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The effect of the accumulation of disease resistance genes on the long-term association of a global sample of environments for testing spring bread wheat

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Abstract CIMMYT (the International Maize and Wheat Improvement Center) has routinely conducted international wheat yield trials to study the adaptation of spring bread wheat. The first of these, the International Spring Wheat Yield Nursery (ISWYN), was conducted for 31 years from 1964 to 1994 inclusive (30 cycles were conducted as no nursery was distributed in 1993 because of Karnal Bunt). Recently, pattern analysis methods have been developed and a set of computer programs written, which enable retrospective analyses of such historical databases to appraise the relationships among test environments in a way that discriminates among genotypes. Such an analysis was conducted on the 30 years of yield data from ISWYN and the classification derived from these analyses was compared with an agroecological classification of spring wheat test environments derived by CIMMYT. The incidence of foliar diseases (stem rust, leaf rust, yellow rust, *Septoria spp.* and *Fusarium spp.*) was important in the distinction between the high-rainfall low-latitude (mega-environment 2) and the high-input-irrigated low-latitude (mega-environment 1) environment types. The accumulation of resistance genes for these diseases has been an objective of the CIMMYT wheat breeding program. It was hypothesized that, as the relevant resistance genes were successfully pyramided into the germplasm, the distinction between these two mega-environment types would disappear. The results of the retrospective analyses support this hypothesis.

Keywords CIMMYT · ISWYN · Mega-environments · Retrospective analysis · Pattern analysis

Introduction

Information on genotype×environment (G×E) interactions for yield obtained from multi-environment trials (METs) grown over diverse environments can be studied using pattern analyses (Byth et al. 1976; DeLacy et al. 1996a, c) to identify genotypes with similar responses across environments and those environments which produce similar discriminations among the genotypes grown in them. Pattern analysis involves the joint use of classification (clustering) and ordination (low dimensional representation) techniques to study pattern in any data set (Williams 1976). These two methods are employed in a complementary way to highlight patterns in the data. The clustering approach is used to summarize the data by either enabling genotype responses to be described by relatively few genotype groups, or environment discrimination by relatively few environmental groups, or else a combination of both (Mungomery et al. 1974). Ordination summarizes the data by representing differences and similarities in genotype response and environment discrimination in a small number of dimensions (Williams 1976; Kempton 1984) and the use of the biplot as a graphical display (Gabriel 1971; Kempton 1984).

Retrospective analysis

Pattern analysis methods have been extended for the analysis of historical data accumulated by plant breeding METs conducted over many years (DeLacy and Lawrence 1988; Lawrence and DeLacy 1988; Peterson and Pfeiffer 1989). These methods handle the imbalance which occurs in METs because of a change of entries over time and the differing locations (environments) used in years, by averaging over years the appropriate proximity matrix from each year. The theoretical basis of

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these *retrospective analyses* has been recently reported (Cooper and DeLacy 1994; DeLacy et al. 1996b) and a number of applications have appeared (Peterson 1992; Lawrence and DeLacy 1993; DeLacy et al. 1994; Ouyang et al. 1995; Abdulla et al. 1996; DeLacy et al. 1996d). These studies, termed cumulative analyses, show that, as data from more years are included in the analysis, the emphasis of the study changes from the response patterns of entries to the relationships among the environments in the way they discriminate among the entries grown in them and the impact of these relationships on genetic gain in the target population of environments (DeLacy et al. 1996d).

Mirzawan et al. (1994) reported two variations of these retrospective analyses. In the first, the relative relationships among environments is built up over time by adding data from each year's MET one at a time to the analysis and the full sequence is then interpreted. When each year in the sequence is interpreted the procedure is referred to as a sequential analysis, as distinct from a cumulative analysis where only the final relationship is reported. Cumulative analysis produces long-term average relationships among the environments in the way in which they discriminate among the genotypes grown in them. Should a stable configuration be produced, the relationship among the current year's environments can be compared to their long-term discrimination. This method, termed a status analysis, is the second variation reported by Mirzawan et al. (1994). The status analysis allows an assessment to be made on the current discrimination provided by an environment compared to its long-term performance. Mirzawan et al. (1994), using their sugarcane data, were able to demonstrate that a stable discrimination space did occur and that the ordination of current data, when superimposed on the long-term relationship, gave useful information on the discrimination provided in the current year.

The proximity coefficients used to assess the similarity among environments, either the average correlation (a similarity) or the environment standardized squared Euclidian distance (a dissimilarity) matrices, measure the relationship among environments in the way they discriminate among genotypes (DeLacy et al. 1996b). Hence, they called the Cartesian space into which the environments are mapped by the ordination, a discrimination space. Provided the Gower complement is used, the classification measures relationships in the same space. Pattern analysis is most powerful when the Gower (1966, 1967) complementary similarity and dissimilarity measures are used to conduct the ordination and cluster analyses, respectively (DeLacy et al. 1996a).

The International Spring Wheat Yield Nursery (ISWYN)

CIMMYT (the International Maize and Wheat Improvement Center), has routinely conducted international wheat yield trials to study the adaptation of spring bread wheat. In 1960 the Office of Special Studies (the precursor

organisation of CIMMYT), sponsored by the Mexican Government and the Rockefeller Foundation, initiated yield trials for spring wheat (*Triticum aestivum* L.) throughout the Americas. Some entries showed wide adaptation while others, particularly those from latitudes higher than 40°, were poorly adapted outside their areas of origin (CIMMYT 1968, 1979). A parallel series of trials was conducted by the same organisation in cooperation with the Food and Agriculture Organisation (FAO) throughout the Near East. These earliest international wheat nurseries were assembled with the help of trainees who had sent seed of the main wheat cultivars in their countries to Mexico (Rajaram and Hettel 1995). The results were similar and some entries, such as Pitic 62 from Mexico, yielded well in both trial series. The two series of trials were merged and expanded into ISWYN in order to study adaptation wherever spring wheat is grown (CIMMYT 1968). ISWYN-1 was distributed in 1964 and the report was published in 1968. CIMMYT has terminated the series and the last ISWYN, number 30, was distributed in 1994. The ISWYNs were distributed on request to participating countries and the results provide an important database for the study of 30 years of the international breeding of spring wheats.

Entries in ISWYN

The entries in ISWYNs were chosen by the CIMMYT breeders from their lines and nominations from different parts of the world (DeLacy et al. 1996c). The entries in ISWYN-1 and -2 were selected to represent the principal types of spring wheats in the world. From ISWYN-3 onwards some entries were also chosen from submissions for some outstanding trait in specific regions. Breeders sent seed of nominated material to CIMMYT. Prior to final nomination for inclusion in ISWYN the lines were grown at the CIANO experiment station in the Yaqui Valley in north-west Mexico, where they were subjected to considerable pressure from rusts [both stem (*Puccinia graminis* Pers. f.sp. *tritici*) and leaf (*Puccinia recondita* Rob. Ex Desm. f.sp. *tritici*) rusts]. In consequence, all entries included in the ISWYNs needed to perform adequately (show little day length, vernalisation or rust sensitivity) in the Yaqui Valley, Sonora. Selection was based on the above suitability and for as wide a range of country representation as possible. Long-term checks were included and most lines under test for some years were deleted to make room for new entries. There were 25 lines grown in ISWYN-1 and -2, 49 lines and a local check grown in all subsequent ISWYNs, except ISWYN-24 which had 39 lines and a local check. There were 605 lines tested in the 30 ISWYNs.

Locations (environments) in the ISWYNs

The CIMMYT international nurseries are distributed, at request, to cooperators in the National Agricultural Re-

Table 1 Characteristics of spring mega-environments^a as defined by the CIMMYT wheat program

ME	Latitude ^b	Moisture regime ^c	Temperature regime ^d	Habit	When sown ^e	Major breeding objectives ^f	Representative location ^g	Production 1984–1986 ^h
1 ⁱ	Low	Irrigated low rainfall	Temperate	Spring	A	Yield potential, resistance to lodging, SR, LR, YR	IND New Delhi	83
2	Low	High rainfall	Temperate	Spring	A	As ME1+resistance to, <i>Septoria</i> spp., <i>Fusarium</i> spp., sprouting	CHN Nanjing	25
3	Low	High rainfall	Temperate	Spring	A	As ME2+acid soil tolerance	BRA Passo Fundo	3
4A	Low	Low rainfall winter dominant	Temperate	Spring	A	Resistance to drought, common bunt	MAR Settat	10
4B	Low	Low rainfall summer dominant	Temperate	Spring	A	Resistance to drought, <i>Septoria</i> spp., <i>Fusarium</i> spp., LR, SR	ARG Marcos Juarez	4
4C	Low	Mostly residual moisture	Hot	Spring	A	Resistance to drought, heat	IND Dharwar	6
5A	Low	High rainfall, humid	Hot	Spring	A	Resistance to heat, <i>Helminthosporium</i> spp., sprouting	PAR Encarnacion	9
5B	Low	Irrigated, Low rainfall	Hot	Spring	A	Resistance to heat	SUD Wad Medani	3
6	High	Moderate rainfall summer dominant	Temperate	Spring	S	Resistance to YR, LR, <i>Fusarium</i> spp., <i>Helminthosporium</i> ssp., sprout	CHN Harbin	13

^a Source: adapted from Byerlee and Moya (1993), DeLacy et al. (1994) and Rajaram et al. (1994)

^b Low=<about 35–40°

^c Rainfall refers to just before and during the crop cycle. High=>500 mm; low=<500 mm

^d Hot=mean temperature of the coolest month >17.5°C; cold=<5.0°C

^e A=autumn, S=spring

^f Factors additional to yield and industrial quality. SR=stem rust, LR=leaf rust, YR=stripe (yellow) rust

^h Bread and durum wheat, million of tons per year in developing countries

ⁱ Further subdivided into (1) optimum growing conditions, (2) presence of Karnal bunt (*Tilletia indica* Mit.), (3) late planted, and (4) problems of salinity

search Centres (NARS) who grow the trials and record the data. These data are returned to CIMMYT for analysis and a report on each nursery is then compiled. In consequence CIMMYT has compiled information on each of the 964 locations for which data have been returned from all nurseries over the period of this study (1964 to 1994). Strictly, this is 964 environments because some cooperators sow more than one trial at a location. For example, the CIMMYT bread wheat breeding program routinely sows a late trial in addition to their normal trial at Obregon in the Yaqui valley. Other cooperators sow a rainfed and an irrigated trial, while still others sow a high fertility trial. In consequence, since these are distinguished in the records, there are a number of different 'trials' at some locations in some years.

For the 30 ISWYNs, 407 of the above 964 environments have had data reported. It was decided that the retrospective analysis conducted for this study would include only those environments for which data were returned from three or more ISWYNs. Hence 193 environments, mostly distinct locations, were included in the final analysis.

Mega-environment classification

CIMMYT orientates breeding on the concept of mega-environments (MEs) (CIMMYT 1989), defined as broad

(not necessarily contiguous and frequently transcontinental) areas, characterized by similar biotic and abiotic stresses, cropping-system requirements and consumer preferences (Byerlee and Moya 1993; DeLacy et al. 1994; Rajaram and van Ginkel 1994; Rajaram et al. 1995). Germplasm may accommodate major stresses throughout the ME for which it was developed, but perhaps not for all significant secondary stresses. The ME classification, which depends on climatic factors and a knowledge of stresses at locations, has been continually refined and six (Table 1) were considered relevant for spring wheat at the time of this study. The CIMMYT breeders continually refine these definitions, and ME4 and ME5 are subdivided.

The 193 environments used in this study were assigned by one of us (Dr. S. Rajaram) to MEs independently of the statistical analysis. Because ISWYNs grown in a winter wheat environments were sown in spring, the environments concerned were assigned to spring MEs.

Aim

Following the documentation that genotype by environment interaction was significant for grain yield [the ratio of genotypic variance to genotype by environment interaction variance averaged 0.34 for the first 19 IWSYNs

(Bruan et al. 1992)) DeLacy et al. (1994) investigated the relationship among the environments used in the first 26 ISWYNs in the way in which they discriminated among the entries in the trials. DeLacy et al. (1994) found that the major division arising from a cumulative analysis of the environments used in ISWYNs1–26 was between those in ME1 (Gp1) and those in ME2 and ME6 (Gp2). The mean yield of environments in Gp1 exceeded those in Gp2 for ISWYNs1–14, but was less for ISWYN-20 and on. They hypothesized that environments in Gp2 had a higher yield potential than those in Gp1 but that this was not realized until resistance to major pathogens was addressed after major yield gains had been made in ME1. The CIMMYT wheat program has been pyramiding into their germplasm disease resistance genes for the major diseases of ME2. It was hypothesized that as the diverse resistance genes were accumulated in the germplasm the difference between the ME1 and ME2 environments in their discrimination among germplasm present in the earlier ISWYNs, i.e. the difference in the grouping of ME1 and ME2, should disappear over time. This hypothesis is investigated in this paper.

Materials and methods

Identification of important changes in the germplasm tested in the ISWYNs

Successful crosses, those from which important cultivars were selected, have a line or many sister lines tested in the ISWYNs (Table 2). Using this criterion, Veery has been the most successful, with 14 sister lines having been tested a total of 58 times since ISWYN-15. Other important crosses are II19975 with five sibs tested 33 times, Pavon (6 and 26), Inia (5 and 23), Bluebird (8 and 21) and Bluejay (5 and 20). An important later cross is Kauz with five sibs tested 12 times in the last seven ISWYNs. Both Siete Cerros and Anza, important early semi-dwarf lines, were used as check lines for most of the ISWYNs and this accounts for the large number of times they were tested. The number of different sister lines recorded as cultivars confirm that the cross Veery with six recorded cultivars was a successful cross (Table 2). Other crosses with three or more cultivars recorded were Bluebird with five, II19008 and II19975 with four each, and II8156, Pitic, Papaju, Bluejay and Bobwhite with three each.

Using this information and the knowledge of the wheat breeders at CIMMYT, five parallel sequences (Fig. 1) were identified as representing the major phases of improvement in spring wheat germplasm in the ISWYNs. The first change occurred with the arrival of the Bluebirds in ISWYN-7 and the II19975 sibs in ISWYN-8. As the Bluebirds were more successful as parents for later crosses, and the last of the non-semidwarfs had disappeared by ISWYN-7, the second sequence was begun with ISWYN-7. A third change was marked by the entry of the Pavons (26 tests) and the Bluejays (20 tests) in ISWYN-12, and a fourth with the Veerys in ISWYN-15. This last sequence is marked with by entry of the Kauz lines in ISWYN-24. A cumulative analysis was conducted on each of these five sequences using the SEQRET computer package (DeLacy et al. 1998) which was written to implement the retrospective analyses developed by DeLacy et al. (1996b).

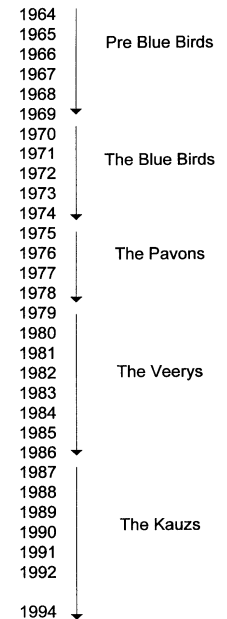
Analytical methods

The cumulative analysis was achieved by using the computer package SEQRET (DeLacy et al. 1998). The principles underlying the method used for the cumulative pattern analyses are given in

Table 2 Crosses for which sibs were tested ten or more times in the 30 ISWYNs

Cross	ISWYN in which the first sib was entered	Number of times a sib was tested	Number of sibs tested	Number of cultivars recorded
II8156 (Siete Cerros)	1	30	3	3
Pitic	1	16	3	3
Penjamo	1	10	1	1
Bajío	2	18	6	1
II19008 (Inia)	3	23	5	4
Anza	5	21	1	1
Giza 155	5	10	1	1
Sonalika	6	15	1	1
Bluebird	7	21	8	5
II19975 (Soltane)	8	33	5	4
Papaju	10	10	3	3
Pavon	12	26	6	1
Bluejay	12	20	5	3
Opata	14	11	1	1
Veery	15	58	14	6
Buckbuck	16	11	3	2
Banks	16	10	1	1
QT4083	16	10	1	1
Bobwhite	18	12	7	3
Junco	22	10	3	2
Kauz	24	12	5	1

Fig. 1 Five sequences of germplasm identified by marked changes in the crosses from which the lines tested in the ISWYNs were derived. There was no ISWYN distributed in 1993 as the seed may have been contaminated with Karnal Bunt (*Tilletia indica* Mit.) spores



DeLacy et al. (1996e). The cumulative pattern analyses were achieved by employing the weighted environment-standardized squared Euclidean distance (esSED) for the proximity matrices, the incremental sum of squares (ISS) for the classification strategy, and the principal coordinate analysis (PCO) by extracting eigenvalues and eigenvectors by spectral decomposition from the Gower complement similarity measures. Empty cells were eliminated by deleting the rows and columns in the proximity matrices associated with environments with the fewest comparisons (Method 2 of DeLacy et al. 1996e). Each vector from the cumulative PCOs was evaluated by estimating the percentage the corresponding eigenvalue was of the trace. The algorithm in SEQRET calculates the trace as the sum of the eigenvalues and stops when the

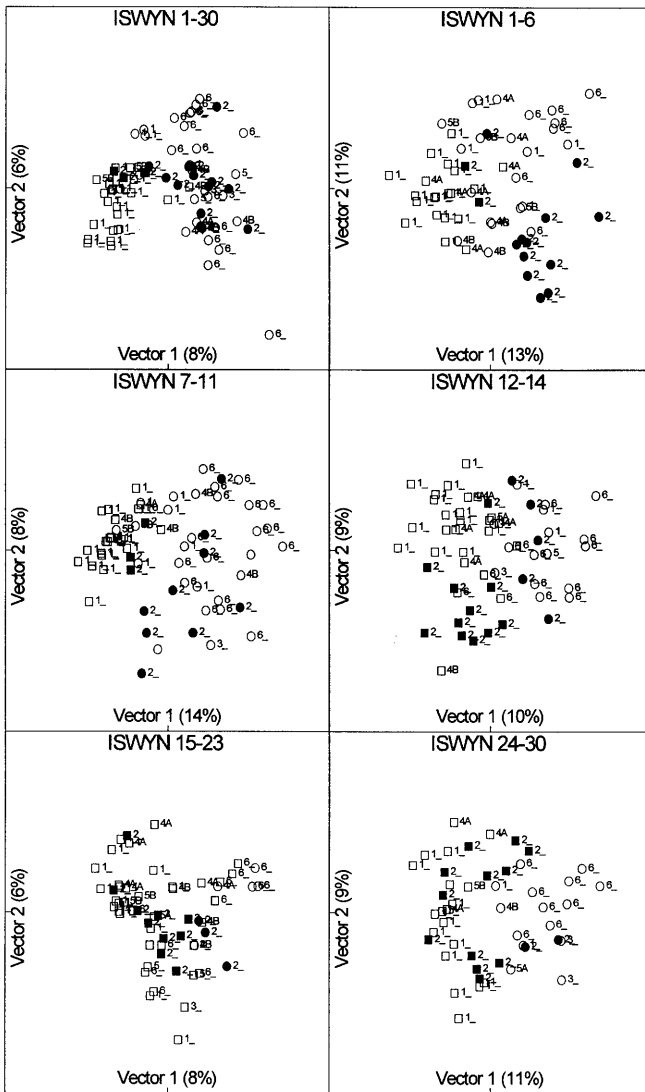


Fig. 2a-f Discrimination plots of the first two vectors from the principal coordinate analysis of the environments in the cumulative sequences (a) ISWYN1–30, and (b–f) the five sequences of germplasm identified by important changes in CIMMYT germplasm (see Fig. 1). The classification at the two-group level is indicated on the plot of each sequence with group A, predominately ME1, represented by the solid symbol and group B, predominately ME6, represented by the open symbol. ME2 environments are indicated by the solid symbols. The name of the sequence is on the top of each figure and the percentage of the total sum of squares explained by each vector is indicated in parentheses in the vector captions

next eigenvalue is less than 1% of this sum. This was interpreted as the percentage of the total sum of squares (TSS) (estimated by the trace) accounted for by the eigenvector. This TSS refers to variation in the standardised discrimination space. An overall evaluation of the cumulative classification was obtained by the percentages of TSS explained by the grouping model. One hundred and ninety three environments, mostly individual locations, were included in the analyses (see above).

Table 3 Percentage of the total sum of squares explained by the model at the two-group level in the hierarchy for the cumulative classifications of the five sequence identified in the ISWYNs

ISWYN sequence	No. of environments		Percentage of total sum of squares explained (R^2) by model at the two-group level	
	Retained ^a	Total ^b	R^2	Range ^c
1–6	57	90	37	33–42
7–11	64	109	30	27–35
12–14	58	108	26	25–27
15–23	58	140	26	21–35
24–30	48	97	29	23–34

^a Retained: refers to the environments retained in the pattern analysis after elimination of those with empty cells in the cumulated matrix of proximity measures

^b Total: total number of environments in each analysis

^c Range of R^2 values for each year in the cumulative classifications

Results and discussion

Cumulative pattern analysis of the 30 ISWYNs

In a previous paper, DeLacy et al. (1994) found that the major division arising from a cumulative analysis of the environments used in ISWYNs1–26 was between those classified as ME1 and those classified as ME2 and ME6. The cumulative pattern analysis of the environments used in ISWYNs1–30 confirmed this separation. Of the 69 environments retained in the analysis, 19 of the 21 ME1 environments were in one group (GpA), while 14 of 17 ME2 and all of the 15 ME6 environments were in the other group (GpB). The discrimination plot, with the results of the classification of the environments used in ISWYNs1–30 superimposed (Fig. 2) from the cumulative PCOs, confirms this separation.

Evaluation of the cumulative pattern analyses

For the two-group level the percentage of the TSS explained varied from a high of 37% for the sequence ISWYNs1–6 to a low of 26% for the sequences ISWYNs12–14 and ISWYNs15–23 (Table 3). There was no relationship between the number of ISWYNs in a sequence and the percentage of TSS accounted for: the correlations at the two-group level were not significant. The range in the percentage SS associated with each year (ISWYN) varied over a reasonably narrow range (Table 3). For instance for the ISWYNs1–6 sequences they varied from 33 to 42%. These figures are high considering that the variation among nearly 77000-means in the complete data set needed to be explained. The variation explained by the first two vectors was lower than that accounted for by the classifications. This varied from 8 to 14% for vector 1, from 6 to 11% for vector 2, and from

Table 4 The number of environments, the mega-environment composition and the mean yield of the two groups at the first split of the hierarchy for the classification of each of five sequences of

the locations identified in the 30 ISWYNs. GpC and GpD are the two groups which split from GpA in the ISWYN15–23 sequence

ISWYN sequence		ME1	ME2	ME3	ME4	ME5	ME6	NC ^a	Total ^b	Mean ^c t/ha
1–6	GpA ^d	16	2		0	0	0		22	3.32
	GpB	6	12		6	3	7		35	2.56
7–11	GpA	18	3	0	3	0	1		25	4.28
	GpB	6	9	1	2	2	17	2	37	3.25
12–14	GpA	15	11	0	6	1	4		37	3.95
	GpB	1	5	1	0	1	10		21	3.32
15–23	GpA	15	11	1	7	5	9	1	49	4.03
	GpC ^e	8	2	0	4	0	0	0	14	
	GpD	7	9	1	3	5	9	1	35	
	GpB	1	3	0	2	0	4		9	3.27
24–30	GpA	13	12	0	3	2	0	1	31	4.63
	GpB	1	2	2	1	1	9		17	3.52

^a NC=environments not classified into mega-environment groups

^b Total number of environments in each group in the analysis

^c Mean yield of all environments in the group over all years in the cumulative sequence

^d GpA the group predominantly ME1, and GpB predominantly ME6

^e GpC and GpD are the two groups formed by the split of GpA in the sequence 15–23

14 to 24% for both together (Fig. 2). These results suggest that conflicts between the interpretations for classification and ordination should be resolved in favour of the classification.

A comparison of the pattern analysis (PA) and mega-environment (ME) classifications of the ISWYN environments

The relationship between the cumulative PA and the ME1, ME2 and ME6 environments

There was a clear and consistent difference between those environments classified as ME1 and ME6 in that they grouped separately in the first split in the hierarchy (Table 4, Fig. 2). This difference is consistent over all ISWYNs and was evident in four of the five cumulative analyses. The exception is the ISWYNs15–23 sequence where the split of ME6 environments was distributed to nine in GpA and four in GpB. However, in the split of GpA into two groups, GpC contains no ME6 environments and GpD all the nine that were originally in GpA. GpC also contains 9 of the 11 ME2 environments from GpA. The 15 ME1 environments from GpA were distributed to eight into GpC (no ME6 environments) and seven into GpD with a majority of the ME2 and all of the ME6 environments. Hence, the grouping in ISWYNs15–23 is consistent with the separation of the ME1 and ME6 environments. There is an equally clear and consistent trend in that the ME2 environments, which, while originally grouped in GpB with the ME6 environments, have been increasingly grouped in GpA with the ME1 environments as the sequences change from earlier to later ISWYNs. In the first sequence 12 out of 14 ME2

environments grouped in GpB with the ME6 environments (Table 4). In contrast, in the last sequence 12 out of 14 grouped with the ME1 environments in GpA.

In ISWYN-1 there was a substantial difference between ME1 and ME2 with 12 of the 13 ME1 environments in GpA, and five of the seven ME2 environments in GpB grouped, with the single ME6 environment. A comparison of the results from the analysis of the individual ISWYNs (data not shown) indicates that the association among environments for their discrimination among genotypes is variable in any one ISWYN (year), even when there are from 60 to 80 environments (as there are in the IWSYNs). For a similar number of environments, however, the relationship would be expected to be more stable in a more-uniform target population of environments than the world spring wheat regions considered here.

The relationship between the retrospective PA and the ME3, ME4 and ME5 groups

No consistent grouping of ME4 environments was observed in these analyses. Both ME4A and ME4B (Fig. 2) environments grouped separately across all groups and there was no recognized tendency for any of these environments to group together. There was a strong tendency (Fig. 2) for the ME5B environments to group with the ME1 (GpB) environment and for ME5 A to group with GpB. The association of ME5B environments with GpB occurs despite their low yield (Table 5). The ME3 environments always grouped in GpB. CIMMYT always recommended that the areas grown for the ISWYNs be limed when the soil was acid. If this practice was fol-

Table 5 Mean grain yield of all environments in each mega-environment classification for the 30 ISWYNs

ISWYN	Mega-environment											Mean
	NC ^a	1	2	3	4A	4B	4	5A	5B	5	6	
1		3.00	2.39		2.58	2.87			1.87		1.96	2.44
2		3.17	2.55		3.01	2.14			1.17	0.53	2.39	2.14
3		3.31	2.60		2.81	0.63			1.35		2.70	2.23
4		3.53	2.75		3.18	0.92			1.94		2.88	2.53
5		3.42	2.23	1.24	2.44	1.77			2.71		2.40	2.31
6	1.62	3.56	2.93		2.00	2.29			2.26		2.67	2.48
7	2.54	3.95	3.61		4.19	2.75			2.68		3.59	3.33
8	2.44	4.33	3.00	0.70	3.75	3.72			3.38		3.05	3.05
9	5.56	4.33	3.45	1.18	4.55	2.27	3.81		2.94		3.93	3.56
10	4.06	4.45	2.89	1.45	3.39	2.69	1.02		2.46		3.44	2.87
11	2.58	4.69	3.46	0.35	5.80	2.99			2.50	2.82	3.37	3.17
12		4.70	3.26	0.81	3.70	3.09				2.49	4.07	3.16
13	3.20	4.02	3.53		2.97	1.68		0.92	2.70	1.47	3.40	2.66
14	2.33	4.25	3.74	1.24	2.63	3.82		1.50	2.61	1.93	3.05	2.71
15		4.04	3.74		2.99	2.50	0.84	1.08	1.58	4.62	3.91	2.81
16	2.62	4.11	3.45	0.47	4.05			2.77	2.53	3.02	3.40	2.94
17		4.41	3.37		3.45			1.65		3.07	3.84	3.30
18	1.64	4.22	4.14	0.51	3.26	2.66		1.27	2.15	3.27	3.90	2.70
19	1.89	5.21	3.41	1.87	2.96	2.83		2.53	2.33	1.62	4.00	2.86
20	1.86	4.40	3.73	1.42	4.39	3.45			0.79	2.40	5.29	3.08
21		3.98	3.87	0.90	2.47	2.52		0.85	3.30	2.95	3.09	2.66
22	2.00	4.41	4.40	1.11	2.50	2.94	0.78		2.11	1.74	3.98	2.60
23		4.40	4.59		4.63	3.56	3.65	1.67	0.81	2.73	3.06	3.23
24		3.90	3.68	2.60	4.19	2.99		1.88	1.46	3.63	2.68	3.00
25		4.30	3.64	2.15	3.08	4.11		1.43		2.66	3.87	3.15
26		4.36	4.36	1.78	3.13	4.10				3.35	3.55	3.52
27	6.26	4.01	4.76	1.38	4.23	5.47		1.03	0.98		4.77	3.65
28	8.97	4.34	4.89		3.16	4.44		1.50	3.09	2.88	4.13	4.15
29	3.08	6.15	4.45		2.58	3.99			3.08		5.58	4.13
30		5.43	2.93		1.51	3.99					3.30	3.43
Mean	3.29	4.21	3.53	1.25	3.32	2.97	2.02	1.54	2.19	2.62	3.51	3.00

^a NC, mega-environment status unknown

lowed and was successful in raising the pH, it is to be expected that the ME3 environments in which the ISWYNs were grown would be converted to ME2-type environments. It would also be expected, if the liming was successful, that yields would be increased; however, the yields of reported ME3 environments were lower than those for ME2 (Table 5).

Environment yields in the ISWYNs

Mean yield of the MEs in the ISWYNs

Those environments classified as ME1 out-yielded those classified as ME2 consistently, until ISWYN.20 when ME2 yields were equal or higher except for the last two ISWYNs (Table 5). The ME1 environments report an exceptionally high yield in ISWYN-29; 0.72 t ha⁻¹ higher than the next highest, ISWYN-30. The ME2 environments reported a good yield in ISWYN-29 and a low yield in ISWYN-30. There was a major change in entries in ISWYN-28 and these remained substantially the same for ISWYN-29 (DeLacy et al. 1996b). There was a further major change for ISWYN-30, only seven lines having been grown in previous ISWYNs. DeLacy et al.

(1994) inferred that the yields of the ME2 environments had increased to match the yields in ME1 environments for the yields of the GpA and GpB environments from the cumulative classification of the ISWYN1–26 sequence. This is confirmed, with the exception of the last two ISWYNs, with the yield of the environments from the ME classification.

ME4 A environments had lower yields on average (3.32 t ha⁻¹) than ME1 (4.21 t ha⁻¹) and slightly lower than ME2 (3.53 t ha⁻¹) (Table 5). However, these yields are higher than expected and eight ISWYNs reported yields over 4 t ha⁻¹ for environments classified as ME4A; ISWYN11 reported an average of 5.8 t ha⁻¹ for three (Table 5) ME4 A environments. The variation of reported yields was higher than the ME1 and ME2 averages but there were fewer environments reporting.

The one or two (Table 5) ME5 A environments which reported each year averaged 1.54 t ha⁻¹ while the ME5B environments averaged 2.19 t ha⁻¹ from one, two or three reporting environments. The ME6 environments averaged the same as the ME2 environments. Even though it was recommended that the environments classified as ME3 be limed for the ISWYNs, the yields were low at 1.25 t ha⁻¹.

Table 6 Number of ISWYNs in which the two groups from the cumulative classification of each of the five sequences had the highest mean yield and the number of environments in each group that was classified as ME2

Sequence	1–6		7–11		12–14		15–23		24–30	
	Highest yield ^a	ME2 membership ^b	Highest yield	ME2 membership	Highest yield	ME2 membership	Highest yield	ME2 membership	Highest yield	ME2 membership
Group A ^c	6	0	5	3	3	11	8	11	7	12
Group B	0	12	0	9	0	5	9	3	0	2

^a Number of ISWYNs where members of groups A or B had the highest mean yield

^b Number of environments classified as ME2 in groups A or B

^c Group A is predominantly ME1 and Group B is predominantly ME6

Mean yield of the retrospective PA groups

GpA environments consistently out-yielded the GpB environments (Table 6). This occurred despite the transfer of many ME2 environments from GpB to GpA, further confirming the increase in yield of ME2 environments.

Conclusions

This retrospective analysis of the ISWYN nursery used a different method of organising the data than the two methods developed by Mirzawan et al. (1994) and described previously as sequential and status analysis. Here a series of five sequences were identified by significant changes in the germplasm and a cumulative analysis was conducted on each. This proved to be a successful method for coordinating the analysis and an understanding of this large data set

The percentage of the TSS explained by the groupings at the two-group level of the classification was relatively high, both in terms of the adequacy of the model and in comparison to the PCO. In the latter the first two vectors accounted for from 14 to 24%, which was relatively low. Nevertheless the discrimination plots reinforced the information and interpretations from the classification, and provided significant and useful extra information. Since the classification explained more of the information, it is recommended that conflicts of interpretation be resolved in favour of the classification.

The analyses provided support for the hypothesis that, as the CIMMYT wheat breeding program successfully pyramided relevant disease resistance genes into their germplasm, the difference in discrimination provided by the ME2 and ME1 environments would disappear over time. It has been a stated objective of the CIMMYT bread wheat breeding program (Rajaram et al. 1995) to accumulate resistance to a wide spectrum of diseases, many of which are important in ME2 environments. DeLacy et al. (1994) argued that the ME2 environments had as high a yield potential as the ME1 environments but that this could not be expressed until the disease problems in the ME2 environments had been addressed. There has been a major shift over the period of the

ISWYNs with an increasing proportion, a shift from a small minority to a large majority, of ME2 environments grouping with ME1 environments.

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