Theor Appl Genet (2005) 110: 688–695
DOI 10.1007/s00122-004-1894-3

ORIGINAL PAPER

S. Grando · M. Baum · S. Ceccarelli · A. Goodchild
F. Jaby El-Haramein · A. Jahoor · G. Backes

QTLs for straw quality characteristics identified in recombinant inbred lines of a *Hordeum vulgare* × *H. spontaneum* cross in a Mediterranean environment

Received: 11 July 2004 / Accepted: 26 November 2004 / Published online: 28 January 2005

Abstract Barley straw is commonly used as animal feed in many developing countries. Even a small increase in its nutritive value can have a large impact on animal production, and hence, on rural livelihood and human nutrition. Straw quality is strongly affected by environmental factors and is, therefore, difficult to improve with empirical breeding. The objective of this study was to identify molecular markers to facilitate the improvement of straw quality in barley. For this purpose, we have used the genetic linkage map that was already developed for recombinant inbred lines (RILs) of the cross between a *Hordeum vulgare* cultivar ('Arta') and a *H. spontaneum* line (*H. spontaneum* 41-1), covering a total of 890 cM. Straw parameters from RILs grown at Tel Hadya and Breda (ICARDA's research stations) in 2 years (1996/1997 and 1997/1998) were analyzed by NIRS for predicted nutritional characteristics including neutral detergent fiber, acid detergent fiber, lignin, digestible organic matter in dry matter, voluntary intake, crude protein, and straw morphology (the percentage of blades, sheaths, and stems). Localization of QTLs was performed using Windows QTL Cartographer, version 2.0. Seventy-three QTLs were identified, the majority of which (17) in the driest of the four environments. Only six QTLs were identified in two environments; in five cases, one of the two was the wettest environment. This is discussed in relation to the possibility of improving straw quality in favorable environments where yields are higher, rather than in dry environments where straw quality is already relatively good.

Keywords QTLs · *Hordeum spontaneum* · Straw quality · NIRS · Crude protein

Introduction

Barley is the main rainfed crop in the dry areas of West Asia and North Africa (WANA) and is largely grown as feed for animals, particularly small ruminants, such as sheep and goats, which play an important role in the economy of farmers in the drier areas of the region. The crop is normally harvested by combine, but when it is too short because of drought, it may either be grazed at maturity or hand-harvested by uprooting. In general, the whole crop is collected, and the straw is chopped for feed. In the case of combine harvesting, the barley stubble is grazed during summer and early autumn. In many countries of WANA, the contribution of pastures to livestock feed has declined in the last 50 years and has been replaced by feed grains and other concentrates, and, to some extent, by straw and other crop residues (Nordblom et al. 1995). In the semi-arid areas of WANA, barley straw and stubble provide between one quarter and one half of the metabolisable energy fed to sheep (Goodchild et al. 1997).

Improving the quality and quantity of these crop residues will increase the availability of nutrients to small ruminants, and the characteristics associated with straw quality are considered so important by farmers that they play a major role in the adoption of new varieties (Traxler and Byerlee 1993). Consequently, breeding programs should enhance the nutritive value of the residues for ruminant production, without causing any associated negative effects on grain yields. Most of the current genetic improvement programs for grain crops do not include direct selection for the quality of

Communicated by G. Wenzel

S. Grando · M. Baum (✉) · S. Ceccarelli · A. Goodchild
F. J. El-Haramein
ICARDA, P.O. Box 5466, Aleppo, Syria
E-mail: m.baum@cgiar.org
Tel.: +963-21-2243433
Fax: +963-21-2243490

A. Jahoor · G. Backes
Plant Biology and Biogeochemistry Department,
Risoe National Laboratory, P.O. Box 49,
Roskilde, 4000, Denmark

their residues as ruminant feed. Also, genetic markers on which to base selection for straw quality have not received enough attention.

The wild progenitor of cultivated barley, *Hordeum vulgare* ssp. *spontaneum* (hereafter referred to as *H. spontaneum*) is a source of useful genes for several characteristics. Resistance to powdery mildew (Moseman et al. 1983, Jahoor and Fischbeck 1987; Gustafsson and Claesson 1988; Nevo 1992; Lehman et al. 1998), leaf rust (Moseman et al. 1990; Nevo 1992), and other diseases (Nevo 1992) have been identified in *H. spontaneum*, and its use in breeding for disease resistance has been reported by several authors (Lehmann and Bothmer 1988; Backes and Jahoor 2001; Pillen et al. 2003, 2004). The species showed variation for important agronomic traits, such as seminal root morphology (Grando and Ceccarelli 1995), floral structure (Giles and Bengtsson 1988), salt tolerance (Nevo et al. 1993), grain size (Giles 1990), milling energy (Ellis et al. 1993), grain protein content (Jaradat 1991), earliness, biomass, grain yield, plant height under drought, and drought tolerance (Nevo 1992; Grando et al. 2001; Ellis 2002; Baum et al. 2003; Pillen et al. 2003; Ceccarelli et al. 2004; Pillen et al. 2004). This vast potential of genetic resources remains largely unexploited. *H. spontaneum* has the potential to contribute useful genes in barley breeding as a donor of adaptive traits to extreme stress conditions, which is suggested by its distribution in the driest areas of the West Asia. However, it is not known whether its use may introduce undesirable straw quality characteristics.

Previous work conducted at ICARDA (Thomson and Ceccarelli 1990) has shown large effects of environmental factors such as rainfall, temperature, soil fertility, and crop management on quality. As many of these factors are unpredictable, pragmatic breeding based on phenotypic assessment of straw quality is not expected to be very effective. Marker-assisted selection (MAS) could be helpful in tackling some of these problems.

The objectives of this study were to identify genes responsible for straw characteristics, their linkages with molecular markers using the QTL approach, and to ultimately increase the efficiency of selection.

Materials and methods

Plant material and growth conditions

A population of 494 F_7 RILs derived by single-seed descent from the cross 'Arta' × *H. spontaneum* 41-1 was developed at ICARDA (the details of the two parents are given by Baum et al. 2003). In the cropping seasons 1996/1997 (hereafter referred to as 1997) and 1997/1998 (hereafter referred to as 1998), the 494 lines and the parental lines were planted at ICARDA's research stations located near Tel Hadya (36°01′ N; 37°20′ E, elevation 300 masl) and near Breda (35°56′ N; 37°10′ E, elevation 354 masl) in Syria. The experimental design, rainfall, and temperature conditions were described in Baum et al. (2003).

Straw-related traits

Complete plants for each plot were hand-harvested. Roots were cut off by scissors, and samples were weighed in the field and collected in plastic bags for further processing. In the laboratory, straw samples were dissected into stems, blades, and sheaths. Percentage of blades (PCB), percentage of sheaths (PCH), and percentage of stems (PCS) by weight of air-dry straw were calculated. PCB, PCH, and PCS were measured only in straw of TH98.

Straw samples were milled by a Wiley mill No. 4 (Thomas Scientific, USA) fitted with a 6-mm screen and analyzed by NIRSystems Model 5000 scanning monochromator (Foss NIRSystems, USA), wave length range 1,100–2,500 mm, using the coarse sample cell (half volume). Correlations among NIRS and reference methods were previously established for acid detergent fiber (ADF), neutral detergent fiber (NDF), digestible organic matter in dry matter (OMD), voluntary intake (INT), crude protein (CP), and lignin content (LIC) (Table 1). ADF measures the total fiber content (cellulose and lignin) or the more slowly digestible components of a straw. NDF has been widely accepted as a determinant for dietary fiber in cereal grains, as it estimates the contents of cellulose, hemi-cellulose, and lignin present mostly in outer grain layers. OMD measures enzymatically the total dry matter digested in the rumen. INT is a reflection of chemical composition, physical characteristics, digestion, and rate of passage through the digestive system of feed that is offered to the animal ad libitum. CP is determined as total nitrogen ×6.25. LIC is the indigestible component of the straw limiting the availability of cellulose carbohydrates in the plant. ADF, NDF, OMD, INT, and CP were measured in the four environments Br97, Br98, Th97, and Th98.

A total of 50 straw samples representing a range of above parameters were selected from several growing seasons (1986–1992). The sample sets were assembled for NIRS calibration and validation in the approximate ratio of 3:1, based on reference data. Near-infrared Spectral Analysis Software, version 3.22 (Foss NIR-

Table 1 Accuracy of prediction of barley straw-quality parameters by NIRSystems 5000. *SEP* Standard error of prediction

Parameter[a]	r^2	SEP	Range	*n*
ADF	0.96	1.35	29.36–56.15	12
NDF	0.69	1.57	69.3–81.6	12
INT	0.94	1.96	7.80–31.79	12
LIC	0.98	0.36	2.11–9.35	12
CP	0.98	0.23	1.69–6.25	12
OMD	0.94	2.35	31.97–65.49	12

[a] *ADF* Acid detergent fiber, *NDF* neutral detergent fiber, *INT* voluntary intake, *LIC* lignin content, *CP* crude protein, *OMD* digestible organic matter in dry matter

Systems), was used to produce NIRS calibrations by multiple regression analysis. Details for sample sets used in validation are provided in Table 1.

DNA extraction

A genetic linkage map was constructed using 194 RILs. Total genomic DNA was extracted following the procedure described by Saghai-Maroof et al. (1984), with minor modifications. Fresh, aboveground parts from 4- to 6-week-old seedlings were collected for DNA isolation from the parents, and a bulk of 10–20 individuals were selected from each of the RILs. The DNA was RNase-treated and quantified using a spectrophotometer (Beckman DU-65). The quality of the extracted DNA was visually checked on a 1% agarose gel.

Analysis of amplified fragment length polymorphic markers and single sequence repeats

Genetic mapping was carried out using amplified fragment length polymorphic markers and microsatellite-based markers (Baum et al. 2003).

Linkage mapping

Segregation analysis was performed according to Lander et al. (1987), with the MAPMAKER software program, and the JoinMap, version 2.0 (Stam and van Ooijen 1995), software package was employed for map construction. Recombination fractions were converted to centiMorgans, according to the Kosambi mapping function (Kosambi 1944).

QTL analysis

The QTL analysis was performed using Windows QTL Cartographer, version 2.0 (Basten et al. 1994, 2002). (For details, see Baum et al. 2003).

Results

Linkage map

Details of the linkage map based on the ‘Arta’ × *H. spontaneum* 41-1 population are described in Baum et al. (2003).

Trait variations and correlations

The RIL population showed a large variation for the traits examined among the four environments. Average grain and biomass yields reflected the difference in rainfall and were higher in Tel Hadya (grain yield was 2,608 kg/ha and 2,536 kg/ha in 1997 and 1998, respectively, and biomass yield was 9,310 kg/ha and 7,047 kg/ha in 1997 and 1998, respectively) than in Breda (grain yield was 936 kg/ha and 1,251 kg/ha in 1997 and 1998, respectively, and biomass yield was 5,625 kg/ha and 3,745 kg/ha in 1997 and 1998, respectively).

The means of ADF, LIC, and NDF were higher in Tel Hadya than in Breda and in 1998 than in 1997, confirming the better quality of the straw produced in dry years and in dry locations (data not shown). This is confirmed by the lower values of INT, OMD, and CP in Tel Hadya and in 1998. The traits measured only in Th98 (PCB, PCH, and PCS) showed a large phenotypic variation, as expected in a population derived from a wide cross. PCB varied from 2.1 to 13.6, PCH from 10.5 to 26.3, and PCS from 65.5 to 84.5.

The simple correlation coefficients among the specific traits in the four environments were calculated (data not shown). In general, relatively high correlations were found among the NIRS-based traits (ADF, NDF, LIC, OMD, INT, and CP). Positive correlations were found within the subgroup of ADF, NDF, and LIC on one side, and the subgroup of OMD, INT, and NIT on the other side, while negative correlations were observed among these subgroups. Low correlations were observed among these traits and the plant architecture-related traits, i.e., PCB, PCH, and PCS. Within the latter, PCS was correlated negatively with PCB and PCH, while no significant correlation was found between PCB and PCH. PCH showed significant positive correlations with OMD and INT and significant negative correlations with NDF and LIC. The most striking difference among the environments was the lack of correlations between INT and other traits in Th97, and the high correlations between INT and the other traits observed in the other environments.

QTL analysis

The QTLs identified in this study are shown in Fig. 1 and Table 2. In Table 2, the QTLs are ordered by chromosomal position, followed by and the LR-value of the locus, either from multi-trait analysis—if a QTL for more than one trait was identified—or from composite interval analysis. The effect and the explained phenotypic variance were estimated by multi-interval mapping.

The numbers on the right side of the chromosomes in the diamond symbol in Fig. 1 correspond to chromosomal position in Table 2 (e.g., 1H-4 corresponds to the diamond symbol with the number 4 at the right side of chromosome 1H)

Ten QTLs were identified for ADF on 1H-2, 3H-3, 6H-1, 7H-6, and 7H-8 in Br97; on 6H-6 in Br98; on 4H-2, 7H-1, and 7H-2 in Th97; and finally, on 2H-1 in Th97; none of them was common among the environments. The QTLs identified in Br97 explained in total 18.6% of the phenotypic variation, and the ones found in Th97 explained 19.2%.

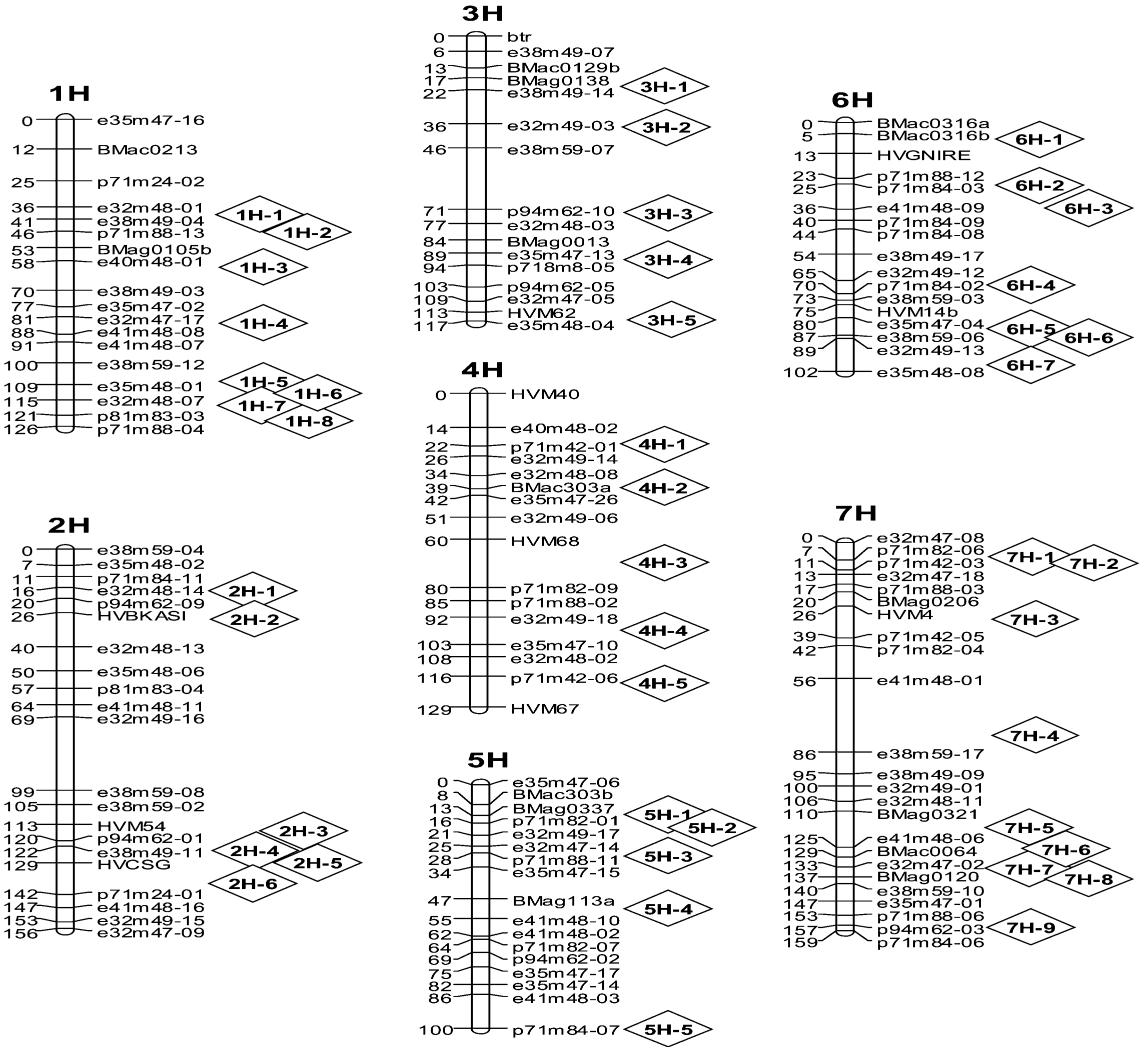

Fig. 1 Linkage map of the cross 'Arta' × *Hordeum vulgare* ssp. *spontaneum* 41-1, with positions of QTLs on the *right side* of the chromosomes. The description of the QTLs indicated by the *diamonds* (e.g., 1H-1s are listed in Table 2)

One QTL was identified for NDF on 1H-1, and this was common to Br98 and Th98. In Br97, four QTLs (on 1H-5, 2H-2, 2H-4, and 6H-3) and one epistatic interaction (among the QTLs on 2H-2 and 2H-4) were found, together explaining 30.1% of the phenotypic variation. For all the QTLs identified for this trait, the *H. spontaneum* parent contributed the allele with the higher value, i.e., that associated with a lower quality.

Eleven QTLs were identified for LIG. One of them was common to two environments (6H-7 in Br97 and Br98), five were specifically identified in Br98 (on 2H-4, 3H-4, 5H-5, and 7H-7), three in Th97 (on 1H-5, 3H-5, and 7H-5), and another three in Th98 (3H-2, 4H-4, and 6H-5). In Br98, an epistatic interaction was identified among the QTLs on 3H-4 and 6H-7. The explained variance in Br98 was 30%, while in Th97 and Th98, the explained variance was around 20% (20.1% in Th97 and 19.7% in Th98, respectively). For all QTLs beside the one on 5H-5, the allele with the higher value (lower quality) originated from the *H. spontaneum* parent.

Twelve QTLs were identified for OMD; one of them was common to Br98 and Th98 (on 5H-4). Four QTLs were identified in Br97, (on 1H-9, 2H-5, 5H-3, and 6H-4) and two QTLs in Th97 (on 5H-5 and 6H-5). In addition to the common QTL, three specific QTLs were found in Br98 (on 2H-3, 3H-3, and 4H-3) and two specific QTLs in Th98 (on 4H-1 and 4H-4). The explained phenotypic variance ranged from 28.8% (Br97) over 19.9% and 15.1% (Th98 and Br98, respectively) to 13.4% (Th97). Besides the QTL on 5H-5, 'Arta' possessed the allele with the higher value for all the OMD QTLs.

Twelve QTLs were identified for INT, one of which was common to Br97 and Th98 (on 1H-8) and one common to Br98 and Th98 (on 5H-5). Only for these two QTLs, the *H. spontaneum* parent contributed the allele with the higher value (better quality), while for all other QTLs identified for this trait, the allele with the higher value was found in 'Arta'. Specific QTLs for INT were identified in Br97 (on 1H-4, 1H-9, 2H-6, and 6H-4), in Br98 (1H-1, 3H-4, 6H-7, and 7H-4) and in Th98 (on

Table 2 Position, statistics, effects, and explained phenotypic variance (*Var. expl.*) of the QTLs detected

QTL[a]	Effect[b]	Var. expl. (%)
1H-1: 37 (LR = 24.1)		
NDF-Br98-01	0.379 [Hs]	3.5
INT-Br98-01	1.006 [Ar]	7.4
CP-Br98-01	3.616 [Ar]	5.3
1H-2: 43 (LR = 20.4)		
ADF-Br97-01	1.381 [Hs]	4.1
PST-Th98-01	1.313 [Ar]	5.2
1H-3: 58 (LR = 8.4)		
PSH-Th98-01	0.987 [Hs]	3.8
1H-4: 81 (LR = 14.3)		
INT-Br97-01	0.983 [Ar]	7.2
1H-5: 105 (LR = 10.9)		
LIG-Th97-01	0.516 [Hs]	7.6
NDF-Br97-01	0.607 [Hs]	3.8
1H-6: 111 (LR = 15.3)		
INT-Th98-01	1.636 [Ar]	13.7
1H-7: 115 (LR = 7.1)		
CP-Th97-01	3.152 [Ar]	6.0
1H-8: 120 (LR = 22.8)		
INT-Br97-02	1.037 [Hs]	2.2
ASH-Br98-01	0.372 [Hs]	4.6
INT-Th98-02	1.232 [Hs]	0.5
1H-9: 125 (LR = 13.5)		
INT-Br97-03	1.487 [Ar]	8.4
DOM-Br97-01	1.378 [Ar]	4.8
2H-1: 17 (LR = 11.2)		
ADF-Th98-01	1.588 [Ar]	6.6
2H-2: 30 (LR = 7.2)		
NDF-Br97-02	0.415 [Hs]	3.1
2H-3: 115 (LR = 11.4)		
DOM-Br98-01	1.193 [Ar]	5.9
2H-4: 122 (LR = 33.3)		
ASH-Br98-02	0.299 [Ar]	2.5
LIG-Br98-01	0.359 [Hs]	5.8
NDF-Br97-03	1.065 [Hs]	14.7
2H-5: 127 (LR = 24.4)		
DOM-Br97-02	2.179 [Ar]	12.0
2H-6: 135 (LR = 19.3)		
INT-Br97-04	1.144 [Ar]	10.1
3H-1: 22 (LR = 11.1)		
ASH-Br98-03	0.496 [Ar]	8.3
3H-2: 38 (LR = 12.0)		
LIG-Th98-01	0.486 [Hs]	8.9
3H-3: 72 (LR = 8.2)		
ADF-Br97-02	1.148 [Hs]	2.5
DOMD-Br98-02	1.086 [Ar]	4.1
3H-4: 94 (LR = 13.9)		
LIG-Br98-02	0.333 [Hs]	4.4
INT-Br98-02	0.763 [Ar]	5.2
3H-5: 116 (LR = 11.2)		
LIG-Th97-02	0.453 [Hs]	5.4
4H-1: 47 (10.5)		
DOM-Th98-01	1.332 [Ar]	4.4
4H-2: 80 (LR = 23.7)		
ADF-Th97-01	1.194 [Ar]	2.3
INT-Th98-03	1.073 [Ar]	11.6
4H-3: 102 (LR = 13.3)		
DOMD-Br98-03	1.226 [Ar]	6.3
4H-4: 108 (LR = 7.8)		
LIG-Th98-02	0.295 [Hs]	3.7
DOM-Th98-02	1.638 [Ar]	6.2
5H-1: 12 (LR = 16.0)		
ASH-Br98-04	0.330 [Ar]	1.1
NDF-Th97-01	0.637 [Hs]	7.8
5H-2: 18 (LR = 10.4)		
ASH-Br98-05	0.554 [Hs]	9.3
PBL-Th98-01	0.988 [Ar]	6.2
5H-3: 28 (LR = 10.5)		
DOMD-Br97-03	1.302 [Ar]	4.2
5H-4: 50 (LR = 21.0)		
DOMD-Br98-04	1.077 [Ar]	3.6
DOMD-Th98-03	1.385 [Ar]	4.5
5H-5: 100 (LR = 23.1)		
INT-Th98-04	0.845 [Hs]	5.6
DOM-Th97-01	2.369 [Hs]	6.1
INT-Br98-03	0.718 [Hs]	4.0
LIC-Br98-03	0.309 [Ar]	4.3
CP-Th97-02	2.537 [Hs]	3.3
CP-Th98-01	1.966 [Hs]	4.2
6H-1: 6 (LR = 8.6)		
ADF-Br97-03	1.380 [Ar]	4.1
6H-2: 25 (LR = 15.1)		
PSH-Th98-02	1.506 [Hs]	7.9
6H-3: 34 (LR = 11.1)		
NDF-Br97-04	0.571 [Hs]	3.8
6H-4: 69 (LR = 11.4)		
DOM-Br97-04	1.700 [Ar]	7.8
INT-Br97-05	0.922 [Ar]	6.0
PSH-Th98-03	1.180 [Ar]	2.3
6H-5: 84 (LR = 24.4)		
DOM-Th97-02	2.567 [Ar]	7.3
LIG-Th98-03	0.423 [Hs]	7.1
6H-6: 89 (LR = 14.1)		
ADF-Br98-01	1.043 [Hs]	3.2
PSH-Th98-04	1.338 [Hs]	3.6
6H-7: 98 (LR = 30.7)		
INT-Br98-04	0.790 [Ar]	5.2
LIG-Br97-01	0.661 [Hs]	4.2
LIG-Br98-04	0.433 [Hs]	7.5
7H-1: 4 (LR = 5.2)		
ADF-Th97-02	3.871 [Hs]	0.7
7H-2: 7 (LR = 12.7)		
ADF-Th97-03	4.715 [Ar]	16.2
7H-3: 28 (LR = 11.0)		
PSH-Th98-02	1.600 [Ar]	7.8
7H-4: 77 (LR = 8.4)		
INT-Br98-05	0.890 [Ar]	4.8
7H-5: 116 (LR = 19.8)		
LIG-Th97-03	0.523 [Hs]	7.1
CP-Th97-03	3.020 [Ar]	5.3
7H-6: 124 (LR = 15.4)		
ADF-Br97-04	2.136 [Hs]	5.9
7H-7: 132 (LR = 12.7)		
LIG-Br98-05	0.346 [Hs]	5.2
7H-8: 137 (LR = 10.5)		
ADF-Br97-05	1.754 [Ar]	2.0
7H-9: 156 (LR = 9.4)		
PSH-Th98-05	1.152 [Ar]	2.5

[a] QTL position: The number connected to the chromosome is the number indicated in Fig. 1. The absolute position of the locus follows the colon and in parentheses, the LR-value. The latter is derived from composite interval mapping: either from a multi-trait analysis if QTLs for more than one trait are detected at this locus or from a single trait composite interval mapping

[b] Difference of the genotype with two alleles of the one parent compared to the genotype with two alleles from the other parent (in brackets): the parent with the higher value trait expression, [Ar] 'Arta,' [Hs] *Hordeum vulgare* ssp. *spontaneum*

2H-6 and 4H-2). Epistatic effects were found in Br98 between the QTL on 5H-5 and the one on 6H-7. No QTLs were found in Th97. The explained phenotypic variance was about 30% (Br97, 33.9%; Br98, 30.3%; and Th98, 31.4%).

For CP, no QTLs were found in Br97, while one QTL was common to Th97 and Th98 (on 5H-5) and three additional specific QTLs were localized. One of them was identified in Br98 (on 1H-1), and two in Th97 (on 1H-7 and 7H-5). All three QTLs in Th97 explained 20% phenotypic variation. As in the case of LIC, OMD, and INT, the origin of the allele with the higher value for the locus on 5H-5 was opposite to the rest of the QTLs; in this case, it was the only QTL where the *H. spontaneum* parent contributed with the allele leading to the higher value of the trait (better quality).

PCB, PCH, and PCS were exclusively measured in Th98. For PCH, five QTLs were identified (on 1H-3, 6H-2, 6H-4, 6H-6, and 7H-9, see Table 2) together explaining 20.1% variation. For two of them, the *H. spontaneum* line contributed the allele for the higher stem percentage, and for three of them 'Arta' contributed to higher stem percentage. For PCS, two QTLs were localized, one on 1H-2 and one on 7H-3, leading to 13% explained phenotypic variance. Finally, one QTL on 5H-2 was localized for PCB.

Discussion

The literature has long provided information on significant genetic variation in the nutritional value of pasture grass and legume species (e.g., Minson and McLeod 1970).

In the present study, 73 QTLs were identified, the majority of which in only one environment (17 in Br97, 21 in Br98, 12 in Th97, and 20 in Th98) and six in two environments. Drought resistance-related traits measure the reaction of the plant to environmental conditions. Therefore, a change in these conditions will necessarily result in differences in QTL localization. Although, e.g., the total rainfall in Breda was similar between the years, large differences in distribution together with differences in temperature have major effects on plant development in that site. This is the reason why we focused on the QTLs in single environments and the relations of the single traits to each other in the different environments, reflected by correlations and the multi-trait analysis and indicated through LR-values and explained variance.

In the driest environment (Br97), the QTLs for ADF, INT, NDF, and OMD explained an amount of phenotypic variance ranging from a minimum of 18.6% (ADF) to a maximum of 33.9% (INT). This would indicate that a dry location such as Breda is a suitable place to select for these four traits related to higher straw quality. However, the greater need is to improve straw quality in wet environments where there is large quantity of straw of poor quality. Therefore, the QTLs identified in Th98, explaining nearly 20% of the phenotypic variance of LIG and OMD and slightly more that 30% of the phenotypic variance of INT, are probably more relevant, because they are the five QTLs identified in two environments.

Two important agronomic traits associated with straw quality are plant height and lodging resistance (Travis et al. 1996). Tall plants are desirable under drought even though the straw quality is inferior, while lodging, associated with soft and palatable straw, affects negatively yield in wet conditions (Ceccarelli et al. 1991). In the case of plant height under drought, the QTLs found in the 'Arta' × *H. spontaneum* 41-1 population, especially the one on 3H (Baum et al. 2003), showed pleiotropic effects on traits such as days to heading, grain yield, and biological yield. However, there was little co-localization of straw-quality QTLs at the same position. Only one QTL for LIG and one for INT, both identified in Breda 1998, were identified in this interval (at 3H-4). Therefore, it should be possible to combine the height under drought contributed by *H. spontaneum* with desirable straw-quality attributes. This is important, because *H. spontaneum* is used in drought resistance breeding at ICARDA, and this study shows that, with few exceptions, the specific *H. spontaneum* line used extensively in the crossing program contributes alleles with a negative effect on straw quality.

The protein concentration of the straw is important for the multiplication and metabolism of rumen microflora, and hence, it affects voluntary intake and digestibility. QTLs for straw crude protein (CP) were identified on chromosomes 1H, 5H, and 7H, with the 5H-5 location appearing in more than one environment. This could coincide with QTLs for leaf nitrogen at maturity identified on 1H and 3H in a recent study by Mickelson et al. (2003). At the 3H location, the alleles with high leaf nitrogen at maturity were associated with low yield, while at the 1H location, alleles were associated with low residual leaf nitrogen but with high yield.

Quality traits such as OMD, water-soluble carbohydrate content, and high digestion rate are consistently rated as the highest priorities for improvement in grazing crops for meat and milk production (Smith et al. 1998). Coefficients of variation of 0.05 –0.16 among genotypes are seen for the in vivo digestibility and voluntary digestible dry matter intake of barley straw (Herbert et al. 1994). Voluntary intake itself has a genotypic coefficient of variation of about 0.10 and is not correlated with grain yield or lodging resistance (Goodchild et al. 1996). However, it is negatively correlated with stem height. Annual differences in springtime drought and heat stress increase intake, and do so to a greater extent than genetic variation (Goodchild 1997). Heritable differences in straw intake are, however, most marked when growing conditions are favorable, so that cultivars whose grain yields are well maintained under drought tend to have the best intake under higher-rainfall conditions (Goodchild 1997).

Correlation and co-localizations

There were four main locations within the barley map where a number of QTLs for traits associated with straw quality were located. The 1H-5–8 interval (105–120 cM) had seven QTLs, the 2H-3–6 interval (115–135 cM) had six QTLs, the 5H-5 (100 cM) interval had six QTLs, and the 7H5–8 interval (116–137 cM) had five QTLs. In particular, the QTLs that were identified in more than one environment are interesting for further characterization and utilization. QTLs for INT were identified in Br97 and Th98 at 1H-8; QTLs for grain yield and biological yield co-located at the same position (Baum et al. 2003): LIC in Br97, Br98 at 6H-7, NDF in Br98 and Th98 at 1H-1; CP in Th97 and Th98 at 5H-5; and OMD in Br98 and Th98 at 5H-4. It is interesting that out of the six QTLs common to two environments, five were identified in Th98, the highest yielding environments and therefore, where straw is expected to be of the poorest quality and where improvement can have greater impact because of the large amount of straw produced.

Favorable wild-species QTL alleles are useful as a breeding resource after they have been fixed in nearly isogenic lines (NILs) and after the superior performance of a QTL-NIL has been confirmed in comparison to the recurrent elite line (Pillen et al. 2003, 2004). Bernacchi et al. (1998) have already validated the effects of exotic tomato QTLs in QTL-NILs. We are developing advanced backcross populations for 'Arta' × *H. spontaneum* 41-1 as well as QTL-NILs mainly for agronomic traits. While numerous positive *spontaneum* alleles have been identified for agronomic traits (Baum et al. 2003), positive *spontaneum* alleles for straw-related traits are rather limited. The 5H-5 location carries *spontaneum* alleles for the improvement of crude protein concentration and for intake and the 1H-8 location for intake. MAS could help to identify the *spontaneum* alleles in further backcross generations and for the development of QTL-NILs. This should allow the improvement of straw quality traits even under the variable West Asian environmental conditions.

Acknowledgements This research was funded by BMZ, by a grant of the Arab Fund for Economic and Social Development, and by the grant of the Danish Research Council for Developmental Research (project no. 90978). We would like to thank Ms. Aman Sabbgh for excellent technical support. We like to acknowledge the input of Bruce Stone, LaTrobe University to initiate the project "Crop Residues in Sustainable Mixed Crop/Livestock Farming Systems," funded by ACIAR, project no. AS2/1997/098. We are grateful to Dr. W. Powell, Scottish Crop Research Institute, for providing barley microsatellite primer sequences even prior to their being published.

References

Backes G, Jahoor A (2001) Wege zur Nutzung des genetischen Potentials der Wildgerste—mit molekularen Markern zu neuen Resistenzgenen. Bericht der Arbeitstagung der 52. Tagung der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreich, Gumpenstein 81–86

Basten CJ, Weir BS, Zeng Z-B (1994) Zmap—a QTL cartographer. In: Smith C, Gavora JS, Benkel B, Chesnais J, Fairfull W, Gibson JP, Kennedy BW, Burnside EB (eds) Proceedings of the 5th world congress on genetics applied to livestock production: computing strategies and software, vol 22, pp 65–66

Basten CJ, Weir BS, Zeng Z-B (2002) QTL Cartographer, version 1.16. Department of Statistics, North Carolina State University, Raleigh

Baum M, Grando S, Backes G, Jahoor A, Sabbagh, A, Ceccarelli S (2003) QTLs for agronomic traits in the Mediterranean environment identified in recombinant inbred lines of the cross 'Arta' × *H. spontaneum* 41-1. Theor Appl Genet 107:1215–1225

Bernacchi D, Beck Bunn T, Emmatty D, Eshed Y, Inai S, Lopez J, Petiard V, Sayama H, Uhlig J, Zamir D, Tanksley S (1998) Advanced backcross QTL analysis of tomato II. Evaluation of near-isogenic lines carrying single-donor introgressions for desirable wild QTL-alleles derived from *Lycopersicon hirsutum* and *L. pimpinellifolium*. Theor Appl Genet 97:170–180

Ceccarelli S, Acevedo E, Grando S (1991) Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. Euphytica 56:169–185

Ceccarelli S, Grando S, Baum M, Udupa SM (2004) Breeding for drought resistance in a changing climate. In: Rao, Ryan J (eds) Challenges and strategies for dryland agriculture. CSSA Spec Publ 32 ASA and CSSA, Madison

Ellis RP (2002) Wild barley as a source of genes for crop improvement. In: Slafer GA, Molin-Cano JL, Savin R, Araus JL, Romagosa I (eds) Barley science: recent advances from molecular biology to agronomy of yield and quality. Haworth, New York, pp 65–83

Ellis RP, Nevo E, Beiles A (1993) Milling energy polymorphism in *Hordeum spontaneum* Koch in Israel and its potential utilization in breeding for malting quality. Plant Breed 111:78–81

Giles BE (1990) The effects of variation in seed size on growth and reproduction in the wild barley *Hordeum vulgare* ssp. *spontaneum*. Heredity 64:239–250

Giles BE, Bengtsson BO (1988) Variation in anther size in wild barley (*Hordeum vulgare* ssp. *spontaneum*). Hereditas 108:199–205

Goodchild AV (1997) Effects of rainfall and temperature on the feeding value of barley straw in a semi-arid Mediterranean environment. J Agric Sci (Cambr) 129:353–366

Goodchild AV, Thomson EF, Ceccarelli S (1996) Optimizing laboratory indicators of the nutritive value of straw, in recent advances in small ruminant nutrition. In: Lindberg JE, Gonda HL, Ledin I (eds) FAO-CIHEAM network of cooperative research on sheep and goats. Subnetwork Nutrition, France, pp 87–92

Goodchild AV, El Haramein FJ, Ceccarelli S, Thomson EF (1997) Near infrared reflectance spectroscopy (NIRS) wavelengths for selecting barley for the genotypic feeding value of its straw. In: International symposium on in vitro techniques for measuring nutrient supply to ruminants. British Society of Animal Science, University of Reading, UK, 8–10 July 1997

Grando S, Ceccarelli S (1995) Seminal root morphology and coleoptile length in wild (*Hordeum vulgare* ssp. *spontaneum*) and cultivated (*Hordeum vulgare* ssp. *vulgare*) barley. Euphytica 86:73–80

Grando S, von Bothmer R, Ceccarelli S (2001) Genetic diversity of barley: use of locally adapted germplasm to enhance yield and yield stability of barley in dry areas. In: Cooper HD, Spillane C, Hodgink T (eds) Broadening the genetic base of crop production. CABI/FAO/IPRI, pp 351–372

Gustafsson M, Claesson L (1988) Resistance to powdery mildew in wild species of barley. Hereditas 108:231–237

Herbert F, Thomson EF, Capper BS (1994) Effect of genotype on the morphological characteristics, chemical composition and feeding value of nine barley straws, and responses to soya-bean meal supplementation. Animal Prod 58:117–126

Jahoor A, Fischbeck G (1987) Sources of resistance to powdery mildew in barley lines derived from Hordeum spontaneum collected in Israel. Plant Breed 99:274–281

Jaradat AA (1991) Grain protein variability among populations of wild barley (*Hordeum spontaneum* C. Koch) from Jordan. Theor Appl Genet 83:164–168

Kosambi DD (1944) The estimation of map distance from recombination values. Ann Eugen 12:172–175

Lander ES, Green P, Abrahamson J, Barlow A, Daly MJ, Lincoln SE, Newburg L (1987) Mapmaker: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174–181

Lehmann LC, von Bothmer R (1988) *Hordeum spontaneum* and landraces as a gene resource for barley breeding. In: Jorna ML, Slootmaker LAJ (eds) Cereal breeding related to integrated cereal production. Pudoc, Wageningen, The Netherlands, pp 190–194

Lehmann LC, Jönsson R, Gustafsson M (1998) Identification of resistance genes to powdery mildew isolated from Hordeum vulgare ssp. spontaneum and landraces of barley. J Swed Seed Assoc 108:94–101

Mickelson S, See D, Meyer FD, Garner JP, Foster CR, Blake TK, Fischer AM (2003) Mapping of QTL associated with nitrogen storage and remobilization in barley (*Hordeum vulgare* L.) leaves. J Ex Bot 54:801–812

Minson DJ, McLeod MN (1970) The digestibility of temperate and tropical grasses. In: Proceedings of the 11th international grassland congress, Surfers' Paradise, Australia, pp 719–722

Moseman JG, Nevo E, Zohary D (1983) Resistance of *Hordeum spontaneum* collected in Israel to infection with *Erysiphe graminis hordei*. Crop Sci 23:1115–1119

Moseman JG, Nevo E, El-Morsidy MA (1990) Reactions of *Hordeum spontaneum* to infection with two cultures of *Puccinia hordei* from Israel and United States. Euphytica 49:169–175

Nevo E (1992) Origin, evolution, population genetics and resources for breeding of wild barley, *Hordeum spontaneum*, in the Fertile Crescent. In: Shewry PR (ed) Barley: genetics, biochemistry, molecular biology and biotechnology. CAB International, UK, pp 19–43

Nevo E, Krugman T, Beiles A (1993) Genetic resources for salt tolerance in the wild progenitors of wheat (*Triticum dicoccoides*) and barley (*Hordeum spontaneum*) in Israel. Plant Breed 110:338–341

Nordblom TL, Goodchild AV, Shomo F (1995) Livestock, feeds and mixed farming systems in West Asia and North Africa. In: Wilson RT, Ehui S, Mack S (eds) Livestock development strategies for low-income countries. Proceedings of the joint FAO/ILRI round table on livestock development 27 Feb 1995. Addis Ababa, Ethiopia, pp 101–123

Pillen K, Zacharias A, Leon J (2003) Advanced backcross QTL analysis in barley (*Hordeum vulgare* L.). Theor Appl Genet 107:340–352

Pillen K, Zacharias A, Leon J (2004) Comparative AB-QTL analysis in barley using a single exotic donor of *Hordeum vulgare* ssp. *spontaneum* . Theor Appl Genet 108:1591–1601

Ramsay L, Macaulay M, Degli Ivanissevich S, Maclean K, Carsle L, Fuller J, Edwards KJ, Tuvesson S, Morgante M, Massari A, Maestri E, Marmiroli N, Sjakste T, Ganal M, Powell W, Waugh R (2000) A simple sequence repeat-based linkage map of barley. Genetics 156:1997–2005

Saghai-Maroof MA, Soliman KM, Gorgensen RA, Allard RW (1984) Ribosomal DNA spacer length polymorphism in barley: Mendelian inheritance, chromosomal location and population dynamics. Proc Natl Acad Sci USA 81:8014–8018

Smith KF, Simpson RJ, Oram RN, Dove H, Culvenor RA, Humphreys MO (1998) Increasing the nutritive value of perennial ryegrass in dairy pastures of temperate Australia. In: Boller B, Stadelmann FJ (eds) Breeding for a multi-functional agriculture. Proceedings 21st EUCARPIA fodder crops and amenity grasses section meeting. FAL, Zurich, Switzerland, pp 16–19

Stam P, Van Ooijen JW (1995) JoinMap Version 2.0: software for the calculation of genetic linkage maps. CPRO-DLO, Wageningen

Thomson EF, Ceccarelli S (1990) Progress and future direction of applied research on cereal straw quality at ICARDA. In: Production and utilization of lignocellulosics: plant refinery and breeding, analysis, feeding to herbivores and economic aspects. COST 84 Workshop, Bologna. Elsevier, London, pp 249–264

Travis AJ, Murison SD, Hirst DJ, Walker, KC, Chesson A (1996) Comparison of the anatomy and degradability of straw from varieties of wheat and barley that differ in susceptibility to lodging. J Agric Sci (Cambr) 127:1–10

Traxler G, Byerlee D (1993) A joint-product analysis of the adoption of modern cereal varieties in developing countries. Am J Agric Econ 75:981–989