Identification of Alleles for Complex Gene Loci *Glu-A1*, *Glu-B1*, and *Glu-D1*, Which Code for High Molecular Weight Subunits of Glutenin in Japanese Hexaploid Wheat Varieties

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Seed storage proteins of Japanese wheat (*Triticum aestivum*) varieties were fractionated by sodium dodecyl sulfate−polyacrylamide gel electrophoresis to identify the alleles for complex gene loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, which code for high molecular weight (HMW) subunits of glutenin in Japanese hexaploid wheat varieties. These were identified by comparison of subunit mobility with those previously found in hexaploid wheat. Twenty-four different, major glutenin HMW subunits were identified, and each variety contained three to five subunits. Seventeen different glutenin subunit patterns were observed for 14 alleles in Japanese varieties. A catalog of alleles for the complex gene loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, that code for HMW subunits of glutenin in hexaploid wheat was compiled. Japanese varieties showed some special allelic variation in glutenin HMW subunits that was different from those in hexaploid wheats of other countries.

Keywords: *Triticum aestivum; Japanese variety; seed storage protein; glutenin subunit composition; allelic variation*

INTRODUCTION

Wheat (*Triticum aestivum*) is hexaploid with three different diploid genomes, AA, BB, and DD. High molecular weight (HMW) glutenin subunits are controlled by codominant alleles. Endosperm storage proteins of hexaploid wheat are important for bread-making quality (Branland and Dardevet, 1985; Blackman and Payne, 1987; Payne et al., 1979, 1981, 1987; Ng and Bushuk, 1989). The major endosperm storage proteins are glutenin, which consists of polypeptides cross-linked by interpolypeptide disulfide bonds, and gliadin, a complex mixture of single polypeptides (Shewry and Tathan, 1990).

Glutenin may be classed as either HMW or low molecular weight (LMW) subunits. HMW glutenin subunits have distinctly slower electrophoretic mobility than gliadin or LMW glutenin subunits and thus can be clearly identified. 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. The composition of HMW glutenin subunits plays an important role in determining the wheat quality. Each hexaploid wheat contains three to five HMW subunits distinguishable by using SDS−PAGE (Payne et al., 1984). The genes that code for endosperm storage proteins in hexaploid wheats (*T. aestivum*) are located at nine complex loci on six different chromosomes. *Glu-A1*, *Glu-B1*, and *Glu-D1* contain genes for the HMW subunits of glutenin and are close to the centromeres on the long arms of homologous group-1 chromosomes 1A, 1B, and 1D, respectively. Each locus displays allelic variation that results in differences in protein compositions and also in bread-making quality (Jackson et al., 1983).

The highest molecular weight subunit, designated the 145 kDa subunit, was found frequently in Japanese varieties (Nakamura et al., 1990a). This subunit has an electrophoretic mobility identical to that of the glutenin HMW subunit 2.2 as reported by Payne et al. (1983b). The frequency of varieties with 145 kDa subunit was higher in the southern part of Japan than in the northern part, and examination 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., 1990a). Studies investigating HMW glutenin composition and/or its relation to bread-making quality have been carried out in virtually all major wheat-producing countries. The results of the recent studies highlighted three important topics: (a) the allelic variation for *Glu-1* loci which exist in *T. aestivum*; (b) the relationship between HMW glutenin subunit composition and quality parameters; and (c) the association between allelic distribution and ecogeographical parameters. Because the HMW glutenin composition of bread wheat varieties from many countries has now been published, an analysis of these data will contribute to our knowledge of the worldwide distribution of *Glu-1* alleles (Payne et al., 1987).

This paper reports the allelic composition at each of the three loci controlling HMW glutenin subunits of the varieties of hexaploid wheat registered in Japan. 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 new lines.

EXPERIMENTAL PROCEDURES

A wheat breeding program was started at the National Agriculture Experimental Station in the early part of the 20th century in Japan. The Norin numbering system has been

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Table 1. *Glu-1* Quality Scores Assigned to Individual or Pairs of HMW Glutenin Subunits

Glu-1 quality score	locus		
	Glu-A1	*Glu-B1*	*Glu-D1*
4			5+10(d)
3	1(a), 2*(b)	17+18(i), 7+8(b), 13+16(f)	
2		7+9(c)	2+12(a), 3+12(b)
1	null(c)	7(a), 6+8(d)	4+12(c)

[a] Payne et al. (1987).

employed in Japan since 1929 to designate the variety. The varieties studied are the major wheats bred and cultivated in Japan and are very important for Japanese wheat production.

The Japanese varieties designated Norin 1−131 were examined in this study. Seeds of these varieties were from the National Institute of Agrobiological Resources, Tsukuba, Japan. To determine the electrophoretic mobility of each HMW glutenin subunit by SDS−PAGE, standards (Bezostaya-1, Champlein, Chinese Spring, Danchi, Dunav, Federation, Gabo, Hobbit, Hope, Lancota, Norin 61, Sappo, and Serbian) that included the subunits expected were used (Payne and Lawrence, 1983a). Varieties and standards were analyzed by SDS−PAGE, according to the procedure of Nakamura et al. (1990a). The discontinuous buffer system of SDS−PAGE to fractionate proteins was based on that developed by Laemmli (1970).

The separation gel contained 1.5 M Tris-HCl, pH 8.8, and 0.27% SDS. Gels were made 7.5% (w/v) acrylamide and 0.2% (w/v) bis(acrylamide). The stacking gel contained 0.25 M Tris-HCl, pH 6.8. Wheat flour (10 mg) was suspended in 300 mL of 0.25 M Tris-HCl buffer, pH 6.8, containing 2% (w/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 12000 rpm, and a portion (30 μL) of the extract was loaded into the gel slot. The electrode buffer was 0.025 M Tris-glycine, pH 8.3, containing 0.1% (w/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 brilliant blue R250 dissolved in water, ethanol, and acetic acid (40:50:10 v/v).

The system for numbering HMW glutenin subunit bands and for allelic classification at the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci proposed by Payne and Lawrence (1983a) was used in this study. Alleles are designated by lower case letters following the locus name, for example, *Glu-A1a*. Overall quality scores of HMW glutenin subunits for a given variety were obtained as the sum of the scores of individual subunits, after the methods found in Anonymous (1983) and Stevens et al. (1984). Table 1 shows the HMW *Glu-1* quality scores that were determined in relation to the actual bread-making quality of various wheat varieties (Payne et al., 1987).

RESULTS AND DISCUSSION

After SDS−PAGE separation of wheat seed proteins extracted in Tris-HCl buffer, pH 6.8, that contained SDS, it was apparent that HMW subunit bands of glutenin had resolved into three to five bands depending on the variety (Figure 1). Subunit mobility was compared with that of hexaploid wheat determined previously (Payne et al., 1984).

Table 2 indicates the catalog of alleles for the complex gene loci, *Glu-A1*, *Glu-B1*, and *Glu-D1*, that code for HMW subunits of glutenin in hexaploid wheat. For the Japanese hexaploid wheats, 14 different alleles were identified, 3 corresponding to the *Glu-A1* locus, 6 to the *Glu-B1* locus, and 5 to the *Glu-D1* locus. It has been demonstrated that HMW glutenin subunit composition is useful for wheat variety identification (Lawrence,

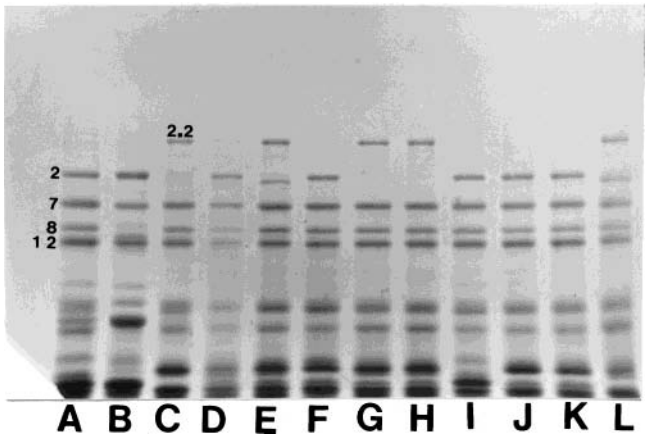

Figure 1. SDS−PAGE patterns of HMW glutenin subunits in Japanese hexaploid wheat varieties; (lane A) Norin 1; (lane B) Norin 16; (lane C) Shiroganekomugi; (lane D) Mikunikomugi; (lane E) Fukuhokomugi; (lane F) Miyaginokomugi; (lane G) Norin 72; (lane H) Nishikazekomugi; (lane I) Norin 66; (lane J) Aobakomugi; (lane K) Kitakamikomugi; (lane L) Norin 61.

1986). In this regard, the Japanese hexaploid wheat varieties in this study could be divided into 17 groups based on this character. The present study also showed specific differences in frequencies of *Glu-1* subunits throughout Japan. There are at least three possible factors influencing the distribution of the *Glu-1* allele: (1) it might be linked to genes of adaptive value, which results in preferential selection of particular alleles for certain areas; (2) the differences in frequency patterns might arise from the use of a particular parental gene pool or introduced gene for each area; (3) each breeding area distribution of *Glu-1* alleles might be influenced by selection pressure toward good bread-making quality or noodle-making quality because these genes contribute to the amount and quality of wheat gluten.

The null allele *Glu-A1c* on chromosome 1A was frequently observed in Japanese varieties, appearing in 74% of the varieties, compared with 36% in 1380 varieties throughout the world reported by Morgunov et al. (1993). The present work indicates that a high proportion, 74%, of the variation at *Glu-A1c* allele. Subunit pair 7+8 controlled by the *Glu-B1b* allele was detected in most Japanese varieties (109 of 131 varieties). It is quite different from that (25%) of 1380 varieties throughout the world. Table 3 shows the list of Japanese varieties analyzed for HMW glutenin subunit composition. The four varieties bred in the Hokkaido district had the somewhat rare subunit pair 6+8 (Takunekomugi), subunit 20 (Tihokukomugi), subunits 13+19 (Haruminori), and subunits 17+18 (Haruyutaka). It is thus clear that allelic variation among the varieties bred in the Hokkaido district (northern part of Japan) is considerable at the *Glu-B1* locus. Haruminori and Haruyutaka are the leading bread wheat varieties, and Tihokukomugi is a leading Japanese soft noodle wheat variety in Japan.

The frequency of the subunit pair 2+12 encoding the *Glu-D1a* allele was high (72 of 131 varieties). It was similar to the proportion, 53%, of the variation at the *Glu-D1a* allele throughout the world. A characteristic apparently unique to Japanese varieties is the high frequency of the 2.2 subunit encoded by the *Glu-D1f* allele. The molecular weight of this subunit exceeded that of any other glutenin subunit present in the varieties analyzed; 35.1% (46 of 131 varieties) of the

Table 2. Identification of Japanese Varieties with Respect to HMW Glutenin Allele Composition

locus and allele			*Glu-1*		no. of	subunit
Glu-A1	*Glu-B1*	*Glu-D1*	quality score	variety	varieties	compositions
a	*b*	*a*	8	Shiranekomugi (Norin 131)	1	1, 7+8, 2+12
a	*b*	*b*	8	Norin 21, Norin 42	2	1, 7+8, 3+12
a	*b*	*c*	7	Norin 8, Norin 24, Nanbukomugi (Norin 82), Mukakomugi (Norin 108)	4	1, 7+8, 4+12
a	*b*	*f*		Norin 41, Norin 59, Junreikomugi (Norin 96)	3	1, 7+8, 2.2+12
a	*c*	*c*	6	Norin 17, Norin 31, Norin 38, Kokeshikomugi (Norin 89)	4	1, 7+9, 4+12
a	*d*	*c*	5	Takunekomugi (Norin 115)	1	1, 6+8, 4+12
a	*i*	*a*	8	Haruyutaka (Norin 130)	1	1, 17+18, 2+12
b	*b*	*a*	8	Ebisukomugi (Norin 87), Sakyukomugi (Norin 91), Hiyokukomugi (Norin 107), Toyohokomugi (Norin 119)	4	2*, 7+8, 2+12
b	*b*	*f*		Norin 60, Norin 61, Norin 62, Yutakakomugi (Norin 92), Danchikomugi (Norin 93), Hayatokomugi (Norin 99), Nichirinkomugi (Norin 103), Ushiokomugi (Norin 105), Kobushikomugi (Norin 110), Sakigakekomugi (Norin 112), Asakazekomugi (Norin 123), Fukuhokomugi (Norin 124)	12	2*, 7+8, 2.2+12
b	*c*	*d*	9	Norin 35	1	2*, 7+9, 5+10
b	*g*	*a*		Haruminori (Norin 111)	1	2*, 13+19, 2+12
c	*b*	*a*	6	Norin 1, Norin 2, Norin 3, Norin 4, Norin 5, Norin 6, Norin 7, Norin 9, Norin 10, Norin 13, Norin 14, Norin 18, Norin 25, Norin 27, Norin 29, Norin 32, Norin 33, Norin 34, Norin 36, Norin 37, Norin 39, Norin 40, Norin 44, Norin 45, Norin 46, Norin 47, Norin 48, Norin 51, Norin 52, Norin 55, Norin 56, Norin 58, Norin 66, Norin 67, Norin 68, Norin 70, Norin 71, Norin 73, Norin 74, Susonokomugi (Norin 77), Iyokomugi (Norin 79), Mutubenkei (Norin 78), Hatamasari (Norin 80), Aobakomugi (Norin 81), Hikarikomugi (Norin 85), Myokoukomugi (Norin 86), Hitumikomugi (Norin 88), Okukomugi (Norin 90), Furutumasari (Norin 94), Kitakamikomugi (Norin 97), Mikunikomugi (Norin 100), Shimofusakomugi (Norin 101), Miyaginokomugi (Norin 102), Zenkoujikomugi (Norin 109), Hatimankomugi (Norin 113), Hanagasakomugi (Norin 116), Gogatukomugi (Norin 118), Wakamatukomugi (Norin 127)	58	null, 7+8, 2+12
c	*b*	*d*	8	Haruhikari (Norin 104)	1	null, 7+8, 5+10
c	*b*	*f*		Norin 15, Norin 19, Norin 20, Norin 22, Norin 23, Norin 26, Norin 28, Norin 30, Norin 43, Norin 49, Norin 50, Norin 53, Norin 54, Norin 57, Norin 63, Norin 64, Norin 65, Norin 72, Shirasagikomugi (Norin 95), Omasekomugi (Norin 106), Shiroganekomugi (Norin 117), Setokomugi (Norin 120), Shirowasekomugi (Norin 122), Nishuikazekomugi (Norin 129)	24	null, 7+8, 2.2+12
c	*c*	*a*	5	Norin 16, Norin 75, Akatukikomugi (Norin 83), Yukichabo (Norin 84), Horoshirikomugi (Norin 114)	5	null, 7+9, 2+12
c	*c*	*f*		Norin 11, Norin 69, Yuyakekomugi (Norin 76), Fujimikomugi (Norin 98), Tikushikomugi (Norin 121), Minaminokomugi (Norin 125), Fukuwasekomugi (Norin 128)	7	null, 7+9, 2.2+12
c	*e*	*a*		Norin 12, Tihokukomugi (Norin 126)	2	null, 20, 2+12

Japanese varieties carried the 2.2 subunit. The high proportion of 2.2 subunit variation contrasts sharply with the situation in 1380 varieties throughout the world (Morgunov et al., 1993). In Japanese varieties, the 2.2 subunit has been shown to be quite high, and in some cases it occurs in unique combinations. The hardness of flour quality 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 Japan, and the frequency of the 2.2 subunit in these lines may, consequently, be correlated with this character. It is particularly high in southern Japan but quite low in northern areas (Nakamura et al., 1990a). In southern Japan, lines good for noodle-making predominate. In the pedigree of the varieties, the many varieties that possess the 2.2 subunit were used by crossing on the Japanese-noodle wheat breeding program. The breeding areas differ in frequencies of HMW glutenin subunit groups throughout Japan. It also may be that some particular characters such as environment in the Japanese area are required.

Subunits 5+10 are seen more frequently in European than Japanese wheat varieties (Payne et al., 1984), possibly because of its correlation with good bread-making quality, although this is not the case in Japan. Only 1.5% (two bread wheat varieties, Norin 35 and Haruhikari, bred in Hokkaido) of varieties 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 2 gives the *Glu-1* quality scores of the Japanese varieties; the scores ranged from 5 to 9. 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 et al., 1990; Khan et al., 1989; Lawrence, 1986; Lukow et al., 1989; Ng and Bushuk, 1989; Payne et al., 1984). Europe may be

Table 3. Japanese Varieties Analyzed for HMW Glutenin Allele Composition

variety	breeding area	variety	breeding area	variety	breeding area	variety	breeding area	variety	breeding area
Norin 1	Tohoku	Norin 28	Tokai	Norin 55	Tohoku	Norin 83	Chugoku	Norin 110	Tokai
Norin 2	Tohoku	Norin 29	Hokkaido	Norin 56	Kinki	Norin 84	Hokuriku	Norin 111	Hokkaido
Norin 3	Hokkaido	Norin 30	Tokai	Norin 57	Kanto	Norin 85	Hokkaido	Norin 112	Kyushu
Norin 4	Chugoku	Norin 31	Hokuriku	Norin 58	Tohoku	Norin 86	Hokkaido	Norin 113	Tohoku
Norin 5	Kyushu	Norin 32	Kinki	Norin 59	Kinki	Norin 87	Kyushu	Norin 114	Hokkaido
Norin 6	Tohoku	Norin 33	Tohoku	Norin 60	Kyushu	Norin 88	Tohoku	Norin 115	Hokkaido
Norin 7	Kanto	Norin 34	Kyushu	Norin 61	Kyushu	Norin 89	Hokuriku	Norin 116	Tohoku
Norin 8	Hokkaido	Norin 35	Hokkaido	Norin 62	Hokkaido	Norin 90	Tohoku	Norin 117	Kyushu
Norin 9	Tokai	Norin 36	Kyushu	Norin 63	Kinki	Norin 91	Tohoku	Norin 118	Kyushu
Norin 10	Tohoku	Norin 37	Shikoku	Norin 64	Kanto	Norin 92	Kyushu	Norin 119	Kanto
Norin 11	Shikoku	Norin 38	Hokuriku	Norin 65	Shikoku	Norin 93	Kyushu	Norin 120	Kyushu
Norin 12	Kanto	Norin 39	Tohoku	Norin 66	Hokuriku	Norin 94	Tohoku	Norin 121	Kyushu
Norin 13	Kanto	Norin 40	Tohoku	Norin 67	Kanto	Norin 95	Chugoku	Norin 122	Kyushu
Norin 14	Tohoku	Norin 41	Kanto	Norin 68	Kanto	Norin 96	Shikoku	Norin 123	Kyushu
Norin 15	Hokuriku	Norin 42	Kanto	Norin 69	Kanto	Norin 97	Tohoku	Norin 124	Kanto
Norin 16	Kanto	Norin 43	Kinki	Norin 70	Kanto	Norin 98	Kanto	Norin 125	Kyushu
Norin 17	Hokuriku	Norin 44	Kanto	Norin 71	Chugoku	Norin 99	Kyushu	Norin 126	Hokkaido
Norin 18	Tohoku	Norin 45	Kyushu	Norin 72	Kinki	Norin 100	Kanto	Norin 127	Tohoku
Norin 19	Kinki	Norin 46	Chugoku	Norin 73	Chugoku	Norin 101	Tohoku	Norin 128	Chugoku
Norin 20	Kyushu	Norin 47	Chugoku	Norin 74	Chugoku	Norin 102	Tohoku	Norin 129	Kyushu
Norin 21	Chugoku	Norin 48	Kanto	Norin 75	Hokkaido	Norin 103	Kyushu	Norin 130	Hokkaido
Norin 22	Tohoku	Norin 49	Kyushu	Norin 76	Kanto	Norin 104	Hokkaido	Norin 131	Nagano
Norin 23	Kinki	Norin 50	Kanto	Norin 77	Tohoku	Norin 105	Chugoku		
Norin 24	Hokuriku	Norin 51	Shikoku	Norin 78	Tohoku	Norin 106	Tokai		
Norin 25	Chugoku	Norin 52	Chugoku	Norin 79	Shikoku	Norin 107	Kyushu		
Norin 26	Kinki	Norin 53	Tokai	Norin 80	Kyushu	Norin 108	Hokkaido		
Norin 27	Tohoku	Norin 54	Hokuriku	Norin 81	Tohoku	Norin 109	Nagano		

considered a bread consumption zone, whereas Asia is a noodle consumption zone, where noodles are made from hexaploid wheats. In the Hokkaido area, the many varieties (Cadet, Dawson, Garnet, Kanred, Manchuria, Martins Amber, Midex Pilot, Marquis, Turkey Red, Turkey RedII, etc.) introduced from the United States and Canada have improved the bread-making quality of varieties. Ten HMW glutenin subunit compositions were observed in 13 varieties bred in the Hokkaido breeding area. The pedigrees of the five principal bread-making varieties of spring or winter wheat bred at the Hokkaido area are investigated. At least half of the crosses made have been aimed at improving bread-making quality to increase the proportion of home-grown wheat in the milling grist. The five varieties have inherited the good glutenin subunits 1, 5+10, and 17+18 introduced from the other country's varieties. It is clear that there is wide wheat genetic variation in this area. Probably 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 district.

The frequency of 13 subunit groups was low, only 0.8−3.8% (1−5 varieties) of the 131 varieties. 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, 44.2% (58 varieties) of the 131 Japanese varieties.

In the Hokkaido breeding area, six rare subunit groups, 1, 6+8, 4+12 (Takunekomugi; Tohoku 118 × Kitakei 221), 1, 17+18, 2+12 [Haruyutaka; (SieteCerros × Pall)F_1 × (Tob-8156 × Haruhikari)F_1)], 2*, 7+9, 5+10 (Norin 35; Hokkai 6 × Manchuria 142), 2*, 13+19, 2+12 (Haruminori; Norin 42 × Hokuiku 1), null, 7+8, 5+10 (Haruhikari; Midex Pilot × Norin 75), and null, 20, 2+12 [Tihokukomugi; ((Kitami 18 × Kitami 19)F_1 × Kitakei 320], were determined. Five of these compositions were found only in the variety bred in Hokkaido. Subunit groups 1, 7+9, 4+12 were noted for four varieties (Norin 17, Norin 31, Norin 38, and Kokeshikomugi) bred only in the Hokuriku district. No varieties possessed this group of subunits except in the Hokuriku breeding area. This subunit composition is unique in Japanese wheats. On the pedigree of the four varieties, the crossing materials varieties (Australia 13, Martins Amber, Turkey Red, Turkey RedII, Velvet, etc.) were introduced from the United States, etc. With the introduction of the genetic resources of other countries in this area, the Japanese varieties can possess thus unique subunit compositions. It also may be that, with regard to some very specific breeding objective, particular characters such as environment in the Hokuriku area are required.

It has been revealed that the variation in HMW glutenin subunit composition in Japanese hexaploid wheats is very different from that of the varieties throughout the world. 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 varieties is a matter of considerable importance. In Asian countries, noodles are made from hexaploid wheats rather than the tetraploid durum wheats preferred as pasta-making material in Western countries. Noodles are eaten in Japan, China, and other East Asian countries. 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). This matter may be of interest to wheat breeders who consider HMW glutenin subunit groups when breeding crossing lines of good quality. White flour of good quality is needed by millers and noodle- or bread-making companies at all times. This is emphasized in production programs. The present data indicate allelic variation in the HMW glutenin subunit loci of *Glu-1* in the Japanese hexaploid wheat varieties to be unique throughout the world, although for these varieties, there

are only 17 HMW glutenin subunit compositions. The results of this study should facilitate the identification of Japanese wheat varieties and their production in the future by using SDS−PAGE. They may offer the prospect of further advancement by combination with the good glutenins. Alleles from the hexaploid wheat varieties of other countries still have limited distribution in Japanese wheats. It can be concluded that greater genetic variation may be possible by introducing the alleles of many countries' varieties into Japanese hexaploid wheats.

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