

Hybridization between landrace varieties of Ethiopian barley (*Hordeum vulgare* ssp. *vulgare*) and the progenitor of barley (*H. vulgare* ssp. *spontaneum*)

ZEMEDE ASFAW¹ and ROLAND VON BOTHMER²

¹Addis Abeba University, Department of Biology, Addis Abeba, Ethiopia

²The Swedish University of Agricultural Sciences, Department of Crop Genetics and Breeding, Svalöv, Sweden

ZEMEDE ASFAW and BOTHMER, R. VON. 1990. Hybridization between landrace varieties of Ethiopian barley (*Hordeum vulgare* ssp. *vulgare*) and the progenitor of barley (*H. vulgare* ssp. *spontaneum*). — *Hereditas* 112: 57–64. Lund, Sweden. ISSN 0018-0661. Received August 30, 1989. Accepted December 6, 1989

Representative landraces of Ethiopian barley (*Hordeum vulgare* ssp. *vulgare*) were reciprocally intercrossed with the wild progenitor (*H. vulgare* ssp. *spontaneum*). Fertilization success, hybrid (F₁ and F₂) performances, and inheritance mechanisms were studied. Grains were obtained in combinations involving each *vulgare* parent and at least one of the *spontaneum* lines. The hybrids were vigorous and fertile. 21 % of the F₂ progeny gave less than 70 % seed-set while a similar proportion seeded fully. The average seed-set for *vulgare* lines varied between 65–90 %, few plants having severe abortions. Some phenotypes segregated differently in different lines, indicating genotypic dissimilarity or varied effects of the genes under different genomic background. Thus, *spontaneum* can be grown under natural conditions in Ethiopia and direct hybridization with indigenous landraces allows for utilization of its genes.

Zemed Asfaw, Addis Abeba University, Department of Biology, P.O. Box 3434, Addis Abeba, Ethiopia

Barley (*Hordeum vulgare* L.) is one of the most extensively studied crops (e.g., ÅBERG 1940; JOHNSON and ÅBERG 1943; SMITH 1951; TAKAHASHI 1955; NILAN 1964; HOCKETT and NILAN 1985). With cultivated barley, various types of hybridization studies (intervarietal, interspecific, intergeneric) have been undertaken (SMITH 1951; THOMPSON 1971; KRUSE 1974; HARLAN 1976; JACOBSEN and BOTHMER 1981; BOTHMER and HAGBERG 1983; BOTHMER et al. 1983; FEDAK 1985). Whereas *Hordeum vulgare* is well known for its strong hybridization barriers (BOTHMER and HAGBERG 1983; BOTHMER et al. 1983), the wild ancestor (*H. spontaneum* C. Koch) is generally fully interfertile with cultivated forms (HARLAN 1976; BROWN et al. 1978; ZEGI and QIUQAN 1981; BOTHMER and HAGBERG 1983; GILES and BOTHMER 1985) and hybrids between the two are formed in nature under sympatric conditions (HARLAN 1976). Such information has led to the lumping of the two taxa into a single species, *Hordeum vulgare*, and with a delimitation at the subspecific level (BOTHMER and JACOBSEN 1985).

The Ethiopian landraces of barley are of high breeding value (ORLOV 1929; CIFERRI 1940, 1944;

HARLAN 1968, 1976; BOTHMER and HAGBERG 1983; MULUGETA 1985; HOYT 1988). To date, direct information about crossability and hybrid fertility between the Ethiopian material and the progenitor of barley is lacking. This is a central issue because cases of partial sterility between some lines of Ethiopian origin and barleys from other sources (Japanese, American, European, Manchurian) have been reported (ÅBERG 1940; SMITH 1951; HARLAN 1968), and this was assumed to be due to geographical differentiation (TAKAHASHI 1955). It has often been stated that Ethiopian barley has been isolated from all other barley for a long period (HARLAN 1968). JONASSEN and MUNCK (1981) obtained variable seed-sets coupled with some sterility in progeny of crosses between hipolyly barley of Ethiopia and barley types from other areas.

Hybridization studies were attempted between selected phenotypically pure lines (as observed for more than 3 years) of Ethiopian barley and *Hordeum vulgare* L. ssp. *spontaneum* (C. Koch) Thell. in order to obtain information on crossability and status of hybrids. This paper presents the results and analysis of the crosses, and of the progeny up to the F₂ generation.

Table 1. Cultivated (*vulgare*) types used in crosses

Code	Spike row number	Caryopsis type	Spike density	Lemma appendages	Outer glumes	General category	Source
V1	6	Hulled	Lax	Hood	Narrow	hooded	Ethiopian/GDR
V2	2	Hull-less	Dense	Long awn	Narrow	nutans	Local
V3	2	Hulled	Lax	Short awn	Narrow	deficiens	Local
V4	2	Hulled	Dense	Long awn	Narrow	nutans	Local
V5	2	Hulled/black	Dense	Long awn	Broad	deficiens	Local
V6	2	Hulled	Lax	Long awn	Broad	deficiens	Local
V7	6	Hull-less	Lax	Long awn	Narrow	coeleste	Local
V8	2	Hulled/black	Lax	Long awn	Narrow	deficiens	Local
V9	6	Hulled	Lax	Long awn	Narrow	pallidum	Local
V10	6	Hulled	Dense	Long awn/smooth	Narrow	parallellum	Local
V11	6	Hulled	Dense	Short awn/smooth	Broad	compact	Local
V12	2	Hull-less/black	Lax	Long awn	Narrow	nutans	Local
V13	6	Hulled	Dense	Long awn	Narrow	pyramidal	Local
V14	2	Hulled	Lax	Long awn	Narrow	nutans	Local/cultivar
V15	2	Hulled	Lax	Long awn	Narrow	nutans	Exotic

Table 2. Frequency of F₂ plants at five levels of seed-set.V = *vulgare*, S = *spontaneum*

% Seed set	Number of plants derived from																			Total	%
	V1	V2	V3	V4	V5	V6	V7	V8	V9	V10	V11	V12	V13	V14	V15	S1	S2	S3			
00- 20	0	3	6	0	0	1	1	2	1	1	0	0	1	1	0	5	8	4	17	1.2	
21- 40	0	3	7	0	3	12	3	6	12	10	0	0	4	3	0	11	29	23	63	4.3	
41- 60	4	9	16	4	5	21	6	15	19	16	0	3	17	7	0	30	64	48	142	9.6	
61- 80	20	5	30	16	30	37	15	51	28	17	7	5	35	6	6	61	132	115	308	21.0	
81-100	16	15	108	26	21	131	59	274	64	24	30	27	76	42	27	204	475	261	940	63.9	
Average	80	65	79	79	71	80	83	89	85	68	88	81	77	79	90	83	80	80	80		

Materials and methods

Three lines of wild barley, *Hordeum vulgare* L. ssp. *spontaneum* (C. Koch) Thell. (CI/PI 284755, CI/PI 466293, CI/PI 466403, hereafter referred to as S1, S2, S3, respectively, or just *spontaneum* collectively) were obtained from Dr. Lehmann (Svalöv) from material received from the USDA world collection (Beltsville, Maryland).

The *spontaneum* lines are of the 2-row, hulled, nutans type, with staminate lateral florets. The leaves, sheaths and spikes are waxless, awns long and densely scabrid, glumes narrow, both glumes and rachises densely hairy. S1 differs from the other two lines in its short height, high and prolonged tillering, semi-prostrate vegetative growth habit, and earliness.

Fifteen lines of cultivated barley (hereafter referred to as *vulgare*) were used. Thirteen of these (V1-V13) are phenotypically pure (as observed for more than 3 years) forms of Ethiopian landraces

selected to give the most heterogeneous and representative group from the morphotypes reported by ZEMEDE (1988). V14 is a malting type obtained from the farmers' fields by whom it is called "birra" (meaning beer), and V15 is a modern high-lysine type (Risø mutant 1508) obtained from the Biotechnology Department of the Carlsberg Research Center (Denmark). Character combinations of the *vulgare* lines are given in Table 1. Voucher specimens of the three *spontaneum* and fifteen *vulgare* lines used in crosses have been deposited at the National Herbarium, Addis Ababa.

Crosses were made following standard procedure (ANDERSON and REINBERGS 1985). The number of pollinated spikes and flowers as well as the seeds produced were recorded. At anthesis of F₁ plants, 250-800 pollen grains were microscopically inspected and categorized as viable or non-viable, based on stainability in 1% cotton blue, after soaking for 24 hours. The F₂ plants were grown in a lath house and allowed to self. At harvest time the spikes were

described, their individual characters scored, and the number of florets and kernels were recorded. Percentage seed-set per plant was calculated, following STØLEN (1981). The chi-square test was used to test the ratio of segregation of the F₂ progeny.

Results

Crossing attempts and successful fertilization

A total of 1411 flowers of 120 spikes were pollinated, representing 35 of the 45 possible combinations, yielding an overall seed-set of 34 %. All *vulgare* lines were crossed with at least one of the *spontaneum* lines. Six of the *vulgare* lines were crossed with each *spontaneum* line, and all combinations except one seeded. Crosses with 2-rowed *vulgare* had an average seed-set of 37 % and those with the 6-rowed, 24 %. When *spontaneum* was used as male, seed-set was 39 % and when used as female 24 %. S1 gave an average seed-set of 26 %, S2 43 %, and S3 28 %, respectively.

Development and fertility of hybrids

The grains from crosses germinated and grew to maturity with the exception of three of the shrivelled grains that failed to germinate and two seedlings that died soon after germination. Hybrids (F₁) with different *vulgare* lines gave pollen fertility values of 72–92 %. For S1 this value was 66 %, and for S2 and S3, 84 % and 86 %, respectively.

In crosses between *spontaneum* and 2-row *vulgare*, the hybrid spikes were 2-rowed. In crosses between *spontaneum* and 6-row *vulgare*, the F₁ hybrids varied in morphology and pattern of seed production. The F₁ progeny of V7 and V10 produced seeds only in the median florets, and the spikes displayed clear 2-rowed morphology. In the others (V1, V9, V11, V13) both the median and the lateral florets gave seeds, and the spikes had an intermediate morphology. However, the lateral florets of the latter group were devoid of lemma appendages (awns and hoods) and had higher proportion of abortion. The fully-formed grains of these florets were smaller compared with those from the median florets and had a reduced 1000 grain weight (18 grams compared with 56 grams).

The F₂ plants were also vigorous and had full seed-set in most cases. The frequency of plants under various seed-set levels are shown in Table 2. The average seed-set for the progeny of individual lines varied between 65 and 90 %; giving 80 % for

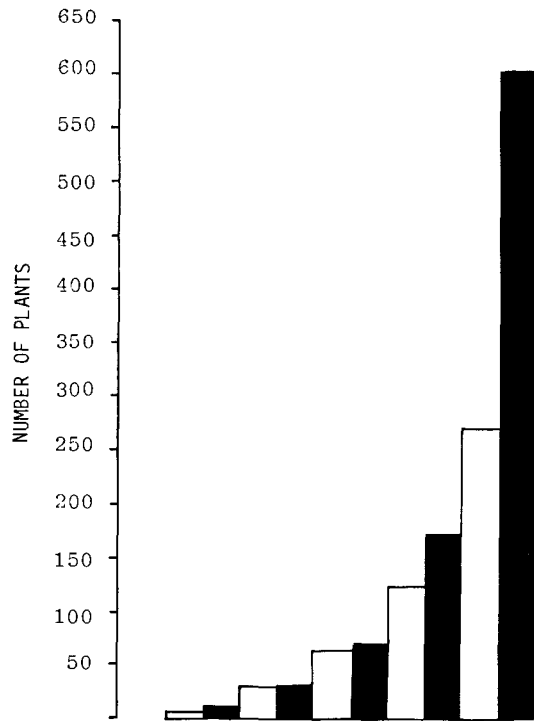


Fig. 1. The pattern of seed-set in F₂ progeny of 2-row [■] and 6-row [□] *vulgare* families at five levels; (0–20, 21–40, 41–60, 61–80, 81–100 %).

the entire sample. The three lines that gave less than 75 % seed-set are all dense types. 86 % of the progeny from 2-rows and 83 % from 6-rows had seed-set values greater than 60 %. 21 % of the whole sample had less than 70 % seed-set, while likewise 21 % had full seed-set. The proportion of seed failure is generally the same for the progeny of the three *spontaneum* lines.

Regardless of the number of plants, the progeny of 2-row and 6-row *vulgare* generally showed the same fertility pattern (Fig. 1).

There were plants that gave less than 5 % seed-set. Severity in grain abortion is higher in the F₂ than in the F₁. Average values did not, however, deviate much. Seed-sets of individual plants in two F₂ families are shown in Fig. 2.

Few cases of very erratic seed development were encountered in the lateral florets. While just one or two seeds per spike were lacking in the progeny of *spontaneum* and 2-row *vulgare*, lacking lateral seeds were more frequent in 2-rowed progeny of 6-row *vulgare*. In the 6-rowed and intermediate progeny groups, a higher proportion of seed failed in the lateral florets than in the median ones, being

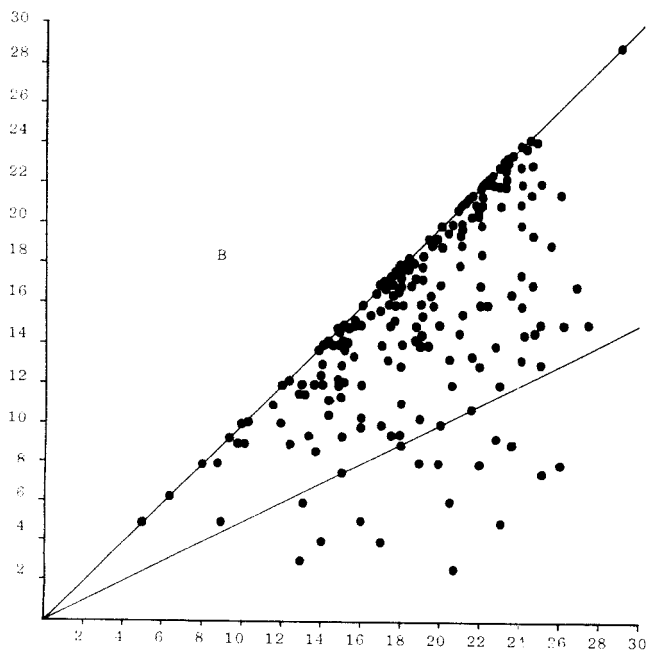
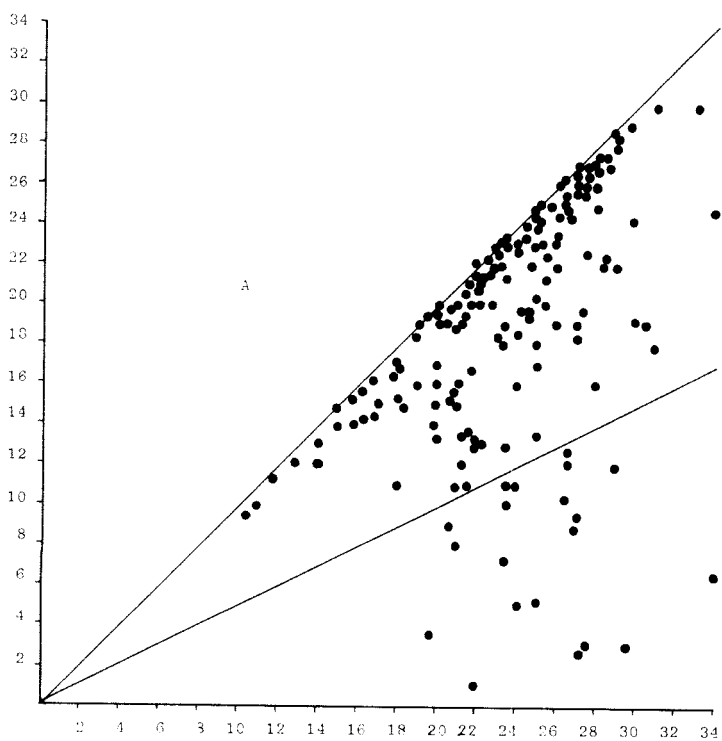


Fig. 2 A and B. Comparison of number of grains (vertical) and florets for the progeny of (A) V3 and (B) V6.

Diagonal and 2nd line mark 100 % and 50 % seed-set, respectively.

Table 3. Segregations of characters in hybrids.

* deviations significant at 5 % probability level

V = *vulgare*, 2-r. = 2-rowed, Int. = intermediate

Character	F ₁	F ₂	No. of plants	Chi-square	Ratio of best fit
	Phenotype	Phenotypes			
1. RACHIS DISARTICULATION					
Progeny of all samples	All brittle	Brittle:tough	1131:339	3.00	3:1
Progeny of 6-row lines	All brittle	Brittle:tough	397: 89	0.05	13:3
Progeny of 2-row lines	All brittle	Brittle:tough	733:251	0.15	3:1
Progeny of <i>deficiens</i> lines	All brittle	Brittle:tough	419:131	0.45	3:1
Progeny of V7	All brittle	Brittle:tough	77: 7	0.62	15:1
Progeny other than V7	All brittle	Brittle:tough	1054:332	0.84	3:1
Progeny of V13	All brittle	Brittle:tough	97: 32	0.003	3:1
2. SPIKE ROW NUMBER					
Progeny of 6-row lines	2-r+Int.	2-r+Int.:6-row	310: 82	3.48	3:1
Progeny of V7+V10	All 2-r	2-r+Int.:6-row	121: 31	1.73	3:1
Progeny of V13	All Int.	2-r+Int.:6-row	106: 23	0.07	13:3
3. LATERAL FLORETS					
Progeny of 6-row lines	Not seeded+seeded	Not seeded:seeded	241:151	4.36*	9:7
Progeny of V7+V10	All not seeded	Not seeded:seeded	111: 41	0.32	3:1
6-rowed other than V7+V10	All seeded	Not seeded:seeded	130:110	0.42	9:7
Progeny of V13	All seeded	Not seeded:seeded	62: 67	0.19	1:1
4. SEEDLESS LATERAL FLORETS (NUTANS vs. DEFICIENS)					
Progeny of <i>deficiens</i> lines	All nutans type	Nutans: <i>deficiens</i>	550:226	6.97*	3:1
Progeny of V3+V8	All nutans type	Nutans: <i>deficiens</i>	388:127	0.03	3:1
Progeny of V6	All nutans type	Nutans: <i>deficiens</i>	125: 77	2.60	9:7
5. SPIKE DENSITY					
Progeny of dense-spiked lines	Lax+dense	Lax:dense	152:100	1.70	9:7
Progeny of V10	All lax	Lax:dense	48: 20	0.71	3:1
Progeny of V13	All dense	Lax:dense	79: 50	1.30	9:7
6. SPIKE WIDTH					
Progeny of wide spiked lines	All narrow spike	Narrow:wide spike	45: 18	0.43	3:1
7. OUTER GLUMES					
Lines with broad outer glumes	All narrow	Narrow:broad	164: 64	1.15	3:1
8. LEMMA APPENDAGES					
Progeny of hooded type	All hooded	Hooded:awned	32: 8	0.43	3:1
Progeny of short awned lines	All long awned	Long:short awned	125: 42	0.002	3:1
Progeny of smooth awned lines	All rough awned	Rough:smooth awned	48: 20	0.71	3:1
9. CARYOPSIS					
Progeny of hull-less lines	All hulled	Hulled:hull-less	60: 24	0.57	3:1
Progeny of black types	All black	Black:white	262: 86	0.01	3:1

more pronounced in the latter group. Some heterozygotes between *spontaneum* and 6-row *vulgare* could be distinguished by their intermediate morphology, by the absence of lemma appendages (awns and hoods) on lateral florets, by the reduced size of lateral kernels, or by the absence of grains in the lower lateral florets.

Segregation and genetic analysis of characters

The expressivity of different characters in crosses

has been given in a number of reviews and publications (e.g., SMITH 1951; NILAN 1964; HOCKETT and NILAN 1985). In this study the obvious morphological characters of *vulgare* that sharply contrasted with the corresponding characters of *spontaneum* were traced through to the F₂ generation. The characters studied, the phenotypes of the two generations, and their segregation ratios are presented in Table 3.

The following spike characters were identified as dominant traits:

brittleness of rachis
 well formed seedless laterals (nutans)
 narrow spike
 narrow outer glumes
 hooded lemma
 long awned lemma
 rough awned lemma
 hulled caryopsis
 black caryopsis

In some characters the relationship varied between lines. Two-rowed spikes exhibited complete dominance in some lines (V7 and V10), and only partially so in others. The same trend was observed for the seed-setting ability of the lateral florets. In the case of spike density, dominance of both the lax and the dense type is evident in different lines.

In the F_2 generation most characters segregated in the 3:1 ratio, while a few deviated from this pattern but were in agreement with the 9:7 ratio or its modifications (13:3, 15:1). Significant deviations ($P \leq 5\%$) from known ratios were observed in the cases of fertility and development of lateral florets. Such differences in segregation pattern between lines are also evident in the case of rachis brittleness, spike row number and density. A graded series was observed in the degree of rachis shattering, and development and fertility of lateral florets.

Discussion

The fifteen *vulgare* and three *spontaneum* lines are interfertile and the resulting hybrids develop normally with full vitality and high seed production. The average seed-set of crosses (34%) is lower compared to the 64–90% reported from pollinating of cultivated types (BRIGGS 1978), but environmental factors may influence the results. Nonetheless, the results show that breeding involving the two materials can be successfully handled by direct hybridization.

Pollen viability and seed-set in F_1 plants did not reveal much correspondence. The pollen viability is relatively high since viabilities of 70% are quoted in the literature (cf. BRIGGS 1978) as encountered within populations of cultivated barley.

Both generations had, on an average, a high seed-set, and differences between lines are not striking enough to warrant attention. The sterility found in some F_2 plants is, however, striking. Seed failure could be brought about by a number of factors including diseases (SANDEFAER 1970), environment

(SANDEFAER 1968), and varietal characteristics (SMITH 1951).

The phenotypes of the F_1 hybrids and most recombinants of the F_2 generation agree with earlier reports (e.g., SMITH 1951; NILAN 1964; HOCKETT and NILAN 1985). In most cases, the data fitted to the 3:1 ratio, indicating single genes. Few cases hinted at actions of complementary genes, while others presuppose interactions of a more complex nature (Table 3).

Disarticulation of rachis generally appeared to fit the 3:1 ratio (chi-square = 3.00), but it varied among lines. There were too many plants with brittle than with tough rachis in the progeny of some lines, and the data of V7 fitted to the 15:1 ratio. If the figures for this line are withdrawn from the analysis of brittle versus tough rachis, the chi-square value falls to 0.84, considerably improving the level of fitness. This character segregated in a perfect 3:1 ratio in the progeny of 2-row *vulgare* and *deficiens* types. Frequently reported ratios for this character are 3:1 and 9:7 (JOHNSON and ÅBERG 1943; SMITH 1951; NILAN 1964). Most investigators agree that rachis brittleness is controlled by two complementary dominant genes designated as *Bt1* and *Bt2*, and tough rachis is a result of either or both of the recessive alleles (SMITH 1951; TAKAHASHI 1955; NILAN 1964; HOCKETT and NILAN 1985). Thus, the *spontaneum* phenotype is represented by the double dominant genotype, *Bt1Bt2* and that of cultivated forms by *Bt1bt2*, *bt1Bt2* or *bt1bt2*. Variation in segregation ratio between lines or groups is suggestive of the occurrence of different genotypes for this character in the *vulgare* lines. Since more genetic affinity is expected between Ethiopian barley and other western barleys which TAKAHASHI (1955) showed to contain more of the western genotype (*bt1Bt2*), it may be deduced that at least part of the single recessives are represented by the same genotype. The data of V7 show consistency with this and earlier findings (JOHNSON and ÅBERG 1943; SMITH 1951), reporting a factor for rachis brittleness in a 6-row hull-less *vulgare*. Generally, this character segregated uniformly among 2-rowed *vulgare*. This may indicate the reported (NILAN 1964) positive association between the brittle gene and spike row number (*bt1bt2 VV*). The double recessive genotype for rachis brittleness is expected to confer some breeding advantages by giving less brittle phenotypes in its progeny compared to the single homozygous genotypes.

Spike row number mostly indicated single locus control with dominance of 2-rowedness, as reported widely (SMITH 1951; NILAN 1964). V13 deviated

from this pattern but gave evidence of modifier gene interactions. It is generally considered that the genetics of row number involves complicated mechanisms. HOCKETT and NILAN (1985) reported that several genetic groups resulting in 6-rowed spikes have been identified and shown to be recessive to their allelic genes but epistatic to 2-rowedness. According to LUNDOVIST (1981), the 6-row phenotype results from homozygosity of one hexastichon or two intermedium genes, or interactions of these. Evidence for co-operation between intermedium genes and six-row genes has been provided recently (LUNDOVIST and LUNDOVIST 1989). Simple inheritance is evident in V7 and V10 and a relatively complex one in V13.

The lateral florets of the *vulgare* parents can be categorized as seeding, seedless (nutans) and missing (deficiens). Seeding ability of laterals, assessed from progeny of 6-row lines, displayed inheritance modes that varied between lines. Evidence for control by single or multiple genes in different lines has been reported (NILAN 1964). The morphology as well as seeding ability of the laterals are shown to be under the control of hexastichon and intermedium genes (LUNDOVIST 1981). Inheritance of seedless laterals suggested single gene pairs in some and complementary genes in other lines, with their presence dominant over their absence. GYMER (1977) has described a different allele for the deficiens phenotype. GUSTAFSSON and LUNDOVIST (1980) and LUNDOVIST and LUNDOVIST (1988) concluded that genes promoting the development of lateral florets may interact in an unexpected and reinforcing or disturbing manner.

Spike density showed both monogenic and complementary gene actions. Several studies reported a monofactorial mode with lax as dominant (SMITH 1951; NILAN 1964) while some obtained evidence for multiple factors (NILAN 1964). The genetics of spike density has been thoroughly investigated with barley *erectoides* (PERSSON and HAGBERG 1969) and *laxatum* (LARSSON 1985) mutants. These studies, noting that spike density is a quantitative character, provided evidence for control by polymeric genes, involving a large number of loci with unequal effects and various pleiotropic syndromes. Cases of complete and partial dominance of the lax trait (LARSSON 1985) and both partial and reversal in dominance of the erectoides gene under different genetic backgrounds (HOCKETT and NILAN 1985) are reported. While V10 shows consistency with the monofactorial mode, V13 illustrates dominance of the dense trait.

The data of hooded versus awned lemma agreed

with previous results (SMITH 1951; NILAN 1964; HOCKETT and NILAN 1985) with respect to dominance and segregation. The progeny of short awned *vulgare* and *spontaneum* (which were long awned) showed monofactorial inheritance, with the long being dominant over the short awned condition. It is also reported as monogenic but with two additional factors affecting only the size of the awns (NILAN 1964). Further elaboration on the genetics of awn length has been provided by KUCERA et al. (1975), whose analysis of *breviaristatum* mutants enabled recognition of three main loci that determine lemma awn size. The case of rough versus smooth awn, for which one or two factor pairs have been reported (NILAN 1964), indicated a single gene pair with rough as dominant.

The other characters studied (spike width, outer glume width, caryopsis type) displayed simple inheritance in conformity with other reports (SMITH 1951; NILAN 1964; HOCKETT and NILAN 1985).

Acknowledgements. — We are very grateful to professor Olov Hedberg, without whose help in obtaining wide contacts this work would not have been attempted. We thank Professor Lars Munk and Dr. Bodil Stilling for their good will and generous provision of materials needed, as well as for the practical training in crossing given to the senior author. Dr. Ib Friis is acknowledged for comments on the manuscript. We also thank Ato Damtew Tefera for the help in the preparation of the figures. The financial support came from SAREC through the Ethiopian Flora Project.

References

- ÅBERG, E. 1940. The taxonomy and phylogeny of *Hordeum* L. Sect. Cerealia Ands. with special reference to Thibetan barleys. — *Symb. Bot. Ups.* 4(2): 1–156
- ANDERSON, M. K. and REINBERGS, E. 1985. Barley breeding. — In: *Barley* (ed D. RASMUSSEN), *Agron. Monogr. no.26, ASA, Madison*, p. 231–268
- BOTHMER, R. VON and HAGBERG, A. 1983. Pre-breeding and wide hybridization in barley. — *Genetika, Ser. F. Suppl.* 3: 41–53
- BOTHMER, R. VON and JACOBSEN, N. 1985. Origin, taxonomy and related species. — In: *Barley* (ed D. RASMUSSEN), *Agron. Monogr. no.26, ASA, Madison*, p. 19–125
- BOTHMER, R. VON, FLINK, J., JACOBSEN, N., KOTIMÄKI, M., and LANDSTRÖM, T. 1983. Interspecific hybridization with cultivated barley (*Hordeum vulgare* L.). — *Hereditas* 99: 219–244
- BRIGGS, D. E. 1978. Barley. — *Chapman & Hall, London*
- BROWN, A. H. D., ZOHARY, D. and NEVO, E. 1978. Outcrossing rates and heterozygosity in natural populations of *Hordeum spontaneum* Koch in Israel. — *Heredity* 41: 49–62
- CIFERRI, R. 1940. Saggio di classificazione degli orzi con speciale riguardo a quelli Etiopici. — *Nuovo G. Bot. Ital.* 47: 424–434. *Societa Italiana, Firenze (English translation used)*
- CIFERRI, R. 1944. Osservazioni ecologico-agrarie e sistematiche su piante coltivate in Etiopia. — *20-C-1(38)*: 179–200. (*English translation used*)
- FEDAK, G. 1985. Wide crosses in *Hordeum*. — In: *Barley* (ed D. RASMUSSEN), *Agron. Monogr. no.26, ASA Madison*, p. 155–186

- GILES, B. E. and BOTHMER, R. VON 1985. The progenitor of barley (*Hordeum vulgare* ssp. *spontaneum*) — its importance as a gene resource. — *Sver. Utsädesfören. Tidskr.* 95: 53–61
- GUSTAFSSON, Å. and LUNDOVIST, U. 1980. *Hexastichon* and *intermedium* mutants in barley. — *Hereditas* 92: 229–236
- GYMER, P. T. 1977. The *deficiens* allele. — *BGN* 7: 34
- HARLAN, J. R. 1968. On the origin of barley. — In: *Barley, Origin, Botany, Culture, Winter-hardiness, Genetics, Utilization and Pests*. — *USDA, Agric. Handb.* 338: 12–34
- HARLAN, J. R. 1976. *Hordeum vulgare* (Gramineae — Triticinae). — In: *Evolution of Crop Plants* (ed N. W. SIMMONDS), Longman
- HOCKETT, E. A. and NILAN, R. A. 1985. Genetics. — In: *Barley* (ed D. RASMUSSEN), *Agron. Monogr. no. 26*, ASA, Madison, p. 187–230
- HOYT, E. 1988. Conserving the wild relatives of crops. — *IBPGR, IUCN, WWF, Switzerland*, p. 1–45
- JACOBSEN, N. and BOTHMER, R. VON 1981. Interspecific hybridization in the genus *Hordeum*. — In: *Barley Genetics IV, Proc. 4th Int. Barley Genet. Symp.* (ed R. N. H. WHITEHOUSE), *Edinburgh University Press, Edinburgh*, p. 710–715
- JOHNSON, J. and ÅBERG, E. 1943. The inheritance of brittle rachis in barley. — *J. Agron.* 35(2): 101–105
- JONASSEN, I. and MUNCK, L. 1981. Biochemistry and genetics of the SP II albumin in hiproly barley. — In: *Barley Genetics IV, Proc. 4th Int. Barley Genet. Symp.* (ed R. N. H. WHITEHOUSE), *Edinburgh University Press, Edinburgh*, p. 330–335
- KRUSE, A. 1974. *Hordeum* × *Agropyrum* hybrids. — *Hereditas* 78: 291–294
- KUCERA, J., LUNDOVIST, U. and GUSTAFSSON, Å. 1975. Induction of brevistaratum mutants in barley. — *Hereditas* 80: 263–278
- LARSSON, H. E. B. 1985. Genetic analysis of *laxatum* barley mutants. — *Hereditas* 103: 255–267
- LUNDOVIST, U. 1981. *Intermedium* and *hexastichon* mutants in barley. — In: *Barley Genetics IV, Proc. 4th Int. Barley Genet. Symp.* (ed R. N. H. WHITEHOUSE), *Edinburgh University Press, Edinburgh*, p. 908–912
- LUNDOVIST, U. and LUNDOVIST, A. 1988. Induced *intermedium* mutants in barley: origin, morphology and inheritance. — *Hereditas* 108: 13–26
- LUNDOVIST, U. and LUNDOVIST, A. 1989. The co-operation between *intermedium* genes and the six-row gene *hex-v* in a six-row variety of barley. — *Hereditas* 110: 227–233
- MULUGETA NEGASSA 1985. Patterns of phenotypic diversity in an Ethiopian barley collection, and the Arsi-Bale Highlands as the centre of origin of barley. — *Hereditas* 102: 139–150
- NILAN, R. A. 1964. The cytology and genetics of barley, 1951–1962. — *Monogr. Suppl. 3 Res. Stud.* 32(1), *Washington State University Press, Pullman, W. A.*
- ORLOV, A. A. 1929. The barley of Abyssinia and Eritrea. — *Bull. Appl. Bot. Genet. Plant Breed.* 20: 283–345. (English translation used)
- PERSSON, G. and HAGBERG, A. 1969. Induced variation in a quantitative character in barley: morphology and cytogenetics of erectoides mutants. — *Hereditas* 61: 115–178
- SANDEFAER, J. 1968. Induced sterility as a factor in the competition between barley varieties. — *Nature* 218: 241–243
- SANDEFAER, J. 1970. Barley stripe mosaic virus as the cause of sterility interaction between barley varieties. — *Hereditas* 64: 150–152
- SMITH, L. 1951. Cytology and genetics in barley. — *Bot. Rev.* 17: 1–51, 133–202, 285–355
- STØLEN, O. 1981. Some aspects of cross-pollination in barley. — In: *Barley Genetics IV, Proc. 4th Int. Barley Genet. Symp.* (ed R. N. H. WHITEHOUSE), *Edinburgh University Press, Edinburgh*, p. 118–129
- TAKAHASHI, R. 1955. The origin and evolution of cultivated barley. — *Adv. Genet.* 7: 227–266
- THOMPSON, R. K. 1971. Barley as a cross-pollinated crop. — In: *Barley Genetics II, Proc. 2nd Int. Barley Genet. Symp.* (ed R. A. NILAN), *Washington State University Press, Washington*, p. 319–322
- ZEGI, Z. and QIUQUAN, S. 1980. Genetic analysis of F₁ hybrids in wild barley from Qing-Zang Plateau. — *Annu. Report Inst. Genet. Acad. Sinica*, p. 139–140. (printed 1981)
- ZEMEDE ASFAW 1988. Variation in the morphology of the spike within Ethiopian barley, *Hordeum vulgare* L. (Poaceae). — *Acta Agric. Scand.* 38: 277–288