Path analysis of genotype $\times$ environment interactions of wheats to nitrogen

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Abstract – To determine the effect of the application of different levels of nitrogen on grain yield and its components, nine genotypes of bread wheat (*Triticum aestivum* L.), five of durum wheat (*T. turgidum* L. var. *durum* Desf.) and a triticale ($\times$ Triticosecale Wittmack) were subjected to three levels of N (0, 65 and 130 kg N ha⁻¹) at three dates of planting: late planting, early planting and mid-season planting, over two growing seasons. A mathematical model based on the method of path analysis was used to study the relationship between grain yield and its components under different N levels. The main effect of N was highly significant for grain yield, aboveground dry matter at anthesis, number of kernels per spike and kernel weight. Genotype $\times$ N interaction was significant for these characters, except number of kernels per spike. The greatest variability among the genotypes in response to N occurred during vegetative growth, followed by the seed setting and grain filling periods. Seven genotypes showed sensitivity to N during vegetative growth and seed setting, two during seed setting and grain filling, one during vegetative growth and grain filling and three during both vegetative and reproductive phases. Only 'Express' and to some extent 'Yecora Rojo' were adapted to limited N during the reproductive phase. Development and cultivation of cultivars such as Express that are adapted to limited N could reduce the amount of N required to grow an economic crop and thus reduce the cost of inputs and the possibility of polluting natural resources with the application of excess N. (© Inra/Elsevier, Paris.)

common wheat / durum wheat / yield components / stress / path analysis

Résumé – Analyse de piste des interactions génotype $\times$ environnement chez des blés traités à l'azote. Pour définir l'effet de différents niveaux d'apport d'azote sur le rendement en grains et ses composantes, neuf génotypes de blé tendre (*Triticum aestivum* L.), cinq de blé dur (*T. turgidum* var. *durum* Desf.) et un triticale ($\times$ Triticosecale Wittmack) ont été soumis à trois traitements d'azote (de 0,65 à 130 kg/ha⁻¹) à trois dates de semis sur deux saisons de culture. Un modèle mathématique basé sur l'analyse de piste a été utilisé pour étudier la relation entre le rendement en grains et ses composantes dans ces différentes conditions. L'effet principal de l'azote a été hautement significatif pour le rendement,

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la matière sèche aérienne, le nombre de grains par épi et le poids de grain. L'interaction $G \times N$ a été significative pour ces caractères, sauf pour le nombre de grains par épi. La plus grande variabilité génotypique pour la réponse à l'azote a été constatée pendant la croissance végétative, suivie par les périodes de nouaison et de remplissage. Sept génotypes ont montré une sensibilité à l'azote pendant la croissance végétative et la nouaison, deux pendant les phases de nouaison et de remplissage, un pendant la croissance végétative et le remplissage et trois pendant les deux périodes végétative et reproductrice. Seuls « Express » et, dans une moindre mesure, « Yecora Rojo » sont apparus adaptés à des faibles doses d'azote pendant la période reproductrice. Le développement et la culture de cultivars comme « Express », adaptés à de faibles niveaux d'azote, pourraient réduire la quantité d'azote requise pour exploiter une plante d'intérêt agronomique et par conséquent réduire le coût des intrants et les risques de pollution des ressources naturelles par des apports excessifs d'azote. (© Inra/Elsevier, Paris.)

blé tendre / blé dur / composantes du rendement / analyse de piste

1. INTRODUCTION

Little is known of the differential response of cereal crops to nutrient-limited conditions. Nitrogen is the most important and most expensive fertilizer nutrient used in agriculture. A large portion of applied N is lost by leaching and denitrification [9]. It has been reported that plants use as little as 50 % of applied N [4]. Environmental and economic considerations require the effective use of resources in crop production systems. The use of high N inputs might result in nitrate pollution of underground water and the atmosphere. In developing countries, small-scale farmers often cannot afford to invest in large applications of N because of credit constraints, low income, or high risk of crop loss, especially in rainfed areas.

In wheat breeding programs, testing and selection is generally performed under high N application with adequate amounts of water. Modern bread wheat (*Triticum aestivum* L.) and macaroni wheat (*T. turgidum* L. var. *durum* Desf.) cultivars require high-input growing conditions to reach yield potentials. In contrast, landraces of wheat, which are still cultivated in traditional and sustainable agriculture are grown under low-input farming conditions [12, 27].

Reports on the response of different wheat cultivars to changing N levels in terms of grain yield production are contradictory. Non-significant genotype $\times$ N interactions have been reported for grain yield in some studies [3, 5, 15–17, 21, 28]. In other studies, however, significant interactions were reported [14, 20].

Wheat grain yield is a complex character and is a product of yield components such as aboveground biomass at anthesis, number of spikes per plant, kernels per spike and kernel weight. The ontogeny of these components follows a sequential development during the growth of the wheat crop. Genotype $\times$ environment (GE) interactions are induced by differential responses of genotypes to environmental factors present during the development of component traits. Grafius and his colleagues [8, 29] suggested that environmental stresses that occur during the sequential development of yield components constitute the major ingredients of GE interactions of yield. Adams [1] suggested that the negative relationships observed among yield components are developmental rather than genetic per se, but are caused by genetically independent components developing in a sequential manner in response to environmental resources.

Tai [23–25] developed a statistical method based on path analysis [30] to investigate GE interactions associated with sequential yield components. There are two important assumptions of the method: 1) the chronological sequence in the development of yield components is X to Y to Z, and yield, W, is the final multiplicative product of the sequential development process; and 2) the environmental response can be separated into three independent groups – R1, R2 and R3 – where each group supports the development of a component trait. The path analysis method has been used to investigate genotype $\times$ environment interactions of eight potato (*Solanum tuberosum* L.) cultivars grown under water-stress conditions [11] and of 20 potato cultivars under heat stress [26].

In the present study, we investigated genotype $\times$ N interactions of grain yield and its components for a diverse set of field-grown cereal cultivars to determine their differential responses under N-limited conditions.

2. MATERIALS AND METHODS

Nine hexaploid and five tetraploid wheat cultivars, along with a triticale cultivar, were used. The hexaploid cultivars included 'no. 14' and 'no. 49', two tall landraces introduced from Iran, 'Ramona 50', a tall older cultivar previously grown in California [2, 6], 'G 4843', a genotype with superior N accumulation capacity [5], 'Yecora Rojo', 'Klasic', 'Yolo', 'Serra' and 'Express', dwarf and semidwarf cultivars grown locally in California [10]. The tetraploid cultivars included 'Aldura', 'Mexicale 75', 'Yavaros 79', 'Westbred 881' and 'Westbred Turbo', semidwarf cultivars, and a tall triticale cultivar, 'Juan', grown locally in California [10]. The commercial seeds were kindly donated by K-F Seeds Company, Brawley, CA; Adams Seed Inc., Woodland, CA; and Dr C.O. Qualset, Department of Agronomy and Range Sciences, University of California, Davis, CA.

These genotypes were grown in a randomized complete block design with three replicates at three different soil N levels over three planting dates; 5 February, 26 October and 6 December 1993, in a Ramona type A sandy loam soil (fine-loamy, mixed, thermic Typic Haploxeralf) at the Moreno Farm of the University of

California Agricultural Experiment Station, Moreno Valley, CA. The late planting (5 February) was harvested in June 1993, and the early (26 October) and mid-season (6 December) plantings were harvested in June 1994. Plot size was six rows, 5 m long, with an interrow spacing of 20 cm. Seeds were planted within the row 4–5 cm apart. Seeds were sown with an Oyjord experimental seed drill (Jens A. Schou Mek Verksted A/S 1973, Norway), which has a cone-type planter with splitter that distributed the seeds into six rows.

Three levels of N were created by applying N at rates of 0.0 (N1), 65.0 (N2) and 130.0 (N3) kg ha⁻¹ in the form of urea before sowing. The residual soil N in the field station was reported to be 75 kg ha⁻¹ in the upper 60-cm profile [5]. The optimal rate of N application in California is between 190 and 260 kg N ha⁻¹. The experiment was irrigated with sprinklers as needed for optimal growth until plants reached maturity. The description of the experiment is given in *table I*. Since all N was applied before sowing in this study, the seed setting and grain filling periods were particularly subjected to limited N.

Days to anthesis were determined as the number of days from planting until 50 % of the plants in a plot showed extruded anthers. At this time, a 1-m length of one of the inner rows was harvested and immediately dried in a forced-air drier at 60 °C for 6 d, and weighed. At maturity, ten spikes were randomly collected from the plants of the inner rows in each plot to determine number of kernels per spike. Before harvesting, 0.5 m of each end of the rows were discarded, and only the three inner rows were harvested to measure grain yield. Mean number of kernels per spike and kernel weight were also measured. Other agronomic characteristics measured

Table I. Description of the experiments used to evaluate mean grain yields of 14 wheat and one triticale cultivars grown over three planting dates and three levels of N.

Planting date in 1993	Applied N ¹ (kg ha ⁻¹)	Irrigation and rain (mm)	Anthesis date	Harvesting date in June
Feb. 5	0.0	355	Apr. 20/93	1993
Feb. 5	65.0	355	Apr. 20/93	1993
Feb. 5	130.0	355	Apr. 20/93	1993
Oct. 26	0.0	580	Mar. 15/94	1994
Oct. 26	65.0	580	Mar. 15/94	1994
Oct. 26	130.0	580	Mar. 15/94	1994
Dec. 6	0.0	480	Apr. 5/94	1994
Dec. 6	65.0	480	Apr. 5/94	1994
Dec. 6	130.0	480	Apr. 5/94	1994

¹ Nitrogen fertilizer applied before planting.

were days from sowing to booting, to harvesting, and to maturity; plant height at anthesis and at maturity; number of spikes per meter in the first planting; number of tillers per meter in the second and third planting at maturity; aboveground dry matter at maturity; and harvest index (ratio of grain yield to aboveground dry matter at maturity). Not all characters are reported here.

2.1. Statistical analysis

Analyses of variance were carried out on grain yield and its components, namely aboveground dry matter at anthesis, number of kernels per spike and kernel weight, assuming fixed effects for dates of planting, N levels and genotypes [22]. The association among characters was examined by correlation analysis.

To investigate the relationship between grain yield, its components and environmental resources in terms of applied N, a model proposed by Tai [23] was used. The causal relationship between the N treatments, components of grain yield and grain yield is shown in *figure 1*. The multiplicative product of the three yield components forms grain yield. In wheat, the first component is usually considered to be number of spikes per plant or per unit area, rather than aboveground dry matter at anthesis. However, in the first date of planting, the correlation coefficient between aboveground dry matter at anthesis and grain yield ($r = 0.55$) was stronger ($P < 0.17$) than

that between number of spikes per meter and grain yield ($r = 0.39$) [22]. Therefore, only aboveground dry matter at anthesis was measured in the second and third dates of planting. Furthermore, the aboveground dry matter at anthesis represents not only the integrated number of tillers and spikes and plant height but also preanthesis assimilates stored in plant parts that could contribute to kernel weight during the grain filling period and thus to grain yield [7, 18].

In Tai's model [23], it is assumed that the environmental resources can be separated into independent groups. These resources are available to the process of plant development at sequential stages in which the yield components are formed. In this model, the yield of the i th genotype ($i = 1, \dots, m$) in the j th environment ($j = 1, \dots, n$) W_{ij} is composed of a mean genotypic effect, μ_{wi} ; three multiplicative terms of the GE interaction formed by three genotypic components, v_{1i} , v_{2i} and v_{3i} ; three environmental components, r_{1j} , r_{2j} , and r_{3j} ; and an error deviate, e_{ij} . It can be expressed as follows:

$$W_{ij} = \mu_{wi} + v_{1i} r_{1j} + v_{2i} r_{2j} + v_{3i} r_{3j} + e_{ij}$$

The environmental components are measured in standard deviation units, and genotypic components represent the efficiency of the genotype to use one standard unit input of the three environmental components during the ontogeny of grain yield development. The genotypic components are estimated by path analysis [30]. The environmental components are then estimated by least squares, using the observed yields and estimates of the genotypic components. Mathematical details are provided by Tai [23–25].

Grain yield stability of each cultivar over nine environments generated by combinations of three dates of planting and three levels of N was determined using estimates of Shukla's stability variance [19].

3. RESULTS AND DISCUSSION

The ranking of wheat genotypes for grain yield in different environments is usually changed because of the presence of genotype $\times$ environment interactions. In this study, the dates of planting, which covered two growing seasons, were chosen to create different environments in which genotype $\times$ N interactions for grain yield and its components could be studied. In the first date of planting (D1), plants reached physiological maturity within 115 d, and they received only 335 mm of water (*table 1*).

Figure 1. A causation diagram showing the developmental relationship between grain yield (W) and its components: aboveground dry matter at anthesis (X), number of kernels per spike (Y) and kernel weight (Z) in cereals. Path coefficients between grain yield and the components are $a_1, \dots, a_6$, and between the three independent groups of environmental resources R1, R2, and R3 and grain yield are u_1, u_2 and u_3 (After Tai [23]).

This was due to late (February) planting and accelerated plant growth in response to relatively higher temperatures. In contrast, plants in the second (D2) and third (D3) dates of planting, late October and early December, respectively, reached physiological maturity within 200 and 180 d, and received 580 and 480 mm of water, respectively (*table I*). The recommended planting date in California is between mid-October to mid-December. For D1, D2 and D3, mean aboveground dry matter at anthesis was 149.5, 380.9 and 355.8 g m⁻¹; mean number of kernels per spike were 32, 34 and 37; mean kernel weight was 36.5, 50.2 and 50.6 mg, and mean grain yield was 4.3, 7.2 and 7.1 t ha⁻¹, respectively. Mean values of these characters were the same for D2 and D3 but were significantly higher than those of D1, except for mean number of kernels per spike, which was similar for D1 and D2.

Mean aboveground dry matter at anthesis was highest for N3 (348.4 g m⁻¹) followed by N2 (314.2 g m⁻¹) and N1 (223.8 g m⁻¹). Mean number of kernels per spike was similar for N1 (36.9) and N2 (35.6), but they were significantly greater than that for N3 (30.6). The highest mean kernel weight was observed for N2 (47.1 mg) followed by N3 (45.3 mg) and N1 (44.9 mg). Mean grain yield was

greatest for N2 (7.0 t ha⁻¹), followed by N1 (6.1 t ha⁻¹) and N3 (5.6 t ha⁻¹).

The analysis of variance indicated significant differences among dates of planting and among N levels (*table II*). The N × date of planting interaction was significant for aboveground dry matter at anthesis, number of kernels per spike and grain yield but not kernel weight (*table II*).

The genotype × date of planting interaction was highly significant for grain yield and its components (*table II*). The genotype × N interaction and genotype × N × date of planting interaction were either significant or highly significant for aboveground dry matter at anthesis, kernel weight and grain yield (*table II*). These results indicated that genotypes responded differently to date of planting and N levels, and for further analysis of response to N levels, the combinations of three dates of planting and three N levels were considered as nine different environments.

The correlation coefficients between grain yield and its components and between the components are shown in *table III*. The correlation structure of the cultivars were different from each other. Among the grain yield components, kernel weight exhibited the most consistent pattern of correlation with

Table II. Mean squares for effects due to nitrogen (N) and interaction with date of planting (D) and genotype (G) for aboveground dry matter at anthesis (AGDMA), number of kernels per spike (KN/S), kernel weight (KW) and grain yield (GY).

Source of variation	df	Mean squares			
		AGDMA	KN/S	KW	GY
D	2	2 176 260 **	1 080 *	8 751 **	373.0 **
Error	6	9 191	155	60	6.2
N	2	560 231 **	1 496 **	175 **	74.8 **
N × D	4	41 238 **	522 **	51	48.2 **
Error	12	4 692	35	24	2.1
G	14	108 571 **	1 677 **	1 194 **	27.3 **
G × D	28	23 448 **	160 **	56 **	8.8 **
G × N	28	4 840 *	52	15 **	6.4 **
G × N × D	56	6 206 **	53	13 **	3.8 **
Error	252	2 937	43	7	1.1

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

Table III. Correlation coefficients between grain yield (GY) and its components aboveground dry matter at anthesis (AGDMA), number of kernels per spike (NK/S) and kernel weight (KW), for 15 bread and durum wheat and triticale cultivars grown over three planting dates and three levels of N.

Cultivar	GY and AGDMA	GY and NK/S	GY and KW	AGDM and NK/S	AGDM and KW	NK/S and KW
No. 14	0.72*	0.90**	0.81**	0.65*	0.75*	0.66*
No. 49	0.37	0.72*	0.29	0.00	0.93**	-0.02
Ramona 50	0.00	0.69*	0.47	0.03	0.81**	0.36
G 4843	0.78**	0.39	0.85**	0.04	0.83**	0.15
Yecora Rojo	0.76*	0.57+	0.59	0.48	0.70*	0.04
Klastic	0.82**	0.57+	0.75*	0.31	0.73*	0.48
Yolo	0.61+	0.48	0.70*	0.11	0.82**	0.62+
Serra	0.48	0.86**	0.65*	0.37	0.83**	0.70*
Express	0.84**	0.30	0.77**	0.25	0.81**	0.45
Aldura ¹	0.39	0.21	0.78**	-0.52	0.78**	-0.01
Mexicale 75 ¹	0.68*	0.41	0.82**	-0.13	0.86**	0.14
Yavaros 79 ¹	0.82**	0.12	0.86**	-0.01	0.80**	0.25
Westbred 881 ¹	0.31	0.22	0.58+	-0.48	0.83**	-0.60+
Westbred Turbo ¹	0.75*	0.50	0.76*	-0.12	0.64+	0.49
Juan ²	0.68*	0.84**	0.58+	0.37	0.81**	0.32

+ * ** Significant at the 0.10, 0.05 and 0.01 probability levels, respectively.

¹ Durum wheats.

² Triticale.

grain yield followed by aboveground dry matter at anthesis and number of kernels per spike (*table III*). The correlation between kernel weight and aboveground dry matter was positive and significant for all cultivars, indicating importance of the latter character in determination of kernel size. Only one cultivar (no. 14) showed a positive correlation between aboveground dry matter and number of kernels per spike and one cultivar (Westbred 881) showed a negative correlation between number of kernels per spike and kernel weight. The correlation coefficients in *table III* were used to estimate the genotypic and environmental components of GE interactions for the 15 cultivars.

Although aboveground dry matter at anthesis was used as one of the primary components of grain yield in the model instead of number of spikes per plant or per unit area, the correlation between observed mean grain yields and the values fitted by the model for the 15 cultivars was high, except for Yecora Rojo and Yolo (*table IV*). Yecora Rojo was one of the two earliest genotypes to reach anthesis

(101 days after sowing), had the least height at anthesis (62 cm), and produced the least aboveground dry matter at anthesis (206.7 g m⁻¹) and at maturity (13.41 t ha⁻¹) (*table V*). Yolo was intermediate in reaching anthesis (108 days after sowing) and in height (76 cm) but had the highest number of tillers and spikes, 169 and 94 m⁻¹, respectively, at maturity, with the lowest kernel weight (34 µg) (*table V*). The relationship ($r = 0.89$) between observed mean grain yields and the values fitted by the model for all cultivars combined is presented in *figure 2*. This demonstrated that the yield model used was suitable for analysis of the genotype × N interaction for grain yield. The correlation coefficients between the observed marketable yield of eight potato cultivars grown in seven environments and the fitted values using the same model ranged from 0.92 to 0.99 [11].

The magnitude of the genotypic components of the genotype × N interaction represents the response of the genotype to standardized unit N input at the various growth stages (*table IV*). All

Table IV. Estimates of mean grain yields, genotypic components of genotype $\times$ environment interactions (GE) and stability variances ($\hat{\sigma}_i^2$) of 15 bread and durum wheat and triticale cultivars and correlation coefficients between observed and fitted grain yield for each cultivar.

Cultivar	Grain yield (t ha ⁻¹)	Genotypic components of GE interactions				Correlation coefficient
		$\hat{v}_1$	$\hat{v}_2$	$\hat{v}_3$	$\hat{\sigma}_i^2$	
No. 14	4.989 ab ¹	0.932	0.762	0.299	2.11	0.89
No. 49	5.691 abc	0.764	1.487	-0.282	8.19	0.86
Ramona 50	4.178 a	0.005	1.212	0.873	4.63	0.97
G 4843	6.121 bcd	1.721	0.737	0.683	1.36	0.95
Yecora Rojo	5.841 bcd	1.458	0.449	0.437	13.08	0.52
Klasic	7.490 de	2.222	0.897	0.252	8.51	0.93
Yolo	6.829 cd	1.392	0.935	-0.203	15.03	0.46
Serra	6.260 bcd	0.980	0.905	-0.336	5.58	0.74
Express	6.403 bcd	1.864	0.219	0.270	3.07	0.92
Aldura ²	6.472 bcd	0.910	1.117	1.396	1.60	0.98
Mexicale 75 ²	6.238 bcd	1.513	1.126	0.572	1.58	0.97
Yavaros 79 ²	6.043 bcd	1.630	0.262	0.629	1.60	0.89
Westbred 881 ²	5.580 abc	0.447	0.605	1.183	1.99	0.87
Westbred Turbo ²	6.472 bcd	1.497	1.194	-0.222	1.55	0.92
Juan ³	8.558 e	2.355	2.199	0.131	15.57	0.92

¹ Means in the same column followed by the same letter are not significantly different at the 0.05 probability level using LSD test.

² Durum wheats.

³ Triticale.

Figure 2. Grain yield of 15 wheat and triticale cultivars grown in nine environments generated by combinations of different levels of N and dates of planting fitted by a mathematical model (Tai [23]) compared with the observed values.

cultivars showed positive estimates of v_1 and v_2 components. Thus, all cultivars used a positive unit of the first and second environmental components

toward producing more aboveground dry matter and number of kernels per spike for more grain yield. However, there were marked differences among the cultivars for $\hat{v}_1$ and $\hat{v}_2$. Ramona 50 had a distinctly low value for $\hat{v}_1$ (0.005), indicating that aboveground dry matter at anthesis had practically no impact on production of grain yield in this cultivar. Ramona 50 was one of the two earliest genotypes to reach anthesis (101 days after sowing) and had one of the lowest number of spikes at maturity (62 m⁻¹), number of kernels per spike (22), and aboveground dry matter at maturity (13.57 t ha⁻¹) (table V). In contrast, Juan and Klasic had the highest values for $\hat{v}_1$, indicating that aboveground dry matter at anthesis had the greatest influence on production of grain yield in these two cultivars. Juan was one of the latest genotypes to reach anthesis (114 days after sowing), had the maximum height at anthesis (112 cm), and produced the least number of spikes at maturity (49 m⁻¹) but showed the great-

Table V. Mean values for days to anthesis (DA), plant height at anthesis (PHA), aboveground dry matter at anthesis (AGDMA), number of kernels per spike (NK/S), kernel weight (KW) and aboveground dry matter at maturity (AGDMM) for 15 bread and durum wheat and triticale cultivars grown over three planting dates and three levels of N.

Cultivar	DA d	PHA cm	AGDMA g m ⁻¹	NK/S no.	KW µg	AGDMM t ha ⁻¹
No. 14	111	107	370.1	30	34	16.22
No. 49	119	106	452.9	25	46	19.41
Ramona 50	101	93	252.8	22	48	13.57
G 4843	112	79	284.9	43	45	15.25
Yecora Rojo	101	62	206.7	28	46	13.41
Klasic	103	62	244.2	32	48	15.60
Yolo	108	74	264.5	40	34	15.95
Serra	107	76	260.7	39	42	14.78
Express	113	77	289.6	47	37	15.34
Aldura ¹	113	67	299.2	31	47	15.00
Mexicale 75 ¹	107	77	262.5	31	53	15.13
Yavaros 79 ¹	116	73	262.7	33	52	14.40
Westbred 881 ¹	108	71	276.2	27	50	14.70
Westbred Turbo ¹	117	82	317.6	38	50	15.51
Juan ²	114	112	386.3	48	55	20.13

¹ Durum wheats.

² Triticale.

est number of kernels per spike (48), heaviest kernel weight (55 µg), and produced the greatest aboveground dry matter at maturity (20.13 t ha⁻¹) (table V). Juan also had the highest value for $\hat{v}_2$, followed by no. 49 and Ramona 50, suggesting the importance of number of kernels per spike in formation of grain yield in these cultivars. Among the cultivars, Express, Yavaros 79 and Yecora Rojo had the lowest values for $\hat{v}_2$ (table IV). Estimates of the v_3 component were negative for no. 49, Yolo, Serra and Westbred Turbo, indicating that these cultivars favored environments that suppressed kernel weight (i.e. negative $\hat{v}_3$). The highest values of $\hat{v}_3$ belonged to Westbred 881 and Aldura, suggesting the importance of kernel weight in determination of grain yield in these two cultivars. The $\hat{v}_1$ and $\hat{v}_2$ genotypic components were larger in absolute value than the corresponding $\hat{v}_3$, except for Ramona 50, Express, Aldura, Yavaros 79 and Westbred 881. Therefore, most cultivars were sensitive to N application during the vegetative phase up to anthesis and also during seed setting, which affects kernel number, especially in Juan, Westbred Turbo, Mexicale 75,

Klasic, Yolo and Serra. Morgan [13] reported that generation of larger photosynthetic surface area by N-fertilized wheat plants early in development was the major factor accounting for greater grain yield, compared with unfertilized plants. Mossedaq and Smith [14] concluded that application of N early in plant growth resulted in significantly greater assimilation capacity, both before and after anthesis, which increased grain yield production. Considering both $\hat{v}_2$ and $\hat{v}_3$ values, Express and Yecora Rojo were the only cultivars with reasonable tolerance to limited N during the reproductive phase.

Variation in $\hat{v}_1$ values among the cultivars was greatest, followed by $\hat{v}_2$ and $\hat{v}_3$, suggesting that genotypic differences in response to N were associated more with aboveground dry matter at anthesis than with number of kernels per spike and kernel weight. Thus, only $\hat{v}_1$ was positively and significantly correlated with grain yield ($r = 0.83$, $P < 0.01$). Correlation coefficients between grain yield and $\hat{v}_2$ ($r = 0.40$) and $\hat{v}_3$ ($r = -0.30$) were not significant. No significant correlation coefficient was

observed between the three genotypic components, indicating that the genotypic response of the cultivars to the three groups of environmental resources were most probably controlled by separate genetic systems. No consistent pattern was observed between values of $\hat{v}_1$, $\hat{v}_2$ and $\hat{v}_3$ with polyploidy levels (i.e. tetraploids and hexaploids).

The durum wheats, namely Aldura, Mexicale 75, Yavaros 79, Westbred 881 and Westbred Turbo, along with a bread wheat, G 4843, showed the least values for the stability variance (*table IV*). The cultivars were classified into three groups of stability according to $F_{\max}$ statistic, with Juan, Yolo and Yecora Rojo showing the least stability for grain yield, followed by Klasic, no. 49, Serra and Ramona 50 as the second group; and G 4843, Westbred Turbo, Mexicale 75, Yavaros 79, Aldura, Westbred 381 and Express making up the most stable group. Mean grain yield and the stability variances were not correlated. However, a negative correlation ($r = -0.45$, $P < 0.10$) was found between $\hat{v}_3$ and the stability variance, indicating the importance of kernel weight as the last component in stabilizing grain yield across different environments.

The mean grain yield at the nine environments generated by combinations of N levels and dates of planting, the values of environmental indices (I) and

estimates of the three environmental components are presented in *table VI*. The correlations of I with $\hat{r}_1$, $\hat{r}_2$ and $\hat{r}_3$ were, respectively, 0.74 ($P < 0.05$), 0.59 ($P < 0.10$) and 0.94 ($P < 0.01$). It appeared that the third and first environmental components that affected kernel weight and aboveground dry matter production at anthesis, respectively, reflected the same environmental effect that influenced grain yield production.

The first three environments corresponding to N1, N2 and N3 in the first date of planting (D1, late planting in February), respectively, had the lowest mean grain yield (*table VI*). The estimates of the three environmental components, $\hat{r}_1$, $\hat{r}_2$ and $\hat{r}_3$ were negative for these environments, suggesting the prevalence of stressed conditions during the development of preanthesis aboveground dry matter, seed setting and grain filling for late planting. The impact of environmental stress was much greater in the first and the third components of grain yield than in the second component, as indicated by the relative magnitude of the $\hat{r}_i$ components for these three environments (*table VI*). However, both the first and the third environmental components showed a clear positive relationship with decreased N stress, whereas the second component showed a negative trend. It appeared that in late planting,

Table VI. Estimates of mean grain yields, environmental index (I)¹, and environmental components of the genotype $\times$ environment interactions (GE) of nine environments using 15 wheat and triticale cultivars.

Environment No.	Grain yield (t ha ⁻¹)	I	Environmental components of GE interactions		
			$\hat{r}_1$	$\hat{r}_2$	$\hat{r}_3$
1 (D1N1) ²	3.735 a ³	-2.476	-1.589	-0.165	-0.541
2 (D1N2)	4.330 ab	-1.881	-0.963	-0.450	-0.509
3 (D1N3)	4.811 b	-1.400	-0.511	-0.560	-0.488
4 (D2N1)	6.680 d	0.469	-0.658	1.534	-0.196
5 (D2N2)	8.833 f	2.622	1.029	1.162	0.950
6 (D2N3)	6.115 cd	-0.096	0.901	-1.235	0.035
7 (D3N1)	7.756 e	1.545	0.408	0.757	0.570
8 (D3N2)	7.899 e	1.688	0.461	0.658	0.601
9 (D3N3)	5.740 c	-0.471	0.923	-1.701	-0.423

¹ Environmental index = mean grain yield in each environment – mean of all environments.

² D1, D2, and D3 are three planting dates and N1, N2, N3 are three levels of N.

³ Means in the same column followed by the same letter are not significantly different at the 0.05 probability level using LSD test.

grain yield of the genotypes was affected more severely by N stress during preanthesis growth and development and grain filling rather than during the seed setting phase, which affected kernel number.

In the early (D2) and mid-season (D3) date of planting (environments 4–9, *table V*), the $\hat{r}_2$ component was larger in absolute size than $\hat{r}_1$ and $\hat{r}_3$ in all cases, and $\hat{r}_1$ in turn was larger than $\hat{r}_3$ in most cases. The $\hat{r}_2$ component, which supported the process of seed setting and kernel number, again showed a clear negative relationship with application of higher levels of N (*table VI*). The highest mean grain yield was obtained in environment 5 (8.833 t ha⁻¹) when date of planting was early and N2 was applied. In this environment the values of $\hat{r}_i$ components were positive and greatest. It appeared that in this environment, the environmental conditions were most favourable for growth and development of the three components of grain yield. The second level of grain yield production was obtained in environments 7 (7.756 t ha⁻¹) and 8 (7.899 t ha⁻¹), when date of planting was mid-season and N1 and N2, respectively, were applied. In these two environments, the values of $\hat{r}_i$ components were also positive but lower than the corresponding ones in environment 5 (*table VI*). The third level of grain yield production was achieved in environments 4, 6 and 9, when date of planting was either early or mid-season, but either one or two of $\hat{r}_i$ components were negative. The negative component was either $\hat{r}_1$, $\hat{r}_2$ or $\hat{r}_3$, and it associated with either N1 or N3. The least favorable environments were 1, 2 and 3, where the corresponding $\hat{r}_i$ components were all negative (*table VI*).

4. CONCLUSIONS

The model used in this study, in which above-ground dry matter at anthesis was used as one of the primary components of grain yield instead of number of spikes per plant or per unit area, was appropriate for estimating grain yield for all cultivars examined except Yolo and Yecora Rojo. It also allowed an insight into the study of GE interactions

based on the concept of sequential development of grain yield components.

This study showed differential responses to N among the 15 cereal cultivars studied. Significant differences were found among the cultivars in terms of grain yield production and relationships between grain yield and its components. In general, above-ground dry matter at anthesis was more sensitive to limited N than number of kernels per spike and kernel weight. Kernel weight was the least sensitive component and showed a negative correlation with the stability variance. However, there were marked differences among the cultivars, which suggested the need for different procedures of N management for specific cultivar(s). Results from this study indicated that for Ramona 50 and Westbred 881, limited application of N before anthesis had, respectively, no or smaller effect on grain yield production than after anthesis. For Yavaros 79, N stress before anthesis and during grain filling had a greater influence on grain yield than during seed setting. For the two landraces (no. 14 and no. 49), Klasic, Yolo, Serra, Westbred Turbo, and particularly Juan, N stress before anthesis and during seed setting had a greater effect on grain yield than during grain filling. Aldura, G 4843 and Mexicale 75 were sensitive to N stress during both vegetative and reproductive phases of growth and development. The only two cultivars that showed adaptation to limited N during the reproductive phase were Express and Yecora Rojo. However, the former one was identified as one of the most stable cultivars, whereas the latter was one of the least stable. The durum wheats, as a group, were more stable in grain yield production under N-limited conditions than the bread wheats.

Our study indicated that a late planting in February had a detrimental effect on grain yield and its components. The maximum grain yield was achieved either at early (late October) or mid-season (early December) planting dates and with application of intermediate N, 65 kg N ha⁻¹ (N2). The development and use of cultivars such as Express could reduce the amount of N required to grow an economic crop and thus reduce the cost of inputs and the possibility of polluting natural resources with the application of excess N.

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