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The Transfer and History of "Reduced Height Genes" (Rht) in Wheat from Japan to Europe

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Wheat is the main crop and often a strategic crop in many European countries. From a historical perspective, we describe the transfer of ''reduced height genes'' (Rht genes) from Japanese wheat varieties to wheat varieties in Europe and their influence on the increase of the total wheat production in the last century. Historic pathways of Rht genes were influenced directly or indirectly by wheat breeders exchanging seed samples and by some governments importing large quantities of wheat during historically critical periods for their countries.

Introduction

During the last hundred years, wheat breeders in Europe and other parts of world were working on increasing the yield of wheat by reducing plant height, to make the plants resistant to lodging in conditions of intensive agriculture. For this reason, breeders selected plants with short and stiff straw, based on their phenotypic expression, from natural populations or from generations that had been crossed with dwarf varieties. Many wheat breeders were successful in breeding semi-dwarf, high-yielding varieties that were well adapted to intensive agriculture. By tracing back the wheat pedigrees, it has been shown that most of the dwarf and semi-dwarf European wheat varieties have the Japanese variety Akakomugi in their genetic background (Rabinovich 1972; Borojevic 1990a, 1990b). In the last quarter of the twentieth century, it was proved that the wheat variety Akakomugi is the donor of a "reduced height gene" called Rht8 and a daylight-insensitive gene called Ppd-D1, both on the 2D chromosome, which together reduce plant height by 10 cm, increase spikelet fertility, and bring flowering forward by 8 days (Gale and Youssefian 1985). These two genes are closely linked (Korzun et al. 1998) and they were transmitted by cross breeding to many Italian wheat varieties in the beginning of twentieth century. From the Italian wheat varieties, they were further transmitted by cross-breeding to many winter semi-dwarf high-yielding varieties to the former Yugoslavia and from there to South and Central Europe (Borojevic and Potocanac 1966; Worland et al. 1998a; Worland 2000).

Origin of Rht Genes in Wheat

According to Cho et al. (1993), short wheat varieties originated in Korea, where they were grown in wheat mixture as early as the third and the fourth centuries C.E. It seems that the short wheat varieties came from Korea to Japan during the Korean-Japanese War in the sixteenth century. In Japan, the short straw varieties were used by plant breeders in the nineteenth century and throughout the twentieth century (Nonaka 1995). Microsatellite analyses of wheat indicated that three major wheat microsatellite alleles of the WMS 261, the diagnostic locus for dwarfing genes, were included in Japanese varieties by the early decades of twentieth century. The variety Akakomugi (the source for most European varieties for Rht8 gene) carries WMS 261–192 bp; variety Saitama 27 carries WMS 261–165 bp; and Norin 10 carries WMS 261–174 bp (Worland et al. 1998b).

Import of Rht8 Genes from Japan to Italy

In the beginning of the twentieth century, Italian politicians strongly supported research that would increase wheat yield to reach self-sufficiency in wheat production of the country. The project is known in history as the Wheat Battle (it occurred during Mussolini's time). Italian wheat breeder Nazareno Strampelli was one of the most important pioneers in this field. In 1913, Strampelli had already crossed the Japanese wheat variety Akakomugi (the source variety for Rht8 and PpD1 genes) with the cross of Wilhelmina Tare × Rite to shorten the straw and obtain resistance to lodging, as well as early ripening. From this cross, the new varieties Villa

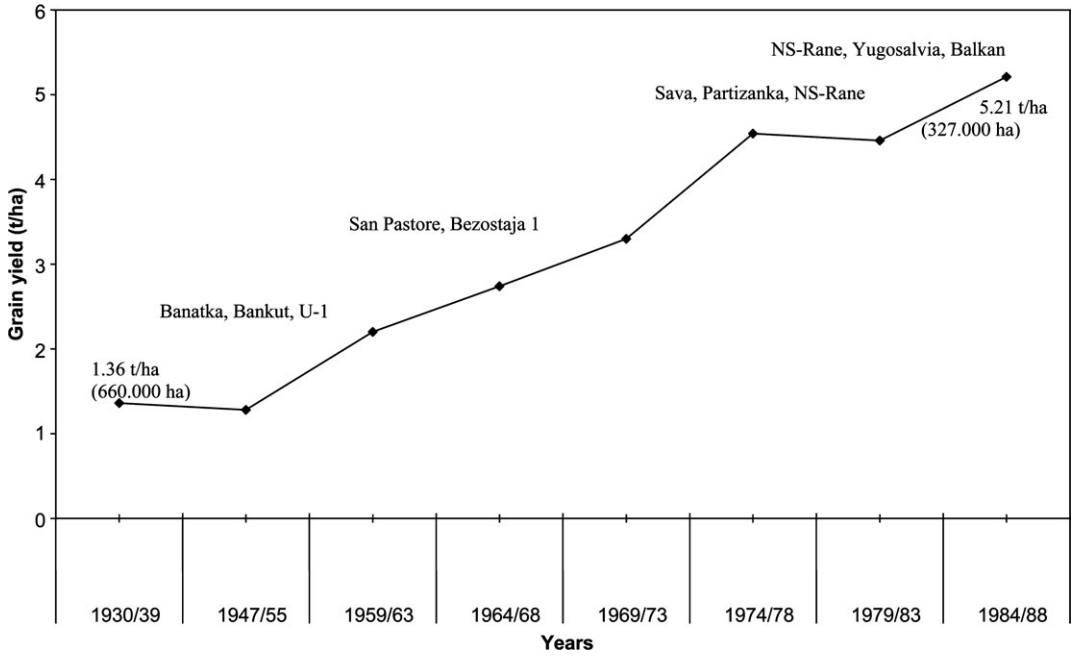

Figure 1. Five-year average yields of wheat in Vojvodina and leading wheat cultivars in various periods (Borojevic 1990b).

Gloria, Ardito, Mentana, and Damiano were obtained in 1918. These varieties were very well known and were grown in Italy, South America, and especially in Argentina because of the short straw, early maturity, and high yield potential (Lorenzetti 2000). Later, around 1925, Strampelli crossed Villa Gloria with the variety Balilla (obtained from the cross Duro di Puglia × Akakomugi). From this complex cross, Strampelli created the variety San Pastore in 1931 (Strampelli 1932). San Pastore was grown with extraordinary success in Italy and many other countries for more than 35 years (Borojevic 2000, 2003; Boggini et al. 2003).

Import of Rht8 genes from Italy to South and Central Europe

After World War II, San Pastore and 30 other Italian wheat varieties were imported by the Yugoslav government from Italy during the 1950s with an aim to make the country self-sufficient in wheat production. The imported Italian varieties were grown on a large scale and were used by plant breeders in crosses with winter wheat varieties (Borojevic and Potocanac 1966; Borojevic 1990b). Thanks to Rht genes (mostly Rht8) and PpD-D1 genes (although at the time unknown), semi-dwarf and daylight-insensitive high-yielding winter wheat varieties were developed and grown in large-scale production. Total wheat production was increased several times over, and record yields of over 10 t/ha were not rare in the former Yugoslavia. In Vojvodina Province, the breadbasket of the Pannonian Plain, the average wheat yield increased from 1.36 t/ha up to 5.21 t/ha, as illustrated in Figure 1 (Borojevic 1990b).

Similar results were obtained in Hungary, Bulgaria, Romania, the former Czechoslovakia, as well as in other neighboring countries. Some of the countries in the region turned from importers of wheat to exporters of wheat (Borojevic 2000). In 1959, in the former Soviet Union, the semi-dwarf winter wheat variety Bezostaja 1 was created by Lukyanenko in Krasnodar (Lukyanenko 1973; Rabinovich 1972). Bezostaja had good quality and winter hardiness. It was widely spread in East and Central Europe, including the former Yugoslavia. Coincidentally, Bezostaja is also a carrier of the Rht8 gene, which was not known at that time. Bezostaja 1 came from a cross in which one of the parents was Skorospelka. Skorospelka came from a cross in which one of the parents was Klein 33 from Argentina, and Klein 33 came from a cross in which one parent was Ardito (Strampelli wheat). Ardito came from a cross in which one parent was the Japanese variety Akakomugi (Worland 1998a). Later, Bezostaja was included in pedigrees in more than 200 wheat varieties worldwide (Sozinov 2000). The complex pedigrees of some of semi-dwarf wheat varieties derived at an early stage in Yugoslavian breeding programs (carriers of Rht8 and Ppd-D1 genes) are presented in Figure 2 (Worland et al. 1998).

Import of Rht1 and Rht2 genes from Japan to America and from America to Europe

The dwarfing Rht1 and Rht2 genes from the Japanese variety Norin 10 came to the United States through a completely different geographic route and after World War II (Reitz and Salmon 1968). S. D. Salmon, a leader of wheat breeding

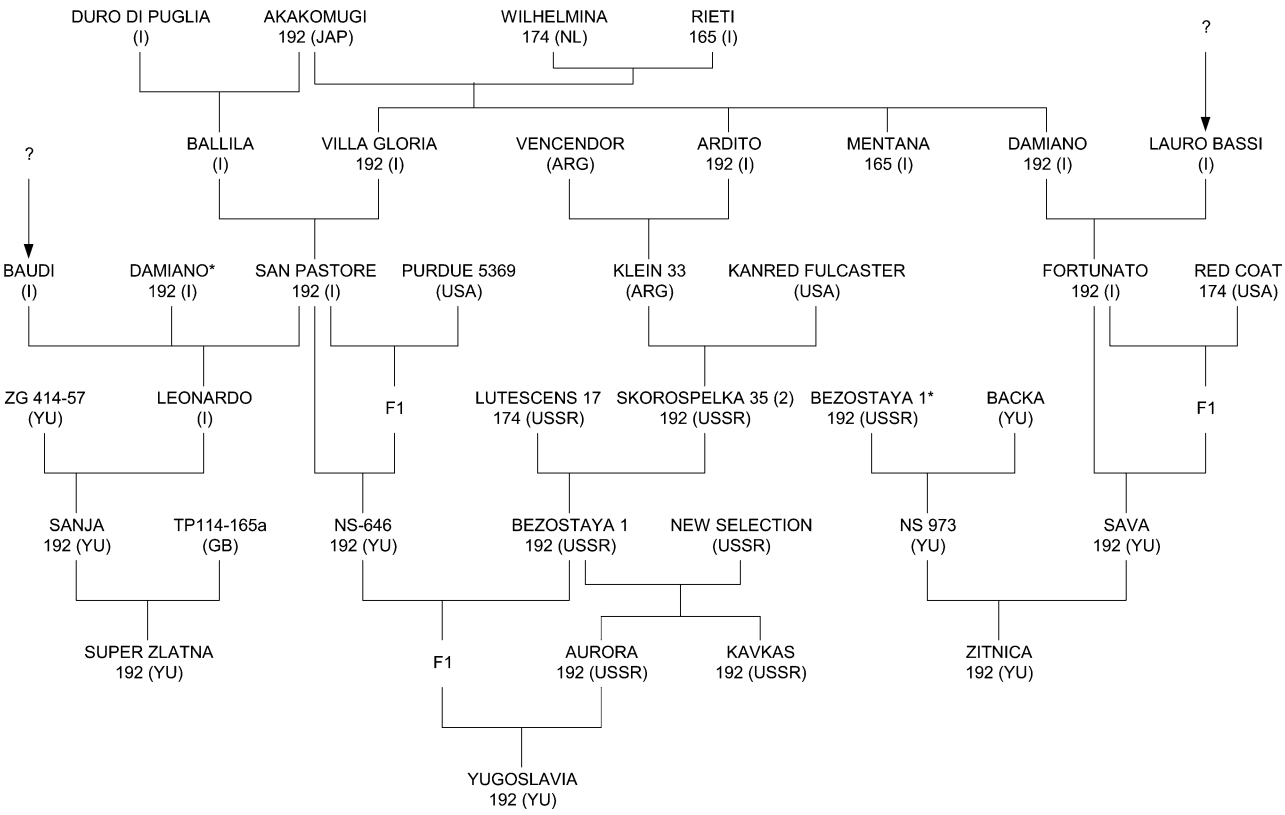

Figure 2. The pedigree of semi-dwarf wheat varieties derived at an early stage in the Yugoslavian breeding program, detected by diagnostic molecular markers. Letters in brackets indicate the country of origin; numbers indicate alleles of the microsatellite locus WMS 261 (Worland et al. 1998a).

research in the U.S. Department of Agriculture (USDA), visited Marioka Agriculture Research Station on Honshu in Japan as an advisor of the occupation army. On his return to the United States, Salmon brought with him 10-g wheat samples, which he received from Japanese scientists on the occasion of his visit. One of the samples was Norin 10. He sent the sample for further experimentation to the Joint USDA/Washington State University project at Pullman, Washington. In 1952, O. A. Vogel, a USDA agronomist at Washington State University at Pullman, crossed Norin 10 with Brevor, a variety that was popular at the time in Washington. Selection from this cross led to a new variety called Gaines. Gaines dominated production in the Pacific Northwest in the late 1960s. Individual farmers have obtained yields exceeding 130 hl/ha (150 bu/acre), and one obtained even 183 hl/ha (209 bu/acre) (Reitz and Salmon 1968). From Washington State, Norin 10 and its derivatives were transferred to the CIMMYT (International Maize and Wheat Improvement Center in Mexico) where new dwarf daylight-insensitive wheat varieties carriers of Rht genes (mostly Rht1 and Rht2) were developed by Norman Bourlag (1968), the 1970 Nobel Peace Prize winner. The CIMMYT wheat varieties were distributed all over the world and increased wheat production several times in Mexico, India, Pakistan, and Turkey. In Europe, the CIMMYT material was mostly used in crosses with winter wheat varieties and contributed greatly to the increase of wheat yields in north and central Italy, as well as in South and Central Europe (Borghi 2000).

Discussion and Conclusion

The transfer of Rht genes followed long and complex pathways, from Japan to all around the world, to improve wheat production. Wherever Rht genes were transferred to commercial wheat varieties, the production of wheat increased several times. Locally in national programs, as well as in international programs, many of the wheat breeders were competing in carrying out complicated long-term multiple crossings in their effort to reduce plant height to achieve high yield, without knowing that they were often transferring the same genes for short straw and daylight insensitivity. Numerous crosses were unnecessary, leading to competition between and within institutes and between plant breeders. Decades later, after the discovery of the diagnostic molecular markers (especially wheat microsatellite analyses), it was possible to identify donor genes and

accelerate the long and complex process of traditional plant breeding. It was also possible to follow the routes of genes more precisely and to detect the three geohistorical pathways:

1. The first pathway of the Rht8 gene (of the variety Akakomugi) was from Japan to Italy at the beginning of the twentieth century (Strampelli 1932). In the 1950s, Italian short straw varieties, mostly carriers of Rht8 and Ppd-D1genes (at the time unknown) were transferred to the former Yugoslavia and to South and Central Europe, where they were incorporated into semi-dwarf winter wheat varieties (Borojevic and Potocanac 1966).
2. The second pathway of Rht8 (of the variety Akakomugi) was from Japan to Italy, from Italy (by derivatives of Akakomugi) to Argentina before and during World War II (1940–45) (Lorenzetti 2000), and from Argentina to Europe and the former Soviet Union after World War II.
3. The third pathway of the Rht genes was through the Japanese wheat variety Norin 10 (source of Rht1 and Rht2 genes). Norin 10 was transferred from Japan to the United States after World War II, and from the United States to the CIMMYT in Mexico. From the CIMMYT, Rht1 and Rht2 genes were distributed all around the world, including Europe (Borlaug 1968; Kronstad 1997).

If we look at the geographic pathways and the timing of the introduction of wheat varieties, carriers of Rht genes, they might appear incidental. However, if we examine them more closely from a historical perspective, the countries where the wheat varieties, were initially introduced—Italy, Argentina, the former Yugoslavia, the former Soviet Union, India, Pakistan, and Turkey—and the time when they were introduced—before and immediately after World War II—a pattern starts to emerge. The high-yielding short wheat varieties were introduced to these countries to increase total wheat production, not only through free exchange of wheat seeds by breeders but also by the initiative and perhaps orders of governments during periods when the countries were struggling with famine, and when one of the main social goals of the regimes was to provide a daily quota of bread. It is interesting to note that short varieties from Korea came to Japan after the Korean-Japanese War. This emerging pattern of seed exchange among breeders and governments' impact on growing these wheat varieties should be investigated further, to explore the underlying sociohistorical influences that may have played a role in determining the pathways of these genes.

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