The Relationship between High-Molecular-Weight Glutenin Subunit Composition and the Quality of Japanese Hexaploid Wheat Lines

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To reveal the high-molecular-weight (HMW) glutenin subunit composition, the seed storage proteins of 40 Japanese wheat (*Triticum aestivum*) lines were fractionated by sodium dodecyl sulfate−polyacrylamide gel electrophoresis to determine their HMW glutenin subunit composition. These were identified by comparison of subunit mobility with that previously found in hexaploid wheat. Twelve different, major glutenin HMW subunits were identified. Each line contained three to five subunits, and 11 different glutenin subunit patterns were observed for 11 alleles in Japanese lines. The *Glu-1* quality scores were not particularly high for most of the Japanese wheats in the southern part of Japan (Kyushu district). However, the *Glu-1* quality scores of several wheat lines in the Hokkaido area (north Japan) were high. South Japanese wheat lines showed specialty allelic variation in the glutenin HMW 145 kDa subunit, different from those in non-Japanese hexaploid wheats.

Keywords: *Hexaploid wheat; HMW glutenin; subunit composition; bread-making quality*

INTRODUCTION

High-molecular-weight (HMW) glutenin subunits represent a group of wheat seed storage proteins characterized by molecular weights between 80 000 and 145 000 and a complex biochemical structure involving disulfide bonds. This group of storage proteins has been extensively explored during the last 20 years. The HMW glutenin subunits were identified electrophoretically in a range of hexaploid wheat varieties (Nakamura et al., 1999). Genetic analysis revealed that each locus displays allelic variation, and this is responsible for some of the differences among varieties in protein quality for making bread. The information on the relative qualities of different alleles at each locus indicates the following order in importance of bread-making potential *Glu-1* > *Gli-1* > *Gli-2* (Payne et al., 1984). The genes for some of these alleles are being incorporated into the genomes of commercial wheats (Payne et al., 1984). Each hexaploid wheat contains three to five HMW subunits distinguishable by using SDS−PAGE (Payne et al., 1984). The high-molecular-weight subunit designated as the 145 kDa subunit was found frequently in Japanese commercial varieties (Nakamura et al., 1990). This subunit has an electrophoretic mobility identical to that of glutenin HMW subunit 2.2 as reported by Payne et al. (1983a).

The major endosperm storage proteins of wheat are glutenins, which consist of polypeptides cross-linked by interpolypeptide disulfide bonds, and gliadins, a complex mixture of single polypeptides (Shewry and Tatham, 1990). The storage proteins of wheat flour typically consist of approximately 50% gliadin, 10% HMW glutenin subunits, and 40% LMW glutenin subunits. HMW glutenin subunits are essential for gluten elasticity and bread-making quality (Payne et al., 1984) and Chinese noodle-making quality (Huang et al., 1988) of wheat flour. It has been well-known that HMW glutenin subunit composition plays an important role in determining the wheat quality. Wheat is imported from the United States and Canada for bread-making purposes. Historically, wheat breeding for quality in Japan has received little attention; industrial quality research efforts started only 20 years ago. In Japan, a major objective of wheat breeders is to develop new, high-yielding varieties with improved bread-making qualities. Wheat for making bread must have certain minimum levels of protein content and protein quality. At the wheat breeding institute, a greater effort is being placed on the improvement of protein quality in the Japanese breeding programs (Nakamura et al., 1999). To date, the HMW glutenin subunit composition of Japanese wheats remains unexplored. Some wheat breeding programs such as those at wheat breeding institutes outside of Japan and the International maize and wheat improvement center (CIMMYT) have already used HMW glutenin subunit composition as a criterion of selecting parents for improving bread-making quality. The protein content of cereal grains is low and for wheat is normally between 9% and 16% of the dry weight. Nevertheless, world production of wheat grain protein is vast. As well as being of great importance nutritionally to many peoples of the world, wheat grain protein plays a fundamental part in food processing, for instance, in bread manufacture, biscuits, breakfast cereals, pasta, and Japanese noodle products (Nakamura et al., 1999).

The frequency of varieties with a 145 kDa subunit was higher in the southern part of Japan than the northern part, and investigation of pedigrees shows that the genotypes with and without the 145 kDa subunit were preferably selected in each step of the wheat breeding procedures in the southern and northern parts of Japan, respectively (Nakamura et al., 1999). The studies investigating HMW glutenin composition and/or its relation to bread-making quality were carried out in virtually all major wheat-producing countries. Because the HMW glutenin composition of bread wheat varieties from many countries has now been published,

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an analysis of these data will contribute to our knowledge of the worldwide distribution of *Glu-1* alleles (Morgunov et al., 1993).

The objective of this study was to investigate the allelic composition at each of the three loci controlling HMW glutenin subunits of the advanced lines of hexaploid wheat registered in northern or southern Japan and to provide information for improving the industrial quality of Japanese commercial wheat varieties. The results are presented in the form of a key to aid in the identification of unknown samples. This key should provide a useful supplement to other keys of Japanese wheat varieties based on glutenin and gliadin patterns. The information may also be of interest to plant breeders, because breeders are now taking HMW glutenin subunit composition into account when choosing patterns for crosses intended to produce lines in Japanese bread or noodle wheat breeding programs.

EXPERIMENTAL PROCEDURES

The 40 Japanese wheat lines in this research originated from the northern or southern part of Japan, respectively. Seeds of these wheat lines were from the National Institute of Agrobiological Resources, Tsukuba, Japan. To determine the electrophoretic mobility of each HMW glutenin subunit by sodium dodecyl sulfate−polyacrylamide gel electrophoresis (SDS−PAGE), standards (Bezostaya-1, Champlain, Chinese-Spring, Danchi, Dunav, Federation, Gabo, Hobbit, Hope, Lancota, Norin 61, Sappo, and Serbian) that included the spectra of the subunits expected were used (Payne and Lawrence, 1983b). These lines were analyzed by SDS−PAGE, according to the procedure of Payne et al. (1979).

The separation gel contained 1.5 M Tris−HCl, pH 8.8, and 0.27% SDS. Gels were made from 7.5% (v/v) acrylamide and 0.2% (v/v) bis-acrylamide. The acrylamide, which is toxic, must be carefully used in the experiment. The stacking gel contained 0.25 M Tris−HCl buffer, pH 6.8. Wheat flour (10 mg) was suspended in 300 mL of 0.25 M Tris−HCl buffer (pH 6.8) containing 2% (v/v) SDS, 10% (v/v) glycerol, and 5% 2-mercaptoethanol, and shaken for 2 h at room temperature. The suspension was heated at 95 °C for 3 min. The top portion of the supernatant was collected after centrifugation for 3 min at 12 000 rpm, and a portion (30 μL) of the extract was loaded into individual lanes on SDS−PAGE gels. The electrode buffer was 0.025 M Tris-glycine, pH 8.3, containing 0.1% (v/v) SDS. Electrophoresis was conducted at 10 mA constant current for 15 h until the tracking dye, Bromophenol blue, reached the bottom of the gel. The gels were stained for several hours with a mixture of Coomassie blue R dissolved in aqueous ethanol and acetic acid.

The system for numbering HMW glutenin subunit bands and for allelic classification at *Glu-A1*, *Glu-B1*, and *Glu-D1* loci, proposed by Payne and Lawrence (1983b), was used in this study. In this study, alleles are designated by lower case letters following the locus name, for example, *Glu-A1a*. HMW *Glu-1* quality scores were determined and compared with the official bread-making quality of the wheat varieties (Payne et al., 1987).

RESULTS AND DISCUSSION

Current analysis of high-molecular-weight (HMW) glutenin subunit composition shows a post-factum status of these loci because, until recently, wheat breeders did not manipulate the alleles intentionally in Japan. So the analysis reflects the results of indirect changes in genetic constitution due to selection for related or linked traits in Japan. The HMW glutenin subunits have distinctly slower electrophoretic mobilities than either the gliadins or LMW glutenin subunits and so can be clearly identified on SDS−PAGE gels. The banding patterns are those obtained in a gel of 7.5% acrylamide. Table 1 indicates the alleles for the complex gene loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, which code for HMW subunits of glutenin in hexaploid wheat. For the Japanese wheat lines, 11 different alleles were identified, three corresponding to the *Glu-A1* locus, four to the *Glu-B1* locus, and four to the *Glu-D1* locus. Each pattern included three to five bands of HMW glutenin subunits. It was said that HMW glutenin subunit composition is useful for wheat variety identification (Payne et al., 1984). The Japanese hexaploid wheat lines in this study could be divided into 11 groups on the basis of this parameter.

At the *Glu-A1* alleles, 15 lines in north Japanese lines possessed subunit 1 encoded by the *Glu-A1a* allele; 32.8% in varieties throughout the world possess the *Glu-A1a* allele on chromosome 1A. The null allele *Glu-A1c* was now frequently observed here in Japanese lines, regardless of the breeding area between north and south Japan, compared with 36% in 1380 varieties throughout the world reported by Morgunov et al. (1993).

In *Glu-B1* alleles, subunits 7, 7 + 8, 7 + 9, and 20 are represented. Subunits 7 + 8 controlled by the *Glu-B1b* allele was detected in most Japanese commercial wheats (Nakamura et al., 1999). It is quite different from that (25%) of 1380 varieties throughout the world. By and large, many Japanese wheat lines had subunits 7 + 8 controlled by the *Glu-B1b* allele, regardless of the breeding area (Table 1), which is similar to Japanese commercial varieties (Nakamura et al., 1999). Five wheat lines had the rare subunits in Japan; subunit 7 (three lines in the Hokkaido area; Hokkai 44, Hokkai 61, and Hokkai 64) and subunit 20 (two lines in the Hokkaido area; Hokkai 240 and Kitami 18). The high frequency of subunits 4 + 12 was noted in the Hokkaido district (Table 1). The frequency of subunits 2 + 12 encoding the *Glu-D1a* allele was high and many Japanese lines possessed subunits 2 + 12 (Table 1). It was similar to the proportion, 53%, of the variation at the *Glu-D1a* allele throughout the world.

Only six bread wheat lines in the Hokkaido breeding area, Honiku 52, Hokkai 44, Hokkai 61, Hokkai 62, Hokkai 64, and Hokkai 115, possessed subunits 5 + 10 encoded by the *Glu-D1d* allele: 41% in 1380 varieties throughout the world (Morgunov et al., 1993) contain this subunit. Table 1 also gives the *Glu-1* quality scores of the Japanese lines, the scores ranged from 5 to 10. However, the quality scores for nine lines were distributed across five subunit groups (1, 7 + 8, 145 kDa + 12; 2*, 7 + 8, 145 kDa + 12; Null, 7 + 8, 145 kDa + 12; null, 7 + 9, 145 kDa + 12; null, 20, 2 12) were not determined because 145 kDa glutenin subunit was a rare subunit in non-Japanese wheats and a rare subunit 20 in the 1380 varieties throughout the world (Morgunov et al., 1993) whose effects on bread-making quality have yet to be determined. Average *Glu-1* quality scores of Japanese wheats have been shown to be less than those of known quality wheats from Europe, Australia, Canada, and the United States (Graybosch

Table 1. Relationship between High-Molecular-Weight (HMW) Glutenin Subunit Composition and *Glu-1* Quality Score in Japanese Wheat Lines

wheat lines		HMW glutenin subunit composition			*Glu-1* bread-making quality score	N/S	wheat breeding area
Honiku	37	null	7 + 9	2 + 12	5	N	Hokkaido
Honiku	50	1	7 + 8	4 + 12	7	N	Hokkaido
Honiku	51	null	7 + 8	2 + 12	6	N	Hokkaido
Honiku	52	1	7 + 8	5 + 10	10	N	Hokkaido
Honiku	53	1	7 + 8	4 + 12	7	N	Hokkaido
Honiku	54	1	7 + 8	4 + 12	7	N	Hokkaido
Honiku	68	1	7 + 8	4 + 12	7	N	Hokkaido
Honiku	133	1	7 + 8	4 + 12	7	N	Hokkaido
Hokkai	44	1	7	5 + 10	8	N	Hokkaido
Hokkai	61	1	7	5 + 10	8	N	Hokkaido
Hokkai	62	1	7 + 8	5 + 10	10	N	Hokkaido
Hokkai	63	null	7 + 9	2 + 12	5	N	Hokkaido
Hokkai	64	1	7	5 + 10	8	N	Hokkaido
Hokkai	65	null	7 + 9	2 + 12	5	N	Hokkaido
Hokkai	106	null	7 + 8	2 + 12	6	N	Hokkaido
Hokkai	115	1	7 + 8	5 + 10	10	N	Hokkaido
Hokkai	116	null	7 + 9	2 + 12	5	N	Hokkaido
Hokkai	138	1	7 + 9	2 + 12	7	N	Hokkaido
Hokkai	153	null	7 + 8	4 + 12	5	N	Hokkaido
Hokkai	165	null	7 + 8	2 + 12	6	N	Hokkaido
Hokkai	180	1	7 + 8	4 + 12	7	N	Hokkaido
Hokkai	183	null	7 + 8	4 + 12	5	N	Hokkaido
Hokkai	195	null	7 + 8	2 + 12	6	N	Hokkaido
Hokkai	240	null	20	2 + 12		N	Hokkaido
Kitami	17	1	7 + 8	4 + 12	7	N	Hokkaido
Kitami	18	1	7 + 8	4 + 12	7	N	Hokkaido
Kitami	22	null	20	2 + 12		N	Hokkaido
Igatikugo	1	null	7 + 8	2 + 12	6	S	Kyushu
Igatikugo	2	null	7 + 8	2 + 12	6	S	Kyushu
Igatikugo	3	null	7 + 8	2 + 12	6	S	Kyushu
Minamikyushu	62	2*	7 + 8	2 + 12	8	S	Kyushu
Saikai	95	2*	7 + 8	2 + 12	8	S	Kyushu
Saikai	98	null	7 + 8	145kDa + 12		S	Kyushu
Saikai	104	null	7 + 8	145kDa + 12		S	Kyushu
Saikai	113	2*	7 + 8	145kDa + 12		S	Kyushu
Saikai	149	2*	7 + 8	145kDa + 12		S	Kyushu
Saikai	150	2*	7 + 8	145kDa + 12		S	Kyushu
Saikai	151	null	7 + 9	2 + 12	5	S	Kyushu
Saikai	152	2*	7 + 8	145kDa + 12		S	Kyushu
Saikai	153	null	7 + 8	145kDa + 12		S	Kyushu

[a] N/S = The breeding area in northern (Hokkaido area) or southern (Kyushu area) part of Japan.

et al., 1990; Khan et al., 1989; Lawrence, 1986; Lukow et al., 1989; Ng and Bushuk, 1989; Payne et al., 1984). The *Glu-1* quality scores were not particularly high for most of the Japanese wheats in southern part of Japan (Kyushu district). The lower *Glu-1* quality scores of southern wheats are not unexpected since most wheat breeding programs in the Kyushu district have focused on noodle quality or yield improvement. In this Kyushu district (south Japan) wheat has been mainly used to make Japanese soft noodles, this could be another reason Japanese wheats have poor bread-making quality because the quality requirements for soft noodles are very different, until recently to have limited interest in bread-making quality.

However, the *Glu-1* quality scores of several wheat lines in the Hokkaido area (north Japan) were high. In the Hokkaido district, the wheat breeding program has been mainly used to make breads with good bread-making quality. Eleven HMW glutenin subunit compositions were observed in 40 lines, and it was also found that three lines possessed the subunit combination (subunits 1, 7 + 8, and 5 + 10) in Japan. Judging by the HMW glutenin composition, only three lines (Honiku 52, Hokkai 62, and Hokkai 115) are expected to have very good bread-making quality, due to the presence of subunits 1, 7 + 8, and 5 + 10, which was an exceptionally positive effect on highest bread-making quality grade (Payne et al., 1987). Japanese commercial varieties do not currently possess this subunit group (Nakamura et al., 1999).

Table 1 also shows that three subunit groups 1, 7 + 8, 4 + 12; 1, 7, 5 + 10, and 1, 7 + 8, 5 + 10 in the north area, but, it was rare subunit groups in Japanese commercial varieties (Nakamura et al., 1999). However, three subunit groups 2*, 7 + 8, 145 kDa + 12; null, 7 + 8, 2 + 12, and null, 7 + 8, 145 kDa + 12 were found between north and south breeding areas, respectively. Null (null allele, *Glu-A1c*), and subunits 7 + 8 and 2 + 12 controlled by the *Glu-B1b* and *Glu-D1a* alleles, respectively, were found in many Japanese wheats (Nakamura et al., 1999), but, the 27 lines in the Hokkaido district were different. It is evident from the present study that the Japanese wheat breeding lines do not vary widely in HMW glutenin subunit groups, and the subunit compositions were different from between north and south districts in Japan, respectively. Hexaploid wheat landraces or old varieties have more variability compared to modern varieties (Lagudah et al., 1987; Pogna et al., 1989). The relative uniformity of bread wheat varieties for the *Glu-D1* alleles may be explained by tremendous selection pressure toward alleles with particular effect on bread-making quality.

A characteristic apparently unique to Japanese lines is the high frequency of the *Glu-D1f* allele in the Kyushu district, which is similar to Japanese commercial varie-

ties (Nakamura et al., 1999). Wheat lines ideal for Japanese noodle-making quality are of course preferred in Japan, and the frequency of the 145 kDa subunit in these lines is high. It is particularly high in southern Japan, but quite low in northern areas (the Hokkaido area). In southern Japan, lines good for noodle-making quality are used most. In the pedigree of the commercial varieties, the many landraces and lines that possess 145 kDa subunit were used by crossing within the soft noodle wheat breeding programs. Japanese wheat lines in southern Japan, differ considerably from non-Japanese wheats in allelic variation in HMW glutenin subunits at loci, *Glu-A1*, *Glu-B1*, and *Glu-D1* (Payne et al., 1983b). HMW subunits of glutenin have different properties from other smaller and more abundant subunits (Payne et al., 1981) and thus allelic variation in HMW glutenin subunits of the Japanese lines is a matter of considerable importance. In the Kyushu lines, the frequency of the 145 kDa subunit is very high and in some cases occurs in unique combinations. Hard Japanese wheats do not possess this 145 kDa subunit, instead of many Japanese commercial soft wheats possess this 145 kDa subunit (Nakamura et al., 1990). Wheat kernel hardness is correlated with Japanese noodle-making quality, with hard wheat varieties having poor quality. Wheat lines ideal for Japanese noodle-making are of course preferred in south Japan and the frequency of the 145 kDa subunit in these lines may, consequently, be associated with this character. The 145 kDa subunit is characterized by high frequency of alleles with exceptionally negative effect on bread-making quality (Nakamura et al., 1990). This might be due to HMW glutenin subunit interaction and some other factors that also determine Japanese soft noodle-making quality. Likewise, the high rainfall or warmth mega-environment includes Kyushu district in south Japan.

The frequency of subunits related to good bread-making quality, such as subunit group 1, 5 + 10, and 7 + 8 are not present in this south area. Morgunov et al. (1990) pointed out the association between certain HMW glutenin subunits and environmental stresses, breeding objectives, and different wheat types. Differences reports concerning the relationship between subunit composition and environment might be influenced by inadequate selection of wheat varieties and wheat variety number used in each study (He et al., 1992). Research on wheat flour component contribution to noodle quality indicates proteins to be of primary importance in this regard, and quantitative and qualitative aspects should be considered in explaining variation in the quality of noodles made from different wheats (Miskelly, 1981; Miskelly and Moss, 1985). Variation in HMW glutenin subunit composition in the Kyushu wheat line is very different from that of the 1380 varieties throughout the world, according to Morgunov et al. (1993). Especially, the frequency of the 145 kDa subunit in the Japanese wheat lines is quite different from that of the 1380 varieties throughout the world reported by Morgunov et al. (1993). The results of this study indicate the Japanese hexaploid wheat lines not vary widely in HMW glutenin subunit group, although unique HMW glutenin subunit combinations have been observed in some cases. Judging by the HMW glutenin subunits in seed storage proteins, the wheat lines in Kyushu area, are expected to have good soft noodle quality, the wheat grain hardness is correlated with Japanese soft noodle quality, with hard bread wheat varieties do not possess the 145 kDa subunit (Nakamura et al., 1990). The concern of plant breeders about genetic uniformity of modern varieties is well-known. This matter may be of interest to wheat breeders who consider HMW glutenin subunit groups when breeding crossing lines of good quality.

The present data indicates allelic variation in the HMW glutenin subunit loci of *Glu-1* in the Japanese hexaploid wheat lines to be unique throughout the world, although for these lines, there are only 11 HMW glutenin subunit compositions. The present results should facilitate the identification of Japanese wheat varieties and their production in the future by using SDS−PAGE. As introducing the alleles of lines Honiku 52, Hokkai 62, or Hokkai 115 in Japanese commercial varieties of the Japanese bread wheat breeding programs, the Japanese bread variety can possess this subunit composition with the highest bread-making quality grade. They may offer the prospect of further advancement by combination with the good glutenins.

The above results demonstrate that the pattern of HMW glutenin subunits in northern part of Japanese wheat lines is distinct from that observed in the lines from southern Japan. Japanese wheat lines are similar to those from Japanese commercial varieties (Nakamura et al., 1999) in the Kyushu district. Common parentage can influence the distribution of *Glu-1* alleles. Frequent involvement of the same successful parents in crosses will result in a large similarity in genetic structure. The present study showed wheat breeding area, specific differences in frequencies of *Glu-1* subunits. There are three factors influencing the distribution of *Glu-1* alleles: (1) they might be linked to genes of adaptive value, which results in preferential selection of particular alleles for certain area, (2) the differences in frequency parents arise from the use of a particular parental gene pool for each wheat breeding area, and (3) the Japanese distribution of *Glu-1* alleles is influenced by selection pressure toward good bread-making quality or Japanese soft noodle-making quality since these genes contribute to the amount and quality of wheat gluten. Thus the geographical distribution of *Glu-1* alleles appears to be based on product use and market demand rather than on environment.

The most influential factor affecting the composition of the *Glu-1* loci is a breeding strategy in relation to bread-making quality in the Hokkaido area, and soft Japanese noodle-making quality in the Kyushu area, respectively. Much evidence has been reported that *Glu-1* alleles directly affect gluten quality (Khan et al., 1989; Lukow et al., 1989; Rogers et al., 1989; Uhlen et al., 1990). It is likely that each wheat breeding area-specific differences in *Glu-1* patterns results from the intensity of selection pressure toward good bread-making quality or Japanese soft noodle-making quality, respectively. Especially, Japan has a long history of Japanese soft noodle wheat breeding, which has an exceptionally negative effect on bread-making quality (Nakamura et al., 1990). It can be concluded that Japanese breeding area distribution of *Glu-1* HMW glutenin alleles in hard bread or soft noodle wheats are influenced most by selection pressure toward good quality, respectively. Common parentage could also contribute to the similarity in *Glu-1* HMW glutenin pattern, Hokkaido or Kyushu breeding area, respectively.

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