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# Physiological factors associated with genotype by environment interaction in wheat

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**Abstract**

Wheat cultivars often show highly significant genotype by environment interaction (G × E) for yield, even when comparing different years within a relatively stable location. This study attempts to explain some of the physiological bases of G × E in two experiments: (i) historic yield potential trials (HYPTs) of bread wheat (*Triticum aestivum* L.), durum (*T. durum* Desf.) and triticale (X *Triticosecale* Wittmack) cultivars grown under agronomically optimal conditions; (ii) an elite spring wheat yield trial (ESWYT) of 30 bread wheat genotypes cultivated at 27 international locations. For the HYPT, the main objectives were to determine the environmental variables during different phenological stages associated with: (i) G × E among the three crop species, (ii) G × E within each species, and (iii) underlying physiological causes of G × E. For ESWYT, meteorological data were not available and so mean site values of certain crop parameters were used as proxy environmental data to determine whether conditions either pre- or post-anthesis were more influential in determining G × E. Partial least-squares analysis and factorial regression models were used to identify the environmental factors best explaining G × E independent of the main effects. Of the three crops, durums were shown to be the most sensitive to conditions pre-anthesis, requiring higher radiation and cooler average temperatures in order to set high grain number. Triticale, despite having the highest average yield and biomass, performed relatively poor when conditions from spike growth stage onwards were sunny and warm. Bread wheat appeared to be the most robust of the three species. Considering yield, biomass, and yield components, it was apparent that the spike primordia growth stage was generally the most sensitive to environmental factors causing G × E. Results for the ESWYT suggested that conditions post-anthesis were more influential on G × E than conditions pre-anthesis. Implications for how such analysis may assist with both conventional and molecular approaches to breeding are discussed. 

*Keywords:* Wheat; G × E; Climate; Phenology; Yield; Breeding

## 1. Introduction

Wheat is one of the most widely adapted of any crop; it survives extremes of temperature, from under −35 °C in the vegetative phase in Ontario (Haji and Hunt, 1999) to over 40 °C during grainfilling (GF) in the Sudan (Elahmadi, 1994), drought stress resulting in grain yields well under 1.0 Mg ha$^{-1}$ (Morris et al., 1991), and at the same time is highly responsive to favorable conditions where yields as high as 17 Mg ha$^{-1}$ have been reported on experimental plots

*Abbreviations:* G × E, genotype by environment interaction; HYPT, historic yield potential trial; ESWYT, elite spring wheat yield trial; PLS, partial least-squares analysis; FR, factorial regression; MX, maximum temperature; MI, minimum temperature; Tx, average temperature; PTQ, photothermal quotient; BW, bread wheat; DW, durum wheat; TCL, triticale; BM, biomass; RD, solar radiation; G/M2, grains m$^{-2}$; TKW, thousand kernel weight; G/SP, grains/spike; SP/M2, spikes m$^{-2}$; HGT, plant height; HEAD, heading; MAT, maturity; GF, grainfilling; PGF, proportion of time in grainfilling; GFR, grainfilling rate

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in Chile (Hewstone, 1998). Wheat is cultivated over a wide range of latitudes and altitudes (herein we report data from international yield trials with latitudes varying from 3° in Tanzania to 60° in Norway and at elevations as a high as 2400 m in Guatemala; Appendix A). Such adaptability reflects the diversity of the wheat genome, and it follows that when comparing different genotypes, their interaction with environment is often highly significant. The fact that crop performance is strongly influenced by weather conditions (and is therefore unpredictable) is an important food security issue, especially in light of predicted climate change. Furthermore, vulnerability of cultivars to environmental variation can also be viewed as a barrier to improving yield potential. This is apparent when considering the fact that any breeding program, no matter how localized, must create lines which are adapted to a range of environments, at the very least those representing yearly weather fluctuations as well as those imposed by varying farmers practices. If wheat yield potential is to meet future demand (Rosengrant et al., 1995), targeting the underlying physiological causes of $G \times E$ for genetic improvement would be worthwhile investment.

Relatively little is known about the genetic and physiological bases of $G \times E$ in wheat. Austin (1989) concluded that despite our knowledge of the physiology of wheat, it is generally impossible to apply it to a quantitative assessment of the effect of a given difference in environment. More recently, moisture has been shown to be a factor that interacts with genotype, especially water deficits prior to anthesis (Baker, 1996; Haji and Hunt, 1999). The latter also showed that January temperatures in Ontario contributed to $G \times E$, where average daily minimum values ranged from −10 to −22 °C.

This study attempts to identify factors associated with $G \times E$ in two different types of trials: (i) historic yield potential trials (HYPTs) of bread wheat (BW), durum wheat (DW) and triticale (TCL) cultivars grown in NW Mexico, at the International Maize and Wheat Improvement Centre's (CIMMYT's) main wheat breeding station for temperate, irrigated spring wheat, under agronomically optimal conditions over six cycles from 1990 to 1995. (The trials are 'historic' in the sense that they represent key cultivars released over three decades.) (ii) The 11th Elite Spring Wheat Yield Trial (ESWYT), sown at 27 different international locations in 1990. For the HYPT, the principal objective was to establish a relationship between meteorological data occurring at specific growth stages (e.g., vegetative, spike development, etc.) and the observed $G \times E$ as it related to the differential performance among the three species, as well as for cultivars within species. For the ESWYT, meteorological data were not available. Instead mean site values for certain crop parameters were used as proxies for environmental data to test whether conditions affecting traits pre-anthesis (e.g., average plant height) or post-anthesis (e.g., average kernel weight) were more or less influential on $G \times E$. Partial least-squares (PLSs) regression (Aestveit and Martens, 1986; Vargas et al., 1998, 1999) and factorial regression (FR) models (Van Eeuwijk et al., 1996; Vargas et al., 1999) were used to identify the growth stages most sensitive to meteorological conditions being associated with $G \times E$, independent of the main effects of genotype and environment on performance.

One of the difficulties in understanding $G \times E$ is the statistical complexity presented by the large number of environmental variables that may influence genotypes. When the number of variables are large and some of them are correlated, results of ordinary least-squares methods are difficult to interpret. In non-water, non-nutrient-limited situations, crop models use daily maximum and minimum temperatures and radiation as the environmental inputs (from which mean temperature and photothermal quotient can be calculated) and these variables are assumed to drive productivity. In our study, these variables were calculated for five cardinal growth phases in each of 6 years, making a total of 150 separate environmental variables. Clearly, interpretation of $G \times E$ using conventional graphical inspection methods would be prohibitively slow (and increasingly unfeasible with larger data sets). PLS analysis offers a statistical method where the interactions between genotypes and years can be explained by the environmental variables collected in each year. Genotypes, years and the environmental co-variables can be graphically represented in a biplot. The approach offers a powerful technique for evaluating the response of genotypes in various environments as a function of a large set of explanatory variables comprising the environmental variables collected every year.

Results were interpreted with the principal objectives of determining the environmental variables during different phenological stages that contributed to: (i) G $\times$ E between crop species; (ii) G $\times$ E within species; (iii) the underlying physiological causes of G $\times$ E.

## 2. Materials and Methods

### 2.1. Growing conditions

#### 2.1.1. HYPT

Experiments were sown for 6 successive years at CIMMYT's research station located near Cd. Obregon (27°N, 38 m a.s.l.); seedling emergence dates were 21, 12, 21, 3, 9, and 11 December, respectively, in consecutive years from 1989 to 1994. Trials were managed as optimally as possible with respect to irrigation, fertility and weed, pest and disease control. In addition, support nets were used which prevented lodging. A complete description of growing conditions is described in Sayre et al. (1997).

#### 2.1.2. ESWYT

The ESWYT trial was sent to more than 100 locations around the world representing irrigated, high rainfall and dry areas. The trials were sown in the 1990–1991 wheat crop cycle using local agronomic practices as close as possible to the optimal date of planting. The 27 locations used in the analysis represent those trials where the regional cooperators returned complete data on yield, heading and maturity date, plant height and average kernel weight.

### 2.2. Germplasm

#### 2.2.1. HYPT

The HYPT consisted of seven BW, seven DW and four TCL cultivars released between 1962 and 1989 (Table 1). The cultivars were chosen for being landmark cultivars, which as well as having been released as varieties in Mexico, have been widely used by national wheat programs worldwide.

#### 2.2.2. ESWYT

The 29 genotypes distributed in the ESWYT were bred in Mexico by shuttling segregating materials between Cd. Obregon and CIMMYT's Toluca research station in the central Mexican highlands (19°N, 2640 m a.s.l.). Elite cultivars were selected for inclusion in the ESWYT based on their yield performance under optimal agronomic conditions at Cd. Obregon. An extra entry was sown to the best local check variety resulting in a two replicate trial of 30 genotypes at each location.

Table 1
Average yield of cultivars of the three wheat species used in the HYPT, NW Mexico, 1990–1995[a]

| | Yield (Mg ha$^{-1}$) |
|---|---|
| Bread wheat | |
| PITIC-62 | 6.13 |
| 7 CERROS-66 | 6.45 |
| YECORA-70 | 6.82 |
| NACOZARI-76 | 6.97 |
| CIANO-69 | 7.10 |
| SERI-82 | 7.51 |
| SUPER KAUZ-88 | 7.78 |
| LSD for yield | 0.25 |
| Durum | |
| CHAPALA-67 | 4.44 |
| JORI-69 | 5.19 |
| COCORIT-71 | 6.99 |
| MEXICALI-75 | 7.12 |
| YAVAROS-79 | 7.61 |
| ALTAR-84 | 7.60 |
| ACONCHI-89 | 7.66 |
| LSD for yield | 0.25 |
| Triticale | |
| CANANEA-79 | 7.04 |
| ALAMOS-83 | 7.34 |
| BEAGLE-82 | 6.58 |
| ERONGA-83 | 7.61 |
| LSD for yield | 0.32 |

[a] Cultivar numbers 1–18 correspond with numbers used in biplots (Figs. 1–3).

### 2.3. Environmental variables

#### 2.3.1. HYTP

The following daily meteorological data were available: maximum temperature (MX), minimum temperature (MI), and total solar radiation in MJ m$^{-2}$ per day (RD). From these, the following parameters were calculated: average temperature (Tx) and photothermal quotient (PTQ). Average temperature was calculated as $(\mathrm{MX}+\mathrm{MI})/2$. PTQ was calculated as RD/Tx (base temperature of zero was used to avoid unrealistically high values for PTQ when Tx is low).

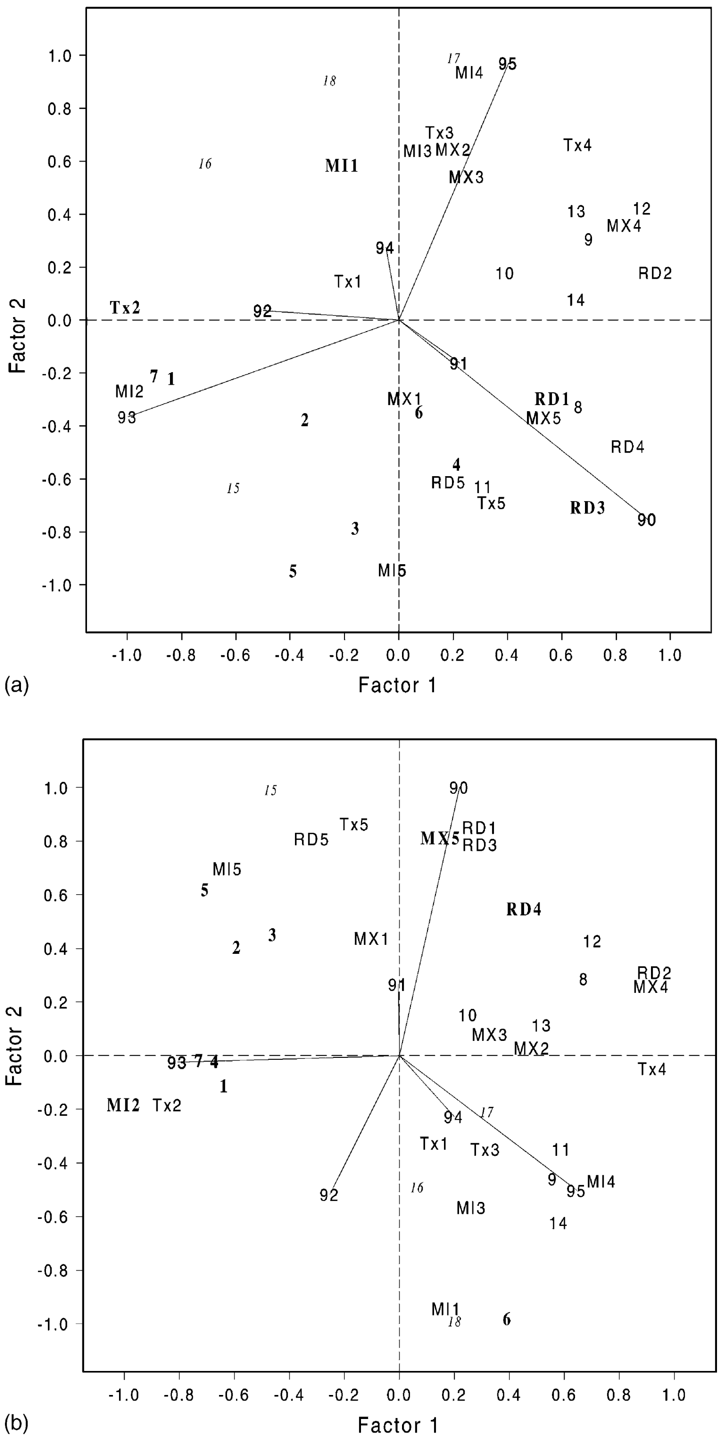


Fig. 1. Biplot based on PLS analysis of G × E for bread wheat (1–7), durum wheat (8–14) and triticale (15–18) cultivars showing the relationship with environmental variables and years, NW Mexico, 1990–1995. Environmental variables are abbreviated as follows: minimum temperature (MI), maximum temperature (MX), mean temperature (Tx), radiation (RD); growth stages are abbreviated as follows: 1, vegetative; 2, spike primordia; 3, spike growth; 4, first half of grainfilling; 5, second half of grainfilling (environmental variables identified by factorial regression in larger font) for: (a) yield; (b) biomass; (c) grains $m^{-2}$.

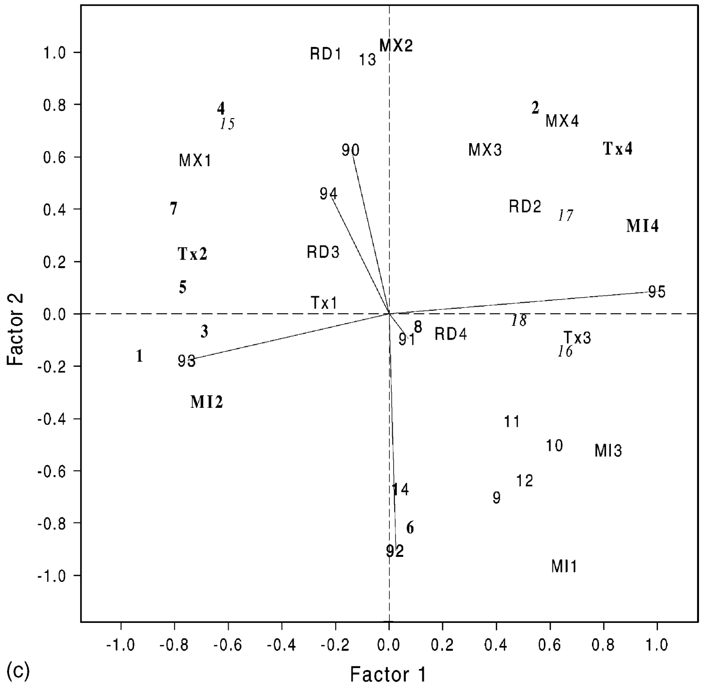


Fig. 1. (*Continued*).

Each of these parameters was calculated each year for the following approximate growth stages: vegetative (stage 1), spike primordia (stage 2), spike growth (stage 3), milk stage of GF (stage 4) and dough stage of GF (stage 5). The vegetative, spike primordia and spike growth stages were assumed to occupy approximately the same amount of thermal time each and their duration was calculated as a third of the number of day degrees from crop emergence to anthesis; GF was divided into two periods, GF1 and GF2, each having an equal number of day degrees; these assumption (while roughly based on previous observations for a few BW cultivars) were very approximate but considered unbiased given the lack of specific information for each cultivar. The meteorological data for each growth stage was calculated using the average anthesis and maturity date across all cultivars. In the PLS biplots (Figs. 1–3), the stages are numbered chronologically from 1 to 5, such that MI in the vegetative stage is denoted MI1, and MX in the spike primordia stage MX2, RD in the spike growth stage, RD3, Tx in the first and second half of GF Tx4 and Tx5 respectively, etc. Initial analyses indicated that the environmental variables PTQ and RD gave very similar results and subsequent analyses were run with only RD. The following dependent variables were analyzed: yield, total aboveground biomass (BM), grains $m^{-2}$ (G/M2), thousand kernel weight (TKW), grains/spike (G/SP), and spikes $m^{-2}$ (SP/M2).

### 2.3.2. ESWYT

Other than latitude and altitude, no other environmental variables were available from most of the ESWYT sites of which a total of 71 returned yield data. However, the following trait data were available for 27 sites: days to heading (HEAD) and maturity (MAT), plant height (HGT), TKW and yield. From these it was possible to calculate G/M2, grainfilling rate (GFR) (=Yield/[MAT − HEAD]), and the proportion of time in grainfilling (PGF) =([MAT− HEAD]/MAT). For PLS regression, the average site values of these crop parameters were used as proxies for environmental data. It was assumed, e.g., that the average site value for anthesis and HGT were influenced exclusively by prevailing conditions prior to anthesis, and that TKW and GFR would be influenced largely by environmental conditions during GF (Appendix A). Analyses were made only for the dependent variable yield.

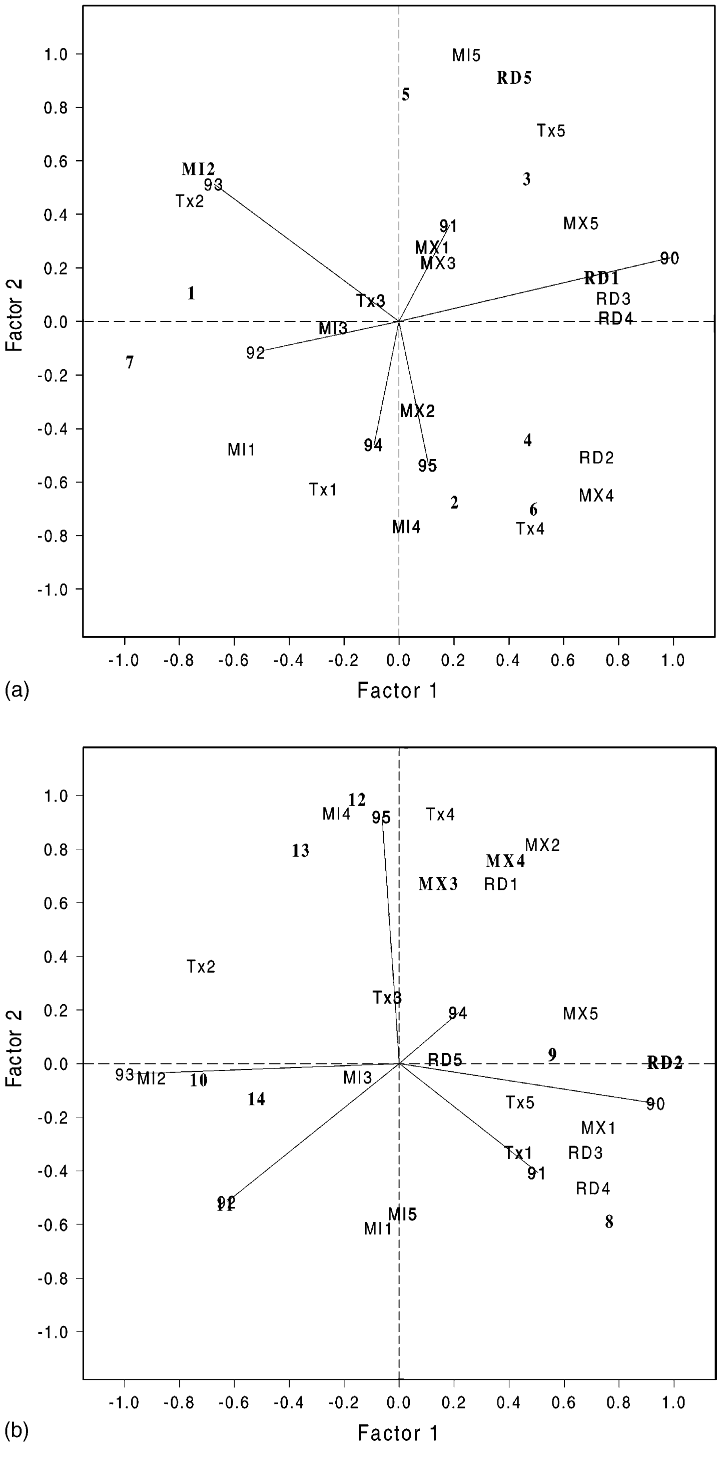


Fig. 2. Biplot based on PLS analysis of G × E showing the relationship between genotypes, environmental variables and years, NW Mexico, 1990–1995. Environmental variables are abbreviated as follows: minimum temperature (MI), maximum temperature (MX), mean temperature (Tx), radiation (RD); growth stages are abbreviated as follows: 1, vegetative; 2, spike primordial; 3, spike growth; 4, first half of grainfilling; 5, second half of grainfilling (environmental variables identified by factorial regression in larger font) for: (a) yield of seven bread wheat cultivars (numbered 1–7); (b) yield for seven durum wheat cultivars (numbered 8–14).

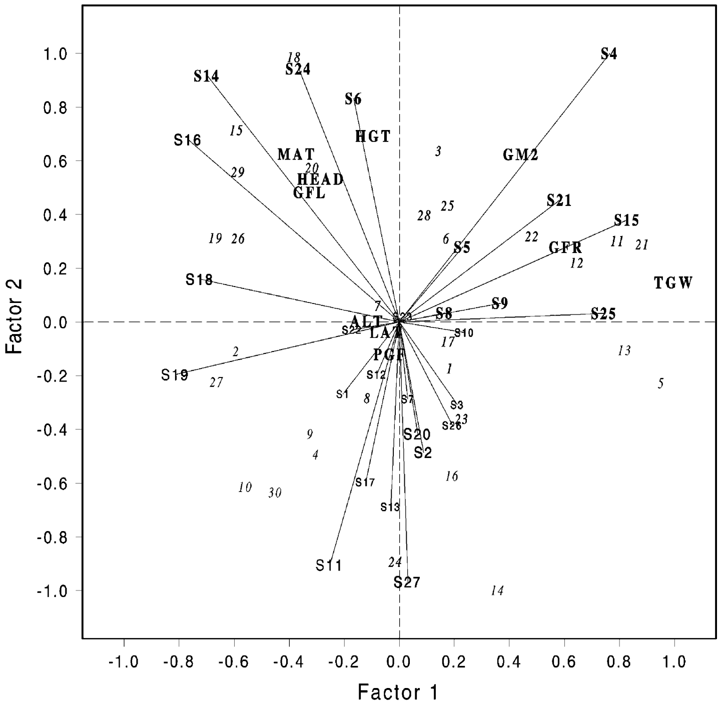

Fig. 3. Biplot based on PLS analysis of G × E for yield for 30 bread wheat lines (numbered) of the 11th ESWYT over 27 international sites (S) (high yield sites large bold **S-#**, low yield sites large S-#, other sites smaller S-#) in 1990 (site numbers correspond to the order of Table 1) showing the relationship with the following environmental variables: altitude (ALT) and latitude (LAT); and the following proxy environmental variables: average site values for days to heading (HEAD), days to maturity (MAT), days in grainfilling (GF), proportion of time in grainfilling (PGF), grainfilling rate (GFR), height (HGT), thousand kernel weight (TKW), and grains $m^{-2}$ (GM2).

### *2.4. Statistical methods*

#### *2.4.1. PLS regression and the biplot*

The PLS extracts the main variation patterns from one data table **X** that have relevance also to another data table **Y** from the same individuals. The PLS can be seen as an extension of principal component analysis because it allows extraction of the main variation patterns within **X** and **Y** permitting study of the structure between **X** and **Y**. Thus, the latent variables extracted are the essence contained in the variables of **X** that are also relevant to **Y** so that both matrices are modeled simultaneously. Thus the bilinear representation of X and Y are as follows:

$$\mathbf{X} = \mathbf{t}_1\mathbf{p}_1' + \mathbf{t}_2\mathbf{p}_2' + \cdots + \mathbf{E} = \mathbf{TP}' + \mathbf{E},$$
$$\mathbf{Y} = \mathbf{t}_1\mathbf{q}_1' + \mathbf{t}_2\mathbf{q}_2' + \cdots + \mathbf{F} = \mathbf{TQ}' + \mathbf{F}$$

where the matrix **T** contains the Z scores, matrix **P** contains the Z loadings, matrix **Q** contains the Y loadings and **F** and **E** are the residual matrices. The basic idea is that the relationship between **Y** and **X** is transmitted through the latent variables **t**. The choice of what is **X** and what is **Y** does not have to follow the traditional: **X** = cause and **Y** = effect like in the classical regression where **X** are called independent (or regressor) variables and **Y** are called dependent variables (Martens and Martens, 2001). In the context of multi-location trials, the **Y** matrix consists of variables (grain yield, days to maturity, etc.) measured on genotypes in different environments (locations) and the **X** matrix comprises co-variables that have been measured in either the genotypes (diseases tolerances, maturity, etc.) or in the locations (MX and MI, precipitation, sun hours, etc.). In this context, the co-variables measured in **X** can explain some of the variability existing in **Y**. In other words, genotypic or environmental co-variables can help us to explain G × E interaction.

The results of the PLS can be graphically displayed in the form of biplots (Gabriel, 1971) in which coordinates for environments, genotypes and environmental co-variables corresponding to the first two PLS components are simultaneously depicted by vectors in a space with starting points at the origin $(0, 0)$ and end points determined by the value of the coordinate. Genotypes and environments having the same directions have positive interactions and those having opposite directions have negative interaction. Details of the univariate and multivariate PLS regression algorithms are given in Vargas et al. (1998, 1999).

#### 2.4.2. Factorial regression

The FR models are ordinary linear models that allow the $G \times E$ interaction to be modeled directly as function of the environmental variables. An FR model for $h = 1, \ldots, H$ environmental co-variables (centered) represented by $z_{j_1}, \ldots, z_{j_H}$ the mean of the *i*th genotype in the *j*th environment, $\bar{y}_{ij}$, is

$$\bar{y}_{ij} = \mu + \tau_i + \delta_j + \sum_{h=1}^{H} \varsigma_{ih} z_{jh} + \bar{\varepsilon}_{ij}$$

where $\mu$ is the grand mean over all genotypes and environments, $\tau_i$ the additive effect of the *i*th genotype, $\delta_j$ the additive effect of the *j*th environment; the non-additivity interaction $G \times E$ of the *i*th genotype in the *j*th environment that is represented by the $\varsigma_{ih}$ that are genotypic sensitivity (regression coefficient) with respect to the to the environmental co-variable, $z_{jh}$ and $\bar{\varepsilon}_{ij}$ is the average error.

## 3. Results and discussion

### 3.1. Historic yield potential trials

The irrigated plains of NW Mexico provide a higher yielding and relatively stable environment for wheat production during the winter cycle. Farmers in the region grow DW for the most part, BW was dominant until the early 1990s and TCL has never been grown commercially. However, these patterns are based entirely on economic rather than biological factors, and all three crops express high yield potential in this environment. Our objective was to evaluate the physiological basis for $G \times E$ among as well as within the three crops that is observed when comparing crop cycles in this environment. The historical sets of cultivars reported in this study represent breeding progress since the 1960s; BW cultivars used in these analyses have been previously characterized agronomically (Sayre et al., 1997) and physiologically (Fischer et al., 1998).

#### 3.1.1. Performance data of the three crop species

When considering performance over 6 years, it was clear that BW, DW and TCL crops were favored by different years (Table 2). The cycle 1990 favored DW, BW ranked highest in 1993, and TCL in 1991, 1994 and 1995. The three years 1990, 1993 and 1995 showed crossover interactions among crop species, indicated by rank differences among crop average yields and the fact that range of crop means exceeded

Table 2
Average yield and days to maturity of seven bread wheat, seven durum wheat and four triticale lines NW Mexico, 1990–1996[a]

| Year | Bread wheat | | | Durum | | | Triticale | | | Average yield ($Mg\ ha^{-1}$) | LSD yield |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Yield | % diff[b] ($Mg\ ha^{-1}$) | Maturity (days) | Yield ($Mg\ ha^{-1}$) | % diff | Maturity (days) | Yield ($Mg\ ha^{-1}$) | % diff | Maturity (days) | | |
| 1990 | 7.54 | 2 | 125 | 7.51 | *2* | 123 | 6.80 | −8 | 125 | 7.28 | 0.63 |
| 1991 | 7.02 | −3 | 131 | 6.99 | −3 | 132 | 7.59 | 6 | 136 | 7.2 | 0.63 |
| 1992 | 6.15 | 2 | 120 | 5.98 | −2 | 123 | 6.09 | 0 | 125 | 6.07 | 0.61 |
| 1993 | 7.34 | *10* | 122 | 5.74 | −14 | 126 | 7.16 | 7 | 127 | 6.75 | 0.93 |
| 1994 | 7.57 | −2 | 127 | 7.48 | −3 | 126 | 8.08 | 5 | 131 | 7.71 | 0.65 |
| 1995 | 6.18 | −4 | 119 | 6.24 | −3 | 120 | 7.14 | *11* | 126 | 6.52 | 0.65 |
| Average | 6.97 | 1 | 124 | 6.66 | −3 | 125 | 7.14 | 4 | 128 | 6.89 | |
| LSD | 0.26 | | 1.5 | 0.25 | | 1.9 | 0.33 | | 1.3 | | |

[a] Highlighted values indicate years when a respective crop showed best (italic) and worst (bold) performance, respectively.
[b] Percent difference between individual crop mean and mean of all crops within each year.

LSD values in these years. Considering yield across all crops, the G × E sums of squares accounted for 20% of the total, with genotypes accounting for 57% and years 23%. For the other traits, the total G × E sums of squares was lowest for G/M2, G/SP, and SP/M2 which accounted for 12% of the total, highest for BM (21%), with TKW accounting for 16%.

### 3.1.2. *Genotype by environment interaction across crop species*

The product of PLS in this study is represented as a biplot in which data are shown as coordinates; environmental and genotypic variables are shown as points, and years as vectors. The relative position of a genotype with respect to a year vector or with another environmental point is based on their interaction (not on main effects). The significance of a genotype, year, or co-variable on the G × E biplot is related to distance from the origin. Thus in the biplot for the dependent variable yield (Fig. 1a), the fact that the year vectors for 1990, 1993 and 1995 are the longest indicates that G × E was most significant in those years; and environmental variables which were furthest from the origin (e.g., Tx2 or RD3) are likely to have a greater influence in determining the G × E. The relationship between any two environmental variables, genotypes, or years is defined by the angle formed when the two coordinates are projected as straight lines back to the origin. The more acute the angle, the greater is the relatedness. Angles of 90° indicate a zero relationship, angles greater than 90° a negative relationship and angles approaching 180° indicate strong negative relationships. Hence, 1990 was associated with relatively high values of the environmental variable RD3, while 1993 and 1995 were associated with relatively low values, and 1990 was associated with relatively good response of DW cultivars and relatively poor response of TCL (Fig. 1a).

The PLS biplot showed a fairly clear grouping of crop species in different parts of the biplot, indicating that in terms of G × E, genotypes responded to environment more similarly within a species than between species. The most obvious exception was cultivar 15 (TCL: Cananea-79) which did not cluster with the TCL group but with BW. As mentioned above, the vector for 1990 is in the direction of DW and away from TCL corresponding to the fact that 1990 was the best year for DW and the worst for TCL (Table 2). Similarly, the vector for 1993 is towards the BW cultivars and away from the DW, and that of 1995 in the direction of TCL and away from BW, corresponding also to their respective best and worst years (Table 2). The vectors for the other years (1991, 1992, and 1994) are shorter indicating less overall contribution of those years to the G × E, a result confirmed by the non-significant differences between crop means in those years (Table 2).

Factorial regression is used to select a subset of environmental variables that between them explain a large proportion of the total G × E. For example, if more than 60–70% of the total G × E can be explained by a small number of environmental variables at specific growth stages, interpretation of the basis for G × E in terms of how temperature or RD is affecting a specific physiological process is feasible. However, variables selected by FR should not be emphasized to the exclusion of other variables indicated by the biplot for the following reason. FR chooses the best subset of variables in a stepwise manner to maximize the variation explained with as few degrees of freedom as possible. Hence in a group of potentially related variables (e.g., RD, MX, MI and Tx at a given growth stage), those best related to each other over years, are likely to be represented by only one variable from the group, even though more than one may be significantly associated with G × E.

The FR indicated that four environmental variables best explained G × E for yield, the most important being Tx in the spike primordia stage (Tx2) and RD in the spike growth stage (RD3), which together explained 61% of the total variation in G × E. When two more variables were added, RD in vegetative stage (RD1) and MI in the vegetative stage (MI1), 80% of the G × E was explained (Table 3). The biplot for yield indicates that 1993 had higher values for the environmental variable mean temperature in spike primordia stage (Tx2), which was positively associated with BW yield, and negatively with DW located on the other side of the biplot. Year 1990 showed higher values of the environmental variables RD in vegetative phase (RD1), spike growth stage (RD3) and the first half of GF (RD4) suggesting that these variables are positively associated with DW performance and negatively with TCL (located on the other side of the biplot). Year 1995 had higher values of MI in the first half of GF (MI4) and this favored TCL and negatively affected DW and BW. The actual yearly values of environmental variables are

Table 3
Growth stages sensitive to weather identified by PLS analysis and factorial regression considering G × E among seven bread wheat, seven durum, and four triticale lines, NW Mexico, 1990–1995

| Growth stage | Meteorological data[a] | Yield components | | | | | |
|---|---|---|---|---|---|---|---|
| | | Yield | Biomass | Grains $m^{-2}$ | Kernel weight | Grains per spike | Spikes $m^{-2}$ |
| Vegetative | RD | 3[b] | | | 1 | | |
| Vegetative | MX | | | | | | 2 |
| Vegetative | MI | 4 | | | | | |
| Vegetative | Tx | | | | | | |
| Spike primordia | RD | | | | | | |
| Spike primordia | MX | | | | 2 | 2 | |
| Spike primordia | MI | | 1 | 4 | | | 3 |
| Spike primordia | Tx | 1 | | 1 | | | 1 |
| Spike growth | RD | 2 | | | 4 | | |
| Spike growth | MX | | | | | | |
| Spike growth | MI | | | | | | |
| Spike growth | Tx | | | | | | |
| Grainfill-1 | RD | | 2 | | | | |
| Grainfill-1 | MX | | | | | | |
| Grainfill-1 | MI | | | 2 | | 1 | |
| Grainfill-1 | Tx | | | 3 | 3 | | |
| Grainfill-2 | RD | | | | | | |
| Grainfill-2 | MX | | 3 | | | | |
| Grainfill-2 | MI | | | | | | |
| Grainfill-2 | Tx | | | | | | |
| G × E explained by FR± (%) | | 80 | 82 | 79 | 80 | 63 | 77 |

[a] RD: solar radiation; MX: maximum temperature; MI: minimum temperature; Tx: mean temperature.
[b] Numbers refer to factors explaining significant amounts of G × E in rank order, i.e. 1, the factor explaining most G × E; 2, the factor explaining most G × E after factor 1, etc., according to FR ± G × E explained by factorial regression (FR), total amount of G × E explained by the 3–4 factors for each trait.

presented in Table 4. The effect of environmental factors identified at specific crop stages will be discussed for each crop species with reference to physiological processes that appear to be influencing G × E.

PLS analysis for the dependent variables BM (Fig. 1b), G/M2 (Fig. 1c), and SP/M2 (not shown) demonstrated the same tendency in the biplots for crop species to cluster together. For G/SP, DW and TCL clustered but not BW, while for TKW, TCL and BW clustered but not DW (not shown). Overall the data support the conclusion that there is more G × E between these crop species than within, as might be expected. The FR analysis with 3–4 environmental variables explained between 63% (G/SP) and 82% (BM) of the total G × E for these traits (Table 3).

A major objective of the analyses was to identify environmental factors at specific stages of crop development that could account for crossover interactions of the crop species. PLS analysis, in contrast to principal component or regression type analyses, is powerful in that it separates interaction from main effects enabling the partitioning of G × E sums of squares to environmental conditions during specific growth stages and years. To assist with physiological interpretation of PLS results, the relative variation in yield of cultivars over years was compared with relative variation in the other performance traits (Appendix C).

#### *3.1.3. Physiological bases for* G × E *of the BW species*

Considering the results obtained from the yield biplot (Fig. 1a), it is apparent the best and worst year for BW were 93 and 95, respectively, and a number of environmental variables can also be seen to be either

Table 4
Meteorological data for different approximate growth stages (averaged from daily values) for six wheat cycles, Obregon, NW Mexico, 1990–1995

| Growth stage/year | MX[a] (°C) | MI[b] (°C) | Tx[c] (°C) | RD[d] (Mg $m^{-2}$ per day) | PTQ[e] (Mg $m^{-2}$ per day) |
|---|---|---|---|---|---|
| 1990 | | | | | |
| Vegetative | 24.13 | 8.83 | 16.48 | 14.22 | 0.88 |
| Spike primordia | 23.81 | 7.41 | 15.61 | 16.49 | 1.08 |
| Rapid spike growth | 25.30 | 7.74 | 16.52 | 20.33 | 1.25 |
| Grainfill-1 | 28.19 | 9.89 | 19.04 | 23.47 | 1.27 |
| Grainfill-2 | 32.53 | 12.41 | 22.47 | 27.50 | 1.23 |
| Average cycle | 26.40 | 9.10 | 17.70 | 19.90 | 1.13 |
| 1991 | | | | | |
| Vegetative | 22.57 | 10.98 | 16.78 | 12.14 | 0.75 |
| Spike primordia | 25.10 | 7.75 | 16.43 | 16.32 | 1.00 |
| Rapid spike growth | 27.16 | 12.39 | 19.78 | 17.92 | 0.92 |
| Grainfill-1 | 26.07 | 9.58 | 17.83 | 22.10 | 1.24 |
| Grainfill-2 | 31.84 | 12.00 | 21.92 | 27.20 | 1.25 |
| Average cycle | 26.20 | 10.40 | 18.30 | 18.60 | 1.02 |
| 1992 | | | | | |
| Vegetative | 22.30 | 11.62 | 16.96 | 11.12 | 0.67 |
| Spike primordia | 22.52 | 10.45 | 16.48 | 13.52 | 0.83 |
| Rapid spike growth | 23.92 | 10.79 | 17.35 | 17.09 | 0.99 |
| Grainfill-1 | 26.25 | 10.31 | 18.28 | 21.21 | 1.17 |
| Grainfill-2 | 28.62 | 10.99 | 19.81 | 24.88 | 1.25 |
| Average cycle | 24.60 | 10.80 | 17.70 | 17.40 | 0.98 |
| 1993 | | | | | |
| Vegetative | 23.43 | 10.05 | 16.74 | 12.14 | 0.75 |
| Spike primordia | 23.94 | 13.97 | 18.96 | 10.93 | 0.58 |
| Rapid spike growth | 25.12 | 9.03 | 17.08 | 16.23 | 0.95 |
| Grainfill-1 | 25.74 | 10.09 | 17.91 | 19.28 | 1.08 |
| Grainfill-2 | 29.67 | 11.51 | 20.59 | 26.18 | 1.28 |
| Average cycle | 25.50 | 10.80 | 18.20 | 16.90 | 0.93 |
| 1994 | | | | | |
| Vegetative | 24.94 | 10.47 | 17.70 | 12.60 | 0.72 |
| Spike primordia | 25.94 | 8.64 | 17.29 | 15.65 | 0.91 |
| Rapid spike growth | 24.83 | 7.78 | 16.30 | 17.41 | 1.08 |
| Grainfill-1 | 27.50 | 10.65 | 19.08 | 20.48 | 1.09 |
| Grainfill-2 | 30.46 | 9.87 | 20.16 | 24.83 | 1.24 |
| Average cycle | 26.70 | 9.40 | 18.11 | 18.10 | 1.01 |
| 1995 | | | | | |
| Vegetative | 22.21 | 10.59 | 16.40 | 12.81 | 0.79 |
| Spike primordia | 25.15 | 7.76 | 16.45 | 15.54 | 0.96 |
| Rapid spike growth | 27.23 | 12.43 | 19.83 | 16.60 | 0.83 |
| Grainfill-1 | 28.52 | 11.95 | 20.24 | 20.85 | 1.03 |
| Grainfill-2 | 30.27 | 10.09 | 20.18 | 25.68 | 1.28 |
| Average cycle | 26.60 | 10.40 | 18.50 | 18.30 | 0.98 |

[a] Maximum temperature.
[b] Minimum temperature.
[c] Mean temperature.
[d] Radiation.
[e] Photothermal quotient.

positively or negatively associated with BW. The traits G/M2 and BM showed a similar interaction with year when considering all 6 years (Figs. 1b and c, Appendix C). By considering this information together, it is possible to speculate as to the physiological basis for the interaction of BW performance with years. In 1993, BW was positively associated with MI and Tx in the spike primordia stage (MI2 and Tx2), and negatively with RD2. In fact 1993 had exceptionally high MI2, Tx2, and low RD2 and thus very low PTQ (Table 4), suggesting that BW are favored relative to the other crops by warmer night temperatures and lower PTQ during the spike primordia stage when potential grain number is being determined. This is consistent with the fact that BW had its highest value for G/M2 relative to the other crops (20% higher than the annual mean) in 1993 (Appendix C).

Fischer (1985) showed that BW yield is most sensitive to environmental conditions during the rapid spike growth stage (stage 3 in this study), grain number being increased by lower Tx and higher RD, and therefore high PTQ. The biplot (Fig. 1a) showed weak associations of BW with RD3 (positive) and Tx3 (negative), consistent with Fischer's observation. It is, therefore, interesting that $G \times E$ for BW appears to be associated with a weak positive interaction with PTQ in stage 3, but a strong negative association with PTQ in the previous stage. (In a subsequent section, evidence for variation within the BW group for sensitivity to conditions in these stages will be presented.) The biplots for BM (Fig. 1b) and G/M2 (Fig. 1c) showed similar associations as yield, and MI2 and Tx2 were identified by FR for the two traits, respectively (Table 3). With the data available, it is not possible to say whether conditions during growth stage 2 were favoring BW biomass which permitted higher grain number (i.e., source driving sink) or whether higher grain number created a greater demand for assimilates (i.e., sink driving source). The other factors identified by FR explaining $G \times E$ for yield, i.e., RD in the vegetative stage (RD1) and MI in the vegetative stage (MI1) were not, according to their positions in the biplot for yield (Fig. 1a) explaining much of the $G \times E$ for BW.

### 3.1.4. *Physiological bases for* $G \times E$ *of the DW species*

Considering $G \times E$ for DW yield (Fig. 1a), the best year for DW (1990) was associated with high RD throughout the pre-anthesis period (RD1, RD2 and RD3). MI2 was low in that year and exceptionally high in 1993, the worst year for DW. In fact, averaged over stages 1–3, RD and PTQ were highest in 1990 and lowest in 1993, while MI showed the opposite trend (Table 4). Traits showing the same pattern of $G \times E$ as yield for DW were BM and G/M2. High DW biomass was also associated with high RD in stages 1–3 (Fig. 1b), while high G/M2 was only weakly associated with RD2 (Fig. 1c). Similarly, MI2 showed a stronger negative relationship with BM than G/M2. This may suggest that in the case of DW, high yield was being driven more by source (BM) than sink (G/M2) at least in the pre-anthesis stage.

Previously, it has been suggested that the major driving force for higher yield and total biomass was higher fertility, theoretically (Slafer et al., 1999; Reynolds et al., 2000) as well as in substitution lines for chromosome 7DL.7Ag associated with *Lr19* (Reynolds et al., 2001). However, the current data, as well as more recent data from *Lr19* isolines (unpublished), suggest that intrinsically higher radiation use efficiency pre-anthesis may also play an important role. Clearly, a major factor explaining $G \times E$ when comparing BW and DW are sensitivity to conditions during spike development. Considerably more work has been published on BW than DW, and while sensitivity of BW to conditions during spike growth stage has been reported by different authors (Fischer, 1985; Abbate et al., 1997), it seems that DW may be the more sensitive of the two species.

### 3.1.5. *Physiological bases for* $G \times E$ *of the TCL species*

For 3–4 TCL cultivars (those clustering together), the most favorable year was 1995, while the worst year (1990) was associated with very high RD from spike growth onwards (RD3-5) (also associated with high MX during GF), and low MI in the vegetative stage (MI1). The traits showing similar $G \times E$ to yield were BM, GR/SP, and HI (Appendix C). The biplot for BM (Fig. 1b) showed a similar pattern to yield. The biplot for GR/SP (not shown) was similar except for MI1, which was negatively associated with TCL and close to the origin suggesting that it was not influential in explaining $G \times E$ for that trait (HI was not analyzed by PLS). The apparent sensitivity of TCL to low temperature in the vegetative stage is hard to explain; one of its genomes is from rye, a cold-tolerant species. However, this origin would be consistent with the apparent sensitivity of TCL to high RD from spike growth stage onwards and perhaps to high temperatures during GF. This may have a metabolic cause and could partly explain the strong association of variation of yield with variation for harvest index (Appendix C).

#### 3.1.6. *Factors influencing* G × E *for yield components*

A summary of environmental factors identified by FR that affect G × E for yield components is presented (Table 3). As might be expected, factors affecting G × E for yield were in many cases in common with factors influencing BM and yield components. For example, Tx in the spike primordia stage (Tx2) is the factor explaining most of the G × E for yield, G/M2 and SP/M2, while MI2 (related to Tx2) is the factor explaining most G × E for BM. Clearly, temperatures during this stage can have a direct influence on tiller growth and survival (SP/M2) and potential grain number (G/M2), and thus an indirect effect on BM and yield. The G × E for both yield and TKW are explained by two environmental variables in common: RD1 and RD3. For the latter, RD in the rapid spike growth phase has been shown to influence kernel weight potential (Calderini and Reynolds, 2000; Calderini et al., 2001); for the former (RD1), G × E for TKW may be influenced indirectly by tiller number (i.e., via compensation among yield components). Both TKW and G/SP were affected by MX2 (higher temperatures were generally associated with higher RD in stage 2), which could influence kernel weight potential as well as G/SP.

A more comprehensive review of G × E for yield components and their interactions will be presented in a subsequent study. However, it is clear even from this cursory analysis that certain stages of development appear to be more sensitive to environmental conditions than others in terms of G × E. Sensitivity during the spike primordia stage appears to be responsible for the largest proportion of G × E for yield, BM and most yield components.

#### 3.1.7. *Genotype by environment interaction within crop species*

On an individual crop basis, crossover interaction was also apparent from the fact that quite large rank changes were obvious from year to year (Appendix B). The G × E sums of squares accounted for 15, 5 and 27% of the total for BW, DW and TCL, respectively. Analyses using PLS and FR were made in exactly the same way within the crops. The objective was to assess cultivar differences in sensitivity to environmental factors at different crop stages. Such information could be used to breed germplasm with less sensitivity to G × E if lines with complementary adaptation can be crossed and selected appropriately. Our analyses did not suggest any decrease in G × E in the historic set of BW (Fig. 2a), DW (Fig. 2b) or TCL (not shown). In the case of BW, new varieties were generally located further from the origin than older ones, although this could also be related to their higher yield potential.

#### 3.1.8. *Physiological bases for* G × E *among BW genotypes*

Considering yield of the seven BW cultivars only, the PLS biplot (Fig. 2a) showed clustering of certain cultivars. The largest and tightest cluster was for cultivars 2, 4, and 6 (7Cerros-66, Nacozari-76 and Seri-82) all of which performed well in 1995 and poorly in 1993, relative to the other BW cultivars in those years. Traits showing similar interaction with year for this group (based on correlation over 6 years of relative variation of traits in this cluster with the yearly average for BW; see also Appendix B) were BM, G/M2 and G/SP. Factorial regression indicated the environmental variables RD1, MI2 and RD5 explained 68% of their G × E. Inspection of the biplot showed that MI2 and Tx2 were the factors showing a significant negative association with performance of this group, suggesting that these cultivars lose potential grain number (G/M2, G/SP) when temperatures are high in stage 2. The group was also associated positively with warm temperatures in stage 4, suggesting that GF in these cultivars is favored by warmer conditions in the milk stage.

Cultivars 1 and 7 (Pitic-62 and Super Kauz-88) also formed a cluster, associated best with poor performance, and high values of radiation and temperature in stage 5. This suggests that these two cultivars (representing the highest and lowest yield potential of the set) are both relatively sensitive to the warmer temperatures that are common during with GF. Cultivar 3 (Yecora-70), the only double dwarf of the group, performed worst in 1992 having a yield of 12% lower than the BW mean (compared with an average of 2% lower in other years); however, no traits were significantly associated with G × E for yield of Yecora-70. None of the clusters for BW or DW showed any correspondence to coefficients of parentage between cultivars that were calculated (theoretically) using pedigrees information.

#### *3.1.9. Physiological bases for* G × E *among DW cultivars*

The PLS biplot (Fig. 2b) showed three clusters of DW cultivars which corresponded with the two oldest (lowest yielding) cultivars (8-Chapala-67 and 9-Jori-69), two of the three highest yielding cultivars (12-Yavaros-79 and 13-Altar-84) and three cultivars which included two intermediate yielding cultivars and one high yielding cultivars (10-Cocorit-71 and 11-Mexicali-75, and 14-Aconchi-89, respectively). Factorial regression indicated the environmental variables RD2, MX3 and MX4 explained 66% of their G × E. Inspection of the biplot suggested that RD2 was best associated with the low yielding group as well as Tx2 (negatively); traits showing similar G × E to yield of this group were G/M2, G/SP, HI and BM. Together these observations suggest that the lower yielding cultivars are especially sensitive to RD and PTQ in the primordia stage; supported by the fact that 1990 (the best year for the low yield DW) was the year with the highest PTQ in growth stage 2.

When considering G × E for all three crops (above), it was concluded that DW was the most sensitive to low PTQ during the pre-anthesis stages; the fact that the oldest cultivars are most sensitive among the DW would suggest that breeding progress in DW has been associated with decreasing their sensitivity to conditions pre-anthesis resulting in more stable grain number (Appendix B). The cluster of three cultivars (Cocorit-71, Mexicali-75 and Aconchi-89) best represent this progress. These three cultivars were associated with MI2 and negatively with RD2 and yielded best relative to the other DW in 1993 (Appendix B), a year with an exceptionally low PTQ in stage 2 (Table 4). Traits showing similar G × E were G/SP, G/M2 and HI. Unlike the other DW cultivars (and especially the low yield group), these cultivars showed great stability in terms of environmental effects on grain number determination in stage 2; G/M2 was extremely stable across years compared with the other DW cultivars (Appendix B).

The cluster of high yield durums were associated with high temperatures in stages 3 and 4, which were on average highest in 1995, the best year for this group. Presumably these cultivars are well adapted to warmer conditions during grain set.

#### *3.1.10. Physiological bases for* G × E *among TCL cultivars*

For TCL, it is more difficult to draw conclusions since only four cultivars were represented. The PLS biplot showed the four cultivars to be well distributed (not shown), although cultivar 1 (Cananea-79) was the most isolated of the four, consistent with the analysis of all three crop species (Fig. 1a) where it was also the cultivar that did not cluster with the TCL group. Performance of Cananea-79 was associated generally with higher RD from stage 3 onwards, suggesting that it may be useful source for improving the crops apparent vulnerability to sunny conditions during rapid spike growth and GF.

### *3.2. Factors influencing* G × E *for yield for ESWYT data*

The ESWYT (one of several international nurseries coordinated by CIMMYT and tested by national wheat programs worldwide) consists of materials of diverse pedigrees with genetic resistance to a broad range of prevalent diseases (Rajaram and Hettel, 1995). Results from the international trials encompassed a wide range of yields, ranging from 1.5 to 9.4 Mg ha$^{-1}$ (Appendix A). The sums of squares for G × E accounted for 7% of the total variation, with genotype and environment accounting for 1 and 84%, respectively.

PLS analysis showed a clear grouping of relatively high versus relatively low yielding sites (i.e., average site yields of 4.1–9.4 Mg ha$^{-1}$ versus 1.5–2.6 Mg ha$^{-1}$, respectively; Fig. 3). Using average site values as proxy environmental variables, FR identified TKW as the one best explaining G × E, although it only accounted for 11% of the total. This suggests that conditions post-anthesis were accounting for more of the G × E than those prior to anthesis (since TKW is largely determined in GF). This could be accounted for by a number of different factors occurring during GF, including G × E for sensitivity to moisture stress which almost certainly accounted for poor performance in many of the lower yielding sites. Terminal heat stress is another factor for which genotypes may show differential response and is typical of many countries growing the ESWYT. Finally disease incidence, which is usually more severe during GF, was reported at 10 of the 27 sites used in this study, and differential susceptibility to these could also account for G × E for yield. The results suggest that greater yield stability could be achieved by emphasizing improved genetic tolerance to these factors. Obviously using mean site variables as indicators of environmental conditions is far from satisfactory, and highlights the need for international breeding programs such as CIMMYT's to obtain better environmental data if G × E is to be understood to benefit global breeding strategies.

## 4. Conclusions

In terms of factors explaining G × E among the three crop species, DW cultivars were shown to be the most sensitive to conditions in the pre-heading phase, preferring higher RD and cooler average temperatures in order to set high grain number. TCL, despite having the highest average yield, and BM yielded relatively poorly in years when conditions were sunny and warm from booting stage onwards suggesting poor heat tolerance. BW appeared to be the most robust of the three species. Such information could be used in conjunction with long-term weather data to predict the relative yield stability of these crops in new environments or in response to climate change.

The type of information obtained on G × E within species could be applied strategically in breeding. For example, in choosing complementary parents with the view to improving robustness in new progeny, as well as to determine in which years/environments to increase selection pressure so as to reduce vulnerability of the crop to G × E. For example, Cananea-79 was identified as a potential source for improving the generally poor heat tolerance of TCL during GF. Likewise a group of DW was shown to be more robust than the rest with respect to conditions pre-anthesis when grain number is determined.

Improving the understanding of how genotype, environment and phenology interact to determine adaptation, could also increase the efficiency of molecular breeding applications, e.g., functional genomics (Brownstein et al., 1998). The main drawback of this approach is the analytical limitations imposed by overwhelming data sets associated with thousands of genes and their interaction with environment and phenology. The analytical approaches described in this paper enable the statistically most relevant environmental and phenological factors to be pinpointed in terms of their interaction with genotype, thus providing a basis for focusing molecular studies. For example, results presented here (Table 3) indicate that gene expression during spike primordia stage would be highly relevant in terms of understanding G × E for wheat species.

## Appendix A

Environmental variables, mean yield and average site values of traits used as proxy environmental variables in PLS analysis of CIMMYT's 11th Spring Wheat Yield Trial (ESWYT) of 30 lines (global), 1991

| Site | Environmental variables | | Yield ($Mg\ ha^{-1}$) | Traits related to conditions | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Pre-anthesis | | Post-anthesis | | |
| | Latitude (°) | Altitude (m) | | Heading (days to) | Height (cm) | Grainfilling (days) | Thousand kernel weight (g) | Grainfilling rate (kg $ha^{-1}$ per day) |
| South Africa | 28 | 1687 | 3.0 | 72 | 80 | 41.1 | 31.9 | 72.9 |
| Malawi | 14 | 1560 | 2.6 | 60 | 68 | 52.0 | 40.5 | 51.6 |
| Tanzania | 3 | 1372 | 3.4 | 59 | 78 | 47.5 | 39.7 | 72.0 |
| Libya | 25 | 415 | 9.4 | 90 | 98 | 56.4 | 43.9 | 167.5 |

**Appendix A.** (*Continued*)

| Site | Environmental variables | | Yield ($Mg\ ha^{-1}$) | Traits related to conditions | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Pre-anthesis | | Post-anthesis | | |
| | Latitude (°) | Altitude (m) | | Heading (days to) | Height (cm) | Grainfilling (days) | Thousand kernel weight (g) | Grainfilling rate ($kg\ ha^{-1}$ per day) |
| Iran | 31 | 20 | 5.3 | 92 | 86 | 49.6 | 41.1 | 91.5 |
| Iran | 37 | 5 | 5.1 | 118 | 94 | 55.6 | 36.1 | 92.2 |
| Bangladesh | 24 | 8 | 2.9 | 67 | 82 | 42.5 | 35.6 | 68.6 |
| India | 27 | 450 | 4.1 | 83 | 87 | 37.0 | 35.1 | 111.1 |
| India | 26 | 123 | 4.8 | 74 | 83 | 49.1 | 41.0 | 99.1 |
| India | 29 | 215 | 3.5 | 87 | 87 | 34.0 | 37.5 | 104.7 |
| Myanmar | 22 | 110 | 1.5 | 57 | 55 | 48.9 | 33.5 | 31.0 |
| Nepal | 27 | 105 | 2.8 | 76 | 85 | 39.9 | 33.9 | 70.0 |
| China | 40 | 50 | 2.9 | 54 | 72 | 34.3 | 29.8 | 83.5 |
| China | 31 | 506 | 4.1 | 130 | 92 | 60.5 | 29.9 | 67.6 |
| China | 38 | 1118 | 8.6 | 64 | 85 | 40.4 | 35.7 | 212.3 |
| China | 32 | 67 | 2.5 | 159 | 90 | 40.0 | 29.5 | 62.9 |
| China | 49 | 288 | 2.9 | 43 | 82 | 39.4 | 29.4 | 73.3 |
| Guatemala | 15 | 2407 | 2.6 | 64 | 86 | 73.5 | 31.2 | 36.1 |
| Brazil | 24 | 340 | 1.9 | 66 | 74 | 67.2 | 27.3 | 28.6 |
| Argentina | 38 | 212 | 2.1 | 89 | 69 | 39.4 | 40.0 | 53.7 |
| Chile | 34 | 479 | 6.0 | 108 | 84 | 42.3 | 44.2 | 141.1 |
| Paraguay | 27 | 200 | 3.1 | 76 | 86 | 49.3 | 34.4 | 62.8 |
| Yugoslavia | 44 | 860 | 3.4 | 79 | 81 | 55.4 | 40.7 | 60.9 |
| Greece | 41 | 10 | 4.6 | 144 | 90 | 53.4 | 35.0 | 87.1 |
| Spain | 37 | 20 | 4.5 | 81 | 85 | 27.8 | 38.0 | 190.7 |
| Spain | 37 | 72 | 3.2 | 87 | 67 | 34.5 | 36.9 | 94.9 |
| Norway | 60 | 90 | 1.7 | 55 | 55 | 45.7 | 38.5 | 36.7 |
| Average | 31.1 | 474 | 3.8 | 83 | 81 | 46.5 | 35.9 | 86.1 |
| Maximum | 60 | 2407 | 9.4 | 159 | 98 | 74.0 | 44.0 | 212.0 |
| Minimum | 14 | 5 | 1.5 | 43 | 55 | 28.0 | 27.0 | 29.0 |

## Appendix B

Yield and other traits for BW, DW and TCL cultivars averaged for six cycles, and % difference of individual cultivars from mean of all crops (dAvg all), Obregon, NW Mexico, 1990–1995

| | Yield (Mg ha$^{-1}$) | dAvg all (%) | Harvest index (%) | dAvg all (%) | Biomass (Mg ha$^{-1}$) | dAvg all (%) | Spikes m$^{-2}$ | dAvg all (%) | Grains m$^{-2}$ | dAvg all (%) | Grain/spike | dAvg all (%) | Thousand kernel wt (g) | dAvg all (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PITIC-62 | 6.1 | −11 | 35.3 | −10 | 17.4 | −1 | 449 | 5% | 16200 | −4 | 36.6 | −11 | 38.0 | −9 |
| 7 CERROS | 6.5 | −6 | 37.2 | −5 | 17.4 | −1 | 434 | 2 | 18700 | 11 | 44.1 | 8 | 34.8 | −16 |
| YECORA-70 | 6.8 | −1 | 43.7 | 12 | 15.6 | −11 | 518 | 21 | 16800 | −1 | 33.1 | −19 | 40.8 | −2 |
| NACOZARI-76 | 7.0 | 1 | 39.0 | 0 | 17.9 | 2 | 453 | 6 | 20100 | 19 | 45.0 | 10 | 34.8 | −16 |
| CIANO-79 | 7.1 | 3 | 38.8 | −1 | 18.3 | 4 | 473 | 11 | 20700 | 22 | 44.2 | 8 | 34.6 | −17 |
| SERI-82 | 7.5 | 9 | 43.7 | 12 | 17.2 | −3 | 392 | −8 | 18900 | 12 | 48.8 | 19 | 39.8 | −5 |
| SUPER KAUZ | 7.8 | 13 | 41.9 | 7 | 18.6 | 5 | 525 | 23 | 22100 | 31 | 42.4 | 3 | 35.6 | −15 |
| Avg BW | 7.0 | 1 | 39.9 | 2 | 17.5 | −1 | 463 | 9 | 19100 | 13 | 42.0 | 3 | 36.9 | −11 |
| CHAPALA-67 | 4.4 | −36 | 29.1 | −26 | 15.1 | −14 | 479 | 12 | 9300 | −45 | 20.2 | −51 | 47.4 | 14 |
| JORI-69 | 5.2 | −25 | 33.4 | −14 | 15.4 | −13 | 358 | −16 | 10100 | −40 | 29.0 | −29 | 51.2 | 23 |
| COCORIT-71 | 7.0 | 1 | 43.7 | 12 | 16.1 | −9 | 455 | 7 | 15700 | −7 | 34.7 | −15 | 44.6 | 7 |
| MEXICALI-75 | 7.1 | 3 | 42.2 | 8 | 16.9 | −4 | 462 | 8 | 15400 | −9 | 33.3 | −19 | 46.6 | 12 |
| YAVAROS-79 | 7.6 | 11 | 42.2 | 8 | 18.1 | 3 | 427 | 0 | 16400 | −3 | 39.2 | −4 | 46.4 | 11 |
| ALTAR-84 | 7.6 | 10 | 41.6 | 6 | 18.4 | 4 | 437 | 3 | 17000 | 1 | 39.7 | −3 | 45.2 | 8 |
| ACONCHI-89 | 7.7 | 11 | 41.1 | 5 | 18.7 | 6 | 438 | 3 | 16600 | −2 | 38.8 | −5 | 46.3 | 11 |
| Avg DW | 6.7 | −3 | 39.0 | 0 | 17.0 | −4 | 436 | 2 | 14400 | −15 | 33.6 | −18 | 46.8 | 12 |
| CANANEA-79 | 7.0 | 2 | 38.8 | −1 | 18.2 | 3 | 389 | −9 | 17500 | 4 | 45.9 | 12 | 40.5 | −3 |
| ALAMOS-83 | 7.3 | 7 | 39.0 | 0 | 18.9 | 7 | 377 | −12 | 19700 | 17 | 52.7 | 29 | 37.1 | −11 |
| BEAGLE-82 | 6.6 | −5 | 34.2 | −13 | 19.3 | 9 | 302 | −29 | 15500 | −8 | 51.8 | 26 | 42.8 | 3 |
| ERONGA-83 | 7.6 | 11 | 38.4 | −2 | 19.9 | 13 | 305 | −28 | 17400 | 3 | 57.9 | 41 | 43.7 | 5 |
| Avg TCL | 7.1 | 4 | 37.6 | −4 | 19.1 | 8 | 343 | −19 | 17500 | 4 | 52.1 | 27 | 41.0 | −2 |
| Avg all crops | 6.9 | | 39.1 | | 17.6 | | 426 | | 16900 | | 41.0 | | 41.7 | |
| F-Y | 69 | | 57 | | 51 | | 86 | | 72 | | 58 | | 30 | |
| F-G | 82 | | 48 | | 21 | | 41 | | 109 | | 77 | | 111 | |
| F-G × Y | 5.5 | | 2.5 | | 2.3 | | 2.4 | | 3.6 | | 2.5 | | 4.6 | |

**B.1.**

Yield and other traits for BW, DW and TCL cultivars, and % difference of each cultivar from annual mean of all crops (dAvg all), Obregon, NW Mexico, 1990

| | Yield ($Mg\ ha^{-1}$) | dAvg all (%) | Harvest index (%) | dAvg all (%) | Biomass ($Mg\ ha^{-1}$) | dAvg all (%) | Spikes $m^{-2}$ | dAvg all (%) | Grains $m^{-2}$ | dAvg all (%) | Grain/ spike | dAvg all (%) | Thousand kernel wt (g) | dAvg all (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PITIC-62 | 6.0 | −19 | 33.2 | −14 | 18.1 | −6 | 468 | 8 | 18500 | −4 | 40.2 | −11 | 32.4 | −17 |
| 7 CERROS | 7.2 | −3 | 37.7 | −2 | 19.0 | −1 | 414 | −5 | 22000 | 15 | 53.2 | 17 | 32.7 | −17 |
| YECORA-70 | 7.8 | 6 | 45.2 | 17 | 17.2 | −10 | 498 | 15 | 20500 | 7 | 41.2 | −9 | 38.1 | −3 |
| NACOZARI-76 | 7.7 | 5 | 40.7 | 6 | 19.0 | −1 | 454 | 5 | 22700 | 18 | 49.9 | 10 | 34.1 | −13 |
| CIANO-79 | 8.1 | 10 | 38.9 | 1 | 20.8 | 9 | 468 | 8 | 23600 | 23 | 51.0 | 12 | 34.3 | −13 |
| SERI-82 | 8.2 | 11 | 44.6 | 16 | 18.3 | −4 | 357 | −18 | 20800 | 8 | 58.2 | 28 | 39.5 | 1 |
| SUPER KAUZ | 7.9 | 7 | 39.7 | 3 | 19.8 | 4 | 517 | 19 | 24300 | 27 | 47.0 | 4 | 32.5 | −17 |
| Avg BW | 7.5 | 2 | 40.0 | 4 | 18.9 | −1 | 454 | 5 | 21800 | 14 | 48.7 | 7 | 34.8 | −11 |
| CHAPALA-67 | 6.0 | −19 | 33.9 | −12 | 17.6 | −8 | 522 | 21 | 12200 | −36 | 23.4 | −48 | 49.0 | 25 |
| JORI-69 | 5.8 | −21 | 35.2 | −9 | 16.6 | −13 | 344 | −21 | 11000 | −43 | 32.4 | −29 | 53.4 | 36 |
| COCORIT-71 | 7.7 | 5 | 41.8 | 8 | 18.6 | −3 | 501 | 16 | 18200 | −5 | 36.9 | −19 | 42.6 | 9 |
| MEXICALI-75 | 7.8 | 6 | 42.8 | 11 | 18.2 | −5 | 490 | 13 | 18400 | −4 | 37.4 | −17 | 42.5 | 8 |
| YAVAROS-79 | 8.4 | 14 | 41.0 | 6 | 20.6 | 8 | 442 | 2 | 18800 | −2 | 42.7 | −6 | 44.8 | 14 |
| ALTAR-84 | 8.4 | 14 | 40.8 | 6 | 20.5 | 7 | 439 | 1 | 20400 | 6 | 46.7 | 3 | 41.1 | 5 |
| ACONCHI-89 | 8.4 | 15 | 42.6 | 10 | 19.9 | 4 | 453 | 5 | 19300 | 1 | 42.9 | −5 | 43.9 | 12 |
| Avg DW | 7.5 | 2 | 39.7 | 3 | 18.9 | −1 | 456 | 5 | 16900 | −12 | 37.5 | −17 | 45.3 | 16 |
| CANANEA-79 | 7.3 | −1 | 36.1 | −6 | 20.3 | 6 | 416 | −4 | 20300 | 6 | 49.0 | 8 | 36.2 | −8 |
| ALAMOS-83 | 6.5 | −12 | 33.3 | −14 | 19.5 | 2 | 380 | −12 | 20100 | 5 | 53.3 | 18 | 32.2 | −18 |
| BEAGLE-82 | 6.5 | −11 | 32.3 | −16 | 20.2 | 6 | 299 | −31 | 16800 | −13 | 56.3 | 24 | 38.9 | −1 |
| ERONGA-83 | 6.9 | −7 | 34.3 | −11 | 20.1 | 5 | 337 | −22 | 18400 | −4 | 54.7 | 21 | 37.5 | −4 |
| Avg TCL | 6.8 | −8 | 34.0 | −12 | 20.1 | 5 | 358 | −17 | 18900 | −2 | 53.3 | 18 | 36.2 | −8 |
| Avg all crops | 7.4 | | 38.6 | | 19.1 | | 433 | | 19200 | | 45.4 | | 39.2 | |

## B.2.

Yield and other traits for BW, DW and TCL cultivars, and % difference of each cultivar from annual mean of all crops (dAvg all), Obregon, NW Mexico, 1993

| | Yield ($Mg\ ha^{-1}$) | dAvg all (%) | Harvest index (%) | dAvg all (%) | Biomass ($Mg\ ha^{-1}$) | dAvg all (%) | Spikes $m^{-2}$ | dAvg all (%) | Grains $m^{-2}$ | dAvg all (%) | Grain/ spike | dAvg all (%) | Thousand kernel wt (g) | dAvg all (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PITIC-62 | 6.7 | 0 | 35.3 | −8 | 18.8 | 9 | 534 | 5 | 16900 | 2 | 31.6 | −5 | 39.4 | −4 |
| 7 CERROS | 6.7 | 0 | 36.4 | −5 | 18.4 | 6 | 561 | 10 | 16700 | 1 | 29.7 | −11 | 40.1 | −2 |
| YECORA-70 | 7.6 | 13 | 43.0 | 12 | 17.6 | 2 | 701 | 37 | 19800 | 19 | 28.3 | −15 | 38.2 | −7 |
| NACOZARI-76 | 6.5 | −2 | 35.5 | −8 | 18.4 | 7 | 567 | 11 | 19900 | 20 | 35.3 | 6 | 33.0 | −20 |
| CIANO-79 | 8.1 | 21 | 38.9 | 1 | 20.8 | 20 | 627 | 23 | 24400 | 47 | 39.0 | 17 | 33.3 | −19 |
| SERI-82 | 7.3 | 9 | 45.6 | 19 | 16.0 | −7 | 440 | −14 | 18000 | 8 | 41.2 | 24 | 40.7 | −1 |
| SUPER KAUZ | 8.5 | 28 | 42.1 | 9 | 20.3 | 17 | 665 | 30 | 24300 | 46 | 36.5 | 10 | 35.4 | −14 |
| Avg BW | 7.3 | 10 | 39.5 | 3 | 18.6 | 8 | 585 | 15 | 20000 | 20 | 34.5 | 4 | 37.1 | −10 |
| CHAPALA-67 | 2.6 | −61 | 20.9 | −46 | 12.7 | −27 | 549 | 8 | 5600 | −66 | 10.4 | −69 | 46.6 | 14 |
| JORI-69 | 3.7 | −44 | 27.8 | −28 | 13.5 | −22 | 434 | −15 | 8000 | −52 | 19.0 | −43 | 46.5 | 13 |
| COCORIT-71 | 6.1 | −8 | 45.6 | 19 | 13.4 | −22 | 426 | −17 | 13800 | −17 | 32.5 | −2 | 44.5 | 8 |
| MEXICALI-75 | 6.7 | 1 | 43.6 | 13 | 15.4 | −11 | 505 | −1 | 14800 | −11 | 29.2 | −12 | 45.6 | 11 |
| YAVAROS-79 | 6.9 | 3 | 42.0 | 9 | 16.4 | −5 | 465 | −9 | 15900 | −4 | 34.3 | 3 | 43.4 | 6 |
| ALTAR-84 | 7.2 | 8 | 41.0 | 7 | 17.8 | 3 | 547 | 7 | 16900 | 2 | 31.5 | −5 | 43.0 | 5 |
| ACONCHI-89 | 6.8 | 3 | 41.2 | 7 | 16.6 | −4 | 543 | 6 | 15300 | −8 | 28.5 | −14 | 44.7 | 9 |
| Avg DW | 5.7 | −14 | 37.4 | −3 | 15.1 | −13 | 496 | −3 | 12900 | −22 | 26.5 | −20 | 44.9 | 9 |
| CANANEA-79 | 7.3 | 10 | 40.0 | 4 | 18.3 | 6 | 481 | −6 | 18300 | 10 | 38.7 | 16 | 40.0 | −3 |
| ALAMOS-83 | 7.5 | 12 | 42.1 | 10 | 17.7 | 3 | 426 | −17 | 19100 | 15 | 44.7 | 34 | 37.7 | −8 |
| BEAGLE-82 | 6.3 | −6 | 32.7 | −15 | 19.4 | 12 | 365 | −29 | 14900 | −10 | 41.0 | 23 | 42.3 | 3 |
| ERONGA-83 | 7.6 | 13 | 38.8 | 1 | 19.5 | 13 | 359 | −30 | 17000 | 2 | 47.7 | 43 | 44.6 | 9 |
| Avg TCL | 7.2 | 7 | 38.4 | 0 | 18.8 | 9 | 408 | −20 | 17300 | 4 | 43.0 | 29 | 41.1 | 0 |
| Avg all crops | 6.7 | | 38.5 | | 17.3 | | 511 | | 16600 | | 33.3 | | 41.1 | |

### B.3.

Yield and other traits for BW, DW and TCL cultivars, and % difference of each cultivar from annual mean of all crops (dAvg all), Obregon, NW Mexico, 1995

| | Yield ($Mg\ ha^{-1}$) | dAvg all (%) | Harvest index (%) | dAvg all (%) | Biomass ($Mg\ ha^{-1}$) | dAvg all (%) | Spikes $m^{-2}$ | dAvg all (%) | Grains $m^{-2}$ | dAvg all (%) | Grain/spike | dAvg all (%) | Thousand kernel wt (g) | dAvg all (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PITIC-62 | 5.3 | −18 | 32.4 | −14 | 16.3 | −4 | 403 | −5 | 13800 | −15 | 34.1 | −15 | 38.4 | −5 |
| 7 CERROS | 5.9 | −9 | 36.3 | −4 | 16.2 | −5 | 393 | −7 | 19400 | 20 | 49.5 | 24 | 30.3 | −25 |
| YECORA-70 | 6.0 | −6 | 41.2 | 9 | 14.7 | −14 | 485 | 15 | 14600 | −10 | 30.1 | −25 | 41.4 | 2 |
| NACOZARI-76 | 6.3 | −2 | 39.3 | 4 | 16.1 | −5 | 435 | 3 | 19000 | 17 | 44.0 | 10 | 33.0 | −19 |
| CIANO-79 | 5.9 | −8 | 39.2 | 4 | 15.1 | −11 | 431 | 2 | 18200 | 12 | 42.4 | 6 | 32.4 | −20 |
| SERI-82 | 6.9 | 8 | 40.3 | 7 | 17.1 | 1 | 424 | 0 | 17800 | 10 | 42.2 | 6 | 38.8 | −4 |
| SUPER KAUZ | 7.0 | 9 | 40.9 | 8 | 17.1 | 1 | 472 | 12 | 19700 | 22 | 41.6 | 4 | 35.7 | −12 |
| Avg BW | 6.2 | −4 | 38.5 | 2 | 16.1 | −5 | 435 | 3 | 17500 | 8 | 40.6 | 1 | 35.7 | −12 |
| CHAPALA-67 | 3.3 | −48 | 22.4 | −41 | 14.9 | −12 | 501 | 19 | 6900 | −57 | 13.9 | −65 | 48.3 | 19 |
| JORI-69 | 4.9 | −24 | 31.3 | −17 | 15.5 | −9 | 385 | −9 | 9400 | −42 | 24.4 | −39 | 51.7 | 27 |
| COCORIT-71 | 6.6 | 3 | 44.2 | 17 | 14.9 | −12 | 470 | 11 | 16100 | −1 | 34.2 | −15 | 41.0 | 1 |
| MEXICALI-75 | 6.4 | 0 | 38.7 | 3 | 16.7 | −2 | 458 | 8 | 15500 | −4 | 33.9 | −15 | 41.5 | 2 |
| YAVAROS-79 | 7.5 | 17 | 41.4 | 10 | 18.2 | 7 | 508 | 20 | 16300 | 1 | 32.2 | −20 | 46.3 | 14 |
| ALTAR-84 | 7.6 | 18 | 40.2 | 7 | 19.0 | 12 | 492 | 16 | 16500 | 2 | 33.7 | −16 | 46.1 | 14 |
| ACONCHI-89 | 7.4 | 15 | 39.4 | 4 | 18.7 | 10 | 442 | 4 | 15000 | −7 | 33.8 | −15 | 49.4 | 22 |
| Avg DW | 6.2 | −3 | 36.8 | −2 | 16.8 | −1 | 465 | 10 | 13700 | −15 | 29.4 | −26 | 46.3 | 14 |
| CANANEA-79 | 6.0 | −6 | 37.4 | −1 | 16.1 | −5 | 344 | −19 | 16400 | 1 | 49.7 | 24 | 36.7 | −10 |
| ALAMOS-83 | 7.1 | 10 | 37.9 | 0 | 18.7 | 10 | 396 | −6 | 20900 | 29 | 52.3 | 31 | 33.9 | −16 |
| BEAGLE-82 | 7.6 | 18 | 36.8 | −2 | 20.6 | 21 | 297 | −30 | 18200 | 12 | 62.3 | 56 | 41.6 | 3 |
| ERONGA-83 | 7.9 | 23 | 39.6 | 5 | 20.0 | 18 | 277 | −35 | 18100 | 12 | 65.7 | 64 | 43.6 | 7 |
| Avg TCL | 7.1 | 11 | 37.9 | 1 | 18.9 | 11 | 328 | −22 | 18400 | 14 | 57.5 | 44 | 39.0 | −4 |
| Avg all crops | 6.4 | | 37.7 | | 17.0 | | 423 | | 16200 | | 40.0 | | 40.6 | |

## Appendix C

Average yield and performance traits of BW, DW and TCL, % variation (% var) of each crop from the yearly average for all crops, correlations (*r*) of trait with yield (*italics*), and correlation (**r**) between % variation of traits with % variation of yield across years (bold), Obregon, NW Mexico, 1990–1995

| Year | Crop | Yield (Mg ha$^{-1}$) | % var | Harvest index (%) | % var | Biomass (Mg ha$^{-1}$) | % var | Spike m$^{-2}$ | % var | Grains m$^{-2}$ | % var | Grains/ spike | % var | Thousand kernel wt (g) | % var |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1990 | BW | **7.5** | **2** | 40.0 | 4 | 18.9 | −1 | 454 | 5 | 21800 | 13 | 48.7 | 7 | 34.8 | −11 |
| 1991 | BW | **7.0** | **−2** | 41.9 | 0 | 16.8 | −1 | 448 | 13 | 18400 | 12 | 41.9 | −2 | 38.6 | −13 |
| 1992 | BW | **6.2** | **1** | 39.6 | 3 | 15.6 | −1 | 387 | 5 | 16300 | 12 | 42.5 | 5 | 38.1 | −10 |
| 1993 | BW | **7.3** | **10** | 39.5 | 3 | 18.6 | 8 | 585 | 15 | 20000 | 20 | 34.5 | 4 | 37.1 | −10 |
| 1994 | BW | **7.6** | **−1** | 40.0 | 2 | 18.9 | −3 | 471 | 10 | 20600 | 12 | 44.0 | 0 | 37.2 | −13 |
| 1995 | BW | **6.2** | **−4** | 38.5 | 2 | 16.1 | −5 | 435 | 3 | 17500 | 8 | 40.6 | 1 | 35.7 | −12 |
| *r*/**r** | | | | *0.55* | **0.44** | *0.73* | **0.96** | *0.43* | **0.50** | *0.81* | **0.96** | *0.33* | **0.49** | *0.00* | **0.77** |
| 1990 | DW | **7.5** | **2** | 39.7 | 3 | 18.9 | −1 | 456 | 5 | 16900 | −12 | 37.5 | −17 | 45.3 | 16 |
| 1991 | DW | **7.0** | **−2** | 42.8 | 2 | 16.3 | −4 | 388 | −2 | 14400 | −12 | 37.5 | −12 | 48.8 | 10 |
| 1992 | DW | **6.0** | **−2** | 38.9 | 1 | 15.3 | −3 | 385 | 5 | 13000 | −11 | 33.9 | −16 | 46.2 | 10 |
| 1993 | DW | **5.7** | **−14** | 37.4 | −3 | 15.1 | −13 | 496 | −3 | 12900 | −23 | 26.5 | −20 | 44.9 | 9 |
| 1994 | DW | **7.5** | **−2** | 38.5 | −1 | 19.4 | −1 | 428 | 0 | 15400 | −16 | 36.5 | −17 | 49.2 | 15 |
| 1995 | DW | **6.2** | **−3** | 36.8 | −2 | 16.8 | −1 | 465 | 10 | 13700 | −16 | 29.4 | −26 | 46.3 | 14 |
| *r*/**r** | | | | *0.83* | **0.70** | *0.82* | **0.92** | *0.00* | **0.55** | *0.95* | **0.89** | *0.87* | **0.28** | −*0.20* | **0.59** |
| 1990 | TCL | **6.8** | **−8** | 34.0 | −12 | 20.1 | 5 | 358 | −17 | 18900 | −2 | 53.3 | 18 | 36.2 | −8 |
| 1991 | TCL | **7.6** | **6** | 40.6 | −3 | 18.7 | 10 | 313 | −21 | 16700 | 1 | 53.5 | 25 | 45.9 | 4 |
| 1992 | TCL | **6.1** | **0** | 36.2 | −6 | 16.8 | 7 | 301 | −18 | 14300 | −2 | 48.5 | 20 | 42.5 | 1 |
| 1993 | TCL | **7.2** | **7** | 38.4 | 0 | 18.8 | 9 | 408 | −20 | 17300 | 4 | 43.0 | 29 | 41.1 | 0 |
| 1994 | TCL | **8.1** | **6** | 38.3 | −2 | 21.1 | 8 | 351 | −18 | 19500 | 7 | 56.7 | 29 | 41.5 | −3 |
| 1995 | TCL | **7.1** | **11** | 37.9 | 1 | 18.9 | 11 | 328 | −22 | 18400 | 14 | 57.5 | 44 | 39.0 | −4 |
| *r*/**r** | | | | *0.69* | **0.98** | *0.71* | **0.94** | *0.24* | **−0.82** | *0.68* | **0.80** | *0.44* | **0.86** | *0.20* | **0.46** |
| Avg | BW | **7.0** | 1 | 39.9 | 2 | 17.5 | −1 | 463 | 9 | 19100 | 13 | 42.0 | 3 | 36.9 | −11 |
| Avg | DW | **6.7** | −3 | 39.0 | 0 | 17.0 | −4 | 436 | 2 | 14400 | −15 | 33.6 | −18 | 46.8 | 12 |
| Avg | TCL | **7.1** | 4 | 37.6 | −4 | 19.1 | 8 | 343 | −19 | 17500 | 4 | 52.1 | 27 | 41.0 | −2 |
| | Avg | **6.9** | | **39.1** | | **17.6** | | **426** | | **16900** | | **41.0** | | **41.7** | |
| 1990 | All crops | **7.4** | | **38.6** | | **19.1** | | **433** | | **19200** | | **45.4** | | **39.2** | |
| 1991 | All crops | **7.1** | | **42.0** | | **17.0** | | **395** | | **16400** | | **42.7** | | **44.2** | |
| 1992 | All crops | **6.1** | | **38.6** | | **15.8** | | **367** | | **14600** | | **40.5** | | **42.2** | |
| 1993 | All crops | **6.7** | | **38.5** | | **17.3** | | **511** | | **16600** | | **33.3** | | **41.1** | |
| 1994 | All crops | **7.6** | | **39.0** | | **19.6** | | **428** | | **18300** | | **43.9** | | **42.8** | |
| 1995 | All crops | **6.4** | | **37.7** | | **17.0** | | **423** | | **16200** | | **40.0** | | **40.6** | |

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