

Variation for yield and quality components in durum wheat backcross inbred lines derived from ssp. *dicoccoides*

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Variation der Ertrags- und Qualitätskomponenten von Durumweizen-Rückkreuzungsinzuchtlinien der ssp. *dicoccoides*

1. Introduction

The use of wild germplasm as a source of qualitative and quantitative trait allelic variation is important for crop improvement. The wild tetraploid wheat *Triticum turgidum* (L.) Thell. ssp. *dicoccoides* (Korn.) Thell. shows particular promise as a donor of useful genetic variation for several traits, including disease resistance, drought tolerance, yield components, protein quality and quantity (FELDMAN and MILLET, 1993). However, wild germplasm contains both favourable traits and many commercially unacceptable characters such as fragile spikes, small seeds, tallness, and low grain yield. In early interspecific generations, plants are segregating for many agronomically important traits that may interact with the trait being introgressed and confound measurements. Backcrossing has been extensively used in self-

pollinating crops to transfer simply inherited characters, such as disease resistance, to cultivars which are deficient only in the characters being transferred. The main advantage of backcrossing in breeding for simply characters has been that it enables to reconstitute the genotype of the recurrent parent except for desirable genes and small chromosomal segment adjacent to these genes from the donor parent. The application of backcrossing to the improvement of quantitative characters has been limited mainly because of the low heritability of these characters and the difficulty of transferring, simultaneously, relatively large number of genes. In contrast to more traditional procedures of wheat breeding, the backcross inbred line method, first described by WEHRHAHN and ALLARD (1965), produces backcross inbred lines (BILs) that can be tested in replicated trials over environments prior of selection. Some experimental evidences for grain yield in

Zusammenfassung

Die Verwendung von Wildformen der Allelvariation von quantitativen Merkmalen ist wichtig für Züchter und Sortenentwicklung. Der wilde tetraploide Weizen *Triticum turgidum* (L.) Thell. ssp. *dicoccoides* (Korn.) erweist sich teilweise als ein vielversprechender Spender von wertvoller genetischer Variation für verschiedene Merkmale, wie Krankheitsresistenz, Trockentoleranz, Ertragskomponenten, Eiweißmenge und -qualität eingeschlossen. Untersucht wurde die Effektivität der Inzucht-Rückkreuzungsmethode zur Einkreuzung quantitativer Merkmale der Subspezies *dicoccoides* (als Spenderelter) in die Kulturdurumweizensorte cv. ‚Latino‘ (als rekurrenter Elter). Eine Inzucht-Rückkreuzungspopulation wurde auf der BC₃-Stufe erzeugt und über zwei Jahre (2001 und 2002) an zwei Standorten (Valenzano und Gaudiano) geprüft auf Eiweißgehalt der Körner, Kornertrag, Hektolitergewicht, Tausendkorngewicht, Pflanzenhöhe und Reifezeit. Die Variation innerhalb der Rückkreuzungsinzuchtlinien (BIL) wurde für alle Merkmale beobachtet. Signifikante Linie x Umwelt-Wechselwirkungen legen nahe, dass Genotyp X Umwelt-Wechselwirkungen für jede Eigenschaft wichtig sein dürften. Deutliche phänotypische Korrelationen zwischen Kornertrag und Eiweißgehalt wurden geschätzt. 6 überragende Rückkreuzungsinzuchtlinien wurden wegen ihres höheren Eiweißgehaltes und eine wegen ihres höheren Kornertrages selektiert, wobei gleichzeitig die erwünschten Eigenschaften des rekurrenten Elters erhalten blieben und keine anderen unerwünschten Merkmale des Spenderelthers auftraten. Die Rückkreuzungsinzuchtlinien und die im Zuge der Studie gesammelten Informationen könnten hilfreich sein sowohl für das Kartieren neuer Allele von agrarisch wichtigen quantitativen Merkmalen als auch für die Festlegung von Strategien zur Erzeugung von Elite-Hartweizen-Linien durch markergestützte Selektion.

Schlagnworte: Hartweizen, Rückkreuzungsinzuchtlinien, Kornertrag, Eiweißgehalt.

Summary

The use of wild germplasm as a source of quantitative trait allelic variation is important for crop improvement and breeders. The wild tetraploid wheat *Triticum turgidum* (L.) Thell. ssp. *dicoccoides* (Korn.) shows particular promise as a donor of useful genetic variation for several traits, including disease resistance, drought tolerance, yield components, protein quantity and quality. The effectiveness of the inbred backcross method for introgressing quantitative traits from the ssp. *dicoccoides* (donor parent) into the cultivated durum wheat cv. 'Latino' (recurrent parent) was examined. An inbred backcross population at BC₃ level was developed and tested over two years (2001 and 2002) at two locations (Valenzano and Gaudio) for grain protein content, grain yield, test weight, 1000-grain weight, plant height and heading time. Variation among backcross inbred lines (BILs) was observed for all traits. Significant line x environment interactions suggest that genotype x environment effects may be important for every traits. Large phenotypic correlations between grain yield and related traits and between grain yield and protein content were estimated. Six superior BILs were selected for increased protein content and one BIL for increased grain yield, while retaining the desirable agronomic characteristics of the recurrent parent and without other undesirable characteristics of the donor parent. The backcross lines and the information gathered during this study will be useful for mapping novel alleles for agriculturally important quantitative traits and will be exploited to formulate strategies for producing elite durum lines by marker-assisted selection.

Key words: durum wheat, ssp. *dicoccoides*, backcross inbred lines, grain yield, protein content.

maize (DUVICK, 1974), oat (LAWRENCE and FREY, 1975) and spring rape (THURLING, 1982), large leaf area (BERDAHL et al., 1972) and yield components (GRAFIUS et al., 1976) in barley, seed protein and nitrogen fixing ability in common bean (SULLIVAN and BLISS, 1983; ST. CLAIR and BLISS, 1991), fruit mass in cucumber (OWENS et al., 1985), soluble solids (TRIANO and ST. CLAIR, 1995) and insect resistance (HARTMAN and ST. CLAIR, 1998) in tomato, has indicated that backcrossing may be effectively employed in the improved of continuous variation traits. The development of molecular markers and the derived molecular maps (see review by PATERSON, 1998), and the recently proposed strategy for molecular breeding, referred to as advanced backcross QTL (AB-QTL) analysis (TANKSLEY and NELSON, 1996), have shown that the backcrossing method has considerable potential for the genetic analyses of quantitative traits and as a method of breeding higher yielding and quality crop varieties (TANKSLEY et al., 1996; FULTON et al., 1997; BERNACCHI et al., 1988a, b; XIAO et al., 1998).

This study was initiated to introgress alleles for high grain protein content from *Triticum turgidum* ssp. *dicoccoides* into more adapted and agronomically acceptable durum wheat germplasm by means of the BIL method, and to identify superior BILs. Others objectives were to estimate the phenotype, genotype, environmental, and genotype x environment interaction variances as well as the heritability of protein content, grain yield and related traits in a set of backcross lines, and to evaluate the consistency of QTLs effects across environments.

2. Materials and Methods

A population of 92 BILs was developed using a procedure similar to that of WEHRHAHN and ALLARD (1965). The semi-dwarf and high yielding cultivar 'Latino' of durum wheat was used as a recurrent parent, and the accession MG29896 of *Triticum turgidum* (L.) Thell. ssp. *dicoccoides* (Korn.) was used as donor parent because of its high grain protein content and the acceptable seed size, respectively. The F₁ generation was produced in 1991. Three successive backcrosses were made to cv. 'Latino' followed by four generation of self-pollination. After the first backcross, 120 random BC₁ plants were chosen to initiate backcross inbred lines. No selection was applied in any generation, and plants were chosen randomly for additional backcrossing or selfing. However, some plants were lost in the subsequent generations and a total of 92 BC₃F₅ lines were obtained and multiplied to have sufficient seed for use in replicated trials.

The BIL population was evaluated in southern Italy at Valenzano (Bari) and Gaudio (Potenza) for two years (2001–2002). A randomized complete block design with three replications and 2 m² (in 2001) or 5 m² (in 2002) plots with plants grown under normal field conditions (350 seeds/m²) was used. Each block contained one plot of each BIL, three plots of the recurrent cv. 'Latino'. Additionally, one plot per block of the accession MG29896 of the ssp. *dicoccoides* was included for observation both years. There was a 30-cm break containing no plants between

each plot. During the grow season, standard cultural practices were used.

Heading date was recorded for each plot when 70 % of plants had flowered and heading time expressed as number of days from the 1st of March. Plant height was taken from the base to the top of the spike, excluding awns. Plots were harvested with a small plot combine and grain yield was expressed in terms of t/ha on a 13 % moisture basis. A 15-g seed sample per plot was used to determine 1000-grain weight. Test weight was measured using the Shopper chondrometer. Protein percentage was evaluated on a 2-g sample of whole-meal flour by near-infrared reflectance spectroscopy and expressed on a 13 % moisture basis.

Each year-location combination was treated as an environment in the subsequent statistical analyses of grain protein content, grain yield per area, test weight, 1000-grain weight, plant height and heading time. Standard procedures for analysis of variance were used to partition the total variance into environments, BILs, BILs x environment interaction, and error, by taking both factors as random for each trait. Genetic variance and broad-sense heritability (line mean basis) were obtained using variance component estimates. Pearson phenotypic correlation coefficients were calculated between traits in each environment and across environments.

Dunnett's t test at a probability level of 0.05 and 0.01 was used to test the difference between each BIL and the recurrent parent cv. 'Latino'. Given the highly significant BIL x environment interaction effects in the combined analysis across environments, the Dunnett's difference for the pairwise comparisons between the mean values of each BIL and the cv. 'Latino' was calculated using the BIL x environment mean square. Superior BILs for protein content and grain yield were selected when the difference between each BIL

and the recurrent parent cv. 'Latino' was significant at 0.05P in at least three environments or at 0.01P in at least two of the four environments.

3. Results

The analysis of variance revealed highly significant differences among BILs for all measurements of grain protein content, grain yield per area, test weight, 1000-grain weight, plant height and heading time in each of the four field trials conducted at Valenzano and Gaudio in 2001 and 2002 (data not shown). When combined over environments, environments, BILs, and BIL x environment effects were highly significant for all traits (Table 1). The means of parental lines and means and ranges of the BIL population, variance components and broad-sense heritability estimates for each trait over the four environments are presented in Table 2. The frequency distribution of the 92 BILs for each trait is shown in Fig. 1. The recurrent parent (cv. 'Latino') was significantly different from the donor parent (ssp. *dicoccoides* acc. MG29896) for each measured trait in each environment and across environments. It always had significant lower protein content and higher grain yield per area than ssp. *dicoccoides*. It also had higher test weight and 1000-grain weight, shorter height and flowered earlier. Differences in mean values and variances of parental lines and BIL population were observed among the trials conducted in different years and locations presumably due to the different climatic conditions. As no selection was imposed during the development of the population, the BIL population means for each trait, as expected, were toward the 'Latino' parent in all trials. BIL variance and broad sense heritability estimates for

Table 1: Analysis of variance of a backcross inbred line (BIL) population derived from the cross *Triticum turgidum* ssp. durum cv. 'Latino' x *T. turgidum* ssp. *dicoccoides* acc. MG29896. Data from a randomized complete block design of BILs grown in 2001 and 2002 in field plots at Valenzano (Bari) and Gaudio (Potenza)

Tabelle 1: Varianzanalyse der Rückkreuzungsinzuchtlinienpopulation aus der Kreuzung von *Triticum turgidum* ssp. durum cv. 'Latino' x *T. turgidum* ssp. *dicoccoides* acc. MG29896. Daten stammen von einer randomisierten, vollständigen Blockanlage von Rückkreuzungsinzuchtlinien aus den Jahren 2001 und 2002 auf Versuchspartzellen in Valenzano (Bari) und Gaudio (Potenza)

Source	Mean squares						
	df	Grain protein content	Grain yield per area	Test weight	1000-grain weight	Plant height	Heading time
Environments	3	726.731***	631.907***	1740.184***	2508.502**	20730.066***	31753.447***
Blocks (environments)	8	4.891	8.872	17.463	260.376	401.778	10.320
BILs	95	7.268***	8.216***	19.096***	86.748***	746.833***	32.191***
BILs x Environments	285	1.218***	1.107***	2.045***	21.288***	38.236***	5.172***
Error	760	0.383	0.362	0.420	14.009	13.568	1.269

*, **, *** Significant difference at 0.05P, 0.01P and 0.001P, respectively

Table 2: Means of recurrent parent (cv. 'Latino') and donor parent (MG29896), and means, ranges, variances and heritability for grain protein content, grain yield and related characters of a backcross inbred line (BIL) population grown at Valenzano and Gaudio in 2001 and 2002
 Tabelle 2: Mittelwerte des rekurrenten Elters (cv. 'Latino') und des Spenderelers (MG29896) sowie Mittelwerte, Streuungen und Heritabilität beim Eiweißgehalt, Korntrag und damit verbundenen Eigenschaften einer in Valenzano und Gaudio 2001 und 2002 kultivierten Rückkreuzungszuchtlinienpopulation

Line or population	Grain protein content (%)	Grain yield per area (t/ha)	Test weight (kg)	1000-grain weight (g)	Plant height (cm)	Heading time (days)
'Latino'	13.0	5.75	85.3	49.4	79.0	42.4
MG 29896	16.4	1.71	77.9	46.7	117.0	46.7
BIL population (means)	13.3	5.56	84.5	49.0	83.2	41.3
(ranges)	(12.2-16.4)	(1.96-6.80)	(80.3-86.4)	(43.9-55.4)	(72.3-117.0)	(39.3-49.0)
C.V.(%)	5.57	10.94	0.92	7.64	4.42	2.71
Genotypic variances	0.504	0.592	1.421	5.455	59.050	2.252
Heritability	0.80	0.84	0.87	0.73	0.94	0.81

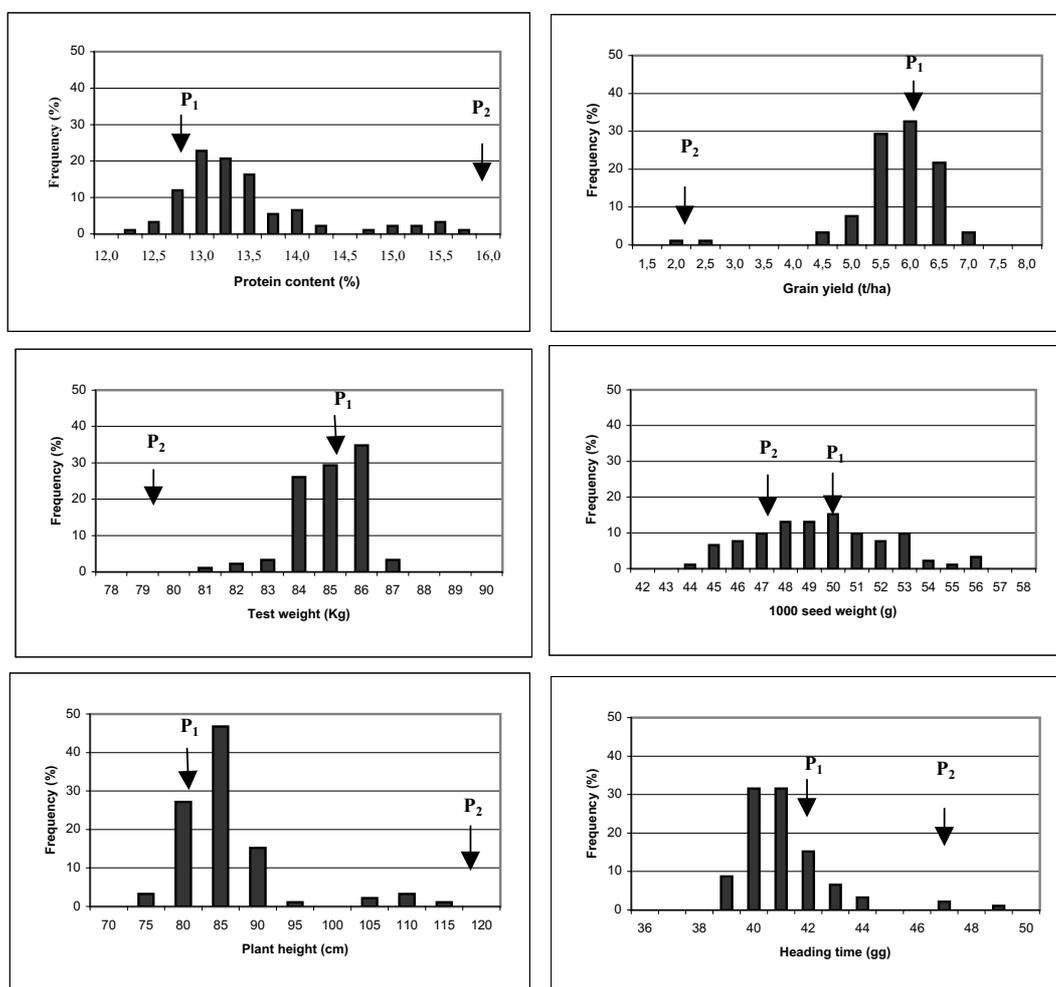


Figure 1: Distributions of backcross inbred lines for protein content, grain yield and related traits. Histograms include observations from four environments. The mean values of the recurrent parent cv. 'Latino' (P₁) and the donor parent ssp. *dicoccoides* acc. MG29896 (P₂) are indicated by arrows.

Abbildung 1: Verteilung der Rückkreuzungszuchtlinien hinsichtlich Eiweißgehalt, Korntrag und damit verbundenen Eigenschaften. Die Histogramme beinhalten Beobachtungen unter 4 Umweltbedingungen. Die Mittelwerte des rekurrenten Elters cv. 'Latino' (P₁) und des Spenderelers ssp. *dicoccoides* acc. MG29896 (P₂) sind durch Pfeile dargestellt.

Table 3: Correlation coefficients (r) between traits in the BIL population grown in 2001 and 2002 in field plots at Valenzano and Gaudio
 Tabelle 3: Korrelationskoeffizienten zwischen Merkmalen der 2001 und 2002 auf Versuchspartzen in Valenzano und Gaudio kultivierten Rückkreuzungsinzuchtlinienpopulation

	Grain yield per area	Test weight	1000-grain weight	Plant height	Heading time
Grain protein content	-0.64***	-0.11***	0.17***	-0.25***	-0.42***
Grain yield per area		0.85***	0.04	0.29***	0.35***
Test weight			0.44***	0.06	0.02
1000-grain weight				-0.04	-0.18***
Plant height					0.10***

*, **, *** Significant difference at 0.05P, 0.01P and 0.001P, respectively

protein content and grain yield, as measured on entry mean basis, were moderately high.

Minimal differences were observed among the phenotypic correlations of the traits in the four environments; therefore, only phenotypic correlations across environments are reported in Table 3. Significant positive correlations were observed for grain yield per area with test weight, plant height and heading time, but not with 1000-grain weight. Grain protein content was negatively correlated with grain yield per area, test weight, plant height and heading time, and positively correlated with 1000-grain weight.

Given the significant line \times environment interactions and the inherently large effects of the environment on grain yield and protein content, BIL performance was compared with the recurrent parent (cv. 'Latino') by the Dunnett's t test at significant levels of 0.05 and 0.01P. The grain char-

acteristic data for all BILs in each of the four environments were analysed but only the characteristics of the superior BILs are presented. Table 4 shows the performance of the selected BILs with significantly higher protein content than 'Latino' either at 0.05P in at least three environments, or at 0.01P in at least two environments, and grain yield not significantly different from the recurrent parent. The percentage of phenotypic difference between the high protein content BILs and the mean of the recurrent parent ranged from 6.2 % to 17.7 % over environments. Two BILs (3BIL-69 and 3BIL-48) had higher protein content at four environments, three BILs (3BIL-85, 3BIL-29, 3BIL-41) in three environments, and one BIL (3BIL-31) only in two environments. No BIL had protein content as the donor parent MG29896 (16.4 %). Surprisingly, one BIL (3BIL-83) had significantly higher grain yield than 'Latino' at

Table 4: Performance of selected BILs for higher protein content and similar grain yield or higher grain yield and similar protein content than the recurrent parent cv. 'Latino' at single environments and across environments

Tabelle 4: Leistung von auf höheren Eiweißgehalt und ähnlichen Kornertrag oder höheren Kornertrag und ähnlichen Eiweißgehalt wie der rekurrente Elter cv. 'Latino' selektierten Rückkreuzungsinzuchtlinien innerhalb und zwischen den Umweltbedingungen

Lines	Environments				
	Valenzano 2001	Gaudio 2001	Valenzano 2002	Gaudio 2002	Across environments
	Grain protein content (%)				
3BIL-85	18.0**	13.3*	14.2**	15.4	15.3**
3BIL-69	16.1**	13.2*	13.9**	16.9**	15.0**
3BIL-48	15.3**	14.1**	13.8**	16.2**	14.9**
3BIL-29	15.0**	11.8	14.0**	17.3**	14.5**
3BIL-41	15.1**	11.5	13.3**	15.8**	13.9
3BIL-31	14.0	11.8	13.8**	15.6**	13.8
'Latino'	13.2	11.5	12.4	14.9	13.0
t Dunnett (0,05P)	1.5	1.7	0.6	0.6	1.1
t Dunnett (0,01P)	1.7	2.0	0.7	0.7	1.3
	Grain yield (t/ha)				
3BIL-83	7.97**	7.43**	7.70**	4.11	6.80*
'Latino'	6.10	6.20	6.86	3.83	5.75
t Dunnett (0,05P)	1.44	1.03	0.71	1.25	1.03
t Dunnett (0,01P)	1.68	1.20	0.83	1.47	1.20

*, ** Significant difference at 0.05P and 0.01P, respectively

0.01P in three environments, and protein content not different from the recurrent parent. The percentage of phenotypic difference between the selected 3BIL-83 and the mean of the cv. 'Latino' was 18.3 % over environments. Means of selected BILs relative to that of the recurrent parent are shown in Fig. 2 for all measured traits. Lines in each case are arranged in descending order of protein content from left to right. The dotted and straight lines are located from the central line representing the mean of cv. 'Latino' at a distance equivalent to the significant difference between the BILs and the cv. 'Latino' calculated with the Dunnett's t test at 0.05 and 0.01P, respectively.

4. Discussion

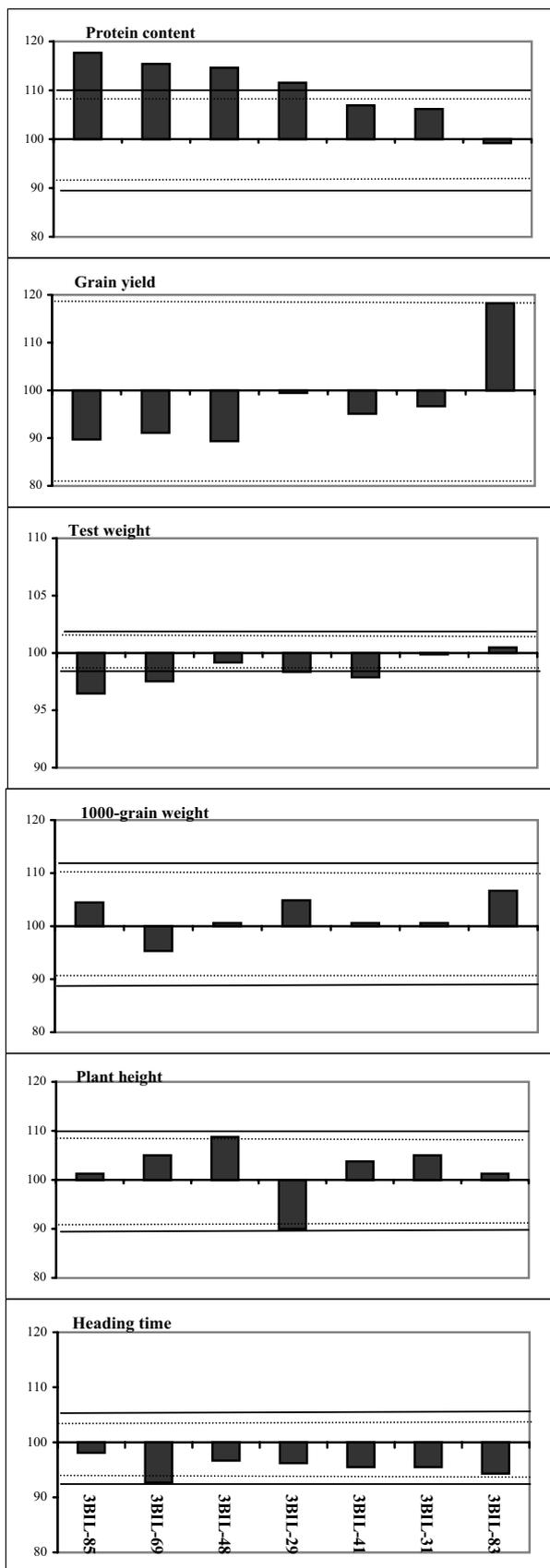
The relatively low heritability of quantitative traits makes it difficult to select for useful alleles from wild germplasm based on phenotypic evaluation of single plants and/or in single environment. The production of backcrossing lines is a laborious and sometimes expensive procedure, but the availability of BILs for quantitative traits facilitates isolation and identification of the genes involved in the inheritance of continuous variation (WEHRHAHN and ALLARD, 1965), as BILs can be evaluated in replicated trials in different environments to identify those which deviate significantly from the recurrent parent.

A set of 92 BILs was developed in durum wheat using the accession MG29896 of the ssp. *dicoccoides* as donor parent by three successive backcrosses followed by four successive generations of selfing. Since no selection pressure was applied during the backcrossing or selfing generations, the BIL population should consist of highly homozygous lines genotypically identical to the recurrent parent (93.75 %) and having a mean of 6.25 % of genome donor segments. Significant variation among BILs for protein content, grain yield and related traits were observed in field plot trials over four environments. BILs genetic variance was moderately high and can be attributed to alleles introgressed from the ssp. *dicoccoides*. A number of BILs had significantly higher protein content than the recurrent parent cv. 'Latino', most of them associated to poor grain yield or other unfavourable related traits. The high number of lines with high protein percentage can be attributed to the increased amount of accumulated proteins in relation to a constant amount of carbohydrates, or conversely to the reduced amount of carbohydrates while the total protein fraction remains unchanged. The results may be similar but the basis for the

altered protein percentage may be quite different and may reflect differences in the genetic control of synthesis and accumulation of the main constituent fractions of the grain (carbohydrates and proteins) (SULLIVAN and BLISS, 1983).

One of the major objectives of wheat breeding programs has been to increase grain protein content while maintaining or increasing the grain yield of cultivars released for commercial production. Simultaneous improvement in both traits has been limited by the generally negative relationship between protein content and grain yield components in wheats, as well as in barley, maize, oat and sorghum, with reported correlations ranging from -0.2 to -0.8 (see reviews by FREY, 1977, and SIMMONDS, 1995). As a result of these generally inverse relationships, high yielding wheat cultivars have generally low increase of grain protein content, especially when grown under fertile areas or under irrigation and where nitrogen is not a limiting factor. Since a significant negative correlation was observed between protein content and grain yield also in the present studies, precautions are necessary to avoid reduced grain yield when protein percentage is increased by selection. Six superior BILs have been selected for increased protein content, while retaining the desirable agronomic characteristics of the recurrent parent and without other undesirable characteristics of the donor parent, such as fragile spikes, hard glumes, low grain yield, late maturity, tallness (Fig. 2). Surprisingly, the BILs testing over four environments showed that one of these lines (3BIL-83) to be consistently higher yielding than the recurrent parent cv. 'Latino'. Although the donor parent, the acc. MG29896 of the wild tetraploid wheat ssp. *dicoccoides*, has proved to be consistently low yielding in a number of trials, it apparently possesses genes which when associated with the genetic background of the cv. 'Latino' cause a significant increase in grain yield. Similar results were observed for flowering time in spring rape (THURLING and VIJENDRA DAS, 1979), grain yield in oat (LAWRENCE and FREY, 1975), and fruit quality components in tomato (FULTON et al., 2000). These results were not predetermined by an appropriate choice of parental lines and were a result of the backcrossing procedure used where the unknown primary determinants of high yield differ between the parental lines.

The performance of the BILs was variable across environments. Only two BILs had significantly higher protein content than the recurrent parent in all trials tested. Since locations differ in environmental conditions, it is likely that some QTL-alleles interact with the environment resulting in the variable performance of the BILs across environments. Thus genes for increased protein content or increased grain



yield were transferred to a desirable agronomic background and suggested that improvement for quantitatively inherited traits could be attained using the BIL method. To facilitate marker-assisted selection for high grain protein content without significant losses in grain yield, DNA sample from each line is being analysed with microsatellite markers to locate quantitative trait loci (QTL) associated with protein content. The microsatellite polymorphism between the cv. 'Latino' of durum wheat and the accession MG29896 of the *ssp. dicoccoides* was found to be 50–55 %, much higher than within the cultivated wheat germplasm, permitting QTL mapping and the use of marker-assisted selection in wheat breeding (data not shown).

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Figure 2: Means of the selected backcross inbred lines (BILs) relative to that of the recurrent parent (cv. 'Latino') for protein content, grain yield and related traits. BILs in each case are arranged in descending order of protein content from left to right. The dotted and straight lines are located from the central line representing the mean of cv. 'Latino' at a distance equivalent to the significant difference between the BILs and the cv. 'Latino' calculated with the Dunnett's t test at 0.05 and 0.01, respectively.

Abbildung 2: Mittelwerte selektierter Rückkreuzungszuchtlinien in Relation zu denen des rekurrenten Elters (cv. 'Latino') für Eiweißgehalt, Kornertag und damit verbundene Eigenschaften. Die BIL sind von links nach rechts entsprechend ihrem Eiweißgehalt in abfallender Folge angeordnet. Die punktierten bzw. durchgezogenen Linien sind im Abstand zur die Mittelwerte der cv. 'Latino' repräsentierenden Zentrallinie äquivalent der signifikanten Differenz zwischen den Rückkreuzungszuchtlinien und der cv. 'Latino' bei einer Irrtumswahrscheinlichkeit für den Dunnett t-Test von 0,05 bzw. 0,01.

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