Yield and adaptation of hexaploid spring triticale*

P.N. Fox,[1] B. Skovmand,[1] B.K. Thompson,[2] H.-J. Braun[3] and R. Cormier[1]
[1] CIMMYT, Apdo. Postal 6-641, 06600 México D.F., México; [2] Engineering and Statistical Research Centre, Research Program Service, Agriculture Canada, Ottawa, Ontario K1A 0C6, Canada; [3] CIMMYT, P.K. 39, Emek, Ankara, Turkey

Summary

Gains in yield and stability were analysed using grain yield data from the 8th to the 14th International Triticale Yield Nursery (ITYN) and differences in adaptation between complete and substituted triticales (X *Triticosecale* Wittmack) were examined. A trend of improving yield and adaptation was observed. As highly significant genotype × site interaction each year was not adequately described using regression analysis, yield stability was examined by ranking genotypes within sites and summarizing scores for individual genotypes across sites. Cluster analysis was used to study the relationships among sites and among genotypes. There was little evidence of sites grouping on a geographical basis. Grouping of genotypes showed a tendency for complete and substituted triticales to perform differently, suggesting that diversity for adaptation is maximized by utilizing both types in breeding.

Progress for grain yield is compared with more spectacular gains in test weight and reasons for the different rates of improvement are postulated.

Abbreviations: CIMMYT – International Maize & Wheat Improvement Centre; ITYN – International Triticale Yield Nursery

Introduction

Two distinct types of hexaploid triticale (X *Triticosecale* Wittmack) have been grown commercially in recent years (Skovmand et al., 1984). These are complete triticales, which have all seven pairs of chromosomes from rye (*S. cereale* L.), and substituted triticales, having rye chromosomes replaced with D-genome chromosomes from hexaploid wheat (*T. aestivum* L.). One substitution involves the replacement of chromosome 2R of rye

by 2D from wheat and probably arose from a natural outcross between hexaploid triticale and hexaploid wheat (Gustafson & Zillinsky, 1973). Other wheat-rye substitutions appear to be discarded during selection and have not been identified in commercial or advanced lines (Lukaszewski, 1988).

Lukaszewski & Gustafson (1984) suggested that the 2D(2R) substitution in spring triticale was established and spread rapidly because it introduced a potent gene for daylength insensitivity located on Chromosome 2D from hexaploid wheat. Zillinsky

(1980) stated that the substitution was also associated with reduced spike length, shorter plumper kernels, decreased plant height, erect spike morphology and an increase in number of kernels per spikelet. Skovmand et al. (1985) examined 272 genotypes from the 14th International Triticale Screening Nursery (ITSN) and found that completes tended to have higher falling number, flour yield and grain hardness than substituted triticales. As a group, substituted genotypes had higher flour protein percentage, gluten content and loaf volume. Completes showed more variation for falling number and flour protein and gluten content, while greater variation for loaf volume and grain hardness was found in substituted germplasm. Some propose that the 2D(2R) substitution occurred at the expense of tolerance to drought stress. Varughese et al. (1986) suggested triticales with this chromosome substitution show a slight disadvantage in dryland conditions with below 400 mm rainfall and generally have narrower adaptation than genotypes with the complete rye genome. Osmanzai et al. (1984) studied six complete and six substituted triticales in Sonora, Mexico, reporting superiority of completes in regimes of both restricted and full irrigation.

Because extrapolation of conclusions from one year's results, or from one region to another, may not be justified, seven years' data from CIMMYT's ITYN, widely distributed in spring cereal areas of the world, were used to examine improvements in yield and stability as well as adaptation differences between complete and substituted hexaploid spring triticales.

Materials and methods

The ITYN was established to distribute a broad range of materials, representing the genetic variation in elite spring triticale germplasm, and to generate a data base for studying the crop. A randomized complete block design with three replicates was used. Grain yield data from ITYN-8 to -14, conducted from 1976 to 1983, were analysed and related to a study of test weight in the ITYN (Skovmand et al., 1983). Table 1 shows the number of sites and number of triticale genotypes, all of which were hexaploid, for individual ITYNs. Data for the variable local check, which was not always a triticale and somet unidentified, as well as bread and durum wheat checks were not analysed. The percentage of triticale genotypes maintained in two consecutive years was variable and generally low, while the sites used were more consistent, but did vary from year to year.

An analysis of variance was conducted on each year's data, before and after a logarithmic transformation, with the genotype × site interaction partitioned into two components. One was due to linear regressions of yields of individual genotypes on site mean yields, based on all genotypes, and the other to deviations from regressions (Finlay & Wilkinson, 1963). Variance components were estimated using a random effects model.

The substituted triticale Cananea 79 (formerly called Mapache) and Beagle, a complete, represent the first high yielding commercially accepted spring triticales and remain as long term check genotypes in the ITYN. Dunnett's (1955) test for multiple comparison was used to determine how many genotypes had significantly higher or lower yields than Cananea 79 and Beagle in ITYN-8 to ITYN-14.

For each year, the number of sites for which Cananea 79 and Beagle occurred in the top, middle and bottom third of trial genotypes was determined. This stratified ranking procedure was repeated in ITYN-14 using Boa, a substituted line, and Juanillo 97, a complete, as thesetwo newer triticales represent the best material from the early 1980s.

In each of the seven ITYNs studied, the similarities among sites and among genotypes were examined using cluster analysis of yield data (Byth et al., 1976). In addition, genotypes common to ITYN-13 and -14 were clustered using the two years' data and site-year combinations from both nurseries were grouped, as though they were sites, to examine repeatability of sites.

Data were standardized prior to clustering, giving each site a mean of zero and a phenotypic standard deviation of one. This removes site main effects, allowing genotype × site interaction to de-

termine the clustering (Fox & Rosielle, 1982; Fox et al., 1985). The clustering program HACLUS from the University of Queensland was used with the incremental sum of squares fusion option (Burr, 1970).

Results and discussion

Analyses of variance within individual ITYNs showed sites, genotypes and genotype × site interaction to be significant (P < 0.01) each year. In only one year did regression explain more than 5% of genotype × site interaction sums of squares. Therefore, regression was not considered adequate for examining the interaction. Apparently, site mean yield did not explain the ecological variability encompassed and consequently linear or curvilinear functions of mean yield explained little of the interaction. Logarithmic transformation did not improve the fit of the linear model for interaction.

An examination of variance components for grain yield showed that genotype × site interaction components were generally 3 to 4 times the size of the genotypic variance (Table 1). This contrasts the situation for test weight data from ITYN-8 to -13 (Skovmand et al., 1983) where genotype and genotype × site components were approximately equal, indicating that test weight is more environmentally stable than yield.

In this section, all comparisons of genotypes with

Table 1. Variance components ($\times 10^3$) for grain yield (kg/ha) calculated using a random effects model in ITYN-8 to -14 and numbers of sites and genotypes in each

	ITYN						
	− 8	− 9	− 10	− 11	− 12	− 13	− 14
Site (S)	3233	3780	2890	3465	2455	2829	2736
Genotype (G)	63	61	61	63	67	46	50
G × S	246	219	188	130	232	174	159
error	329	338	295	451	329	435	465
No. of:							
Sites	59	62	50	59	57	59	58
Genotypes	21	20	21	21	21	46	36

Cananea 79 or Beagle refer to a two-tailed Dunnett's multiple comparison test with a 10% significance level. As with variance components, grain yield results differed from the equivalent analysis of test weight (Skovmand et al., 1983). There, two genotypes in ITYN-8 had higher test weights than both checks. Between ITYN-8 and ITYN-13 newer entries first equalled and then surpassed test weights of the older checks. In ITYN-8 and -9, no genotype was higher yielding than Cananea 79 or Beagle and most were lower yielding (Table 2). By ITYN-13 and -14, the majority of genotypes were not significantly different from Cananea 79 and Beagle, with a few higher yielding. It should be emphasized that genotypic means over all sites may be somewhat misleading, owing to large genotype × site interaction, but results do suggest different trends for the two variables. Generally, yields of ITYN entries at the end of the period studied were similar to those of Cananea 79 and Beagle, while their test weights were higher.

There are probably two major reasons why progress achieved with test weight was not obtained with grain yield. First, CIMMYT's selection strategy placed more emphasis on test weight than yield during the period considered in this study (Skovmand et al., 1983). This occurred because yield levels seldom limited the acceptance of triticale by farmers from the 1970s onwards, while low test weights retarded the crop's entrance into commercial agriculture (Skovmand et al., 1984). Second, as mentioned above, test weight is a more environmentally stable character for which efficient selection is less likely to be confounded by genotype × environment interaction.

Progress for yield in the period studied was not as rapid as in earlier years, when the first large scale breeding of triticale as a spring cereal resulted in yield breakthroughs (Zillinsky, 1974). While yields of a majority of genotypes in ITYN-13 and -14 were no different from the checks, some genotypes were significantly higher yielding (Table 2), indicating that improvement in yield continued, but at a slower pace than for test weight.

The number of sites for which each genotype occurred in the top, middle and bottom third of entries in each trial produced useful information on

adaptation. A genotype which consistently occurred in the top third of entries across sites was considered relatively well adapted to the broad environmental range sampled in the ITYN. However, it is acknowledged that genotypes adapted to specific sites may not be identified. This stratified ranking technique was used to examine the adaptation of Cananea 79 and Beagle in ITYN-8 and-14 and the adaptation of two newer genotypes, Boa, a substituted triticale, and Juanillo 97, a complete, in ITYN-14 (Table 3). Like most measures of adaptation, the rank measure for a genotype depends on the yields of genotypes with which it is grown. In ITYN-8, Cananea 79 and Beagle were two of the better genotypes, but six years later they appeared poorly adapted relative to more recent materials. Decline relative to newer genotypes was not associated with change in reaction to disease in either Cananea 79 or Beagle. In ITYN-14, Boa and Juanillo 97 demonstrated the superioradaptation of more recently developed substituted and complete genotypes, yielding in the top third of entries in 60% or more of sites.

Other measures of general adaptation, besides regression and use of ranking, have been proposed. With barley trials from eastern Canada, Lin & Binns (1988) used the mean squared distance, across sites, of the difference between a genotype's yields and highest yields achieved. The measure may be influenced by scale of observations, important when ranges of site mean yields are large, as commonly occurs in international trials. For exam-

ple, this range was greater than 7 t/ha in ITYN-14. Therefore, to investigate the ITYN, the stratified ranking measure was favoured because it is independent of scale and places equal weight on each site, by contrast to the parameter of Lin & Binns.

Sixty-four site-year combinations from the 32 common sites of ITYN-13 and -14 were clustered using the 20 common genotypes (Fig. 1). Grouping of sites within years and repeatability of sites across the two years was examined. There was little evidence of sites grouping on a geographical basis within years, as for site clusters from analyses of individual ITYNs. Sites which clustered together across years in the combined analysis of ITYN-13 and -14 were generally from higher latitudes. Daylength may have been important in determining adaptation to higher latitudes which generally have longer, cooler growing seasons associated with less environmental stress than occurs at lower latitudes. Strong seasonal interactions, manifested by switches between major groups from year to year, were typical of lower latitude sites where photoperiod may have had less impact than unpredictable seasonal variation in determining interactions. Quito, Ecuador, near the equator performed similarly in consecutive years. Although a low latitude site, its high elevation (3050 m.a.s.l.) and climatic factors confer a long, relatively cool growing season. In contrast, Prince Edward Island, Canada, is a high latitude (46° N) site which exhibited low repeatability, related to a germination problem in ITYN-13

Table 2. Ranking of genotypes relative to Cananea 79 and Beagle for grain yield in ITYN-8 to -14 using a two-tailed Dunnett's (1955) test for multiple comparison (P < 0.10)

| | ITYN | | | | | | |
	− 8	− 9	− 10	− 11	− 12	− 13	− 14
Cananea 79							
Higher	0	0	2	2	1	14	5
No difference	3	2	8	13	8	29	21
Lower	17	17	10	5	11	2	9
Beagle							
Higher	0	0	1	0	1	5	3
No difference	4	2	7	11	5	31	19
Lower	16	17	12	9	14	9	13

causing low yields and a high coefficient of variation.

There were insufficient numbers of genotypes in common in consecutive nurseries prior to ITYN-13 to permit additional analyses of this type. Observations on repeatability from but two years must be considered tentative and require validation.

Each year, clustering of genotypes showed a tendency for complete and substituted triticales to separate into different groups suggesting adaptation differences between the two types. This confirms the report of Fox & Skovmand (1983) showing separation of four completes from 17 substituted triticales in ITYN-12. Cluster analysis of 20 common genotypes from ITYN-13 and -14 (Fig. 2), using 64 site-years as attributes, also illustrated this trend. This set of 20, while excluding several genotypes, retains the diversity of complete and substituted triticales. At the three-group level, substituted entries form one group and completes comprise the other two groups.

Worldwide there was no overall yield difference between the two types of triticale, but these cluster analyses detected a more subtle adaptation difference. Also, while the majority of individual sites in ITYN-13 and -14 showed no obvious discrimination between types, the data revealed 11 sites, common to ITYN-13 and -14, demonstrating distinct superiority for either complete or substituted triticales in ITYN-13 (Table 4). For example, in Ngaoundéré, Cameroon, the top 10 genotypes were all completes and the yield of the best com-

plete was markedly higher than the yield of the best substituted triticale in ITYN-13. In Caacupé, Paraguay, the trend was reversed and substituted triticales were favoured. Superiority of one type of triticale at a site may be consistent across years or may change with seasonal conditions, as was observed in El Batan, Mexico and Brookings, USA (Table 4) where drier conditions in ITYN-14 favoured completes, despite a markedly reduced growing season compared with ITYN-13 at both sites. In Krakow, Poland, the highest yielding substituted genotype exceeded the corresponding complete by 0.8 t/ha in ITYN-13, while the margin was 0.45 t/ha in favour of the complete the following year (Table 4). This phenomenon was also associated with different moisture conditions at Krakow in the two seasons. ITYN-13 was sown into moist soil, while ITYN-14 was dry sown and experienced a drier than average growing cycle. Results from El Batan, Brookings and Krakow support the conclusion that completes yield more than substituted genotypes in moisture deficient situations.

However, from data collected it was not generally possible to explain relationships between complete and substituted types on the basis of environmental characteristics. Earlier maturity of substituted triticales when compared with completes (Lukaszewski & Gustafson, 1984) explains only a few results in Table 4. General superiority of complete triticales in highland regions has been reported. For instance, when eight highland sites from ITYN-14 were analysed as a group, the 10 highest yielding genotypes were completes (CIMMYT, 1985). In contrast, substituted triticales were superior across nine irrigated subtropical sites (CIMMYT, 1985). A more comprehensive data base may facilitate elucidation of underlying causes of differences.

Yearly variation at many sites points to selection problems inherent in yield tests in one season at a single site and emphasizes the importance of identifying broadly adapted material to overcome temporal variation, even within a narrow geographic range. Such broad adaptation may be enhanced by combining desirable characteristics from the different adaptation patterns of complete and substitut-

Table 3. Percentage of sites for which selected genotypes were ranked in the top, middle and bottom third of entries in ITYN-8 and -14

		Top	Middle	Bottom
ITYN-8				
Cananea 79	(S)	64	24	12
Beagle	(C)	59	24	17
ITYN-14				
Cananea 79	(S)	28	60	12
Beagle	(C)	44	24	32
Boa	(S)	60	25	15
Juanillo 97	(C)	63	25	12

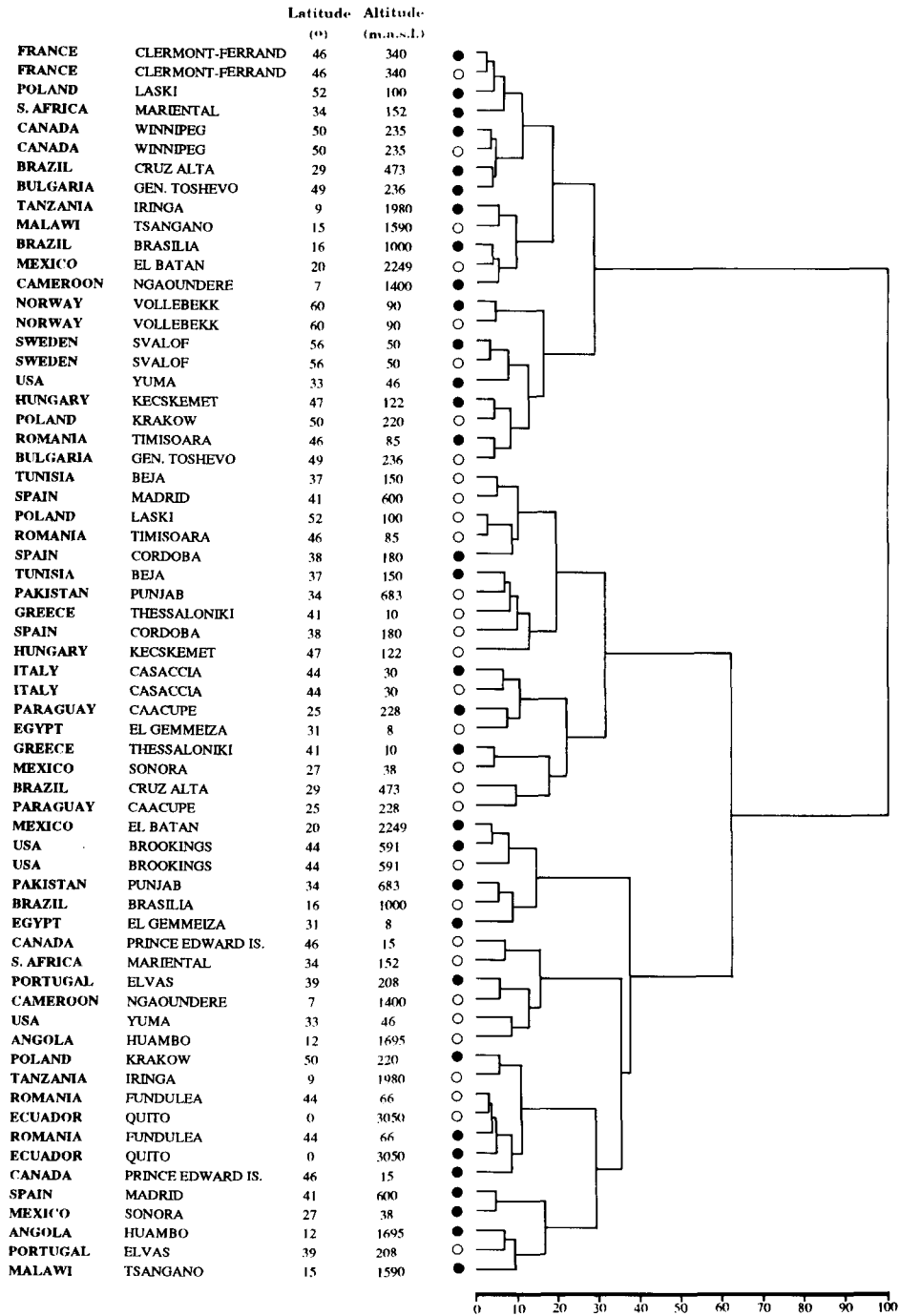S = Substituted; C = Complete.

62

Fig. 1. Dendrogram of relationships among 64 site-year combinations from ITYN-13 and -14 for grain yield of 20 genotypes, showing latitude and altitude. The horizontal axis is proportional to squared Euclidean distance. Filled and open circles represent ITYN-13 and -14 sites, respectively.
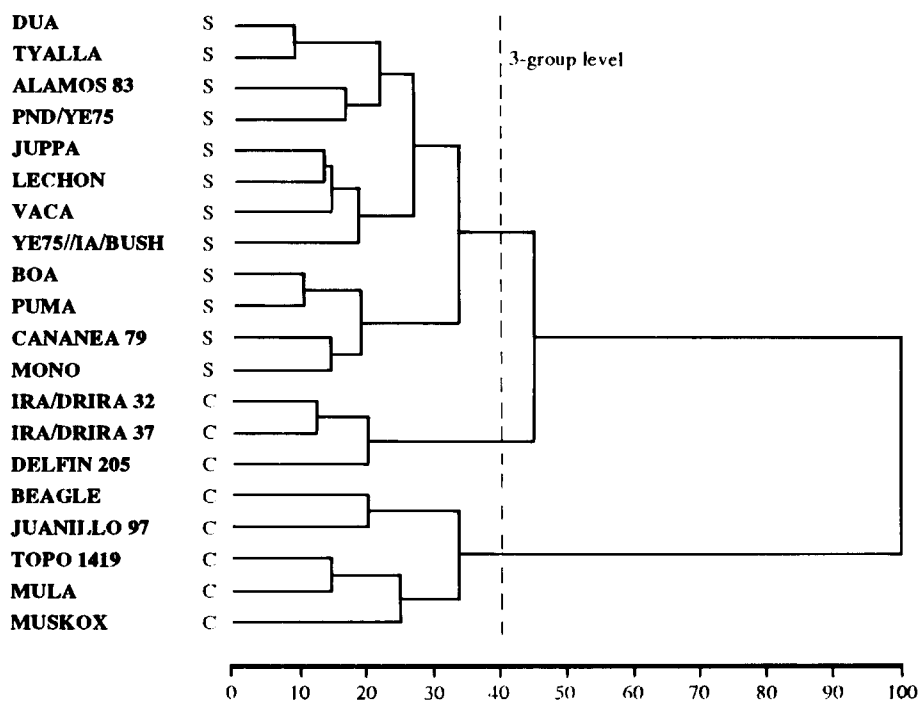
Fig. 2. Dendrogram of relationships among genotypes common to ITYN-13 and ITYN-14 for grain yield in 64 environments. The horizontal axis is proportional to squared Euclidean distance. Complete and substituted triticales are represented by C and S, respectively.

ed triticales as manifested in clustering of genotypes.

Because of their adaptation differences, which are not, as yet, well understood, diversity is en-

hanced by maintaining complete and substituted types in a triticale breeding programme. This applies most obviously to a programme such as CIMMYT's which supplies germplasm for a diverse en-

Table 4. Composition of the 10 highest yielding triticales with respect to karyotype, complete (C) or substituted (S), from 11 sites from ITYN-13 and -14 with highest yields (kg/ha) for C and S types. Sites were selected for marked superiority of one type in ITYN-13

Location	ITYN-13		ITYN-14	
	Composition C/S	Highest yield C/S	Composition C/S	Highest yield C/S
Ngaoundéré, Cameroon	10/0	3677/2285*	7/3	2677/2421
Brasilia, Brazil	9/1	3737/2859*	6/4	5222/4766*
Svalöf, Sweden	8/2	3425/2997	8/2	4639/3730
Winnipeg, Canada	8/2	6757/5855*	7/3	6345/5365*
Krakow, Poland	2/8	3809/4612	5/5	3045/2589
Thessaloniki, Greece	2/8	5436/5705	1/9	2164/3089
Sonora, Mexico	2/8	6976/6837	2/8	3910/4047
El Batan, Mexico	2/8	4952/5077	10/0	2750/1884*
Vollebekk, Norway	1/9	5000/5915*	5/5	4244/4256
Brookings, USA	1/9	2352/2971*	7/3	2624/2473
Caacupé, Paraguay	1/9	1900/2208	4/6	5013/4796

* highest C and S significantly different (LSD, P < 0.05).

64

vironmental range. However, we also suggest that a more narrowly orientated breeding programme, targeted either solely to releasing complete or solely to substituted triticales, may benefit by intercrossing the two types. Complete and substituted triticales were managed separately for many years at CIMMYT, until intercrossing was initiated to combine adaptive advantages of both. A 'blurring' of phenotypic differences between complete and substituted types is becoming more evident in recent material, where complete triticales are found with shorter stature or a degree of earliness formerly limited to substituted germplaem.

Acknowledgement

References

Burr, E.J., 1970. Cluster sorting with mixed character types. II. Fusion strategies. Aust. Comput. J. 2: 98–103.

Byth, D.E., R.L. Eisemann & I.H. De Lacy, 1976. Two-way pattern analysis of a large data set to evaluate genotypic adaptation. Heredity 37: 215–230.

CIMMYT, 1985. Results of the Fourteenth InternationalTriticale Yield Nursery (ITYN) 1982–1983.

Dunnett, C.W., 1955. A multiple comparison procedure for comparing several treatments with a control. J. Am. Stat. Assoc. 50: 1096–1121.

Finlay, K.W. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742–754.

Fox, P.N. & A.A. Rosielle, 1982. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. Euphytica 31: 645–656.

Fox, P.N., A.A. Rosielle & W.J.R. Boyd, 1985. The nature of genotype × environment interactions for wheat yield in Western Australia. Field Crops Res. 11: 387–398.

Fox, P.N. & B. Skovmand, 1983. Relationships between international locations and selection for yield and adaptation in hexaploid triticale. Agron. Abstr. American Society of Agronomy, Madison, WI, p. 63.

Gustafson, J.P. & F.J. Zillinsky, 1973. Identification of D-genome chromosomes from hexaploid wheat in a 42-chromosome triticale. Proc. 4th Int. Wheat Genetics Symp., Columbia, pp. 225–231.

Lin, C.S. & M.R. Binns, 1988. A superiority measure of cultivar performance for cultivar × location data. Can. J. Plant Sci. 68: 193–198.

Lukaszewski, A.J., 1988. Chromosome constitution of hexaploid triticale lines in the recent international yield trials. Plant Breeding 100: 268–272.

Lukaszewski, A.J. & J.P. Gustafson, 1984. The effect of rye chromosomes on heading date of triticale × wheat hybrids. Z. Pflanzenzücht. 93: 246–250.

Osmanzai, M., J.K. Ransom, S.R. Waddington & M. Yoshida, 1984. Performance of complete and substituted triticale in stress and no stress environments. Agron. Abstr. American Society of Agronomy, Madison, WI, p. 81.

Skovmand, B., H.J. Braun & P.N. Fox, 1985. Comparison of agronomic and quality characteristics of complete and substituted hexaploid spring triticales. Proc. Eucarpia Meeting Genetics and Breeding of Triticale, Clermont-Ferrand, pp. 29–34.

Skovmand, B., P.N. Fox & B.K. Thompson, 1983. Improvement and adaptation in test weight of hexaploid triticale (X Triticosecale Wittmack). Proc. 6th Int. Wheat Genet. Symp., Kyoto, pp. 939–943.

Skovmand, B., P.N. Fox & R.L. Villareal, 1984. Triticale in commercial agriculture: progress and promise. Adv. Agron. 37: 1–45.

Varughese, G., E.E. Saari & O.S. Abdalla, 1986. Two decades of triticale breeding and research at CIMMYT. Proc. Int. Triticale Symp., Sydney, Occasional Publications No. 24, pp. 148–169. Aust. Inst. Agric. Sci.

Zillinsky, F.J., 1974. The development of triticale. Adv. Agron. 26: 315–348.

Zillinsky, F.J., 1980. The influence of chromosome substitutions on some agronomic characteristics of hexaploid triticales. Hodowla Ros. Aklim. Nasienn. 24: 383–388.