, has resulted in lower photosynthetic rate (Evans and Dunstone, 1970). Wild relatives of wheat have been reported to have higher photosynthetic rates than modern cultivars (Evans and Dunstone, 1970; Khan and Tsunoda, 1970; Dunstone et al., 1973; Austin et al., 1982; Johnson et al., 1987; Carver et al., 1989). A higher photosynthetic rate may be beneficial when sink (kernel number, kernel weight) strength is increased, as seems to be the case of synthetic-derived wheats (Chapter 1 in this thesis). Zelitch (1982) indicated that increasing the rates of net photosynthesis and translocation while enlarging the

storage capacity may bring about large increases in grain yield, especially in C3 species. Dunstone et al. (1973) found that the higher carbon exchange rate (CER) in wild genotypes was associated with reductions in stomatal and residual resistances, and with increases in stomatal density. Dunstone and Evans (1974) observed that, from wild diploids to modern wheat cultivars, CER fell as mesophyll cell size increased. Number of chloroplasts and content of Rubisco per cell increased almost threefold from diploid to hexaploid (Dean and Leech, 1982). A strong negative correlation between leaf size and CER has been reported for wheat species (Evans and Dunstone, 1970; Austin et al., 1982; Johnson et al. 1987). Planchon and Fesquet (1982) suggested that the D genome, besides being the carrier of baking quality and wide adaptation characteristics, also weakened the negative relation between CER and flag leaf area.

In chloroplast thylakoid membranes there is a variety of photoreceptors, in the form of pigment molecules, that absorb physiologically useful radiation. Among them there are two groups of functionally cooperating chlorophyll molecules consisting of photochemically active chlorophyll a (reaction centers) and photochemically inactive chlorophyll b (antenna pigments). Austin et al. (1987) observed that, under high light intensity, diploids tend to have a higher ratio of chlorophyll a/b than hexaploid wheats. Chlorophyll a is directly involved in the conversion of light energy to chemical energy. Chlorophyll b and carotenoids absorb light at different wavelengths from those absorbed by chlorophyll a. They apparently can transfer the energy to chlorophyll a, extending the range of light

available for photosynthesis. A higher chlorophyll a/b ratio indicates a higher concentration of photosystems per chlorophyll. This condition could be advantageous in high light intensity environments.

The general objective of this study was to explore some physiological features of this relatively new, synthetic-derived, germplasm. Specific objectives were:

- To measure maximum photosynthetic rate (or maximum CO<sub>2</sub> assimilation = A<sub>m</sub>) of synthetic derived genotypes and their respective bread wheat recurrent parents.
- To estimate concentration of photosynthetic pigments by optical density, as well as chlorophyll a to chlorophyll b ratio.
- To assess leaf greenness with a hand-held chlorophyll meter and to relate this score to the total concentration of chlorophyll estimated by optical density.
- To determine responses, by means of regression, of some productivity traits to variable levels of physiological traits.

### III.3. Materials and Methods

Data was collected on seven BC<sub>2</sub>-F<sub>2.6</sub> synthetic-hexaploid derived lines and the recurrent bread wheat parent from three populations. The populations were:

*Population 1:* Altar 84/A.tauschii(219)//2\*Esmeralda

*Population 2:* Altar 84/A.tauschii(223)//2\*Flycatcher

*Population 3:* Duergand 2/A. tauschii(214)//2\*Seri

Details of crosses and pedigrees are provided in Appendix 3. The three populations were evaluated in three adjacent, randomized complete block designs with three replications, during the 1996-97 crop season, at the Agricultural Research Center for the Northwest (CIANO) Experimental Station (40m above sea level and 27°N and 109°W), Yaqui Valley, Sonora, Mexico. Complete description of the experiment, as well as type of soil and climate for the site, is provided in Chapter 1.

#### III.3.1. Photosynthesis measurements

Maximum rate of photosynthesis per unit area ( $A_m$ ) was measured with a CIRAS-1 Portable Photosynthesis System (PP Systems, Hitchin, England) further referred to as PP-system. Stomatal conductance (gs), air temperature, leaf

temperature, and internal carbon (Ci) were simultaneously recorded by the PP-system. Measurements were taken on three flag leaf blades per plot, during the grain filling period (21 to 23 days after anthesis). Data were collected in each replication, on clear days, between 11:00h and 15:30h. Leaf temperature depression ( $\Delta T$ ) was calculated as the difference in °C between air temperature and leaf temperature. Reference CO<sub>2</sub> was set approximately between 380-400 ppm, and it was stable. The reference humidity was set at 70% relative humidity. Photosynthetically active radiation (PAR) was between 1,200 to 1,600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , with most readings between 1,400 and 1,600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

### **III.3.2. Leaf characteristics**

Five healthy and complete flag leaf blades were sampled at random from the central rows of each plot. Sampling was performed during the grain filling stage, simultaneous to photosynthesis measurements. Leaf area of fresh leaves was measured with a Li-Cor Area Meter (Li-3100, Li-Cor Inc., Lincoln, Nebraska, USA).

Leaf greenness was measured on those sampled, fresh leaves using a hand-held leaf greenness meter (SPAD-502, Chlorophyll Meter®, Minolta Camera Co., Ltd., Japan), further referred to as SPAD. The average of three readings (top, center, and base of the leaf blade) per leaf was used as a greenness score.

A leaf disc (5 mm diameter) was removed from each leaf using a hole punch. Leaf specific weight was determined as the mean weight, in  $\text{mg cm}^{-2}$ , of this standard excised area taken from each of the five sampled leaves.

### **III.3.3. Staygreen determination**

Staygreen trait (Stg) was determined by the difference between senescence and physiological maturity (staygreen = days to senescence – days to physiological maturity). Days to senescence were estimated as the number of days from sowing to the date when 50% of the flag leaves turned yellow (50% of chlorophyll remaining) in each plot. Days to maturity were the number of days from sowing to the date when 50% of the peduncles turned yellow. It is crucial for optimum grain filling that flag leaves should remain photosynthetically active until physiological maturity, measured as the cessation of assimilate translocation to the spike when the peduncle starts to lose chlorophyll. A delay of two or fewer days between senescence and maturity is considered “good” (Stg = -2 to 0), a delay of more than 6 days is considered “poor” (Stg = -6)

### **III.3.4. Determination of photosynthetic pigments**

A standard, central portion of each sampled leaf was excised, and the five portions were ground together with 15 ml of acetone 80% in a stone mortar and pestle. The extract with the leaf material was centrifuged at 3,000 rpm for 15

minutes. The optical density values of the supernatant at 750 nm, 663.2 nm, 646.8 nm, and 470 nm were measured with a spectrophotometer (Milton Roy Co., Rochester, N.Y., USA). The blank contained 80% acetone. The reading at 750nm assessed the degree of turbidity, if it was higher than 0.05, centrifugation was repeated. With the other readings, concentration of chlorophyll a (Chl<sub>a</sub>), chlorophyll b (Chl<sub>b</sub>), and carotenoids (Carot.), i.e. xantofils plus carotenes, were calculated from the following equations:

$$\text{Chl}_a = (12.25 A_{663.2}) - (2.79 A_{646.8})$$

$$\text{Chl}_b = (21.50 A_{646.8}) - (5.10 A_{663.2})$$

$$\text{Chl}_{a+b} = (7.15 A_{663.2}) + (18.71 A_{646.8})$$

$$\text{Carot.} = (1000 A_{470} - 1.82 \text{Cl}_a - 85.02 \text{Cl}_b) / 198$$

Where: A is the absorbance at the given wavelength.

The obtained concentrations were expressed in  $\mu\text{g cm}^{-3}$ .

### **III.3.5. Statistical analysis**

Separate analysis of variance for all measured traits and three populations were performed using the Statistical Analysis System Software (SAS Institute Inc., Cary, North Carolina, 1993). Separation of means was computed by Fisher's protected LSD.

Simple linear regression of maximum photosynthetic rate on leaf characteristics, as well as on leaf conductance and leaf temperature depression, was performed to assess the changes in CO<sub>2</sub> assimilation produced by different levels of the independent variable. Simple linear regression of biomass and grain yield on maximum CO<sub>2</sub> assimilation per leaf was also calculated.

#### III.4. Results and Discussion

Observed mean-square values from the analysis of variance for maximum photosynthetic rate per unit area ( $A_m$ ) are presented in Table III-1. Highly significant differences ( $P < 0.01$ ) in CO<sub>2</sub> assimilation rate were detected among genotypes for Population 1. Suggestive differences ( $P < 0.07$ ) were found for Populations 2 and 3. Coefficients of variation ranged between 11.6 and 13.1. The coefficient of determination was higher for Population 1 (0.80) than for Populations 2 and 3 (0.48 and 0.57 respectively).

Mean separation by least significant difference (LSD) is presented in Table III-2. Synthetic derived lines from Populations 1 and 2 had higher or equal  $A_m$  than their respective recurrent parent. Synthetic derived lines from Population 3 were within a LSD of their recurrent parent. No line had lower  $A_m$  than their respective recurrent parent. The staygreen of the genotypes was not substantially shorter for the synthetic derived lines than for their recurrent bread wheat parents. Only two genotypes in Population 1 had lesser staygreen than their bread wheat recurrent

Table III-1. Observed mean squares, F-test level of probability ( $Pr > F$ ), coefficient of variation and coefficient of determination for maximum photosynthetic rate ( $A_m$ ) in three Synthetic derived populations grown at CIANO, 1996-97.

<i>Source of Variation</i>	<i>df</i>	<i>Population 1</i>	<i>Population 2</i>	<i>Population 3</i>
Replications	2	71.07	35.21	121.16
Genotypes	7	96.36	18.06	14.99
Genotypes*replication	14	15.17	7.16	6.02
Error	48	5.38	6.77	6.81
C.V. %		11.65	13.11	12.20
$Pr > F$ (Genotypes)		0.002	0.067	0.069
$R^2$		0.80	0.48	0.57

Table III-2. Mean of maximum photosynthesis rate per unit of area ( $A_m$ ), maturity (Matur.), senescence (Senesc.), staygreen (Stg.) and yield of advanced lines and their recurrent parents from three synthetic hexaploid derived populations.

Genotypes	$A_m$ ( $\mu\text{mCO}_2\text{m}^{-2}\text{s}^{-1}$ )	Matur. (days)	Senesc. (days)	Stg. <sup>†</sup> (days)	Yield (Kg ha <sup>-1</sup> )
<b>POPULATION 1.</b>					
Entry 16	27.2	160	150	-10	2545
Entry 13	21.4	132	134	2	7519
Entry 44	20.1	130	130	0	7592
Entry 21	19.1	129	131	2	6438
Entry 30	18.5	140	136	-4	5649
Entry 17	18.4	129	130	1	7347
Entry 31	17.3	128	129	1	7234
Rec. Par. (Esmeralda)	17.2	133	131	-2	6921
L.S.D. (0.05)	2.8	3.5	3.7		546
<b>POPULATION 2.</b>					
Entry 76	22.0	133	131	-2	4969
Entry 59	21.2	130	129	-1	6842
Entry 81	20.8	131	131	0	4574
Entry 77	20.0	125	127	2	6719
Entry 66	19.6	135	132	-3	7043
Entry 83	18.8	126	126	0	6692
Entry 63	18.2	124	126	2	6474
Rec. Par. (Ocoroni)	18.2	128	127	-1	6516
L.S.D.(0.05)	2.5	3.3	2.7		560
<b>POPULATION 3.</b>					
Entry 116	23.3	134	133	-1	7108
Entry 113	22.8	126	126	0	6200
Entry 141	22.3	127	126	-1	6734
Rec. Par. (Seri)	21.3	133	131	-2	7122
Entry 123	20.7	126	126	0	6505
Entry 127	20.7	136	136	0	5872
Entry 106	20.0	126	126	0	6514
Entry 108	19.9	127	129	2	6081
L.S.D. (0.05)	2.6	2.1	3.2		505

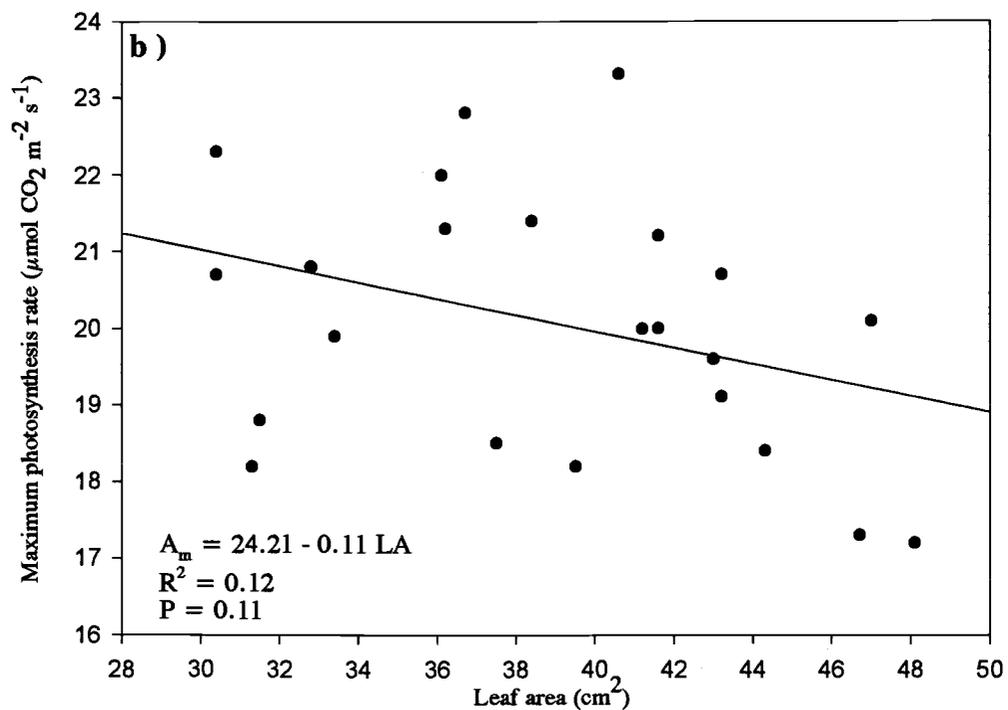
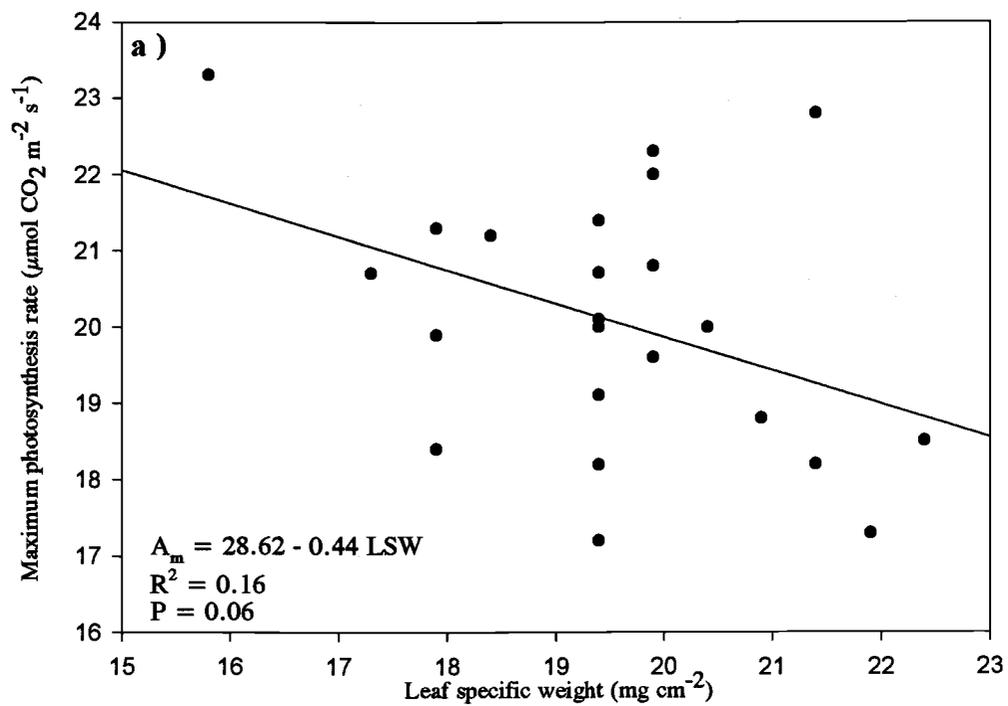
<sup>†</sup> Staygreen = Days to senescence – Days to maturity

parent (Seri). Entry 16, which had the highest  $A_m$ , had a very poor staygreen period (Stg = -10). This entry had a very long phenological cycle, and undoubtedly this characteristic, together with the inferior staygreen period, affected grain filling and yield. Entry 30 also had a less than desirable staygreen period (Stg = -4).

#### **III.4.1. Maximum photosynthesis and leaf characteristics**

Simple linear regressions of  $A_m$  on leaf specific weight, and  $A_m$  on leaf area are shown in Figure III-1. There was a linear and negative response of  $A_m$  on leaf specific weight ( $P=0.06$ ), and of  $A_m$  on leaf area ( $P=0.11$ ). The slope for the regression of  $A_m$  on leaf specific weight was steeper ( $\beta_1 = -0.44$ ) than the slope of  $A_m$  on leaf area ( $\beta_1 = -0.11$ ). These results suggest that genotypes with lighter and smaller leaves tend to have higher levels of  $CO_2$  assimilation per unit area. This observation might explain why synthetic derived lines, in spite of being taller than their bread wheat recurrent parents, had lower biomass (Chapter 1 in this thesis).

The negative association between maximum photosynthetic rate and leaf area has been consistently found between primitive relatives and modern wheats (Evans and Dunstone, 1970; Austin et al., 1982); and also among modern wheat cultivars (Gale et al., 1974; Planchon, 1979). In contrast, the association between maximum photosynthetic rate and leaf specific weight, reported by different authors, has been inconsistent (Khan and Tsunoda, 1970; Dunstone et al., 1973).



**Figure III-1:** Regression of maximum photosynthesis rate ( $A_m$ ) on:

- a) Leaf specific weight (LSW)
- b) Leaf area (LA)

### III.4.2.       Photosynthetic pigments

Observed mean squares for concentration of photosynthetic pigments and greenness rating score are presented in Table III-3. There were no significant differences among genotypes for chlorophyll a, a/b ratio, and total chlorophyll. Population 2 and 3 had significant differences for chlorophyll b. Significant differences among genotypes in carotenoid content was also observed in Population 2. There were also differences among genotypes in leaf greenness rating for the three populations. According to these results, differences in CO<sub>2</sub> assimilation among genotypes cannot be explained either by the ratio of chlorophyll a to chlorophyll b, or by the total chlorophyll content.

Separations of means based on leaf greenness rating (LGR) are presented in Table III-4. Synthetic-derived lines from Populations 1 and 2 tended to have darker green leaves compared to their respective bread wheat recurrent parent. In Population 3, synthetic-derived lines tended to have lighter green leaves than the bread wheat parent.

Table III-3. Observed mean squares and coefficient of variations for chlorophyll a (Chl<sub>a</sub>), chlorophyll b (Chl<sub>b</sub>), total chlorophyll (Chl<sub>ab</sub>), carotenoids (carot.), ratio chlorophyll a/b (a/b ratio), and greenness.

<i>Source of Variation</i>	<i>df</i>	<i>Chl<sub>a</sub></i>	<i>Chl<sub>b</sub></i>	<i>Chl<sub>ab</sub></i>	<i>a/b ratio</i>	<i>Carot.</i>	<i>Greenness</i>
<b><i>Population 1</i></b>							
Replications	2	1.07	0.95*	3.75	0.11	0.13	2.13
Genotypes	7	1.36	0.34	2.95	0.015	0.09	10.77**
Error	14	0.90	0.17	1.83	0.006	0.05	2.01
C.V. %		7.2	8.2	7.4	3.1	7.1	2.8
<b><i>Population 2</i></b>							
Replications	2	3.90**	1.35**	9.7**	0.06**	0.08*	2.09
Genotypes	7	0.81	0.10*	1.4	0.01	0.08*	3.54*
Error	14	0.43	0.03	0.64	0.008	0.02	1.22
C.V. %		4.7	3.5	4.1	3.3	4.1	2.2
<b><i>Population 3</i></b>							
Replications	2	2.28	0.95**	6.21	0.06**	0.50*	4.14
Genotypes	7	2.39	0.43*	4.75	0.02	0.05	14.80**
Error	14	0.98	0.13	1.78	0.01	0.08	1.5
C.V. %		8.2	8.3	8.1	3.4	9.1	2.6

\*, \*\*, significant at the 0.05 and 0.01 probability level.

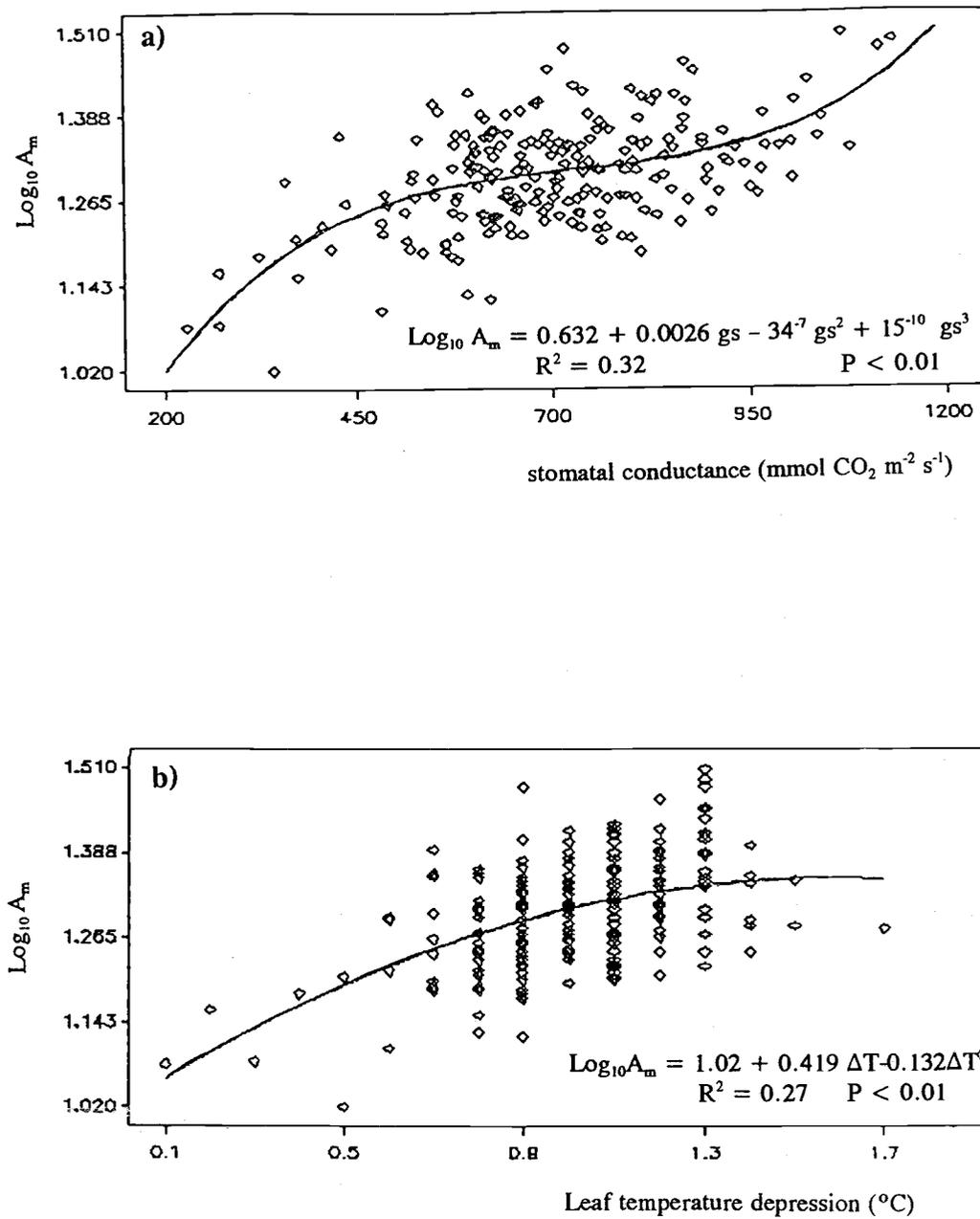
Table III-4. Mean leaf greenness rating (LGR), as measured by the SPAD, for advanced lines and their recurrent parents from three synthetic hexaploid derived populations.

<b>Genotypes</b>	<b>LGR (Spad units)</b>
<i><b>POPULATION 1.</b></i>	
Entry 21	53.1
Entry 44	51.3
Entry 30	51.2
Entry 13	50.4
Entry 17	48.9
Rec. Par. (Esmeralda)	48.7
Entry 31	48.5
Entry 16	47.3
L.S.D. (0.05)	2.5
<i><b>POPULATION 2.</b></i>	
Entry 77	53.0
Entry 83	51.6
Entry 76	51.1
Entry 63	50.9
Entry 66	50.8
Entry 59	50.2
Entry 81	50.2
Rec. Par. (Ocoroni)	49.3
L.S.D.(0.05)	1.9
<i><b>POPULATION 3.</b></i>	
Rec. Par. (Seri)	49.6
Entry 141	49.6
Entry 123	49.0
Entry 113	48.8
Entry 108	48.7
Entry 127	46.2
Entry 106	45.1
Entry 116	43.9
L.S.D. (0.05)	2.6

### III.4.3. Association among maximum photosynthesis, stomatal conductance, and leaf temperature depression

There is strong evidence ( $P < 0.01$ ) that increments in net assimilation of  $\text{CO}_2$  were associated with increments in stomatal conductance. The model that best fit the relationship between maximum photosynthetic rate and stomatal conductance is a cubic regression of the transformed response,  $\log_{10} A_m$ , on  $g_s$ . Figure III-2a depicts the response of  $A_m$  on the cubic form of  $g_s$ . The pattern of the curve suggest that, at lower levels of  $g_s$  ( $< 450$ ), increases in stomatal openings are associated with exponential increases in  $\text{CO}_2$  assimilation. Following this exponential phase, there is a steady state ( $g_s$  between 450 and 950) of  $A_m$  increasing gradually as  $g_s$  increases. Finally, at high levels of  $g_s$  ( $> 950$ ) the curve becomes exponential again, with large increases in  $A_m$  at small expansions in  $g_s$ . Stomatal conductance to water vapor is normally related to photosynthesis because the diffusion pathways for  $\text{CO}_2$  and  $\text{H}_2\text{O}$  are similar. The coefficient of determination ( $R^2$ ) suggests that 32 % of the variation in  $A_m$  can be explained by differences in stomatal conductance.

Increases in  $A_m$  were positively associated ( $P < 0.01$ ) with leaf temperature depression. Thus, genotypes with cooler leaves had a superior assimilation of  $\text{CO}_2$  (Figure III-2b).



**Figure III-2:**

Regression of  $\log_{10}$  of maximum photosynthesis rate ( $\text{Log}_{10} A_m$ ) on:

a) Stomatal conductance ( $\text{gs}$ )

b) Leaf temperature depression ( $\Delta T$ )

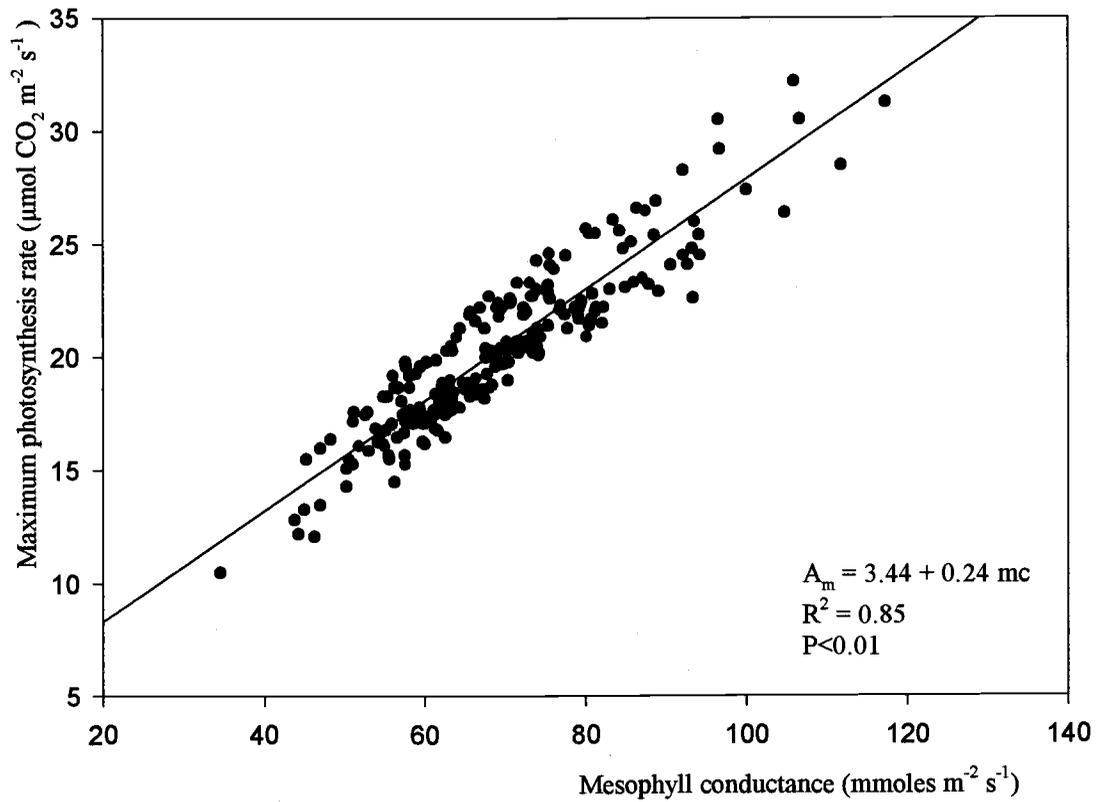
The evaporative cooling, which results from transpiration, influences the difference between air and leaf temperatures. That is why  $\Delta T$  is related to  $g_s$  and, consequently, to  $A_m$ .

#### **III.4.4. Association between maximum photosynthesis and mesophyll conductance**

To further explain variations in  $A_m$ , the apparent mesophyll conductance ( $mc$ ) was calculated from the values of intracellular  $CO_2$  concentration ( $C_i$ ) given by the PP-system and  $A_m$  with the common relationship (Fischer et al., 1998):

$$mc = A_m / C_i$$

There is strong evidence ( $P < 0.01$ ) that increments in net assimilation of  $CO_2$  were associated with increments in mesophyll conductance (Figure III-3). The coefficient of determination ( $R^2$ ) suggests that 85 % of the variation in  $A_m$  can be explained by differences in mesophyll conductance. This result agrees with the explanation given by Evans and Dunstone (1970) for the fall in photosynthetic rate at high light intensities during wheat evolution. They proposed that the decrease in photosynthesis from primitive to modern wheat was likely due to the reduction in surface-volume ratio of the mesophyll cells during wheat evolution. In other words, the larger mesophyll cells of more advanced wheats offer a higher resistance to  $CO_2$  exchange due to their reduced surface-volume ratio. Wilson and Cooper (1969) found that differences in photosynthetic rate at high light intensity among lines of *Lolium perenne* were associated to differences in mesophyll cell size. The



**Figure III-3:** Regression of maximum photosynthesis rate ( $A_m$ ) on mesophyll conductance ( $mc$ ).

same authors (1970) proposed the use of mesophyll cell cross-sectional area as selection criterion for rate of photosynthesis in relatively high light intensity. Furthermore, they indicated that it was possible to select genotypes with small mesophyll cells without reducing leaf size.

The higher rate of photosynthesis mainly due to decreased mesophyll resistances to CO<sub>2</sub> exchange might prove very convenient even at low levels of water supply (Austin, 1980), since increases in photosynthesis will not necessarily result in more water use.

The coefficient of determination ( $R^2$ ) for the multiple regression of  $A_m$  on stomatal and mesophyll conductances (not shown) was 89 %, indicating that conductances in the diffusion pathway of CO<sub>2</sub> were the main reasons for the differences in  $A_m$ .

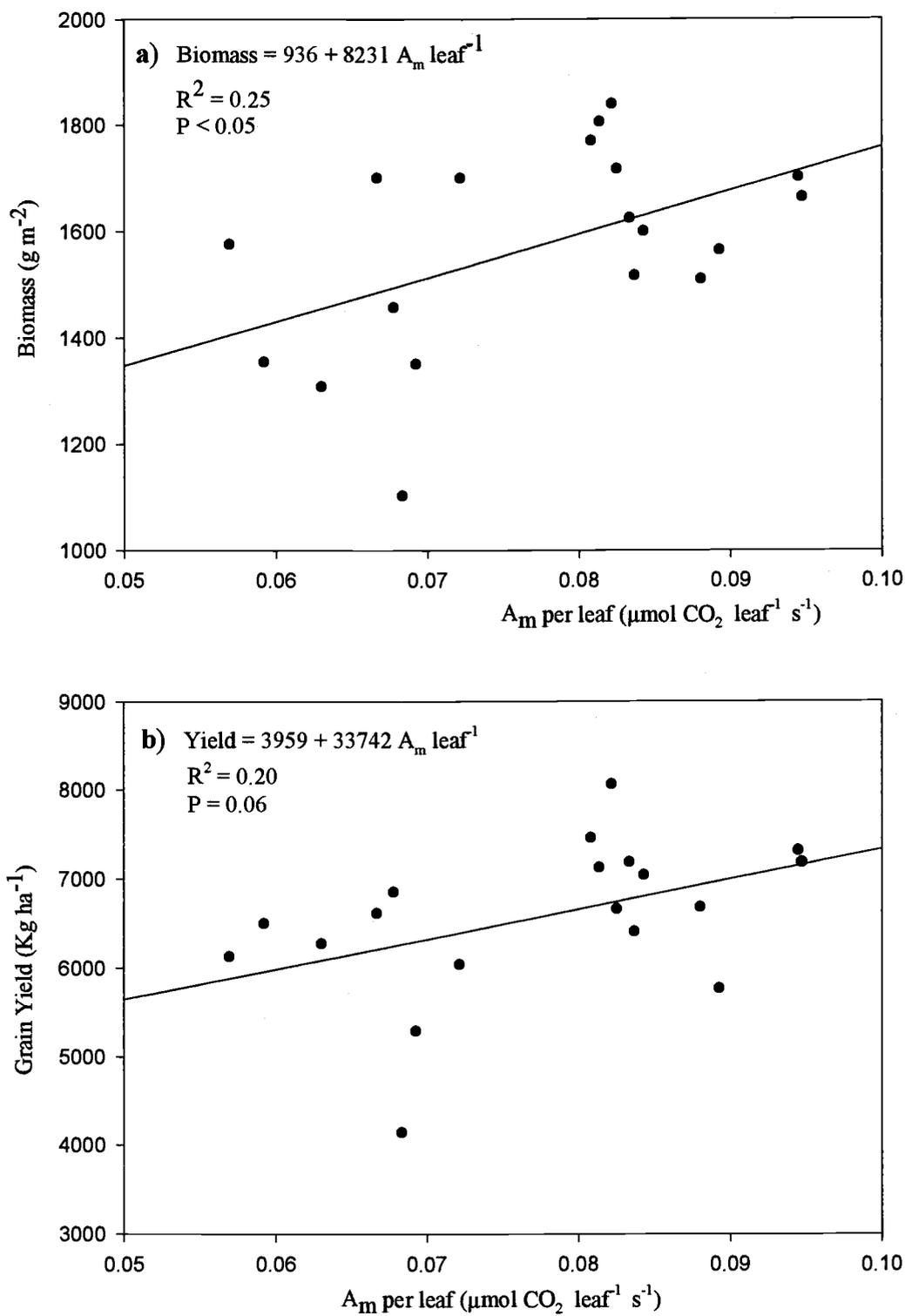
#### **III.4.5 Regression of leaf greenness on chlorophyll content**

To assess the accuracy of the SPAD to ascertain chlorophyll concentration (chlorophyll a+b) among different genotypes, the association of leaf greenness readings and extractable chlorophyll measured by optical density was estimated by linear regression (Figure III-4). The response of greenness on total chlorophyll is linear and positive; hence, increases in greenness of the leaves were associated with increments in chlorophyll content ( $P < 0.01$ ). Nevertheless, the wide spread of the data around the regression line ( $R^2 = 0.35$ ) suggests that the variation in greenness is not completely explained by changes in chlorophyll concentration.

#### **III.4.6 Association of maximum photosynthesis per leaf with biomass and yield**

Linear regressions of biomass and grain yield on  $A_m$  per leaf are presented in Figure III-5. Increases in  $CO_2$  assimilation per leaf were associated with increases in biomass ( $P < 0.05$ ) and grain yield ( $P = 0.06$ ). However, the coefficients of determination were very low for both regressions (0.25 for biomass, and 0.20 for grain yield) suggesting that variables other than  $A_m$  were influencing grain yield.





**Figure III-5:**

- a) Regression of biomass on maximum photosynthesis rate per leaf ( $A_m \text{ leaf}^{-1}$ )  
 b) Regression of grain yield on maximum photosynthesis rate per leaf ( $A_m \text{ leaf}^{-1}$ )

### III.5. Conclusions

- Genetic variability in maximum CO<sub>2</sub> assimilation was detected among genotypes. Synthetic derived lines having higher A<sub>m</sub> than their respective bread wheat recurrent parents were observed in two populations. No synthetic derived line had inferior A<sub>m</sub> compared to their bread wheat parent.
- Staygreen of the synthetic derived lines, with two exceptions, was not substantially shorter than bread wheats.
- Maximum photosynthetic rate was negatively associated with leaf specific weight and leaf area. Nevertheless, these associations were not strong enough to present an obstacle for future selection of genotypes having both desirable traits.
- Differences among genotypes were not detected for chlorophyll concentration and chlorophyll a/b ratio.
- There were differences among genotypes for leaf greenness rating. Synthetic derived lines, in two populations, tended to have darker-green leaves than their bread wheat parent. In Population 3, synthetic derived lines tended to have lighter-green leaves than their bread wheat parent.

- Maximum CO<sub>2</sub> assimilation was positively associated with stomatal conductance, leaf temperature depression, and mesophyll conductance.
- Differences in mesophyll conductance explained most of the differences in A<sub>m</sub>.
- There was a strong association between leaf greenness rating measured with the SPAD, and chlorophyll concentration estimated by optical density.
- Increases in above ground biomass and grain yield were associated with increases in CO<sub>2</sub> assimilation per leaf.

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#### IV. SUMMARY AND CONCLUSIONS

Two studies were undertaken to determine the feasibility of using synthetic hexaploids to enhance wheat yield potential. The major study involved two-hundred eighty-two BC<sub>2</sub> F<sub>2:6</sub> synthetic-derived lines from six different populations and their respective bread wheat recurrent parents. The objective was to ascertain if the introgression of durum wheat and *A. tauschii*, as synthetic hexaploids, into common bread wheat could contribute new variability to quantitative traits such as yield and its components. The second study involved twenty-one BC<sub>2</sub> F<sub>2:6</sub> synthetic-derived lines from three different populations and their respective bread wheat recurrent parents. The objective of this second study was to monitor some selected physiological traits and to detect their associations with several agronomic traits. Both studies were carried out at the Agricultural Research Center for the Northwest (CIANO), Yaqui Valley, Sonora, Mexico. Optimum management conditions and frequent irrigation ensured an adequate environment for the germplasm tested to express its genetic potential.

Results from the first study indicated that the introgression of synthetic hexaploid germplasm did modify the performance of the derived lines for all investigated traits. The greatest impact was in increasing kernel weight; most derived lines had heavier grains compared to their bread wheat recurrent parents. Transgressive segregation for yield was observed in several lines yielding up to 14% higher than their recurrent parents. A simultaneous increase in source and sink, maintaining the harvest index ratio, was observed in outstanding yielding

lines. Grain yield had a strong association with biomass and grains per m<sup>2</sup>. Strong direct effects of biomass and harvest index on grain yield were revealed by path coefficient analysis.

A final consideration to this first study is that it included six synthetic-derived populations derived from only four different *A. tauschii* accessions and three different durum wheats. Taking into account the wide and diverse range of accessions of *A. tauschii*, almost five-hundred in the CIMMYT working collection (Mujeeb-Kazi and Roldan, 1996), and also the possibility of using different durum wheat genotypes, the opportunity for taking advantage of this germplasm to bring into common wheat beneficial alleles for economically important quantitative traits is auspicious.

In the second study, maximum photosynthetic rate per unit area, stomatal conductance, air temperature, leaf temperature, and internal CO<sub>2</sub> were measured with a CIRAS-1 PP-system. Leaf temperature depression and mesophyll conductance were calculated from the previous data. Measurements were taken on three flag leaf blades per plot, during grain filling. Leaf characteristics such as leaf area, leaf specific weight, and leaf greenness, were measured on fresh and healthy leaves. Flag leaf senescence and physiological maturity were recorded to determine the staygreen of the genotypes. Concentration of photosynthetic pigments was determined by optical density.

Conclusions to this second study are that most synthetic-derived lines had higher maximum CO<sub>2</sub> assimilation compared to their bread wheat parents.

Variability in photosynthesis was mainly explained by differences in conductances in the diffusion pathway of CO<sub>2</sub>, i.e., mesophyll and stomatal conductances, with mesophyll conductance being the most important. Differences among genotypes for chlorophyll concentration and chlorophyll a/b ratio were not detected.

Maximum photosynthetic rate was negatively associated with leaf area and leaf specific weight. However, these negative correlations were not very strong and can probably be broken by selection, as Wilson and Cooper (1970) have proven in ryegrass.

Leaf greenness rating was related to chlorophyll concentration estimated by optical density. Thus, the SPAD may be a practical tool to estimate concentration of chlorophyll when precision required is not very high.

Increases in biomass and grain yield were the response to increases in photosynthetic rate per leaf.

From these two studies, we conclude that it can be possible to enlarge the storage capacity of wheat grains and at the same time to increase the efficiency of the photosynthetic apparatus by breeding and selection of synthetic wheat derivatives.

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**APPENDICES**

**Appendix 1.** Meteorological data on per month basis at CIANO, during the 1995-96 and 1996-97 crop season. Mean maximum temperature (Tmax), mean minimum temperature (Tmin), and total month precipitation (Tppt).

Crop Season	Month	Tmax (°C)	Tmin (°C)	Tppt (mm)
<b>1995-96</b>	November	30.5	14.0	61.0
	December	26.0	8.6	0.0
	January	27.2	5.8	0.0
	February	28.3	10.3	0.0
	March	29.2	9.5	0.0
	April	20.2	12.6	1.0
	May	35.9	18.0	0.0
	<i>Total precipitation for growing season</i>			<i>62.0</i>
<b>1996-97</b>	November	29.8	11.8	215.0
	December	26.3	8.0	0.0
	January	24.3	7.9	111.0
	February	25.2	7.6	43.0
	March	30.0	10.8	0.0
	April	30.3	12.2	47.0
	May	36.8	17.7	0.0
	<i>Total precipitation for growing season</i>			<i>416.0</i>

**Appendix 2. Cross and pedigree of two-hundred and eighty-two BC<sub>2</sub> F<sub>2.6</sub> synthetic-derived lines and their recurrent parents used in Experiments I and II, at CIANO, Yaqui Valley, Sonora, Mexico.**

Entry N°	Cross and Pedigree	Entry N°	Cross and Pedigree
1	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-5Y-1M-0Y	31	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-85Y-1M-0Y
2	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-6Y-1M-0Y	32	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-87Y-1M-0Y
3	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-9Y-1M-0Y	33	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-93Y-1M-0Y
4	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-13Y-1M-0Y	34	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-94Y-1M-0Y
5	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-15Y-1M-0Y	35	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-95Y-1M-0Y
6	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-16Y-1M-0Y	36	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-75Y-1M-0Y
7	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-18Y-1M-0Y	37	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-97Y-1M-0Y
8	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-21Y-1M-0Y	38	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-98Y-1M-0Y
9	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-23Y-1M-0Y	39	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-99Y-1M-0Y
10	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-25Y-1M-0Y	40	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-101Y-1M-0Y
11	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-27Y-1M-0Y	41	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-102Y-1M-0Y
12	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-28Y-1M-0Y	42	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-111Y-1M-0Y
13	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-32Y-1M-0Y	43	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-112Y-1M-0Y
14	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-36Y-1M-0Y	44	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-114Y-1M-0Y
15	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-41Y-1M-0Y	45	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-115Y-1M-0Y
16	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-44Y-1M-0Y	46	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-116Y-1M-0Y
17	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-46Y-1M-0Y	47	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-117Y-1M-0Y
18	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-48Y-1M-0Y	48	ESMERALDA M 86 CM49641-9Y-1M-1Y-5Y-0M-0MEX
19	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-49Y-1M-0Y	49	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-3Y-1M-0Y
20	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-50Y-1M-0Y	50	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-7Y-1M-0Y
21	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-51Y-1M-0Y	51	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-13Y-1M-0Y
22	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-53Y-1M-0Y	52	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-16Y-1M-0Y
23	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-54Y-1M-0Y	53	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-21Y-1M-0Y
24	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-63Y-1M-0Y	54	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-22Y-1M-0Y
25	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-64Y-1M-0Y	55	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-24Y-1M-0Y
26	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-70Y-1M-0Y	56	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-29Y-1M-0Y
27	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-76Y-1M-0Y	57	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-32Y-1M-0Y
28	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-79Y-1M-0Y	58	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-35Y-1M-0Y
29	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-83Y-1M-0Y	59	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-37Y-1M-0Y
30	ALTAR 84/AE.TAUSCHII(219)//2*ESDA CMBW91M04380M-050B-84Y-1M-0Y	60	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-41Y-1M-0Y

## Appendix 2. (Continued)

Entry N°	Cross and Pedigree	Entry N°	Cross and Pedigree
61	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-51Y-1M-0Y	91	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-145Y-1M-0Y
62	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-52Y-1M-0Y	92	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-147Y-1M-0Y
63	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-53Y-1M-0Y	93	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-151Y-1M-0Y
64	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-58Y-1M-0Y	94	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-155Y-1M-0Y
65	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-61Y-1M-0Y	95	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-156Y-1M-0Y
66	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-63Y-1M-0Y	96	OCORONI F 86 CM43598-II-8Y-1M-1Y-3M-3Y-0B
67	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-64Y-1M-0Y	97	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-1Y-1M-0Y
68	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-66Y-1M-0Y	98	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-4Y-1M-0Y
69	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-68Y-1M-0Y	99	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-5Y-1M-0Y
70	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-73Y-1M-0Y	100	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-14Y-1M-0Y
71	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-44Y-1M-0Y	101	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-16Y-1M-0Y
72	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-83Y-1M-0Y	102	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-17Y-1M-0Y
73	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-92Y-1M-0Y	103	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-19Y-1M-0Y
74	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-93Y-1M-0Y	104	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-21Y-1M-0Y
75	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-94Y-1M-0Y	105	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-24Y-1M-0Y
76	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-95Y-1M-0Y	106	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-25Y-1M-0Y
77	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-97Y-1M-0Y	107	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-27Y-1M-0Y
78	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-106Y-1M-0Y	108	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-28Y-1M-0Y
79	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-110Y-1M-0Y	109	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-29Y-1M-0Y
80	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-117Y-1M-0Y	110	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-34Y-1M-0Y
81	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-121Y-1M-0Y	111	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-35Y-1M-0Y
82	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-122Y-1M-0Y	112	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-37Y-1M-0Y
83	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-125Y-1M-0Y	113	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-38Y-1M-0Y
84	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-126Y-1M-0Y	114	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-39Y-1M-0Y
85	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-129Y-1M-0Y	115	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-44Y-1M-0Y
86	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-135Y-1M-0Y	116	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-45Y-1M-0Y
87	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-137Y-1M-0Y	117	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-48Y-1M-0Y
88	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-139Y-1M-0Y	118	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-51Y-1M-0Y
89	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-140Y-1M-0Y	119	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-56Y-1M-0Y
90	ALTAR 84/AE.TAUSCHII(223)//2*FCT CMBW91M04381M-050B-144Y-1M-0Y	120	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-57Y-1M-0Y

## Appendix 2. (Continued)

Entry N°	Cross and Pedigree	Entry N°	Cross and Pedigree
121	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-60Y-1M-0Y	151	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-30Y-1M-0Y
122	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-62Y-1M-0Y	152	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-38Y-1M-0Y
123	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-63Y-1M-0Y	153	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-39Y-1M-0Y
124	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-72Y-1M-0Y	154	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-41Y-1M-0Y
125	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-73Y-1M-0Y	155	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-45Y-1M-0Y
126	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-75Y-1M-0Y	156	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-46Y-1M-0Y
127	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-77Y-1M-0Y	157	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-53Y-1M-0Y
128	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-79Y-1M-0Y	158	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-57Y-1M-0Y
129	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-81Y-1M-0Y	159	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-58Y-1M-0Y
130	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-82Y-1M-0Y	160	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-60Y-1M-0Y
131	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-83Y-1M-0Y	161	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-64Y-1M-0Y
132	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-86Y-1M-0Y	162	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-67Y-1M-0Y
133	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-88Y-1M-0Y	163	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-68Y-1M-0Y
134	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-89Y-1M-0Y	164	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-69Y-1M-0Y
135	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-90Y-1M-0Y	165	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-69Y-1M-0Y
136	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-92Y-1M-0Y	166	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-77Y-1M-0Y
137	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-94Y-1M-0Y	167	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-85Y-1M-0Y
138	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-96Y-1M-0Y	168	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-87Y-1M-0Y
139	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-100Y-1M-0Y	169	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-90Y-1M-0Y
140	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-102Y-1M-0Y	170	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-92Y-1M-0Y
141	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-103Y-1M-0Y	171	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-93Y-1M-0Y
142	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-104Y-1M-0Y	172	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-95Y-1M-0Y
143	DVERD 2/AE.TAUSCHII(214)//2*SERI CMBW91M04388M-050B-107Y-1M-0Y	173	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-98Y-1M-0Y
144	SERI M 82 CM33027-F-15M-500Y-0M-87B-0Y-0MEX	174	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-104Y-1M-0Y
145	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-13Y-1M-0Y	175	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-105Y-1M-0Y
146	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-14Y-1M-0Y	176	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-109Y-1M-0Y
147	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-20Y-1M-0Y	177	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-115Y-1M-0Y
148	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-21Y-1M-0Y	178	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-116Y-1M-0Y
149	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-23Y-1M-0Y	179	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-120Y-1M-0Y
150	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-29Y-1M-0Y	180	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-123Y-1M-0Y

## Appendix 2. (Continued)

Entry N°	Cross and Pedigree	Entry N°	Cross and Pedigree
181	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-124Y-1M-0Y	211	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-56Y-1M-0Y
182	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-130Y-1M-0Y	212	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-60Y-1M-0Y
183	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-134Y-1M-0Y	213	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-64Y-1M-0Y
184	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-135Y-1M-0Y	214	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-66Y-1M-0Y
185	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-139Y-1M-0Y	215	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-76Y-1M-0Y
186	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-141Y-1M-0Y	216	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-80Y-1M-0Y
187	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-142Y-1M-0Y	217	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-83Y-1M-0Y
188	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-146Y-1M-0Y	218	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-89Y-1M-0Y
189	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-128Y-1M-0Y	219	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-91Y-1M-0Y
190	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-55Y-1M-0Y	220	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-93Y-1M-0Y
191	DVERD 2/AE.TAUSCHII(214)//2*OPATA CMBW91M04389M-050B-132Y-1M-0Y	221	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-94Y-1M-0Y
192	OPATA M 85 CM40038-6M-4Y-2M-1Y-2M-1Y-0B-0MEX	222	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-96Y-1M-0Y
193	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-1Y-1M-0Y	223	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-97Y-1M-0Y
194	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-2Y-1M-0Y	224	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-100Y-1M-0Y
195	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-3Y-1M-0Y	225	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-104Y-1M-0Y
196	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-5Y-1M-0Y	226	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-105Y-1M-0Y
197	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-8Y-1M-0Y	227	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-106Y-1M-0Y
198	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-20Y-1M-0Y	228	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-111Y-1M-0Y
199	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-22Y-1M-0Y	229	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-115Y-1M-0Y
200	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-23Y-1M-0Y	230	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-117Y-1M-0Y
201	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-27Y-1M-0Y	231	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-118Y-1M-0Y
202	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-33Y-1M-0Y	232	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-119Y-1M-0Y
203	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-36Y-1M-0Y	233	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-120Y-1M-0Y
204	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-37Y-1M-0Y	234	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-122Y-1M-0Y
205	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-38Y-1M-0Y	235	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-124Y-1M-0Y
206	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-39Y-1M-0Y	236	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-127Y-1M-0Y
207	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-46Y-1M-0Y	237	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-129Y-1M-0Y
208	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-50Y-1M-0Y	238	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-137Y-1M-0Y
209	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-51Y-1M-0Y	239	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-145Y-1M-0Y
210	DVERD 2/AE.TAUSCHII(214)//2*ESDA CMBW91M04390M-050B-53Y-1M-0Y	240	ESMERALDA M 86 CM49641-9Y-1M-1Y-5Y-0M-0MEX

## Appendix 2. (Continued)

Entry N°	Cross and Pedigree	Entry N°	Cross and Pedigree
241	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-1Y-1M-1Y-0B	271	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-103Y-1M-1Y-0B
242	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-5Y-1M-1Y-0B	272	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-105Y-1M-1Y-0B
243	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-6Y-1M-1Y-0B	273	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-109Y-1M-1Y-0B
244	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-8Y-1M-1Y-0B	274	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-110Y-1M-1Y-0B
245	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-10Y-1M-1Y-0B	275	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-113Y-1M-1Y-0B
246	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-14Y-1M-1Y-0B	276	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-1Y-1M-1Y-0B
247	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-19Y-1M-1Y-0B	277	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-120Y-1M-1Y-0B
248	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-20Y-1M-1Y-0B	278	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-132Y-1M-1Y-0B
249	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-26Y-1M-1Y-0B	279	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-137Y-1M-1Y-0B
250	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-32Y-1M-1Y-0B	280	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-141Y-1M-1Y-0B
251	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-35Y-1M-1Y-0B	281	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-144Y-1M-1Y-0B
252	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-39Y-1M-1Y-0B	282	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-160Y-1M-1Y-0B
253	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-41Y-1M-1Y-0B	283	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-173Y-1M-1Y-0B
254	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-47Y-1M-1Y-0B	284	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-176Y-1M-1Y-0B
255	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-48Y-1M-1Y-0B	285	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-177Y-1M-1Y-0B
256	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-51Y-1M-1Y-0B	286	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-193Y-1M-1Y-0B
257	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-54Y-1M-1Y-0B	287	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-194Y-1M-1Y-0B
258	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-57Y-1M-1Y-0B	288	OPATA M 85 CM40038-6M-4Y-2M-1Y-2M-1Y-0B-0MEX
259	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-60Y-1M-1Y-0B		
260	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-62Y-1M-1Y-0B		
261	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-63Y-1M-1Y-0B		
262	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-64Y-1M-1Y-0B		
263	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-65Y-1M-1Y-0B		
264	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-66Y-1M-1Y-0B		
265	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-68Y-1M-1Y-0B		
266	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-69Y-1M-1Y-0B		
267	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-75Y-1M-1Y-0B		
268	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-81Y-1M-1Y-0B		
269	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-99Y-1M-1Y-0B		
270	CROC 1/AE.TAUSCHII(205)//2*OPATA CMSS92Y01863M-102Y-1M-1Y-0B		

**Appendix 3.** Cross and pedigree of synthetic-derived advanced lines and their recurrent parents used in the physiological study at CIANO, Yaqui Valley, Sonora, Mexico, 1996-97.

<b>Population N°</b>	<b>Entry N°</b>	<b>Cross and Pedigree</b>	
<b>1</b>	13	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-32Y-1M-0Y	
	16	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-44Y-1M-0Y	
	17	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-46Y-1M-0Y	
	21	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-51Y-1M-0Y	
	30	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-84Y-1M-0Y	
	31	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-85Y-1M-0Y	
	44	ALTAR 84/AE.TAUSCHII(219)/2*ESDA CMBW91M04380M-050B-114Y-1M-0Y	
	48	ESMERALDA M 86 CM49641-9Y-1M-1Y-5Y-0M-0MEX	
	<b>2</b>	59	ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-37Y-1M-0Y
		63	ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-53Y-1M-0Y
66		ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-63Y-1M-0Y	
76		ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-95Y-1M-0Y	
77		ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-97Y-1M-0Y	
81		ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-121Y-1M-0Y	
83		ALTAR 84/AE.TAUSCHII(223)/2*FCT CMBW91M04381M-050B-125Y-1M-0Y	
96		OCORONI F 86 CM43598-II-8Y-1M-1Y-3M-3Y-0B	
<b>3</b>		106	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-25Y-1M-0Y
		108	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-28Y-1M-0Y
	113	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-38Y-1M-0Y	
	116	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-45Y-1M-0Y	
	123	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-63Y-1M-0Y	
	127	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-77Y-1M-0Y	
	141	DVERD 2/AE.TAUSCHII(214)/2*SERI CMBW91M04388M-050B-103Y-1M-0Y	
	144	SERI M 82 CM33027-F-15M-500Y-0M-87B-0Y-0MEX	