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Environmental and genetic determination of protein content and grain yield in durum wheat under Mediterranean conditions

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Abstract

The unpredictability of the Mediterranean climate causes fluctuations in wheat yield and quality, but offers the opportunity for obtaining high-quality durum wheat in terms of grain protein content. Twenty-five durum wheat genotypes were grown under irrigated and rainfed conditions at each of two latitudes in Spain during 1998 and 1999. Differences between latitudes in grain protein content and chlorophyll content in the flag leaf were attributable to nitrogen fertilization management. Cycle length until anthesis was less affected by the environment than grain-filling duration, and was longer under irrigated conditions than in the rainfed sites. A negative asymptotic curve was the best equation to fit the relationship between yield and protein content, suggesting that yield improvements in fertile environments may be attained with negligible reductions in protein content. 'Jabato', 'Waha', 'Lagost-3', 'Massara-1' and 'Vitrón' showed medium to high yield, yield stability and high protein content. Chlorophyll content in the flag leaf, measured at anthesis with the soil–plant analysis development (SPAD) portable field unit, may be useful for the fast and cheap detection of durum wheat genotypes with high grain protein content in drought-stressed Mediterranean environments.

Key words: *Triticum durum* — chlorophyll — protein content — yield — yield stability

In Mediterranean environments, durum wheat is mainly grown under dryland conditions, which makes grain yield uncertain, but offers an opportunity for the production of high-quality wheats (Borghi et al. 1997).

Protein content is known to be influenced by the genotype, but is mainly influenced by the environment (Baenziger et al. 1985), with their interaction being of less importance. The most important environmental factors that affect protein content are nitrogen fertilization rate, time of nitrogen application and residual soil nitrogen (Rao et al. 1993). About two-thirds or more of the protein that is stored in the grain at maturity is present in the plant at anthesis (Austin et al. 1977); the remaining amount is absorbed from the soil during the period of grain development (Kramer 1979).

It is generally accepted that increases in protein content have been made at the expense of yield (Jenner et al. 1991). A negative relationship between both traits has been confirmed in wheat (Peterson et al. 1992, Liu et al. 1995, Boggini et al. 1997, Pleijel et al. 1999) and triticale (García del Moral et al. 1995). However, this is not a universal rule since, in bread wheat, the correlation between grain yield and grain protein content has been found to depend on soil fertility (Kramer 1979) and the level of yield (Stoddart and Marshall 1990). A worthwhile discussion on the relationships between grain yield and grain protein content can be found in the summary by Simmonds (1995).

The development and testing of cultivars with high and stable grain yield and good quality appears to be crucial in durum breeding. However, few studies have focused on the relationship between yield stability and protein content in durum wheat. Cox et al. (1986), Beninati and Busch (1992) and Ali (1995) reported evidence for the feasibility of achieving high-yielding and stable varieties with acceptable protein content.

The objectives of this study were: to assess the influence of environment on durum wheat yield and grain protein content; to investigate the relationship between protein content and grain yield at two different latitudes within the Mediterranean area; to analyse the contribution of cycle length, grain weight and chlorophyll content, to the characterization of environments and genotypes; and to assess whether genotypes combining both high and stable yield and high protein content could be detected within a set of 25 durum wheat genotypes cultivated in the Mediterranean region.

Materials and Methods

Eight experiments were conducted in 1998 and 1999 in two cereal growing zones of Spain (Ebro Valley in the north and Andalucía in the south), under both irrigated and rainfed conditions. The combination of latitude and moisture regime hereafter will be referred to as environment. Table 1 summarizes site description and agronomic details.

Twenty-five genotypes of durum wheat, *Triticum durum* L., including four Spanish commercial varieties, and 21 genotypes from the Eastern Mediterranean basin, were used in the experiments (Table 2). In each trial, genotypes were sown in a randomized complete-block design with four replications. The seed rate was adjusted for a density of 350 viable seeds/m^2 in the south and of 550 seeds/m^2 in the north. Plot size was 12 m^2 (six rows, 20 cm apart). Grain yield was determined on the basis of the harvested plot in all trials and corrected to a 12% moisture level. Grain protein content (PC) was determined in two blocks per trial, by means of the standard Kjeldahl method at Granada, and by near-infrared reflectance spectroscopy (NIRS), adjusted after calibration of the NIRS apparatus to the Kjeldahl results at Centre UdL-IRTA, Lleida. At both latitudes, the percentage of protein was calculated after multiplying Kjeldahl nitrogen by 5.7 and expressed on a dry weight basis. Protein determinations in both laboratories were analogous, since 98% of values differed by less than 1%. Test weight (TW), measured in a sample of 250 g per plot, is

Table 1: Site localization and agronomic details

	North				South			
	Irrigated		Rainfed		Irrigated		Rainfed	
Location	Gimenells		Canós		Granada		Ochíchar	
Coordinates	41°40′N 0°20′E		40°41′N 1°13′E		37°21′N 3°35′W		37°10′N 3°50′W	
Altitude (m)	200		440		650		720	
Soil characteristics:								
Classification	Mesic Calcixerolic Xerochrept		Fluventic Xerochrept		Typic Xerofluvent		Loamy Calcixerolic Xerochrept	
Texture	Fine loamy		Fine		Silty clay		Silty clay	
pH	8.1		8.3		8.0		8.2	
P (mg P/kg soil)	16		12		50		27	
K (mg K/kg soil)	134		184		88		210	
Organic matter (%)	2.40		2.10		2.01		1.86	
	1998	1999	1998	1999	1998	1999	1998	1999
Seasonal rainfall + irrigation (mm)	285 + 100	257 + 150	194	257	311 + 150	128 + 150	188	193
Average temperatures during grain-filling period:								
T_{max}	23.5	26.3	22.7	25.7	26.0	29.7	28.9	30.5
T_{mean}	17.2	19.2	16.3	19.2	19.2	21.9	21.3	21.6
T_{min}	11.5	12.0	10.3	13.2	12.4	14.5	13.8	12.7
Agronomic practices:								
Fertilizers (kg/ha)								
N (seed bed + top dressing)	45 + 100	24 + 100	32 + 84	32 + 60	60 + 20	75 + 20	45 + 20	49 + 20
P_2O_5	115	45	60	60	60	75	45	49
K_2O	120	45	60	60	60	75	45	49
Sowing time	23 Nov. 1997	10 Nov. 1998	17 Nov. 1997	3 Nov. 1998	11 Dec. 1997	15 Dec. 1998	12 Jan. 1998	25 Nov. 1998
Days to anthesis	157	172	163	184	136	138	122	166

Table 2: Genotypic means of grain yield, protein content and plant analysis development (SPAD) values in the flag leaf at anthesis across two seasons (1998 and 1999), two latitudes (north and south) and two moisture regimes (irrigated and rainfed) for 25 durum wheat genotypes grown in Spain. The origin of the genotypes is also given

Genotype	Genotype code	Grain yield (kg/ha)	Protein content (%)	SPAD at anthesis
From Eastern Mediterranean Region				
'Awalbit'	Awa	3816	15.0	52.7
'Bicrecham-1'	Bic	4247	13.6	50.9
'Chacan'	Cha	3848	13.4	45.4
'Chahra-1'	C88	4091	14.5	53.6
'Zeina-1'	Ze1	4635	13.1	47.9
'Haurani'	Hau	3032	14.8	52.1
'Moulchahba-1'	Mol	4283	13.5	50.2
'Korifla'	Kor	4428	13.7	50.6
'Krs/Haucan'	Krs	3701	14.1	48.5
'Lagost-3'	Lag	4089	14.5	51.9
'Lahn/Haucan'	Lah	4358	14.0	50.9
'Massara-1'	Mas	4120	14.2	53.8
'Mousabil-2'	Mou	4030	14.6	49.3
'Omlahn-3'	Oml	3955	13.5	50.7
'Omrabi-3'	Omb	4042	15.1	55.2
'Omruf-3'	Omf	3930	13.3	52.0
'Quadalete'/ 'Erp'/'Mal'	Qua	3567	13.9	54.0
'Sebah'	Seb	3655	15.0	51.6
'Stojocri-3'	Sto	4049	14.1	50.8
'Waha'	Wah	4362	14.9	53.4
'Zeina-2'	Ze2	4152	13.8	48.5
Spanish commercial varieties				
'Altar-aos'	Alt	4285	14.1	55.2
'Jabato'	Jab	4048	14.7	53.9
'Mexa'	Mex	4159	13.1	50.7
'Vitrón'	Vit	3968	14.3	51.2
LSD (0.05)		504	1.0	1.4

expressed as kg/hl. Thousand-kernel weight (TKW) was calculated from the weight of 200 grains per plot. Thermal duration of vegetative plus reproductive (TD_{VR}) and grain-filling periods (TD_{GF}) were determined as cumulative growing degree-days (GDD) from sowing to anthesis (growth stage 65, Zadoks et al. 1974), and from anthesis to physiological maturity (growth stage 91), respectively. Chlorophyll content at anthesis (growth stage 65, $SPAD_{65}$; Soil–plant analysis development) and at milk-grain stage ($SPAD_{73}$) were recorded by a portable chlorophyll meter (Minolta SPAD-502, Osaka, Japan) on the flag leaf of five plants taken at random in each plot.

Combined analyses of variance (ANOVA) were performed over trials. Least significant difference (LSD) values were calculated at the 5% probability level. A regression technique was used when appropriate. Table Curve 2D (Jandel Corp. 1994) was used to adjust the mathematical function that best fitted the relationship between yield and protein content. Principal component analyses (PCA) were performed on the correlation matrix, calculated on the mean data of all the replicates. Stability parameter was calculated as the slope of genotype regression on environment mean yield according to Finlay and Wilkinson's (1963) joint regression analysis. The SAS-STAT package (SAS Inc. 1996) was used for all the calculations.

Results

Environmental and genotypic effects on yield and protein content

Results of the ANOVA for yield and protein content are summarized in Table 3. For grain yield, environmental effects were much more important than those of genotypes. Latitude and moisture regime together explained 62% of total variance observed. Grain yield ranged from 2353 kg/ha in the southern rainfed environment to 6275 kg/ha in the northern irrigated trials (Table 4).

Table 3: Mean squares of the combined analysis of variance for grain yield and protein content of 25 durum wheat genotypes grown in the north and the south Spain during 1998 and 1999

Source of variation[1]	df	Yield × 10^5	df	Protein content
Y	1	1315.02***	1	11.83
L	1	4219.74***	1	943.82***
L × Y	1	1034.74***	1	10.04
MR	1	12186.46***	1	147.63**
Y × MR	1	35.70	1	10.66
L × MR	1	626.76***	1	0.08
L × Y × MR	1	213.24*	1	42.65
Block (L × Y × MR)	24	39.46***	8	11.74***
G	24	33.62***	24	5.94***
Y × G	24	8.0	24	2.39*
L × G	24	10.95**	24	2.69*
L × Y × G	24	9.63*	24	4.33***
MR × G	24	17.56***	24	1.19
Y × MR × G	24	6.20	24	1.89*
L × MR × G	24	11.01**	24	1.09
L × Y × MR × G	24	8.44	24	1.67*
Residual	576		192	
Total	799		399	

*,**,*** Significant at P = 0.05, P = 0.01 and P = 0.001, respectively.
[1] G = Genotype; L = latitude (north and south); MR = moisture regime (irrigated and rainfed); Y = year.

For protein content the effect of latitude was the greatest determinant and explained 45% of total variation. The genotype effect was highly significant despite it explaining only 6.9% of the total variance in protein content. The mean values of grain yield and grain protein content for the 25 genotypes are shown in Table 2.

Relationships between yield and protein content

The relationship between yield and protein content was studied separately in the north and in the south because latitude had a major role in explaining differences in these two traits. Regression of grain protein content on grain yield at both latitudes resulted in negative associations, which best fitted a non-linear asymptotic equation, highly significant both in the north and in the south (Fig. 1). The slope of the curves tended to be very low for yield values of about 4000 and 5000 kg/ha and above in the south and in the north, respectively.

Environment characterization

Differences between environments appeared not only for grain yield and protein content, but for the other traits analysed (Table 4). A significant relationship was found between protein content and SPAD values at anthesis under rainfed conditions, but not under irrigated conditions (Fig. 2).

To detect the combination of variables that best explained the existing variability, PCA was carried out on the correlation matrix based on the eight traits shown in Fig. 3. The first three PCA axes accounted for 78.6% of total variance: 36.5, 26.3 and 15.8% for axes 1, 2 and 3, respectively.

Axis 1 measures cycle length and grain quality. Towards its positive direction, there is a joint increase of thermal duration of TD_{GF}, TKW and PC. Toward its negative direction, there

Table 4: Mean values of the traits studied in 25 durum wheat genotypes for each latitude and moisture regime combination

Latitude	Moisture regime	Yield (kg/ha)	Protein content (%)	Kernel weight (g)	Test weight (kg/hl)	Cycle length until anthesis (GDD)[1]	Grain filling duration (GDD)[1]	Chlorophyll content at anthesis (SPAD units)[2]	Chlorophyll content at milk-grain stage (SPAD units)[2]
North	Irrigated	6275	15.04	50.6	81.9	1344	721	51.1	49.4
	Rainfed	3246	16.28	49.8	82.0	1423	657	49.1	49.4
South	Irrigated	4262	11.97	38.8	80.3	1353	586	54.2	45.4
	Rainfed	2353	13.16	41.2	83.3	1597	624	51.4	48.8
LSD (0.05)		202	0.42	1.1	0.4	10	10	0.6	0.7

[1] GDD = Growing degree-days.
[2] SPAD = Soil–plant analysis development.

was an increase in thermal duration of the vegetative and reproductive periods (TD_{VR}) and chlorophyll content at anthesis ($SPAD_{65}$).

Axis 2 measures cycle length until anthesis, grain yield and test weight. A positive relationship appeared between TD_{VR} and TW, and negative associations between both traits and yield. The negative correlation between yield and TD_{VR} indicates that the longer the vegetative and reproductive developmental phases, the lower the yield.

Axis 3 measures chlorophyll content. This axis is represented by SPAD values at the milk-grain stage and anthesis, with a negligible influence of other variables.

The points plotted on the plane determined by the first two axes (Fig. 3b) are grouped in clusters related to latitude and moisture regime. Axis 1 properly discriminates between latitudes, whereas axis 2 discriminates between moisture regimes. TD_{GF}, TKW, PC and grain yield were higher in the north than in the south, whereas cycle length until anthesis and, to a certain extent, chlorophyll content at anthesis, were higher in the south. Under irrigated conditions, yield and chlorophyll content at anthesis were higher than in the rainfed environment, but test weight and cycle length until anthesis were greater in the absence of irrigation. Environments could not be separated by the chlorophyll content of the genotypes, but genotypic differences were consistent across environments (see Table 2 for genotype means of $SPAD_{65}$ across environments).

Genotype characterization

Genotypic differences were assessed by means of PCA and stability analysis. PCA was performed on genotype mean values across environments of the eight traits shown in Fig. 4a. This analysis revealed significance mostly of two PCA axes, which accounted for 54.7% of total variance. Principal component 1 was related mainly to chlorophyll content ($SPAD_{65}$ and $SPAD_{73}$), PC, and TD_{GF} towards its negative direction, and to cycle length until anthesis (TD_{VR}) towards its positive direction. Chlorophyll content at anthesis and at milk-grain stage appeared to be strongly correlated with protein content ($r = 0.54^{**}$ and $r = 0.60^{**}$, respectively). Again, an inverse relationship appeared between TD_{VR} and TD_{GF} ($r = -0.85^{***}$). Increases in principal component 2 are related to increases in TD_{GF} and decreases in cycle length until anthesis and PC. Genotypes clustered in four groups in the plane formed by the first two PCA axes (Fig. 4b).

The relationship between genotype mean yield and yield stability is shown in Fig. 5a. According to Finlay and Wilkinson (1963), a genotype may be considered stable when its regression slope is close to 1. Thus, from this figure, it may be inferred that 'Moulchahba-1', 'Zeina-2', 'Bicrecham-1', 'Jabato', 'Lagost-3' and, to a lesser extent, 'Massara-1', 'Lahn'/'Haucan', 'Mexa' and 'Vitron' were high- to medium-yielding and stable genotypes. 'Korifla', 'Altar-Aos' and 'Zeina-1' were high-yielding genotypes, with a positive response to favourable environments. In contrast, 'Haurani' was the lowest-yielding genotype with specific adaptation to poor environments. The relationship between genotype mean PC and grain-yield stability, shown in Fig. 5b allows one to separate, within stable genotypes, those having high and low PC. 'Waha', 'Jabato', 'Lagost-3', 'Massara-1' and 'Vitrón' had high and stable yield, and high PC.

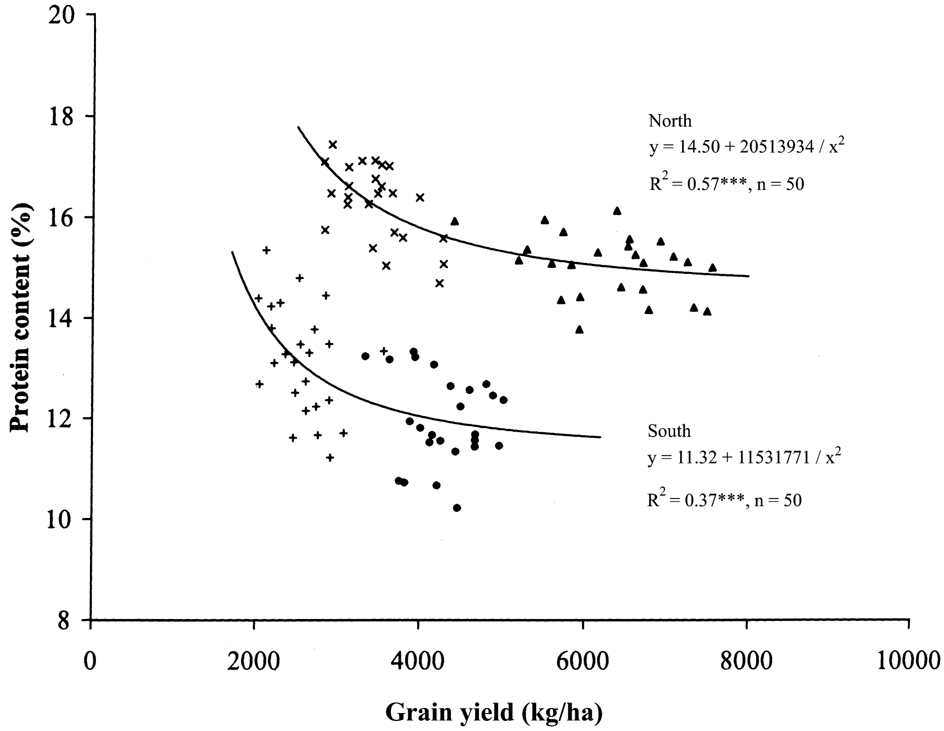

Fig. 1: Regression of grain protein content on grain yield in 25 durum wheat genotypes grown in the north (▲, irrigated and ×, rainfed) and the south (●, irrigated and +, rainfed) of Spain during two seasons. *** Significant at P = 0.001

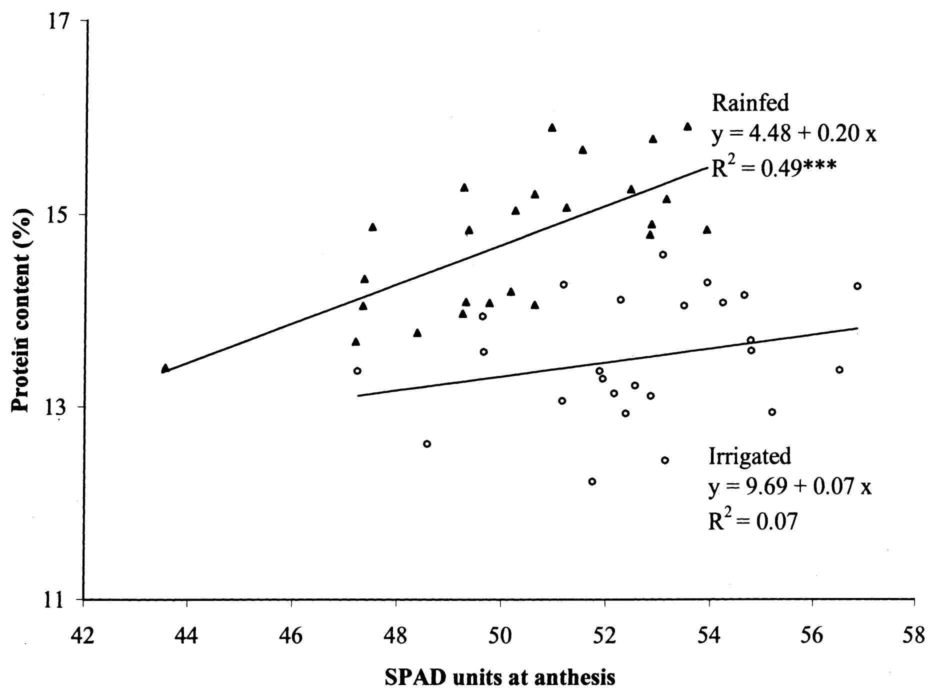

Fig. 2: Relationship between grain protein content and chlorophyll content in the flag leaf at anthesis, measured as soil–plant analysis development (SPAD) units, under rainfed (▲) and irrigated (○) conditions. Points represent genotype means over two seasons and two latitudes. *** Significant at P = 0.001

Discussion

Wide phenotypic variability was found for grain yield and protein content, suggesting the potential for selecting the best genotypes in terms of adaptation and grain quality. Genotypic variation in protein content can be attributed to differences in nitrogen uptake from the soil before anthesis, in activity of the root system during grain filling, in efficiency of translocation of nitrogenous substances from vegetative tissues to the grains and in harvest index (Kramer 1979, Jenner et al. 1991). As reported in many studies (Peterson et al. 1992, Novaro et al. 1997, Uhlen et al. 1998), environmental conditions had a larger effect on grain yield and protein content than did genotype, while the interaction genotype–environment proved less important.

Grain-filling duration, TKW and PC were the traits that best distinguished between latitudes. Despite the longer cycle until anthesis (in calendar terms) in the northern latitude, the highest temperatures recorded in the south led to greater thermal duration until anthesis. It is well known that the higher the mean temperature during grain growth, the shorter the duration (Henry and Kettlewell 1996). However, the rapid

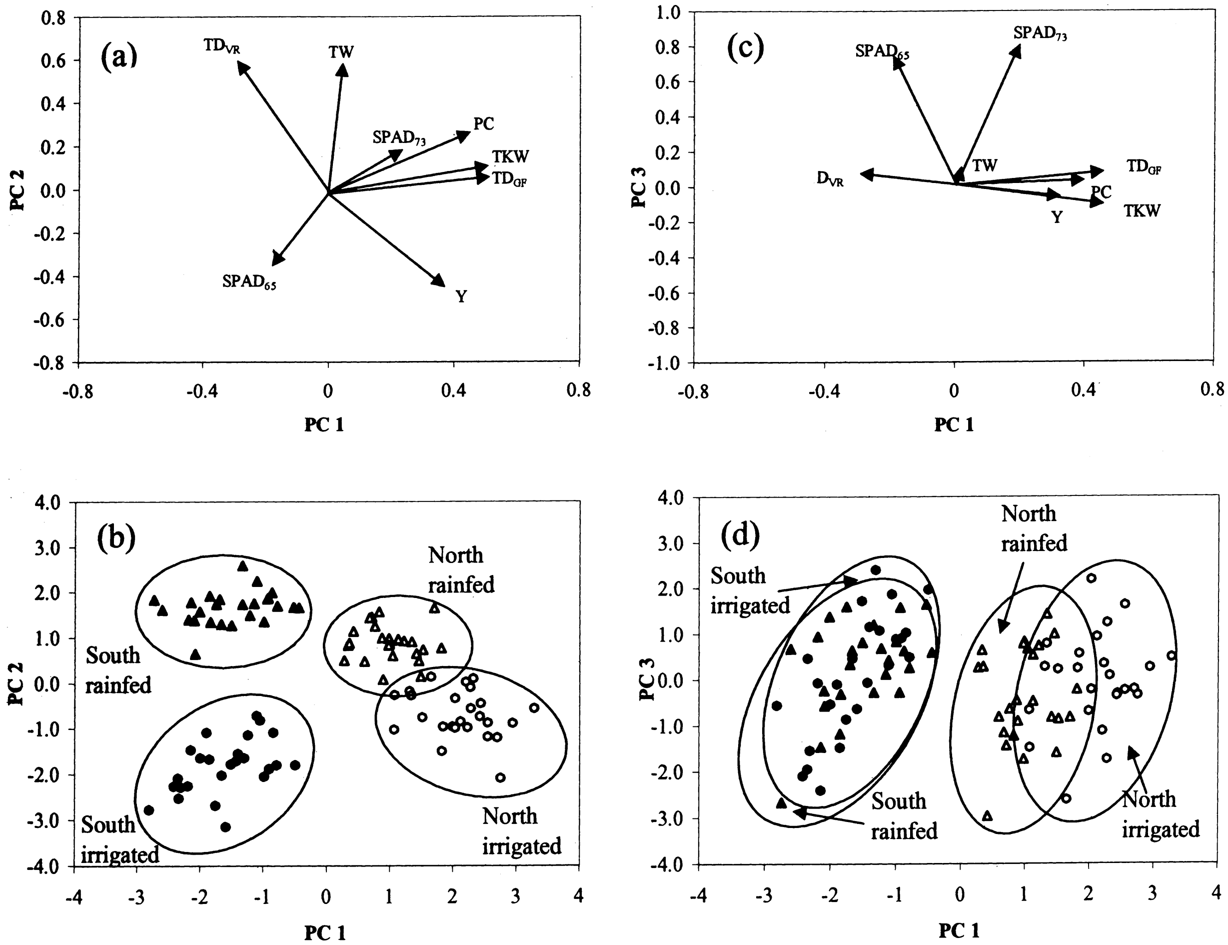

Fig. 3: Principal component analysis (PCA) projections on axes 1 and 2 (a,b), and axes 1 and 3 (c,d), accounting for 62.8% and 52.3% of total variance, respectively. In (a) the eigenvalues of the correlation matrix are symbolized as vectors representing the traits that most influence each axis (see Materials and Methods for definitions of the variables). In (b) and (d) the 100 points representing genotypic means for both latitude and moisture regimes (○, north, irrigated; △, north, rainfed; ●, south, irrigated; ▲, south, rainfed) are plotted on the plane determined by axis 1 and 2 (b) and 1 and 3 (d)

increase of temperatures during spring in the lowest latitude, and the delayed sowing in the south compared with the north, probably shortened the duration of grain filling, as reported in other cereals (Royo et al. 2000). The strong correlation between grain-filling duration and kernel weight may be explained by the dependence of final mature grain weight on the rate of dry weight accumulation and the length of the dry weight accumulation period (Nass and Reiser 1975, Jones et al. 1979). This could partially explain why TKW was higher in the north than in the south. The greater nitrogen availability in the north probably also contributed to a rise in TKW, since nitrogen absorbed after the booting stage may increase grain weight (Spiertz and van der Haar 1978).

Differences between northern and southern conditions in protein content may also be partly attributed to the different fertilization management in both regions. Thus, more than 70% of nitrogen was applied to the crop at the jointing stage in the north, leading to very high protein content in the grain. In this study the latitude effect is confounded by the effect of nitrogen management. Kramer (1979) and Campbell et al. (1981) reported that nitrogen applied near heading tends to increase protein content, but not grain yield. Leaf senescence was earlier in the south than in the north, probably because senescence of the flag leaf was delayed in the north by the application of nitrogen fertilizer at jointing (Thomas et al. 1978).

In this study, the moisture regime effect is mixed with the site effect. In the rainfed trials the length of the cycle until anthesis was longer, grain yield was lower, but grain test weight and protein content tended to be greater than under irrigated conditions. The tendency to produce higher protein contents under rainfed conditions than in the irrigated trials at both latitudes was probably a consequence of the higher temperatures and drought during grain filling under rainfed conditions (Wrigley et al. 1994, García del Moral et al. 1995). This is due to the fact that leaves are the main source of amino acids for grain protein synthesis in temperate cereals. Pigments and the enzyme RuBisCo, the degradation of which is enhanced by the high temperatures and terminal drought at rainfed sites (Jenner et al. 1991, García del Moral et al. 1995, Fernandez-Figares et al. 2000) are principal sources of amino acids.

The negative relationships between protein content and grain yield could result from a dilution of nitrogen compounds when carbohydrate deposition increases throughout photosynthesis (Cox et al. 1986, Jenner et al. 1991). According to Campbell et al. (1981), the highest grain protein contents are usually found under adverse conditions for grain formation, since the production and translocation of compounds such as

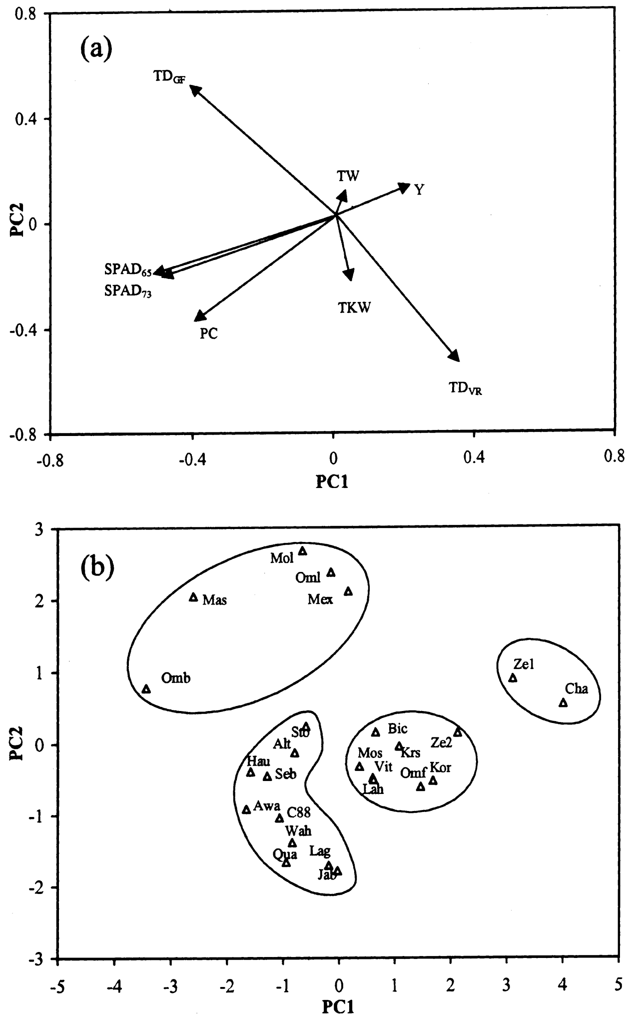

Fig. 4: Principal component analysis (PCA) projections on axes 1 and 2, accounting for 54.7% of total variance. In (a) the eigenvalues of the correlation matrix are symbolized as vectors representing the traits that most influence each axis (see Materials and Methods for definitions of the variables). In (b) the 25 points representing genotypic means are plotted on the plane determined by the first two axes. Genotype codes are given on Table 3

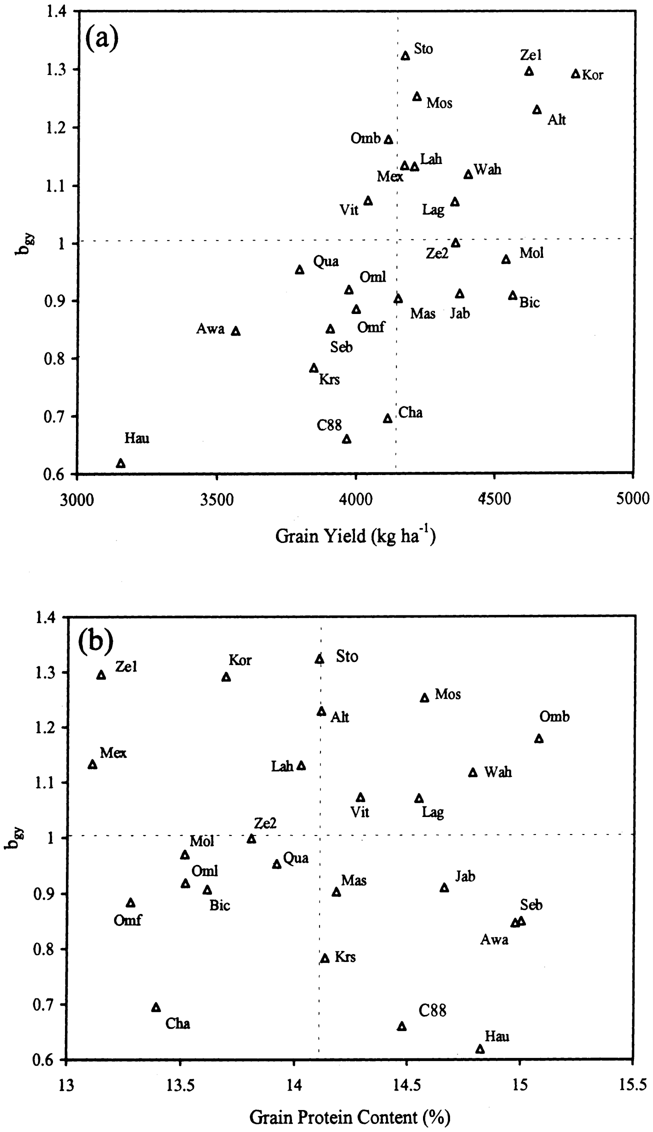

Fig. 5: Relationship between yield stability (b_{gy}: Finlay and Wilkinson's regression slope) and mean of 25 durum wheat genotypes grown at two latitudes, under two moisture regimes, during two seasons. a. grain yield; b. grain protein content. The minimum and maximum values of the root mean square for the regression of the different genotypes were 564 and 1072 kg/ha, respectively, for grain yield and 0.91 and 1.96%, respectively, for protein content. Genotype codes are given in Table 3

carbohydrates to the grain is more sensitive to adverse growing conditions than is protein accumulation. The competition in the transport of proteins and sugars to the grain of triticale has also been demonstrated recently (Fernandez-Figares et al. 2000). However, in the present study, a non-linear asymptotic equation better fitted the observed values than the generally used linear regression. These results support the view that it is possible to increase yield without diminishing grain protein content, as has been demonstrated for bread wheat (Loffler and Busch 1982, Stoddart and Marshall 1990, Gooding and Davies 1997), where breeding efforts have led to simultaneous increases of both grain yield and grain protein concentration, and mutant lines with higher protein content but similar yields to their mother lines have been developed (Ali 1995). Moreover, Cox et al. (1986) and Beninati and Busch (1992) reported good evidence for the existence of major genes conferring increased protein concentration without adverse effects on yield.

The significant correlation found between grain protein content and SPAD units at anthesis (Miller et al. 1999) could indicate a higher dependence of protein deposition on leaf nitrogen under drought stress than under irrigated conditions. The results of this study suggest that genotypes with high protein content may be detected in breeding programmes by measuring the chlorophyll content at anthesis under drought stress conditions. Measurements with the portable field unit (SPAD) are fast and simple, enabling cheap, quick screening of lines.

The study of the grain-yield stability showed different types of adaptation strategies among durum wheat genotypes, ranging from lines specifically adapted to high-yielding environments (such as 'Korifla', 'Altar-Aos' and 'Zeina-1'), to those specifically adapted to low-yielding environments (such as 'Haurani'). However, for a breeding programme, emphasis should be given to those genotypes combining both general adaptation for grain yield and acceptable protein content. In this study, those requirements were fulfilled by the genotypes 'Jabato', 'Waha', 'Lagost-3', 'Massara-1' and 'Vitrón'.

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