

Specific *Glu-D1f* Allele Frequency of Japanese Common Wheat Compared with Distribution of *Glu-1* Alleles in Chinese Wheat

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ABSTRACT

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The quality of wheat (*Triticum aestivum* L.) grain favored in bread-making is strongly affected by components of seed storage protein, particularly high molecular weight glutenin subunits (HMW-GS). The HMW-GS 2.2 controlled by the *Glu-D1f* allele is frequently found in Japanese cultivars and landraces. In the investigation into the factors affecting the distribution of the allele, the available data on HMW-GS of common wheats from Japan were analyzed and compared with the data for intensity of winter habit and wheat flour hardness. We show that the main factors affecting the *Glu-D1f* allele frequency in Japanese wheat

were the intensity of natural selection for winter habit and artificial selection for flour hardness. According to a study of the worldwide distribution of *Glu-1* alleles, the *Glu-D1f* allele is rare. However, *Glu-D1f* allele was the most common Japanese wheat seed storage protein allele. It is well known that Chinese wheat contributed to Japanese landraces, and Japanese landraces contributed to modern cultivars from Japan. However, common Japanese and Chinese wheats differ in the frequencies of *Glu-D1f* allele. These results may be explained either by the founder effect or by a selective bottleneck in Japanese common wheat genetic resources.

To strengthen the international competitiveness of Japanese domestically produced common wheat (*Triticum aestivum* L.), it is essential to improve grain quality and develop a unique product that will satisfy the demands of domestic consumers. The factors determining the quality of grain from Japanese common wheat cultivars must be characterized. High molecular weight glutenin subunits (HMW-GS) represent a group of common wheat seed endosperm proteins characterized by apparent molecular weights of 80,000–145,000 and a complex biochemical structure involving disulfide bonds (Nakamura 2000a). This group of endosperm proteins has been explored extensively during the last 20 years (Payne et al 1979, 1981, 1983; Payne and Lawrence 1983). At least 20 different HMW-GS have been reported (Payne et al 1987). Genetic analysis revealed that variation in HMW-GS is controlled by alleles at the *Glu-A1*, *Glu-B1*, and *Glu-D1* loci on the long arms of chromosomes 1A, 1B, and 1D, respectively (Payne et al 1987). Studies investigating HMW-GS composition or its relationship to bread-making quality have been conducted in all major wheat-producing countries (Morgunov et al 1993). Results of studies involving both cultivars and landraces of common wheat highlighted three important topics: 1) allelic variation for *Glu-1* loci that exists in *T. aestivum*; 2) the relationship between HMW-GS composition and wheat quality parameters, and 3) the association between allelic distribution and ecogeographical parameters. HMW-GS of common wheat cultivars from many countries have now been published so an analysis of these data on Japanese wheat will contribute to our knowledge of the worldwide distribution of *Glu-1* alleles. The objective of this study was to analyze this distribution in Japan, the most geographically remote region for common wheat production in Asia, concentrating mainly on HMW-GS allelic variation within common wheat and the factors that affect it in a worldwide context.

MATERIALS AND METHODS

Allelic composition for the HMW-GS of 131 Japanese improved cultivars, 174 Japanese landraces, and 274 Chinese common wheats was investigated by SDS-PAGE, according to the procedure described by Payne et al (1979). The 274 Chinese wheats consisted

of 98 landraces and 176 cultivars. These landraces and cultivars were from the provinces of Heilongjiang, Jilin, Liaoning, Hebei, Beijing, Shandong, Shanxi, Hangssu, Zhejiang, Henan, Nangjin, Ningxia, Gansu, Xinjiang, Uygur, Sichuan, Anhui, and Jiangxi in China. These Japanese and Chinese materials were provided by the National Institute of Agrobiological Resources in Japan. Gels contained 10% (w/v) acrylamide, 0.2% (w/v) bis-acrylamide, 1.5M Tris-HCl at pH 8.8, and 0.27% SDS. The stacking gel contained 0.25M Tris-HCl at pH 6.8. Wheat flour (10 mg) was suspended in 300 mL of 0.25M Tris-HCl buffer (pH 6.8) containing 2% (w/v) SDS, 10% (v/v) glycerol, and 5% (v/v) mercaptoethanol and shaken for 2 hr 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 30 μ L of the extract was loaded into the gel slots. The electrode buffer was 0.025M Tris-glycine at pH 8.3, containing 0.1% (w/v) SDS (Nakamura et al 1990). Electrophoresis was conducted at 30 mA constant current for 4 hr until the Bromophenol blue ran to the end of the gel. The gels were stained for several hours with Coomassie blue in aqueous ethanol and acetic acid. HMW-GS were identified and numbered according to the system of Shewry and Tatham (1990). In addition, the samples were analyzed using the milled flour of 30 grains from each cultivar or landrace. To determine electrophoretic mobility of each HMW-GS by SDS-PAGE, standard cultivars (Bezostaya, Champlein, Chinese-Spring, Danchi, Dunav, Federation, Gabo, Hobbit, Hope, Norin 61, Lancota, Sappo, and Serbian) were used to exhibit patterns of expected subunits (Payne and Lawrence 1983; Nakamura et al 1999). Chi-square (χ^2) values were calculated to test for frequency differences among the *Glu-1* alleles, the intensity of winter habit, and wheat flour hardness. Frequencies of Japanese improved and Japanese landraces were analyzed relative to those of Chinese wheat through independent pair-wise comparisons. Chi-square values were obtained by considering Chinese frequencies as “expected” values, and frequencies of both Japanese improved and Japanese landraces as “observed” in this study. Chi-square analysis also was used in evaluating frequency differences among growth habit and kernel hardness classes.

RESULTS AND DISCUSSION

We undertook the present study to elucidate the allelic composition of HMW-GS with the objective of improving the grain quality of Japanese common wheat. Common wheat cultivars from different countries differ in frequencies of *Glu-A1*, *Glu-B1* and *Glu-D1* alleles (Morgunov et al 1993). Graybosch (1992) revealed that enhanced quality selection may have resulted in a decline of the *Glu-D1d* gene among U.S. soft red winter wheat, and an increase in frequency among hard red winter wheat. However, the HMW-

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GS composition of U.S. hard winter wheat could have resulted from a chance fixation of *Glu-1* alleles, as the favorable alleles were already present at a high frequency in the ancestral population. In U.S. soft winter wheat, selection for quality resulted in a decline in the frequency of specific HMW-GS, particularly those of strong doughs (*Glu-D1d* allele). But in hard red winter wheats, the ancestral wheats had a high frequency of the favorable allele, and the gene frequencies have not altered much over time (Graybosch 1992). Recently, Takata et al (2000) revealed that, among the HMW-GS, the 2.2 glutenin subunit controlled by the *Glu-D1f* allele is associated with weak gluten doughs and has a highly negative effect on breadmaking quality.

In this study, the HMW-GS 2.2 subunit controlled by the *Glu-D1f* allele was frequently found among improved cultivars as well as in Japanese landraces (Table I). The allelic frequency of this subunit was >35% among improved Japanese cultivars and >25.3% among Japanese landraces, but it was found in only 1.8% of Chinese wheat. The frequency of HMW-GS 2.2 from the *Glu-D1f* allele among Japanese improved and landraces was higher than among Chinese wheats. Significant increases in frequency were observed for subunit 2.2, while the frequency of subunits 5+10 and 2+12 was significantly lower than that of the Chinese wheat. Both Japanese improved and landrace wheat classes have been characterized by consistent and significant increases in the frequency of subunit 2.2 from the *Glu-D1f* allele. Available data on the HMW-GS alleles of common wheats from Japan were analyzed and compared with published data on the worldwide distribution of *Glu-1* alleles (Lawrence 1986; Payne et al 1987; Khan et al 1989; Lukow et al 1989; Ng and Bushuk 1989; Pogna et al 1989; Rogers et al 1989; Graybosch et al 1990; Morgunov et al 1990, 1993; Uhlen et al 1990; Graybosch 1992). In total, 1,380 cultivars from 21 common wheat-producing countries were included. The *Glu-D1f* was reported to be a rare allele in a study of the worldwide distribution of *Glu-1* alleles (Morgunov et al 1993). However, the *Glu-D1f* allele was the most common Japanese wheat seed storage protein allele (Table I). A lower frequency of this allele was observed among wheats of China and other countries.

It is believed that cultivated common wheat originated in the Middle and Near East and traveled via the Silk Road through China to the Far East and to Japan, the most geographically remote region in Asia for wheat production. During the course of its long journey and its adaptation to diverse local environments, Japanese common wheat has developed a unique composition of glutenin genes and a

narrow genetic base. The founder principle can explain many instances of rapid speciation and high local frequencies of alleles that appear rarely in other areas (Templeton 1980).

The N-terminal amino acid sequence of HMW-GS 2.2 was determined by a gas-phase sequencer (Nakamura et al 1990). Examinations of the amino acid sequence and electrophoretic mobility revealed that this subunit was identical to that of the 2.2 band reported by Payne et al (1983). Previous investigation into crosses between variants with and without the 2.2 subunit revealed that the GS expression was controlled by a single dominant allele designated *Glu-D1f* located on the 1D chromosome (Nakamura et al 1990).

Genealogical examinations revealed that the *Glu-D1f* allele was present in the cultivar Nisikaze-komugi, prevalent in the Kyushu district (south Japan), and frequently appeared in its pedigree. It was absent in the cultivar Horoshiri-komugi found in the Hokkaido district (north Japan), and carried only by a few of its remote ancestors (Nakamura et al 1990). A noticeable geographical cline has been reported in the frequency of the *Glu-D1f* allele (Nakamura et al 1999; Nakamura 2000c). We investigated the association of the occurrence of the glutenin *Glu-D1f* gene both with winter habit intensity and with flour hardness (Tables II and III).

In Japan, common wheat-cultivating environments are rendered diverse by the distance of the islands from north to south, by improved Japanese cultivars, as well as by locally grown landraces differentiating into distinct types of winter habit. The intensity of winter habit in Japan is the most important factor affecting common wheat production. Generally, the weaker winter habit (I–III) intensity is found in south Japan, and the stronger winter habit (V–VII) intensity is in north Japan. A strong correlation was observed between intensity of winter habit and occurrence of the *Glu-D1f* allele (Table II). The improved cultivars with the weaker winter habit intensity tended to carry the *Glu-D1f* allele more frequently, but this allele was absent in cultivars with the stronger winter habit intensity. In wheat of the stronger winter habit intensity (V–VII), there is a consistent and significant decrease in the frequency of *Glu-D1f*. The differences between weaker winter habit and stronger winter habit was significant. It was previously reported that, in a worldwide context, *Glu-1* alleles are not associated with ecogeographical parameters (Morgunov et al 1993). In fact, the genes conditioning winter hardness are probably not linked to those producing HMW-GS. Hence, selection for winter-hardiness could only have resulted in a fixation of these specific glutenin subunits through the founder effect. If the original selected lines happened

TABLE I
Comparison of *Glu-1* Allele Frequencies (%) in Chinese and 174 Japanese Wheats

| Locus and Allele | Subunit | Chinese % | Japanese Improved | | Japanese Landraces | |
|------------------|---------|-----------|-------------------|----------|--------------------|----------|
| | | | % | χ^2 | % | χ^2 |
| <i>Glu-A1</i> | | | | | | |
| a | 1 | 5.2 | 12.2 | 9.42*** | 4.6 | 0.07 |
| b | 2* | 14.4 | 13.7 | 0.03 | 8.6 | 2.34** |
| c | Null | 80.4 | 74.1 | 0.49 | 86.8 | 0.51 |
| <i>Glu-B1</i> | | | | | | |
| a | 7 | 12.3 | 0 | 12.30** | 1.7 | 9.14** |
| b | 7+8 | 71.9 | 83.2 | 1.78** | 94.1 | 6.89** |
| c | 7+9 | 8.1 | 12.9 | 2.84** | 1.2 | 5.88** |
| d | 6+8 | 3.9 | 0.8 | 2.46** | 1.2 | 1.87** |
| e | 20 | 1.4 | 1.5 | 0.01 | 0.6 | 0.46 |
| f | 13+16 | 0.7 | 0 | 0.70 | 0 | 0.70 |
| g | 13+19 | 0.4 | 0.8 | 0.40 | 0 | 0.40 |
| i | 17+18 | 0.7 | 0.8 | 0.01 | 1.2 | 0.36 |
| k | 22 | 0.7 | 0 | 0.70 | 0 | 0.70 |
| <i>Glu-D1</i> | | | | | | |
| a | 2+12 | 84.6 | 55.0 | 10.36** | 70.1 | 2.49** |
| b | 3+12 | 1.1 | 1.5 | 0.15 | 0 | 1.10** |
| c | 4+12 | 2.1 | 6.9 | 10.97** | 1.2 | 0.39 |
| d | 5+10 | 10.5 | 1.5 | 7.71** | 3.4 | 4.80** |
| f | 2.2+12 | 1.8 | 35.1 | 616.05** | 25.3 | 306.80** |

a *** = Significant at $P < 0.01$.

to have *Glu-D1f* allele and many subsequent lines were derived from a small number of ancestral lines in south Japan, then *Glu-1* alleles were fixed only because of a lack of genetic polymorphism in the ancestral populations.

It is also believed that the flour hardness of wheat grains is closely related to grain quality. Wheat flour hardness is correlated with Japanese soft-noodlemaking quality; hard common wheat cultivars have poor Japanese soft-noodlemaking quality (Shewry and Tatham 1990; Nakamura 2000a). Thus, the relationship between flour hardness and the occurrence of the *Glu-D1f* allele was investigated in this study. We found that soft flour cultivars tend to exhibit the *Glu-D1f* allele more frequently than hard-flour cultivars (Table III). In the soft wheat flour classes (soft and intermediate) of Japan, no statistically significant differences in *Glu-D1f* frequency were observed. Significant decreases in *Glu-D1f* frequency were observed in the hard wheat flour classes of Japan. Continued selection demands for improved Japanese soft noodle (*udon*) quality might have increased the frequency of *Glu-D1f* allele. However, while breeders of *udon* wheat have been no less diligent in quality selection, yet 2+12 and 5+10 also decreased and *Glu-D1f* allele increased. Alternatively, the increase in the frequency of *Glu-D1f* could be attributed to chance fixation of *Glu-1* alleles based on parental choice by *udon* wheat breeders. The *Glu-D1f* allele was found in many of the important Japanese *udon* noodle wheat (JUNW) ancestral lines (Nakamura 2000b,c, 2001). The effect of the *Glu-D1f* allele on quality has not been established in JUNW. However, the *Glu-D1f* allele has increased dramatically among JUNW at the expense of *Glu-D1a*. In the absence of any selective advantage, the increased allele frequency of *Glu-D1f* among JUNW only can attributed to a more frequent use of *Glu-D1f* carrying parents in JUNW breeding programs.

Research on the wheat flour component contribution to noodle quality indicates that proteins are 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 1981). Current analysis of HMW-GS shows postfactum status of these loci because, until recently, Japanese common wheat breeders did not manipulate the *Glu-1* alleles intentionally. Hence, the analysis reflects the results of indirect changes in common wheat genetic constitution due to selection for related or linked traits in Japanese wheat breeding programs. The average *Glu-1* quality scores relating to good breadmaking quality in Japan and China (within the noodle culture zones of the Far East) (Nakamura et al 1999; Nakamura 2000a,b,c) are lower in Europe, Australia, Canada, and the United States (within the bread culture zones) (Lawrence 1986; Payne et al 1987; Khan et al 1989; Lukow et al 1989; Ng and Bushuk

1989; Pogna et al 1989; Rogers et al 1989; Graybosch et al 1990; Morgunov et al 1990, 1993; Uhlen et al 1990; Graybosch 1992).

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. Chinese wheat contributed to Japanese landraces, and Japanese landraces contributed to modern cultivars from Japan (Nakamura 2000a). However, the common wheats of Japan and China differed in the frequency of *Glu-D1f* alleles in this study. Our findings suggest that the geographical clines in frequency of the *Glu-D1f* allele observed among Japanese improved cultivars as well as landraces may be caused by natural selection for winter habit or by artificial selection for wheat flour hardness. Japanese common wheat is characterized by the high frequency of alleles such as *Glu-B1g* and *Glu-D1f* (Nakamura 2000a,b,c) in the *Glu-1* locus. Natural and artificial selection is thought to have narrowed the genetic base of Japanese wheat. The frequent occurrence of the *Glu-D1f* allele would support this inference. Japanese common wheat breeding objectives are mainly determined by Japanese soft white noodles (*udon*) in noodle culture zones (Nakamura 2000a,c). On the other hand, in bread culture zones, the similarity in *Glu-1* allele composition profile of different countries seemed to be mainly determined by similar breeding objectives (Lawrence 1986; Payne et al 1987; Khan et al 1989; Lukow et al 1989; Ng and Bushuk 1989; Pogna et al 1989; Rogers et al 1989; Uhlen et al 1990; Graybosch et al 1990; Morgunov et al 1990, 1993; Graybosch 1992).

The common wheat brought to Japan likely would have included a very limited subset of the wheat found in China. The founder effect described often in evolutionary literature is associated with gene frequencies on islands such as Japan. This study has shown that the *Glu-1* allele frequencies between noodle culture zones and bread culture zones differ. Probably the most influential factor affecting composition of the *Glu-1* allele is the wheat breeding strategy for breadmaking quality in the bread culture zone. The *Glu-1* alleles directly affect wheat gluten quality (Bushuk 1996; Shepherd 1996). Japanese specific differences in *Glu-1* patterns probably result from selection toward good Japanese soft-noodlemaking quality instead of selecting the good breadmaking quality. It is believed that a cultivated common wheat originated in the Middle and Near East traveled via the Silk Road through China to the Far East and Japan. Japan, therefore, is a remote region in the world for common wheat production. In the course of its long journey and its adaptation to diverse local environments, Japanese common wheat seems to have lost its genetic diversity. As a consequence of its spread, adaptation, and phenotypic refinement, Japanese common wheat has developed a unique composition of *Glu-1* glutenin alleles and a narrow common wheat genetic

TABLE II
Winter Habit Intensity and *Glu-D1f* Allele Occurrence in Japanese Wheat^a

| | I | II | III | IV | V | VI | VII |
|--|-----------------|------|---------------------|---------|---------|---------|---------|
| <i>Glu-D1f</i> allele-carrying cultivars | 10 | 23 | 4 | 9 | 0 | 0 | 0 |
| Total number of cultivars | 19 | 34 | 11 | 40 | 13 | 13 | 1 |
| Frequency (%) | 52.6 | 67.6 | 36.4 | 22.5 | 0 | 0 | 0 |
| χ^2 | .. ^b | 4.28 | 4.99** ^c | 17.22** | 52.60** | 52.60** | 52.60** |

^a Weaker winter habit (I–III) in south Japan. stronger winter habit (V–VII) in north Japan.

^b Intensity of winter habit I: the “expected” class.

^c ** = Significant at $P < 0.01$.

TABLE III
Flour Hardness and *Glu-D1f* Allele Occurrence in Japanese Improved Cultivars

| Flour Hardness | Soft | Intermediate | Semihard | Hard |
|--|-----------------|--------------|----------|----------|
| <i>Glu-D1f</i> allele-carrying cultivars | 26 | 20 | 0 | 0 |
| Total number of cultivars | 59 | 45 | 13 | 14 |
| Frequency (%) | 44.1 | 44.4 | 0 | 0 |
| χ^2 | .. ^a | 0.002 | 44.100** | 44.100** |

^a Flour hardness soft: the “expected” class.

^b ** = Significant at $P < 0.01$.

base. For example, adaptation to the different winter climatic conditions spanning the length of Japan resulted from artificial breeding (Tables II and III). Cultivars with superior breadmaking quality have higher *Glu-1* quality scores and tend to have limited genetic variation in their *Glu-1* loci, such as the *Glu-D1d* gene. This demonstrates a narrowing of genetic glutenin-protein variability when breeding common wheat for its breadmaking quality.

The rich genetic diversity of common wheat landraces confers resistance to multiple diseases, environmental adaptations, and agronomic traits of economic significance. There is a belief that *Glu-1* alleles could serve as markers for genes involved in adaptation (Shepherd 1996). Japanese wheat breeders and cereal chemists could use genetic analysis of endosperm proteins in common wheat to develop new cultivars with improved grain quality. The range of *Glu-1* allelic variation in seed storage proteins that is currently available to the wheat breeder is being extended by the introgression of glutenin alleles from primitive landraces and from alien common wheats (Lagudah et al 1987; Shewry and Tatham 1990). Linkage studies using SDS-PAGE to determine the relationship between seed endosperm glutenin protein genes and genes for other agronomic characters might enable the incorporation of desired traits into new common wheat cultivars. Desirable traits may include improved cold tolerance, disease resistance, and improved quality for Japanese soft noodles. The contribution to Japanese soft-noodle-making quality is of particular interest because HMW glutenin proteins confer elasticity to dough by forming large aggregates. Consequently, the *Glu-D1f* gene is being transferred into the many good soft noodle cultivars at wheat breeding programs in Japan (Nakamura 2000a,b,c). After several generations of backcrossing against good noodle-making cultivars with selection for *Glu-D1f* gene, it will be possible to determine the effect of this gene on dough extensibility and elasticity by comparing the good noodle-making cultivar with the near-isogenic line of this cultivar containing the *Glu-D1f* gene. It may be concluded that worldwide distribution of *Glu-1* alleles in common wheat is influenced most by selection for good breadmaking or noodle-making quality. The frequency of *Glu-D1f* allele differs for Japanese and Chinese wheats. However, a common parentage could also contribute to the similarity in *Glu-1* pattern for Japanese wheat. To further improve grain quality and develop unique grains of common wheat in Japan, the genetic base of domestic wheat will have to be broadened.

The variability released by both environmental and genetic factors could easily lead to different subpopulations of the founders (Templeton 1980). This, in turn, could lead to the establishment of more than one reproductively isolated population from a single founder through population genetic mechanisms for common wheat. Each bottleneck was followed by a flush of rapid population growth, so once again there were optimal conditions for inducing genetic change (Templeton 1980). With this design from China, the common wheats were exposed to a selective bottleneck induced by the external environment, as well as a founder effect (since all populations went through bottleneck of small size). Consequently, the selective bottleneck was extremely intense and, in fact, most ancestral populations may be become extinct in Japan.

We should point out that although the selective bottlenecks discussed in this study were primarily induced by genetic environment, most of the predictions made in this study would also apply if the selective bottlenecks were induced by the external environment. The HMW-GS allele pattern of Japanese common wheat cannot be explained solely by the founder effect because, as we already pointed out, the pattern also was affected by the artificial selection of breadmaking or noodle-making quality in wheat breeding programs. The ease with which genetic changes occur in Japan strongly implies a lack of genetic variability in natural populations of Japanese common wheats. The theory presented here has increased the explanatory powers of wheat genetic revolution model of speciation and, more importantly, has generated testable pre-

dictions that can be examined in both the natural and artificial selection using current methodologies and systems. We hope that this theory of Japanese common wheat demonstrates how population genetic theory can be applied to the problem of speciation in more extensive and thorough fashion than it has in the past.

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