

Genetic diversity in *Hordeum agriocrithon* E. Åberg, six-rowed barley with brittle rachis, from Tibet

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Abstract

Twenty-two accessions of *H. agriocrithon* from Tibet were investigated for morphological and physiological characters, and genotypes combined alleles at the tightly linked *Est1*, *Est2* and *Est4* complex locus encoding esterase isozymes. *H. agriocrithon* was similar in plant type to Tibetan cultivated barley, but different from *H. spontaneum*. The accessions of *H. agriocrithon* were classified by their spike-awn types into vars. *eu-agriocrithon*, *dawoense* and *paradoxon*, with one exceptional accession of the awnless naked type similar to var. *nuditonsum* of cultivated barley. They were characterized by spring growth habit, susceptibility to Japanese race I of powdery mildew, and either of the same three esterase genotypes as those of cultivated barley from Tibet, Bhutan and Ladakh. The similarity suggested that the esterase complex locus on chromosome 3H is closely linked with some QTL for adaptation to Tibetan conditions. On the origin of *H. agriocrithon*, it might be concluded that natural hybridization between *H. spontaneum* and six-rowed barley occurred in northern parts of Afghanistan, Pakistan or India, and seeds of their segregants mixed into barley or wheat were brought up to Tibet, resulting six-rowed barley with brittle rachis.

Introduction

Åberg (1938) discovered three kernels of covered barley in a wheat seed sample collected from Taofu, Sichuan Province of southwest China, by H. Smith in 1935. Out of them, two kernels germinated and grew up to maturity. These plants were six-rowed covered barley with brittle rachis, which were named *Hordeum agriocrithon* E. Åberg, and classified into two botanical varieties by their characteristics. One of the varieties was var. *eu-agriocrithon* characterized by yellow ear and long awn, while another was var. *dawoense* with purple ear and lateral awn shorter than central one (Åberg 1940). This finding stimulated to further intensive studies on the brittle six-rowed barley, and several expeditions have been made to collect seed samples and information of *H. agriocrithon*. German Expedition to Shikkim and Tibet in 1938/1939 conducted by E. Schäfer brought home five seed samples of cereals which were bought at a market near Lhasa, located 1200 km southwest of Taofu. In their

seed samples, Freisleben (1943) also found dark gray kernels of *H. agriocrithon*, and thought them to be primitive cultivated varieties of barley that were still being grown for some agricultural purpose. Another seed sample of *H. agriocrithon* was recognized in seed lots of wheat and naked barley from Tsela Dzong between Taofu and Lhasa, collected by a British Expedition to South-East Tibet in 1947 led by M. Sheriff. One plant of *H. agriocrithon* from a wheat seed lot was var. *eu-agriocrithon* with long awn, whereas four plants had long awns on the central rows but awnless on the lateral rows, similar to the intermedium type of cultivated barley. Schiemann (1951) designated these plants *H. agriocrithon* var. *paradoxon*.

In 1974–76, Academia Sinica conducted the scientific expedition to the Chin-Zhang plateau in Tibet to investigate wild barley (Shao 1981, 1982; Shao and Li, 1987). They collected many specimens of *H. agriocrithon* and two-rowed barley with brittle rachis that they called *H. spontaneum*. The samples of *H. agriocrithon* varied in spike type, so they were classified

Table 1. Accessions of *Hordeum agriocrithon* collected from Tibet.

No.	Accession	OU NO.*	Collection site, Province (Collector, Year)
1	eu-agriocrithon 111 (Type 1)	H767	Taofu, Sichuan (H. Smith, 1935)
2	dawoense 112 (Type 2)	H767	Taofu, Sichuan (H. Smith, 1935)
3	dawoense (HOR2456)	H792	Near Lhasa, Tibet (E. Schäfer, 1938)
4	dawoense (HOR2457)	H793	Near Lhasa, Tibet (E. Schäfer, 1938)
5	dawoense (HOR2460)	H795	Near Lhasa, Tibet (E. Schäfer, 1938)
6	dawoense (HOR2461)	H796	Near Lhasa, Tibet (E. Schäfer, 1938)
7	dawoense (HOR2465)	H800	Near Lhasa, Tibet (E. Schäfer, 1938)
8	dawoense (HOR2466)	H801	Near Lhasa, Tibet (E. Schäfer, 1938)
9	agriocrithon (HOR1645)	H786	Tsela Dzong, Tibet (M. Sheriff, 1947)
10	agriocrithon (HOR2451)	H787	Tsela Dzong, Tibet (M. Sheriff, 1947)
11	agriocrithon (HOR2452)	H788	Tsela Dzong, Tibet (M. Sheriff, 1947)
12	agriocrithon (HOR2453)	H789	Tsela Dzong, Tibet (M. Sheriff, 1947)
13	agriocrithon (HOR2454)	H790	Tsela Dzong, Tibet (M. Sheriff, 1947)
14	agriocrithon (HOR2455)	H791	Tsela Dzong, Tibet (M. Sheriff, 1947)
15	agriocrithon (HOR2462)	H797	Tsela Dzong, Tibet (M. Sheriff, 1947)
16	agriocrithon (HOR2463)	H798	Tsela Dzong, Tibet (M. Sheriff, 1947)
17	agriocrithon (HOR2464)	H799	Tsela Dzong, Tibet (M. Sheriff, 1947)
18	paradoxon (HOR2507)	H808	Tsela Dzong, Tibet (M. Sheriff, 1947)
19	paradoxon (HOR2508)	H809	Tsela Dzong, Tibet (M. Sheriff, 1947)
20	paradoxon (HOR2908)	H810	Tsela Dzong, Tibet (M. Sheriff, 1947)
21	agriocrithon TBT-4	H823	Chaya, Tibet (C. Yen, 1983)
22	agriocrithon TBT-6	H824	Chaya, Tibet (C. Yen, 1983)

*Okayama University Accession Number.

into three groups; convar. *lagunculiforme* characterized by lateral spikelets with a short pedicel, convar. *agriocrithon*, and convar. *nudum* with naked caryopsis (Shao 1982). Two convars. *lagunculiforme* and *agriocrithon* were widely grown in Tibet, while convar. *nudum* was distributed in the eastern part of Tibet. In 1981–84, Agricultural Academia Sinica made a mission to Tibet, and collected many samples of wild barley including *H. spontaneum*, and covered and naked types of *H. agriocrithon* exhibiting a large variation in awn length and kernel color (Ma et al. 1987). Furthermore, several expeditions to Tibet collected many seed samples of *H. agriocrithon*, together with their information (e.g. Yang and Yen 1985; Xu 1987; Bothmer et al. 1989).

The present study was conducted to investigate morphological and physiological characters, and esterase genotypes of *H. agriocrithon* collected in different regions of Tibet, to compare them with six-rowed cultivated barley and *H. spontaneum* which might be assumed the cross parents of *H. agriocrithon*, and to discuss the origin of *H. agriocrithon*.

Materials and methods

Twenty-two accessions of *H. agriocrithon* were investigated, which consisted of two accessions collected at Taofu, Sichuan Province by H. Smith in 1935, six accessions brought at a market near Lhasa, Tibet by E. Schäfer in 1938, 12 accessions collected at Tsela Dzong, Tibet by M. Sheriff in 1947, and two accessions collected at Chaya, Tibet by C. Yen in 1983 (Table 1). These accessions have been preserved at Barley Germplasm Center of Okayama University, which have the Okayama University Barley Accession Number such as OUH767 for eu-agriocrithon 111 (Type 1) sent from E. Åberg (1940). The accessions with HOR were sent from Institute of Plant Genetics and Crop Plant Research, Gatersleben, Germany.

The accessions were sown in the late November at Kurashiki, Japan, and the spike-awn type and kernel color were observed. Further, awn lengths of central and lateral spikelets, and length of pedicel at the base of lateral spikelets were measured in five spikes per accession. Growth habit was determined by days from sowing to the flag leaf emergence and number

of leaves on the main stem, when the seedlings were grown in a growth chamber at 18 °C with 24 h illumination per day. Plants of spring habit (I) showed less than 36 days and had seven to eight leaves, while plants of spring habit (II) needed more than 45 days and possessed nine to ten leaves. Reaction to Japanese major races I, IV and IX of powdery mildew were separately examined by the artificial inoculation with each race. Three sets of the seedlings were grown in a greenhouse. When the first leaf of the seedlings expanded, the conidia of each race were sprayed above the seedlings, and reaction to the mildew was determined as resistant, moderately resistant and susceptible (Hiura 1960). Esterase isozyme alleles were determined by the migration distance and the shape of bands appearing after starch gel electrophoresis and enzyme staining, using the extract from the first leaf of seedlings (Nielsen and Johansen 1986).

To investigate the plant type of *H. agriocrithon*, five accessions of each *H. agriocrithon*, Tibetan barley and *H. spontaneum* from Afghanistan near Tibet were measured in stem length, the first internode length from the top, length of spike elongation from the first leaf sheath (= the first internode length – the first leaf sheath length), and lengths and widths of the first and second leaves at the main stems of five plants per accession, and data were treated by the principal component analysis. Furthermore, on referring to the Catalogue of Barley Germplasm preserved in Okayama University (Takahashi et al. 1983) and Geographical Diversity of Isozyme Genotypes in Barley (Konishi 1995a), *H. agriocrithon* was compared with barley from Tibet and its neighboring regions (Bhutan and Ladakh in India), and *H. spontaneum* from Afghanistan as the most eastern region of the distribution.

Results

Plant type

Quantitative data of plant type in respective five accessions of *H. agriocrithon*, Tibetan barley and *H. spontaneum* were treated by the principal component analysis. The Eigen vectors for their characters and contributions to the total variance of the first and second components were indicated in Table 2. The first and second vectors had 46% and 26% contributions to the total variance. The characters were classified into three groups by the first and second vectors.

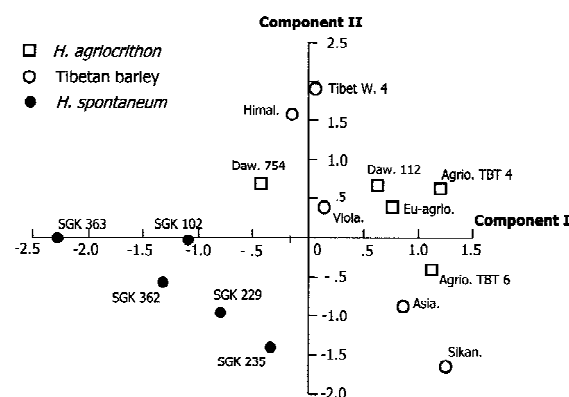


Figure 1. Scatter diagram of *H. agriocrithon*, *H. spontaneum* and Tibetan barley accessions by the first and second scores obtained from the principal component analysis.

Table 2. Eigen vectors for stem and leaf characters.

Character	Eigen vector	
	I	II
Stem length	-0.337	-0.013
1st internode length	-0.484	0.122
Spike elongation	-0.446	0.074
1st leaf length	0.022	0.707
1st leaf width	0.442	0.238
2nd leaf length	-0.117	0.644
2nd leaf width	0.491	0.085
Contribution ratio	0.463	0.260

Lengths of stem, the first internode and spike elongation showed large negative values of the first vector, whereas widths of the first and second leaves had large positive values of the first vector. Lengths of the first and second leaves indicated large positive values of the second vector, respectively. The scores of the first and second components for the accessions were illustrated in Figure 1. Accessions of *H. agriocrithon* were distributed over the first, second and third quadrants overlapping with Tibetan barley accessions, whereas the accessions of *H. spontaneum* were scattered in the fourth quadrant. This indicates that *H. agriocrithon* is similar in plant type to Tibetan barley, and clearly different from *H. spontaneum*.

Spike and kernel characters

All the accessions of *H. agriocrithon* were six-rowed covered barley with brittle rachis, except the naked ac-

Table 3. Spike and kernel characters of *H. agriocrithon* accessions.

No.	Accession	Spike type*	Awn length (cm)		Pedicel lgt. (mm)	Kernel color
			Central	Lateral		
1	eu-agriocrithon 111 (Type 1)	Ll	11.0	8.0	0.0	Blue
2	dawoense 112 (Type 2)	Llb	9.4	0.7	0.5	Blue
3	dawoense (HOR2456)	Ll	8.6	6.4	0.0	Black
4	dawoense (HOR2457)	Ls	7.3	5.0	0.0	Black
5	dawoense (HOR2460)	Ll	9.0	6.5	0.0	Black
6	dawoense (HOR2461)	Ll	9.8	7.4	0.0	Black
7	dawoense (HOR2465)	Ll	8.4	6.0	0.2	Black
8	dawoense (HOR2466)	Ls	7.6	5.6	0.0	Black
9	agriocrithon (HOR1645)	Ll	11.1	7.1	0.2	Yellow
10	agriocrithon (HOR2451)	Ll	11.4	5.2	0.5	Yellow
11	agriocrithon (HOR2452)	Ll	11.3	8.2	0.4	Yellow
12	agriocrithon (HOR2453)	Ll	10.5	8.6	0.0	Yellow
13	agriocrithon (HOR2454)	Ll	11.0	8.8	0.1	Yellow
14	agriocrithon (HOR2455)	Ll	11.4	7.3	0.0	Yellow
15	agriocrithon (HOR2462)	Ll	12.4	9.2	0.0	Blue
16	agriocrithon (HOR2463)	Llb	11.0	2.3	0.3	Blue
17	agriocrithon (HOR2464)	Ll	11.8	8.8	0.2	Yellow
18	paradoxon (HOR2507)	Llp	9.7	5.4	1.0	Yellow
19	paradoxon (HOR2508)	Llbp	10.4	0.3	1.8	Yellow
20	paradoxon (HOR2908)	Llbp	11.5	0.3	1.2	Yellow
21	agriocrithon TBT-4	Llb	8.3	1.6	0.0	Blue
22	agriocrithon TBT-6 [#]	Lo	1.2	0.0	0.5	Blue

*Ll: Lax spike with long awn. Ls: Lax spike with short awn. Lo: Lax and awnless spike.
b: awnless lateral spikelets. lp: lateral spikelets with a pedicel. #: naked.

cession of agriocrithon TBT-6 (No. 22). As shown in Table 3, spike-awn types among the accessions varied in awn lengths of central and lateral spikelets, although all the accessions had lax spikes. Three accessions named 'paradoxon' had a pedicel longer than 1 mm at the base of each lateral spikelet. Referring to awn lengths, most of the accessions corresponded to the botanical varieties designated by Åberg (1940) and Schiemann (1951), but some of them differed from the nomenclature. However, the name of each accession was still used the original name designated by the collector, and written in Roman in this text. Three accessions of dawoense 112, agriocrithon (HOR2463) and agriocrithon TBT-4 had extremely short awn of lateral spikelets, so they might be classified into var. *paradoxon*. Meanwhile, paradoxon (HOR2507) had considerably long awn of lateral spikelets and yellow kernels, suggesting that it might be var. *eu-agriocrithon*. The peculiar spike type was found in the naked agriocrithon TBT-6, which had extremely short-awned or awnless spikes like var. *nuditonsum* (Körn.) Mansf. (Mansfeld, 1950). However, it should be noted

that awn length of lateral spikelets was considerably influenced by growing conditions, especially by temperature during the development of spike primordia differentiation (Hayashi and Yasuda 1989).

Kernel color ranged from yellow to blue in aleurone layers, and from yellow to black in the pericarp of kernels. All the accessions of 'dawoense' had black or dark gray kernels.

Spring growth habit and reaction to powdery mildew

As shown in Table 4, all the accessions of *H. agriocrithon* were spring type of growth habit. Most of the accessions were extreme spring type of grade I that needed no vernalization for heading, while some of the accessions were spring type (II) that required at least 10 days vernalization at the seedling stage.

As to reactions to powdery mildew, no accessions were found to be completely resistant to any races of Japanese major races I, IV and IX. All the accessions were susceptible to race I, and some of them were moderately resistant to either of races IV and IX.

Table 4. Physiological characters and esterase alleles of *H. agriocrithon* accessions.

No.	Accession	Growth habit*	Mildew**			Esterase allele		
			I	IV	IX	<i>Est1</i>	<i>Est2</i>	<i>Est4</i>
1	eu-agriocrithon 111 (Type 1)	Spring (II)	S	S	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
2	dawoense 112 (Type 2)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
3	dawoense (HOR2456)	Spring (I)	S	S	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
4	dawoense (HOR2457)	Spring (I)	S	S	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
5	dawoense (HOR2460)	Spring (I)	S	M	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
6	dawoense (HOR2461)	Spring (I)	S	S	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
7	dawoense (HOR2465)	Spring (I)	S	S	M	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
8	dawoense (HOR2466)	Spring (I)	S	M	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
9	agriocrithon (HOR1645)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
10	agriocrithon (HOR2451)	Spring (II)	S	S	M	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
11	agriocrithon (HOR2452)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
12	agriocrithon (HOR2453)	Spring (II)	S	S	M	<i>Pr</i>	<i>Fr</i>	<i>At</i>
13	agriocrithon (HOR2454)	Spring (II)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>At</i>
14	agriocrithon (HOR2455)	Spring (I)	S	S	M	<i>Ca</i>	<i>Un</i>	<i>Su</i>
15	agriocrithon (HOR2462)	Spring (I)	S	S	M	<i>Al</i>	<i>ne</i>	<i>At</i>
16	agriocrithon (HOR2463)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>At</i>
17	agriocrithon (HOR2464)	Spring (II)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>At</i>
18	paradoxon (HOR2507)	Spring (I)	S	S	M	<i>Pr</i>	<i>Fr</i>	<i>At</i>
19	paradoxon (HOR2508)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
20	paradoxon (HOR2908)	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>
21	agriocrithon TBT-4	Spring (I)	S	S	S	<i>Ca</i>	<i>Un</i>	<i>Nz</i>
22	agriocrithon TBT-6	Spring (I)	S	S	S	<i>Pr</i>	<i>Fr</i>	<i>Su</i>

*Spring (I): Extremely spring type required no vernalization for heading.

Spring (II): Spring type required at least 10 days vernalization for heading.

**Reactions to Japanese races I, IV and IX of powdery mildew. M: moderately resistant.

S: susceptible.

Esterase genotypes

Esterase genotypes are indicated as combinations of alleles at the tightly linked *Est1*, *Est2* and *Est4* loci on the long arm of chromosome 3H. Three kinds of the genotypes, *Ca-Un-Nz* (indicated as an allelic combination at the *Est1*, *Est2* and *Est4* loci), *Pr-Fr-Su* and *Pr-Fr-At* were detected in the accessions, with one exception, agriocrithon (HOR2462) (No. 15), carrying *Al-ne-At*. Six accessions of 'dawoense' from the suburb of Lhasa had the same genotype of *Ca-Un-Nz* and spring growth habit of grade I, whereas they differed in reactions to powdery mildew races.

Discussion

After finding *H. agriocrithon* from Tibet, attention has been extensively paid to six-rowed barley with brittle rachis. Such brittle six-rowed barleys were frequently found in Israel (Kamm, 1954; Zohary,

1959), Cyprus (Hadjichristodoulou, 1992) and Libya (Hammer et al., 1985). Meanwhile, brittle six-rowed barley was discovered in Ladakh, northwestern India, together with brittle two-rowed barley (Witcombe, 1978a). And, Murphy et al. (1982) found two-rowed and six-rowed segregants in the progeny rows from *H. agriocrithon* collected from Ladakh, whereas brittle two-rowed barley remained true to type in the progeny rows. Furthermore, they produced similar material to *H. agriocrithon* by the artificial crosses between *H. spontaneum* and six-rowed cultivated barley, and thought that brittle six-rowed barleys were produced from natural hybridization between *H. spontaneum* and six-rowed cultivated barley. This assumption on the origin of *H. agriocrithon* has been widely accepted (e.g. Zohary, 1964; Kamm, 1977; Yang and Yen, 1985; Bothmer et al., 1989).

Hence, comparison between *H. agriocrithon* and its assumed parents was conducted for several characters, using 24 accessions of *H. spontaneum* from Afghanistan and 31 Tibetan barley accessions includ-

Table 5. Comparison of the spike-awn types in *H. agriocrithon*, *H. spontaneum* and cultivated barley.

Accession	Spike-awn type*								Total
	Ll	Ls	Lo	Llb	Lk	DI	Ds	Dek	
<i>H. agriocrithon</i>	11	5	1	5					22
<i>H. spontaneum</i>	24								24
Cultivated barley									
Tibet	24	1	1			3	2		31
Bhutan	7					5		3	15
Ladakh	37			7	1	6	4	5	60

*Ll: Lax spike with long awn. Ls: Lax spike with short awn. Lo: Lax and awn-less spike. Llb: Lax spike with central long awn but lateral shorter awn. Lk: Lax spike with hooded awn. DI: Dense spike with long awn. Ds: Dense spike with short awn. Dek: Dense spike with elevated hooded awn.

ing 16 accessions cited by Åberg (1940) (from Types 3 to 20 except 16 and 18). Furthermore, 15 accessions from Bhutan (Konishi 1993) and 60 accessions from Ladakh (Witcombe, 1978b) were combined into Tibetan barley, because the tradition said the emigrants from Tibet had brought barley seed into these regions and Ladakh is generally called “Little Tibet”. As indicated in Table 5, every spike-awn type found in *H. agriocrithon* was detected in cultivated barley, but any dense spikes could not be recognized in *H. agriocrithon*. The spike-awn type of *H. spontaneum* commonly was Ll (long spike with long awn), so spike-awn variation of *H. agriocrithon* was caused by gene flow from cultivated barley.

For inferring the parents of *H. agriocrithon*, it is one of the powerful ways to investigate isozyme alleles and their combinations in the accessions of *H. agriocrithon*, since isozyme alleles are neutral to selection (Konishi 1995a). Especially, three loci for esterase isozymes, *Est1*, *Est2* and *Est4*, are tightly linked on the long arm of chromosome 3H (Konishi and Matsuura 1987a), and genotypes combined their alleles are distributed with a geographical regularity in the world (Konishi and Matsuura 1991; Konishi 1995a). The accessions of *H. agriocrithon* carried three major genotypes of *Ca-Un-Nz*, *Pr-Fr-Su* and *Pr-Fr-At*. They were the same genotypes of cultivated barley accessions from Tibet, Bhutan and Ladakh (Table 6), strongly suggesting that Tibetan barley might be one of the parents of *H. agriocrithon*. Dai and Zhang (1989) also reported that the *Pr-Fr-At* genotype dominated in Tibetan barley, followed by the *Pr-Fr-Su* genotype. On the contrary, the both genotypes were not detected in the accessions of *H. spontaneum* from Afghanistan (Table 6). Furthermore,

their genotypes could not be found in the accessions of *H. spontaneum* which were collected from different regions of the world and preserved at Barley Germplasm Center of Okayama University (Konishi 1995a), and the *Pr* allele at the *Est1* locus was extremely rare in the world collection of *H. spontaneum* maintained by USDA (Kahler and Allard 1981). As the exceptional accession, agriocrithon (HOR2462) was pointed out to carry the genotype of *Al-ne-At* for esterase isozymes (Table 4). If the genotype will be detected in *H. spontaneum*, it may be the other parent. The genotype could not be found in the *H. spontaneum* collection of Okayama University, but the *Al-ne-At* genotype was frequently observed in cultivated barley accessions from Afghanistan (Konishi 1995a). This suggests a possibility to find the *Al-ne-At* genotype in *H. spontaneum* populations of Afghanistan, and the other parent of agriocrithon (HOR2462) might be *H. spontaneum* in Afghanistan. To elucidate the origin of *H. agriocrithon* in more detail, it is necessary to get detailed information about *H. spontaneum* and cultivated barley in the northern regions of Pakistan and India.

In this comparison of esterase genotypes, it should be emphasized that all but one accession of *H. agriocrithon* possessed the same genotypes to those of Tibetan barley. Why the esterase genotypes of Tibetan barley were preferentially selected in hybrid populations between *H. spontaneum* and Tibetan barley? We have observed the preferential selection of the specific esterase genotypes in several hybrid populations (Konishi and Matsuura 1987b; Konishi 1995a; b), and considered that the selection could be explained by a linkage drag between this esterase complex locus and some QTL for adaptation. A similar linkage drag for

Table 6. Comparison of esterase genotypes in *H. agriocrithon*, *H. spontaneum* and cultivated barley.

Accession	Esterase genotype					Total
	<i>Ca-Un-Nz</i>	<i>Pr-Fr-At</i>	<i>Pr-Fr-Su</i>	<i>Ca-Fr-At</i>	Others	
<i>H. agriocrithon</i>	8	5	8		1	22
<i>H. spontaneum</i>	1			11	12	24
Cultivated barley						
Tibet	17	12	1		1	31
Bhutan	7	6	2			15
Ladakh	7	33	20			60

adaptation might be found in Tibetan barley, resulting in the preferentially selected esterase genotypes of *H. agriocrithon*. This assumption will be supported by the evidence that the same major alleles at the *Est1*, *Est2* and *Est4* loci in '*H. spontaneum*' from Tibet were *Pr*, *Fr* and *At*, respectively, as those in *H. agriocrithon* and Tibetan cultivated barley (Zhang et al., 1994).

Finally, one of the most important characters for adaptation is growth habit. As mentioned in Table 4, all the accessions of *H. agriocrithon* possessed the spring growth habit. Xu (1987) reported a life cycle of wild barleys in the Qinghai-Tibetan Plateau. They had the spring growth habit, and the maturity was earlier than that of the cultivated barley in autumn. Spikelets with brittle rachis dropped on the ground before harvesting the cultivated barley, and the seeds sprouted in the next spring. Yang and Yen (1985) further observed that the lowest spikelets remained on the spike were harvested with the cultivated barley simultaneously, resulting that the mixed seeds of *H. agriocrithon* were again sown in barley fields. On the contrary, most of the *H. spontaneum* accessions from Afghanistan were characterized by the winter growth habit. In segregants derived from spontaneous hybridization between *H. spontaneum* and Tibetan barley, hybrid swarms with the spring growth habit could survive from natural selection under short summer and low temperature conditions in Tibet and its neighboring regions more than 2500 m above the sea level.

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