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Environments for Selecting Widely Adapted Spring Wheat

Hans-Joachim Braun,* Wolfgang H. Pfeiffer, and Wolfgang G. Pollmer

ABSTRACT

Breeding widely adapted wheat (*Triticum aestivum* L.) genotypes with stable and high yields across environments is particularly important for developing countries since yield stabilizing inputs are often limited or not available. To evaluate the screening ability of locations for identification of such genotypes, data collected for 19 yr by the International Spring Wheat Yield Nursery (ISWYN) were analyzed; 1221 trials at 268 locations in 69 countries were involved. To compare single-experiment parameters, i.e., genotypic variance (σ_g^2)_k, error variance (σ_e^2)_k, heritability (h^2)_k, and coefficient of variation (CV)_k, trials without major biotic stresses were divided into three groups according to mean grain yield. Genotypic variance, error variance, and heritability increased and (CV)_k decreased with yield. Group means for the four parameters were significantly ($P = 0.01$) different. A fourth group containing trials with major biotic stresses had the highest, but not significantly higher, average estimates for (σ_g^2)_k, (h^2)_k, and (CV)_k. The screening ability for each location was calculated as the correlation, r_k , between mean grain yield of genotypes at each location and mean yield across locations. The screening ability was highest for locations with no major abiotic and biotic stress factors

apart from leaf rust (*Puccinia recondita* Roberge ex Desmaz. f. sp. *tritici*) and stem rust (*P. graminis* Pers.:Pers. f. sp. *tritici* Eriks. & E. Henn.). CIMMYT's principal test site, Ciudad Obregón, Sonora, Mexico, was most suitable for screening, with an average r_k of 0.77. Sensitivity to photoperiod, cold tolerance, need for late maturity, tolerance to problem soils, and resistance to diseases other than rusts were the main adaptation-limiting and location-specific factors.

LIMITATIONS in yield-stabilizing inputs in developing countries increase the need for widely adapted genotypes to cope with environmental variation. The International Maize and Wheat Improvement Center (CIMMYT) develops widely adapted wheat germplasm for diverse agroecological zones. Selection of genotypes at one location for all zones is impossible, because diverse environments require different trait combinations. However, certain locations may be more suitable for the selection of widely adapted wheat genotypes, due to the presence of biotic and abiotic factors.

Selection and evaluation of segregating populations are frequently based on phenotypic performance at one or a few locations. Campbell and Lafever (1976) indicated a relationship between the early-selection

H.-J. Braun, CIMMYT, P.K. 39 Emek, 06511 Ankara, Turkey; W.H. Pfeiffer, CIMMYT, Lisboa 27, Apdo Postal 6-641, 00600 Mexico D.F., Mexico; and W.G. Pollmer, Institute of Plant Breeding, Seed Science and Population Genetics, Univ. of Hohenheim, 7000 Stuttgart 70, Germany. Received 29 Nov. 1991. *Corresponding author.

environment and the range of adaptation, and hence genetic gains of resulting advanced lines, in a target area. Hamblin et al. (1980) defined the criteria for optimal selection locations such that the location performance results should be representative of the target area and genotypic differences should be large enough for gain from selection. Temporal constancy of major environmental factors is also required (Braun, 1983).

Several criteria have been suggested to quantify the screening ability of locations. Johnson and Frey (1967) used the heritability $(h^2)_k$ of a trait, calculated from a single experiment k , as an estimation. However, $(h^2)_k$ is inappropriate to evaluate screening ability of locations when the genotype \times environment interaction ($G \times E$) reduces selection gains in other environments (Johnson and Frey, 1967). In contrast, Horner and Frey (1957), Liang et al. (1966), Abou-el-Fittouh et al. (1969), Shorter et al. (1977), Seif et al. (1979), Brennan et al. (1981), Fox and Rathjen (1981), and Crossa et al. (1991) described methods to reduce $G \times E$ by dividing an area into subregions. These procedures identify environmental subgroups with reduced $G \times E$ but fail to discriminate among locations with respect to screening ability. Utz (1972) used the product of across-location heritability, h^2 , and the correlation between cultivar yield at a location and the mean yield across locations, r_k , to estimate screening ability of locations. Peterson and Pfeiffer (1989) used average correlations of winter wheat cultivar yields among 56 locations in 30 countries to apply principal factor analysis to 17 yr of yield data from the International Winter Wheat Performance Nursery and estimated the most representative location for each of seven identified groups of winter wheat environments.

The choice of selection locations may be particularly critical for target areas where levels of abiotic stress fluctuate considerably. Rosielle and Hamblin (1981) concluded on theoretical grounds that selection in stress environments, where genetic variance is generally small, will "result in a reduced mean yield in non-stress environments and a decrease in mean yield. Selection for mean productivity will generally increase mean yields in both stress and non-stress environments" unless "the genetic correlation of yields in stress and non-stress environments is highly negative." Jensen (1978), Richards (1982), and Pfeiffer et al. (1989) substantiated these conclusions. Jensen (1978) showed that wheat improvement over 70 yr was associated with better discrimination among genotypes due to improved agronomic practices. Richards (1982) and Pfeiffer et al. (1989) found that selection in environments without moisture deficiencies was superior in developing wheat germplasm that combined high genetic yield potential with tolerance to moisture stress than was selection under moisture stress. In contrast, Ceccarelli et al. (1987) concluded that barley (*Hordeum vulgare* L.) genotypes targeted for production in unfavorable environments should be selected under representative stress conditions.

Grain yield data collected for 19 yr by the ISWYN were analyzed to evaluate screening ability of locations for selecting widely adapted spring wheats and to identify abiotic and biotic factors that influence this screening ability.

MATERIALS AND METHODS

Grain yield data of 1221 trials from the 1st through the 19th ISWYN distributed by CIMMYT from 1964 to 1982 were analyzed. The ISWYN is a standardized international yield trial arranged as a randomized complete-block experiment. The first and second ISWYNs consisted of 24 spring bread wheats plus one variable local check and four replicates. All subsequent nurseries consisted of 50 entries and three replicates. The local check was excluded from the analysis because it was frequently unidentified or was identical to one of the other entries. In ISWYNs 12 through 19, one spring durum wheat (*Triticum urgatum* L. var. *durum*: syn. *T. durum* Desf.) cultivar and one spring triticale (\times *Triticosecale* Wittmack) cultivar were included as checks. Over the 19-yr period, ISWYNs were grown at 268 locations in 69 countries between 62° N and 35° S latitudes and between 228 m below and 4210 m above sea level. Co-operators reported experimental conditions, climate, agronomic practices, and occurrence and severity of diseases, pests, and abiotic stresses. The most common diseases were leaf rust, stem rust, stripe rust (*P. striiformis* Westend.), septoria tritici blotch (*Septoria tritici* Roberge in Desmaz.), powdery mildew (*Erysiphe graminis* DC. f. sp. *tritici* Em. Marchal), and tan spot [*Pyrenophora tritici-repentis* (Died.) Drechs.]. Fungicides were not used. Common abiotic stresses were drought, heat, and Al-toxic soils.

Grouping of Locations

To investigate if genotypic variance $(\hat{\sigma}_g^2)_k$, error variance $(\hat{\sigma}_e^2)_k$, heritability $(h^2)_k$, and coefficient of variation of the error variance CV_k for single experiments (k) were associated with mean grain yield $x_{.k}$ and presence of biotic stresses, trials from each ISWYN were separated into four groups based on mean yields and information from co-operators. Trials without major disease incidence and a mean yield of 2/3 SD above the across-location mean yield for a particular ISWYN were considered as highly productive environments. Trials with a mean yield of 2/3 SD below the ISWYN mean yield and without major disease incidence were considered as less productive environments. The remaining trials without major disease incidence were considered as environments with medium productivity. Trials where high disease incidence was reported were grouped as disease (i.e., high biotic stress) environments, because disease susceptibility for particular entries can result in markedly reduced mean yields and increase phenotypic variances, thus affecting the overall correlations among mean yields, genetic variances, and heritabilities.

Statistical Analysis

The genotypic variance $(\hat{\sigma}_g^2)_k = (s_i^2)_k - (\hat{\sigma}_e^2)_k/n$ was calculated from the variance of the mean yields of the genotypes i at location k , $(s_i^2)_k$, the error variance $(\hat{\sigma}_e^2)_k$, and the number of replicates n . The broad sense heritability $(h^2)_k$ was calculated as $(h^2)_k = (\hat{\sigma}_g^2)_k / (s_i^2)_k$ and the coefficient of variation CV_k as $100 \times [(\hat{\sigma}_e^2)_k]^{1/2} / x_{.k}$. The productivity of a location was measured by the mean yield, $x_{.k}$. Only 1174 trials were analyzed for single trial parameters because 47 trials were unreplicated. Analyses of variance across locations were conducted for each ISWYN with untransformed and $10 \times$ natural-logarithm transformed data. The analyses, done according to the model of Utz (1972) and Wright (1971), can be derived from the standard model:

$$x_{ik} = x_{.k} + g_i + e_k + (ge)_{ik} + \text{error}$$

where x_{ik} = yield of genotype i at location k , $x_{.k}$ = grand mean, g_i = effect of genotype $i = x_{i.} - x_{.k}$, $x_{i.}$ = mean yield of genotype i across locations, e_k = effect of location

Table 1. Group means and standard deviations of wheat grain yield x_k , genotypic variance $(\sigma_g^2)_k$, error variance $(\sigma_e^2)_k$, heritability h_k^2 , and coefficient of variation CV_k for trials in each of four environmental groups: high-, medium-, and low-productivity and biotic stress.†

Group	Trials no.	x_k — kg ha ⁻¹ —	$(\sigma_g^2)_k$	$(\sigma_e^2)_k$	h_k^2		CV_k
						%	
High	297	5430a‡ ± 1060	84.5a ± 30.2	38.2a ± 20.0	85.6a ± 11.5		9.1a ± 3.2
Medium	371	3410b ± 690	40.3b ± 20.3	26.1b ± 16.1	77.0b ± 15.1		15.2b ± 5.0
Low	263	1640c ± 560	13.1c ± 11.3	15.9c ± 11.9	66.3c ± 16.3		20.6c ± 6.1
Biotic Stress	243	2706b ± 720	87.2a ± 35.3	27.2b ± 15.9	85.9a ± 14.9		22.5c ± 7.1
Mean	294	3379	55.1	27.1	78.6		

† Data from the International Spring Wheat Yield Trials (ISWYN) 1 to 19.

‡ Within columns, means followed by different letters are significantly different at $P \leq 0.01$ using the LSD.

$k = x_k - x_{..}$, $(ge)_{ik}$ = interaction effect of genotype i and environment k . Differing from the standard model, Utz (1972) and Wright (1971) considered the dependency of the interaction effects $(ge)_{ik}$ on the main effects g_i and e_k and subdivided the interaction $(ge)_{ik}$ as follows:

$$(ge)_{ik} = (c \times g_i \times e_k) + (\beta_i \times e_k) + (\tau_k \times g_i) + d_{ik}$$

where c = regression of $(ge)_{ik}$ on $(g_i \times e_k)$, β_i = regression of $(ge)_{ik}$ on e_k , τ_k = regression of $(ge)_{ik}$ on g_i , d_{ik} = deviation from regression.

If $c = 0$, $\tau_k = 1$ for all k , and β_i is substituted by $1 + \beta_i$, the model is identical to that of Perkins and Jinks (1968). If $c = 0$, $\beta_i = 1$ for all i , and τ_k is substituted by $1 + \tau_k$, the model is identical to that of Wricke (1971). The parameter β_i describes the response of a genotype to better growing conditions, while τ_k describes the differentiation of the genotypes at a location. With higher τ_k , genotypes are better differentiated relative to the mean yield of all genotypes across all locations. The significance of the correlation between x_i and β_i and between x_k and τ_k is tested with the F -test for c . The heritability of yield for each year was calculated as $h^2 = \hat{\sigma}_g^2 / s^2(x_i)$ where $\hat{\sigma}_g^2$ is the estimated genotypic variance and $s^2(x_i)$ is the variance of the mean yield of the genotypes. Since the error and deviation variances were shown to be heterogeneous by Bartlett's test, F -tests are approximate. The screening ability of locations was estimated as the correlation r_k between yield of genotype i at location k and average yield of genotype i across all locations. Braun (1983) showed that this correlation can also be expressed as:

$$r_k = \{(\hat{\sigma}_g^2 \times \tau_k) / [(s_i^2)_k \times h^2]\}^{1/2} \\ = \{1 - [(\hat{\sigma}_e^2)_k \times (G - 2)] / [(s_i^2)_k \times (G - 1)]\}^{1/2}$$

where G = number of genotypes and $(\hat{\sigma}_e^2)_k$ = variance of d_k . Since $\hat{\sigma}_g^2$ and h^2 are constant for all trials in a given year, r_k is dependent only on the ratio of the differentiation ability τ_k to the phenotypic variance $(s_i^2)_k$ and the ratio of the deviations from regression $(\hat{\sigma}_e^2)_k$ to $(s_i^2)_k$. Therefore, the higher the τ_k value and the lower the $(\hat{\sigma}_e^2)_k$ value, the better the differentiation of the germplasm at location k and the higher the screening ability. Consequently, a good location for selection should have a high heritability h_k^2 , and a high r_k (Allen et al., 1978). However, locations with high h_k^2 and low r_k values may also be suitable for selection, because a low r_k suggests that germplasm with specific adaptation to such locations is required.

RESULTS AND DISCUSSION

Single Experiment Parameters

Table 1 provides means, genotypic and error variances, heritability, and coefficients of variation for grain yield for the high-, medium-, and low-productivity environments and the biotic stress environ-

ments. Trials ranged from 290 to 9900 kg ha⁻¹ for yield, 0 to 561.9 for genotypic variance, 0.7 to 321.1 for error variance, 0 to 99.6 for heritability, and 3.2 to 58.5 for CV. Genotypic variance $(\hat{\sigma}_g^2)_k$, error variance $(\hat{\sigma}_e^2)_k$, and the ratio of $(\hat{\sigma}_g^2)_k$ to $(\hat{\sigma}_e^2)_k$ increased with yield within the high-, medium-, and low-productivity environments. This relationship with yield is common (Allen et al., 1978). However, the relationship between h_k^2 and yield is unclear. Allen et al. (1978) compared five crops and found h_k^2 to increase with yield for wheat and soybean [*Glycine max* (L.) Merr.], while barley, oat, (*Avena sativa* L.), and flax (*Linum usitatissimum* L.) had a higher h_k^2 in unfavorable environments. Similarly, for experiments conducted in low-yielding environments, St-Pierre et al. (1967), Richards (1978), and Daday et al. (1973) reported higher h_k^2 for barley, rapeseed (*Brassica napus* L.), and alfalfa (*Medicago sativa* L.), respectively. Our results suggest that wheat experiments grown in high-yielding environments have higher h_k^2 than experiments grown in abiotic stress environments.

Trials in biotic stress environments had the highest average CV, genotypic variance, and heritabilities, which indicates good possibilities for phenotypic selection. In contrast, heritabilities of trials in low-yielding environments were small. Low genotypic variances reflected a lack of discrimination due to low inputs, low precision, and relatively greater effects of microenvironmental variation.

Correlations across all trials within the high-, medium-, and low-productivity groups were significant ($P < 0.01$) between yield x_k and $(\hat{\sigma}_g^2)_k$ (0.53), h_k^2 (0.42), and CV_k (-0.61), respectively. However, large standard deviations for the parameters in Table 1 suggest that, in all three groups, experiments can have high heritabilities and low mean yields. For trials in the biotic stress environmental group, correlations between x_k and $(\hat{\sigma}_g^2)_k$ (0.35), and CV_k (-0.52) were smaller but significant ($P < 0.01$), while no correlation was found between x_k and h_k^2 .

Analysis of Variance and Regression Analysis

The genotypic variance $(\hat{\sigma}_g^2)$ was, on average, about one-third of the variance for $G \times E$ $(\hat{\sigma}_{ge}^2)$ (Table 2). Knight (1970) showed that trials in environments with different yield limiting factors can have similar means and produce large $G \times E$. The ratio of $\hat{\sigma}_g^2$ to $\hat{\sigma}_{ge}^2$ reflects this environmental diversity. This ratio decreased in ISWYNs 10 through ISWYN 19 when compared with ISWYNs 1 through 9. The decrease was associated with a decrease in the proportion of locally developed non-CIMMYT genotypes varying

Table 2. Estimates for the components of variance for each ISWYN† for genotypic σ_g^2 , genotype \times environment interaction σ_{ge}^2 , common regression σ_c^2 , regression of locations σ_r^2 , regression of genotypes σ_β^2 , and error σ_e^2 variances (σ_c^2 , σ_r^2 , and σ_β^2 as percent of σ_{ge}^2).

ISWYN	Trials	Entries	Mean	Components of variance							h^2	σ_g^2/σ_{ge}^2
				σ_c^2 †	σ_{ge}^2 ‡	σ_r^2 ‡	σ_β^2	σ_e^2	σ_β^2	σ_e^2		
	no.		kg ha ⁻¹								%	
01	34	24	2730	12.2	44.8	3	9	1	23.9	93.4	0.47	
02	47	24	2790	13.3	39.6	9	3	0	27.9	93.0	0.34	
03	61	49	2810	13.5	38.9	7	8	4**	27.9	94.4	0.35	
04	63	49	2900	18.0	42.0	7	10	3**	25.2	95.7	0.43	
05	63	49	2610	16.1	37.0	11	11	2**	29.2	95.5	0.44	
06	60	49	2790	20.0	38.8	9	17	2**	29.2	96.1	0.52	
07	66	49	3570	16.3	33.0	13	14	1	30.9	96.1	0.49	
08	81	49	3570	18.1	43.9	19	14	1**	38.7	96.2	0.41	
09	69	49	3850	13.8	36.6	10	6	1*	32.7	95.2	0.38	
10	68	49	3500	9.4	34.9	8	6	1**	32.6	93.3	0.27	
11	65	49	3800	8.8	37.8	6	4	2**	33.7	92.1	0.23	
12	76	49	3850	9.3	34.6	6	3	1**	43.3	93.5	0.27	
13	76	49	3280	10.2	41.3	4	6	2**	38.6	93.4	0.25	
14	71	48	3510	7.7	28.1	12	3	3**	32.5	93.3	0.27	
15	73	49	3760	8.4	38.1	4	3	3**	34.2	92.5	0.22	
16	64	49	3520	10.3	36.4	7	4	1**	38.0	91.1	0.28	
17	54	49	3620	7.4	45.8	5	4	3**	34.7	91.8	0.16	
18	66	49	3760	18.6	48.4	14	3	4**	33.2	93.5	0.38	
19	64	49	3640	11.9	34.0	11	7	4**	38.7	93.8	0.35	
Mean	64	46	3361	13.3	38.6	9	7	2	32.8	93.9	0.34	

*** Significant at the 0.05 and 0.01 probability levels, respectively.

† ISWYN, International Spring Wheat Yield Nursery.

‡ In each year significant at $P = 0.01$.

between 22 and 63% in ISWYNs 1 through 9 and between 6 and 16% in ISWYNs 10 through 19. These non-CIMMYT genotypes were generally tall, photo-period-sensitive, and susceptible to prevalent diseases, such as the rusts. Their grand mean yield was therefore low, due to a lack of adaptation at most of the locations, and this increased the estimates for $\hat{\sigma}_g^2$. The ratio of $\hat{\sigma}_g^2$ to $\hat{\sigma}_{ge}^2$ did not decrease after ISWYN 10 when such entries were replaced by widely adapted CIMMYT genotypes.

The subdivision of $\hat{\sigma}_{ge}^2$ attributed, on average, 9% to the common regression c , 7% to the differences among τ_k , and 2% to differences among the coefficient of regression β_i of the genotypes. On average, 18% of the $G \times E$ could be explained by regression. This portion is higher than previously reported for regional experiments (Utz, 1973; Brennan et al., 1981; Münzer, 1981), but low compared with the unexplained variation. Differences among the differentiation ability of locations, τ_k , accounted for 7 to 33% of $\hat{\sigma}_{ge}^2$ (Table 2). The common regression c was significant in all years ($P < 0.01$). This implies a significant correlation between x_i and β_i and between x_k and τ_k (Table 3). The parameters x_i and β_i are, in general, positively correlated (Lin et al., 1986). Thus, high-productivity environments tend to differentiate germplasm better than low-productivity environments and high-yielding genotypes tend to respond better to favorable growing conditions. The average correlation between x_k and τ_k was 0.69 and between x_k and r_k it was 0.50, while in most years no significant correlation was found between r_k and $(\hat{\sigma}_d^2)_k$ (Table 3). This suggests a stronger and more representative discrimination of the entries in high-productivity environments and a higher screening ability of locations in such environments for the selection of widely adapted germplasm.

To evaluate the repeatability of parameters x_k , r_k , $(\hat{\sigma}_d^2)_k$, and τ_k , correlations from one year to the next

for a common set of genotypes and environments were analyzed from ISWYNs 1 vs. 2 to ISWYNs 18 vs. 19. The correlations (not shown) were significant ($P < 0.01$) for all parameters for all 18 combinations of years (e.g., between x_k of year n and x_k of year $n + 1$). The average correlations were 0.76 for x_k , 0.75 for τ_k , 0.71 for $(\hat{\sigma}_d^2)_k$ and 0.72 for r_k . The correlations indicate repeatability over years for different parameters and screening ability of locations.

Average Correlation Values of Locations

The majority of locations with average r_k values higher than 0.60 is located in the irrigated subtropical

Table 3. Correlations between mean yield x_k , coefficient of regression τ_k , deviation from regression $(\hat{\sigma}_d^2)_k$, and r_k .

ISWYN†	Correlations between					
	x_k and		τ_k and		$(\hat{\sigma}_d^2)_k$ and	
	τ_k ‡	$(\hat{\sigma}_d^2)_k$	r_k	$(\hat{\sigma}_d^2)_k$	r_k ‡	r_k
1	0.47	0.14	0.25	0.7	0.76	-0.38*
2	0.74	0.32*	0.52**	0.35*	0.76	-0.22
3	0.66	0.26	0.47**	0.30*	0.77	-0.17
4	0.61	0.19	0.41**	0.18	0.78	-0.33*
5	0.69	0.41**	0.50**	0.43**	0.83	0.03
6	0.57	0.38**	0.41**	0.40**	0.83	0.03
7	0.67	0.27*	0.59**	0.49**	0.82	0.01
8	0.74	0.51**	0.55**	0.61**	0.81	0.13
9	0.75	0.43**	0.57**	0.28*	0.85	-0.14
10	0.70	0.31*	0.41**	0.32*	0.81	-0.19
11	0.71	0.32*	0.54**	0.28*	0.87	0.10
12	0.71	0.29*	0.52*8	0.45**	0.73	-0.13
13	0.57	0.44**	0.46**	0.56**	0.77	0.23*
14	0.84	0.64**	0.67**	0.72**	0.87	0.36**
15	0.66	0.43**	0.42**	0.53**	0.73	0.04
16	0.65	0.17	0.60**	0.35**	0.87	0.03
17	0.75	0.46**	0.46**	0.67**	0.69	0.03
18	0.86	0.39**	0.55**	0.52**	0.71	0.13
19	0.81	0.43**	0.55**	0.57**	0.78	0.19
Mean	0.69	0.36	0.50	0.43	0.79	-0.01

*** Significant at the 0.05 and 0.01 probability levels, respectively.

† ISWYN, International Spring Wheat Yield Nursery.

‡ In each year, significant at $P = 0.01$.

Table 4. Latitude, altitude, number of trials per location (*n*), mean yield, and mean, standard deviation, and range of r_k for 48 locations where the ISWYN was grown seven or more times.

Location	Lat	Altitude	<i>n</i>	Mean yield kg ha ⁻¹	r_k			
					Mean	SD	Min.	Max.
	degree	m						
Obregón, Mexico	27 N	38	17	5475	0.77	0.09	0.56	0.89
Mivhor Farm, Israel	31 N	120	13	5578	0.72	0.13	0.37	0.88
Lyallpur, Pakistan	31 N	213	18	3719	0.67	0.20	0.18	0.83
Davis, CA, USA	38 N	18	17	5139	0.67	0.21	0.09	0.89
Mesa, AZ, USA	33 N	238	8	6034	0.67	0.11	0.49	0.83
Gorgan, Iran	36 N	132	13	4136	0.66	0.13	0.30	0.82
Tandojam, Pakistan	25 N	19	11	2851	0.65	0.19	0.20	0.85
New Delhi, India	28 N	228	12	3411	0.64	0.22	0.18	0.88
Arnab, Pakistan	32 N	340	10	3413	0.62	0.18	0.24	0.80
Elvas, Portugal	39 N	208	16	3706	0.62	0.14	0.34	0.81
Salisbury, Zimbabwe	17 S	1486	13	5841	0.61	0.16	0.25	0.80
Ahwaz, Iran	31 N	20	15	3703	0.60	0.19	0.20	0.85
Sakha, Egypt	30 N	0	14	4071	0.60	0.21	0.02	0.86
Beja, Tunisia	36 N	150	11	4400	0.58	0.16	0.35	0.84
Abu Ghraib, Iraq	33 N	34	12	2853	0.57	0.15	0.36	0.87
El Bajío, Mexico	20 N	1765	13	4995	0.57	0.13	0.33	0.76
Aberdeen, ID, USA	43 N	1341	11	4366	0.55	0.15	0.27	0.76
Tibaitata, Colombia	4 N	2550	14	3081	0.52	0.12	0.24	0.66
La Platina, Chile	33 S	629	15	4273	0.52	0.12	0.30	0.75
Quetzaltenango, Guatemala	14 N	2407	12	2398	0.51	0.16	0.17	0.72
Terbol, Lebanon	34 N	950	11	2720	0.50	0.14	0.27	0.73
Adapazari, Turkey	40 N	30	12	4286	0.50	0.18	0.01	0.80
Quilamapú, Chile	36 S	144	7	3129	0.48	0.14	0.23	0.65
Saskatoon, Canada	52 N	501	13	3149	0.48	0.19	0.03	0.71
Pullman, WA, USA	46 N	762	15	3517	0.47	0.17	0.16	0.82
Deir Alla, Jordan	32 N	- 224	16	3266	0.47	0.29	- 0.16	0.86
Bozeman, MT, USA	45 N	1463	9	3901	0.47	0.24	0.14	0.78
Toluca, Mexico	19 N	2640	13	2955	0.47	0.12	0.24	0.67
Kassala, Sudan	15 N	400	12	2301	0.47	0.17	0.23	0.73
El Batán, Mexico	20 N	1765	13	3438	0.46	0.21	0.11	0.76
Tripoli, Lebanon	33 N	11	12	3104	0.44	0.20	0.11	0.82
St. Paul, MN, USA	45 N	294	10	2208	0.43	0.13	0.10	0.57
Tel Amara, Lebanon	34 N	950	11	3505	0.43	0.25	- 0.15	0.77
Carrillanca, Chile	38 N	200	7	3631	0.42	0.26	0.03	0.69
Winnipeg, Canada	50 N	235	11	3240	0.41	0.16	0.19	0.67
Cochabamba, Bolivia	17 N	2730	8	2842	0.40	0.15	0.11	0.60
Voyvodina, Yugoslavia	45 N	84	12	3223	0.39	0.24	- 0.06	0.70
Kabul, Afghanistan	34 N	1803	11	3274	0.38	0.26	- 0.12	0.72
Palmerston, New Zealand	40 S	15	10	4706	0.37	0.12	0.23	0.64
Njoro, Kenya	0 S	2165	17	1989	0.34	0.15	- 0.19	0.62
Edmonton, Canada	53 N	676	10	4497	0.34	0.12	0.08	0.50
Pergamino, Argentina	34 S	65	12	1809	0.32	0.26	- 0.19	0.81
Cambridge, England	52 N	17	10	4508	0.27	0.19	0.03	0.67
Kitami, Japan	43 N	196	12	2599	0.27	0.26	- 0.30	0.57
Quito, Ecuador	0 S	3050	15	2087	0.25	0.18	- 0.10	0.51
Svålöv, Sweden	56 N	50	10	3783	0.23	0.12	0.06	0.47
Passo Fundo, Brazil	28 S	700	7	1003	0.12	0.24	- 0.18	0.47
Palmer, AK, USA	61 N	61	12	1654	0.10	0.17	- 0.14	0.43
Mean	33	701	12	3566	0.48	0.14		

lowlands and had trial mean yields >3500 kg ha⁻¹ (Table 4). At these locations, semiarid conditions favor leaf and stem rust epidemics (but are unfavorable for stripe rust and other foliar diseases), while irrigation creates a relatively standardized and repeatable environment that permits expression of genetic yield potential. Therefore, geographically dispersed locations in northern Mexico, southern USA, the Middle East, North Africa, southern Africa, and the Indian subcontinent consistently show a high screening ability and suggest the existence of a transcontinental agroecological zone. Furthermore, resistance to leaf and stem rust are prerequisites for wide adaptation, since these diseases are important at >90% (leaf rust) and >50% (stem rust) of the spring wheat growing areas in the developing world (Hanson et al., 1982).

Locations with an average r_k between 0.40 to 0.60 and high standard deviation (e.g., Terbol, (Lebanon) or Deir Alla, (Jordan) are valuable in testing advanced

breeding material in multilocal trials. However, variations in rainfall distribution and amount, disease epiphytotic, and crop losses caused by frost may result in an ineffective selection among segregating populations at locations with unrepeatable environments.

At locations with frequent rust epidemics, high standard deviations are caused by an increase of r_k over time (years), due to improved rust resistance of the top-yielding entries. At Cautin (Chile), significant ($P < 0.01$) correlations between grain yield and stripe rust varied between -0.61 and -0.85 from ISWYNs 10 through 19. During this period, r_k increased from 0.03 (not significant) in ISWYNs 10 and 11 to r_k values between 0.51 and 0.69 after ISWYN 12 ($P < 0.01$). Similar effects of improved rust resistance in high-yielding genotypes on r_k were observed for Njoro, Kenya, El Bajío, Mexico, Quilamapú, Chile, and Quito, Ecuador. Pfeiffer and Braun (1989) reported that the resistance to stripe rust, which was initially limited to

Table 5. Geographical location, latitude, altitude and mean yield for location with maximum r_k for each International Spring Wheat Yield Nursery, r_k for Obregón, Mexico, and average r_k across all locations.

ISWYN	Location	Lat	Altitude	Mean yield	ISWYN maximum	Obregón	ISWYN mean
		degree	m	kg ha ⁻¹			
1	Delhi, India	28 N	228	3133	0.88	---	0.63
2	Obregón, Mexico	27 N	38	3411	0.85	0.85	0.56
	Adelaide, Australia	34 S	123	3275	0.85	0.85	0.56
3	Ludhiana, India	30 N	247	3261	0.80	0.76	0.55
	Syngasst, Cyprus	35 N	152	2629	0.80	0.76	0.55
4	Bet Dagan, Israel	32 N	28	4956	0.89	0.80	0.60
5	Mivhor Farm, Israel	31 N	120	4188	0.88	---	0.58
6	Davis, CA, USA	38 N	18	4863	0.90	0.87	0.61
7	Obregón, Mexico	27 N	38	7072	0.89	0.89	0.60
8	Menara, Morocco	31 N	464	5031	0.87	0.81	0.57
9	Obregón, Mexico	27 N	38	6115	0.85	0.85	0.55
10	Obregón, Mexico	27 N	38	7311	0.85	0.85	0.52
11	Obregón, Mexico	27 N	38	7193	0.83	0.83	0.47
12	Mivhor Farm, Israel	31 N	120	7400	0.80	0.63	0.48
13	Qued Mar, Algeria	35 N	43	5209	0.69	0.64	0.45
14	Jérez, Spain	36 N	21	6055	0.73	0.56	0.45
15	Bozeman, MT, USA	45 N	1463	6173	0.81	0.69	0.44
16	Mivhor Farm, Israel	31 N	120	5209	0.78	0.71	0.44
17	Córdoba, Spain	37 N	220	4770	0.79	0.70	0.44
18	Mesa, AZ, USA	33 N	238	6923	0.83	0.82	0.48
19	Obregón, Mexico	27 N	38	5228	0.80	0.80	0.45
Mean		32	182	5283	0.83	0.77	0.52

a few narrowly adapted Colombian and Bolivian cultivars in the first ISWYNs, was transferred to high-yielding and broadly adapted genotypes such as Pavon 76 and the Veery sibs by ISWYN 12. Since the yield at these locations in absence of disease is high, the differentiation, and hence r_k , became increasingly determined by the yield of genotypes with improved disease resistance.

Low average r_k values were frequently associated with consistent but specific environmental factors. Cambridge, England, Svalöv, Sweden, Edmonton and Winnipeg, Canada, and Palmer, AK, USA all lie between 50 and 61° N lat. Low r_k values at these locations resulted from differences in photoperiod responses of the genotypes. Photoperiod sensitivity, which contributes to yield potential by controlling phenology at such locations constitutes an adaptive disadvantage with associated low yields at middle and lower latitudes. Except for Edmonton, the average r_k of these locations was not significantly different from zero ($P = 0.01$). Other factors that caused low r_k values were tolerance to low temperatures (Kabul, Afghanistan), frost at anthesis (Pergamino, Argentina), acid soils with high levels of soluble Al and low availability of PO_4 (Passo Fundo, Brazil), or specific diseases such as tan spot and septoria tritici blotch.

Significant positive r_k values were obtained for 966 trials indicating that the best performing genotypes across locations performed well in a wide range of different environments. The r_k of 253 trials was not significant different from zero ($P = 0.05$). These trials, located primarily outside the subtropical wheat belt, were in North America (43 trials), tropical highlands (44 trials), South American lowlands (30 trials), northern Europe (36 trials), and central and southern Europe (22 trials). For two trials with CV > 30, significant negative r_k values were obtained.

Table 5 lists the locations with the highest r_k for

each ISWYN. Except for ISWYN 15, all locations were in the subtropical wheat belt. This geographical belt covers the majority of the spring wheat areas in the developing world. Low average r_k values for the ISWYNs occurred when the proportion of test locations outside this belt was high. High standard deviations of r_k values for locations given in Table 5 were caused by nonselective factors. Grain shattering at Davis, CA, USA, weeds at New Delhi, India, and at Ahwaz, Iran, and poor germination at Tandojam, Pakistan, resulted in r_k values < 0.20.

Screening Ability for Locations: CIMMYT Breeding Stations

CIMMYT's main breeding station at Cd. Obregón, Mexico, had the highest average r_k value, 0.77. It also had the highest screening ability of locations in 6 of the 19 ISWYNs. Ciudad Obregón (30 m above sea level, 27° N lat) is a highly productive irrigated environment in the Sonoran Desert of Northwestern Mexico. Temperatures during the growing cycle are moderate, humidity and cloudiness are low, and precipitation is insignificant. Day length increases during the crop cycle (November–May), and leaf and stem rust are the important diseases.

The CIMMYT station for alternate selection at Toluca, Mexico (2640 m above sea level, 19° N lat) is in the tropical highlands. Day length decreases in Toluca during the growing cycle (May–October). The Toluca growing environment is characterized by high rainfall, high humidity, and low night temperatures. Diseases in Toluca include leaf, stem, and stripe rusts; scab (*Fusarium* spp.); pink snow mold [*Microdochium nivale* (Ces. ex Berl. & Vogl.) Samuels & Hallet; syn. *Fusarium nivale* Ces. ex Sacc.]; septoria tritici blotch; glume blotch [*Stagonospora nodorum* (Berk.) Castellani & E.G. Germano; syn. *Septoria nodorum*

(Berk.); barley yellow dwarf; black chaff and bacterial streak [*Xanthomonas campestris* pv. *translucens* (J.J. & R.) Dye]; and a complex of root diseases (*Helminthosporium*, *Fusarium*, *Pythium*, and *Rhizoctonia* spp.).

The contrasting environments are reflected in the low phenotypic correlation between yields at Cd. Obregón and Toluca (Table 6). The correlations were not significant ($P = 0.05$) in 6 out of 12 yr. However, partial correlation between yield at Toluca and grand mean yield, with yield at Cd. Obregón kept constant, was highly significant for 5 of the 6 yr that had non-significant phenotypic correlations. Furthermore, the multiple correlation between grand mean yield and yield at Cd. Obregón and Toluca increased in nurseries released after ISWYN 12 (Table 6) compared with r_k Cd. Obregón (Table 5). This suggests that selection at Toluca does not only reinforce selection made at Cd. Obregón. The shuttle breeding between these two diverse locations allows development of photoperiod insensitive germplasm with wide adaptation, high yield potential, and resistance to a broad spectrum of diseases.

Screening Ability of Locations for Environment Subgroups

Estimates of screening ability of locations would be of little practical value to CIMMYT if the highest yielding entries across locations were not among the top-yielding entries in important wheat growing areas in developing countries. The average phenotypic correlation between mean yield across high- and low-productivity environments was 0.62 ($P < 0.01$), indicating a tendency that lines that perform well in high-productivity environments also perform well in low-productivity environments. This result was confirmed by Pfeiffer and Braun (1989), who used data from ISWYNs 1 through 15. They showed that the highest-yielding entries across all locations in 1 yr were consistently high yielding across 2 consecutive yr and were among the highest-yielding cultivars if experiments were grouped according to geographical or environmental-biological factors.

Natural Log Transformed and Coefficient of Variation Discriminated Analysis

Yield of a genotype in a high-productivity environment contributes relatively more to the mean yield across locations than its yield in low-productivity environments. If the ranking of genotypes in low-productivity environments differed greatly from that in high-productivity environments, an analysis with natural log-transformed data would lead to different conclusions. The ranking of the genotypes across all environments would be different from that using untransformed data, and consequently r_k values would change. A natural log transformation of the data did not influence the interpretation of the r_k values and did not remove heterogeneity of variances. The correlation between the r_k values obtained with untransformed and logarithmic data was always significant ($P < 0.01$) and > 0.9 . While the r_k values were little affected, the natural log transformation removed the correlation between $x_{.k}$ and τ_k and between $x_{.k}$ and $(\hat{\sigma}_g^2)_{.k}$. The ratio of $\hat{\sigma}_g^2$ to $\hat{\sigma}_{ge}^2$ to $\hat{\sigma}_e^2$ remained unchanged.

In analysis where trials with CV > 20 were excluded, neither the ANOVA nor the ranking of the genotypes was influenced and the parameters r_k , $(\hat{\sigma}_g^2)_{.k}$ and τ_k remained unchanged. Since trials with high CV values had often low mean yields caused by stresses, the loss of information due to exclusion of such trials was not compensated for by increased precision or reduced $G \times E$ interaction.

CONCLUSIONS

Irrigated, high-yielding environments in the subtropical semiarid wheat belt have the highest screening ability of locations for selection of widely adapted spring wheat cultivars. Leaf and stem rust are the most important diseases in these environments, which otherwise are generally stress-free. CIMMYT's main breeding station, Cd. Obregón, the location with the highest screening ability, is representative for these environments. Phenotypic correlations between mean grain yields in high- and low-productivity environments were significantly positive indicating correlated

Table 6. Correlations between grand mean yield (GMYLD) in the International Spring Wheat Yield Nursery (ISWYN) trials and yield at Cd. Obregón (Obr) and Toluca (Tol), two contrasting environments in Mexico.

ISWYN	Correlation between				
	Obr-GMYLD†	Tol-GMYLD†	Tol-Obr†	Tol-GMYLD.Obr‡	GMYLD-Obr-Tol§
2	0.85**	0.38**	0.14	0.50*8	0.89**
3	0.76**	0.45**	0.24	0.42**	0.81**
4	0.80**	0.35*	0.16	0.38**	0.83**
6	0.87**	0.41**	0.37**	0.20	0.87**
7	0.89**	0.67**	0.52**	0.55**	0.92**
8	0.81**	0.40**	0.41**	0.13	0.83**
12	0.63**	0.24	0.10	0.22	0.65**
13	0.64**	0.44**	0.23	0.39**	0.71**
14	0.56**	0.62**	0.33*	0.56**	0.73**
15	0.69**	0.42**	0.35**	0.27	0.72**
17	0.70**	0.57**	0.21	0.60**	0.82**
19	0.80**	0.60**	0.36**	0.55**	0.86**
Mean	0.75	0.46	0.29	0.40	0.80

*** Significant at the 0.05 and 0.01 probability levels, respectively.

† Phenotypic correlation.

‡ Partial correlation, with yield at Cd. Obregón held constant.

§ Multiple correlation.

response to selection. The high average coefficient of variation and low heritabilities for trials in low-yielding environments that are free of biotic stresses suggest optimizing agronomic practices and improved experimental design to decrease the error variance and consequently to increase selection efficiencies. Selection of early-generation material may be more efficient in high-yielding, predictable environments. In low-yielding environments, unpredictable variation in rainfall, disease epiphytotics, or losses from frost may result in inefficient selections in segregating populations. If stresses are caused by biotic factors, or predictable abiotic factors, germplasm could be alternately selected in a high-yielding and the respective stress environment. Requirements for photoperiod sensitivity, cold tolerance, late maturity, tolerance to acid soils, and resistance to foliar diseases were suggested as the main location-specific factors limiting broad adaptation. A large $G \times E$ interaction suggests subdivision of locations into homogeneous groups to capitalize on specific $G \times E$ interactions. Locations with the highest screening ability within subgroups and underlying biotic and abiotic factors could be identified for trait-oriented selection to improve both broad and specific adaptation.

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