

Compendium of Plant Genomes
Series Editor: Chittaranjan Kole

M. Timothy Rabanus-Wallace
Nils Stein *Editors*

The Rye Genome

Compendium of Plant Genomes

Series Editor

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Whole-genome sequencing is at the cutting edge of life sciences in the new millennium. Since the first genome sequencing of the model plant *Arabidopsis thaliana* in 2000, whole genomes of about 100 plant species have been sequenced and genome sequences of several other plants are in the pipeline. Research publications on these genome initiatives are scattered on dedicated web sites and in journals with all too brief descriptions. The individual volumes elucidate the background history of the national and international genome initiatives; public and private partners involved; strategies and genomic resources and tools utilized; enumeration on the sequences and their assembly; repetitive sequences; gene annotation and genome duplication. In addition, synteny with other sequences, comparison of gene families and most importantly potential of the genome sequence information for gene pool characterization and genetic improvement of crop plants are described.

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The Rye Genome

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Rye (*Secale cereale* L.)—growing on a field at IPK Gatersleben in 2018 (© Nils Stein)

This book series is dedicated to my wife Phullara and our children Sourav and Devleena

Chittaranjan Kole

Preface to the Series

Genome sequencing has emerged as the leading discipline in the plant sciences coinciding with the start of the new century. For much of the twentieth century, plant geneticists were only successful in delineating putative chromosomal location, function, and changes in genes indirectly through the use of a number of “markers” physically linked to them. These included visible or morphological, cytological, protein, and molecular or DNA markers. Among them, the first DNA marker, the RFLPs, introduced a revolutionary change in plant genetics and breeding in the mid-1980s, mainly because of their infinite number and thus potential to cover maximum chromosomal regions, phenotypic neutrality, absence of epistasis, and codominant nature. An array of other hybridization-based markers, PCR-based markers, and markers based on both facilitated construction of genetic linkage maps, mapping of genes controlling simply inherited traits, and even gene clusters (QTLs) controlling polygenic traits in a large number of model and crop plants. During this period, a number of new mapping populations beyond F₂ were utilized and a number of computer programs were developed for map construction, mapping of genes, and for mapping of polygenic clusters or QTLs. Molecular markers were also used in the studies of evolution and phylogenetic relationship, genetic diversity, DNA fingerprinting, and map-based cloning. Markers tightly linked to the genes were used in crop improvement employing the so-called marker-assisted selection. These strategies of molecular genetic mapping and molecular breeding made a spectacular impact during the last one and a half decades of the twentieth century. But still they remained “indirect” approaches for elucidation and utilization of plant genomes since much of the chromosomes remained unknown and the complete chemical depiction of them was yet to be unraveled.

Physical mapping of genomes was the obvious consequence that facilitated the development of the “genomic resources” including BAC and YAC libraries to develop physical maps in some plant genomes. Subsequently, integrated genetic–physical maps were also developed in many plants. This led to the concept of structural genomics. Later on, emphasis was laid on EST and transcriptome analysis to decipher the function of the active gene sequences leading to another concept defined as functional genomics. The advent of techniques of bacteriophage gene and DNA sequencing in the 1970s was extended to facilitate sequencing of these genomic resources in the last decade of the twentieth century.

As expected, sequencing of chromosomal regions would have led to too much data to store, characterize, and utilize with the then available computer software could handle. But the development of information technology made the life of biologists easier by leading to a swift and sweet marriage of biology and informatics, and a new subject was born—bioinformatics.

Thus, the evolution of the concepts, strategies, and tools of sequencing and bioinformatics reinforced the subject of genomics—structural and functional. Today, genome sequencing has traveled much beyond biology and involves biophysics, biochemistry, and bioinformatics!

Thanks to the efforts of both public and private agencies, genome sequencing strategies are evolving very fast, leading to cheaper, quicker, and automated techniques right from clone-by-clone and whole-genome shotgun approaches to a succession of second-generation sequencing methods. The development of software of different generations facilitated this genome sequencing. At the same time, newer concepts and strategies were emerging to handle sequencing of the complex genomes, particularly the polyploids.

It became a reality to chemically—and so directly—define plant genomes, popularly called whole-genome sequencing or simply genome sequencing.

The history of plant genome sequencing will always cite the sequencing of the genome of the model plant *Arabidopsis thaliana* in 2000 that was followed by sequencing the genome of the crop and model plant rice in 2002. Since then, the number of sequenced genomes of higher plants has been increasing exponentially, mainly due to the development of cheaper and quicker genomic techniques and, most importantly, the development of collaborative platforms such as national and international consortia involving partners from public and/or private agencies.

As I write this preface for the first volume of the new series “Compendium of Plant Genomes,” a net search tells me that complete or nearly complete whole-genome sequencing of 45 crop plants, eight crops and model plants, eight model plants, 15 crop progenitors and relatives, and three basal plants is accomplished, the majority of which are in the public domain. This means that we nowadays know many of our model and crop plants chemically, i.e., directly, and we may depict them and utilize them precisely better than ever. Genome sequencing has covered all groups of crop plants. Hence, information on the precise depiction of plant genomes and the scope of their utilization are growing rapidly every day. However, the information is scattered in research articles and review papers in journals and dedicated Web pages of the consortia and databases. There is no compilation of plant genomes and the opportunity of using the information in sequence-assisted breeding or further genomic studies. This is the underlying rationale for starting this book series, with each volume dedicated to a particular plant.

Plant genome science has emerged as an important subject in academia, and the present compendium of plant genomes will be highly useful to both students and teaching faculties. Most importantly, research scientists involved in genomics research will have access to systematic deliberations on the plant genomes of their interest. Elucidation of plant genomes is of interest not only for the geneticists and breeders, but also for practitioners of an array of plant science disciplines, such as taxonomy, evolution, cytology,

physiology, pathology, entomology, nematology, crop production, biochemistry, and obviously bioinformatics. It must be mentioned that information regarding each plant genome is ever-growing. The contents of the volumes of this compendium are, therefore, focusing on the basic aspects of the genomes and their utility. They include information on the academic and/or economic importance of the plants, description of their genomes from a molecular genetic and cytogenetic point of view, and the genomic resources developed. Detailed deliberations focus on the background history of the national and international genome initiatives, public and private partners involved, strategies and genomic resources and tools utilized, enumeration on the sequences and their assembly, repetitive sequences, gene annotation, and genome duplication. In addition, synteny with other sequences, comparison of gene families, and, most importantly, the potential of the genome sequence information for gene pool characterization through genotyping by sequencing (GBS) and genetic improvement of crop plants have been described. As expected, there is a lot of variation of these topics in the volumes based on the information available on the crop, model, or reference plants.

I must confess that as the series editor, it has been a daunting task for me to work on such a huge and broad knowledge base that spans so many diverse plant species. However, pioneering scientists with lifetime experience and expertise on the particular crops did excellent jobs editing the respective volumes. I myself have been a small science worker on plant genomes since the mid-1980s and that provided me the opportunity to personally know several stalwarts of plant genomics from all over the globe. Most, if not all, of the volume editors are my longtime friends and colleagues. It has been highly comfortable and enriching for me to work with them on this book series. To be honest, while working on this series, I have been and will remain a student first, a science worker second, and a series editor last. And I must express my gratitude to the volume editors and the chapter authors for providing me the opportunity to work with them on this compendium.

I also wish to mention here my thanks and gratitude to the Springer staff, particularly Dr. Christina Eckey and Dr. Jutta Lindenborn, for the earlier set of volumes and presently Ing. Zuzana Bernhart for all their timely help and support.

I always had to set aside additional hours to edit books beside my professional and personal commitments—hours I could and should have given to my wife, Phullara, and our kids, Sourav and Devleena. I must mention that they not only allowed me the freedom to take away those hours from them but also offered their support in the editing job itself. I am really not sure whether my dedication of this compendium to them will suffice to do justice to their sacrifices for the interest of science and the science community.

New Delhi, India

Chittaranjan Kole

Preface

Cultivated rye (*Secale cereale* L.) had undeniably humble origins. Rye's wild ancestors, probably weedy highland grasses from Anatolia, were domesticated partly by mistake—a consequence of unintentional selection exerted by wheat and barley farmers, whose crops rye's ancestors invaded. Rye's domestication therefore proceeded parallel to—if somewhat later than—the North-Western/North-Eastern cultivation range expansion of wheat and barley during the origins of agriculture. Rye's ability to flourish in unforgiving environments and poor-quality soils contributed to its uptake by farmers, and its unique taste and baking qualities have insured that rye breads and fermented drinks are popular cultural staples in a broad range of cuisines across the globe. Alongside human culinary uses, rye is used as a cover crop and a source of animal feed. As of 2019, 10 million tons of rye was annually cultivated, alongside a further 10 million tons of the high-yielding and hardy wheat-rye hybrid *Triticale*. Northern Europe dominates production of both.

Rye has a large and highly repetitive diploid genome (~8 Gbp in length), and most varieties are obligate outcrossers. These factors represented significant hurdles to the development of a high-quality genome sequence, and early efforts to develop sequence-based genetic resources for cereals focused on the most widespread commercial crops, wheat and barley. While several important resources including a draft genome sequence were developed during the 2000s and 2010s, it was only in 2021 that a duo of high-quality full genome sequences for rye was tandemly published.

These achievements represent the perfect prompt to produce an up-to-date summary of the state of rye genome research. This book aims to fill that role, alongside providing much relevant background during the pre-genome-sequencing era. Those interested in learning about the fascinating progression of rye genetic research toward the genomics era would be well advised to consult Rolf Schlegel's *Rye: Genetics, Breeding, and Cultivation* (CRC Press, 2013). Topics covered here include sequencing and assembly approaches, gene prediction, chromosomal genomics, sequence diversity and structural variation, taxonomy, domestication, the repetitive genome, cytogenetics, biotic and abiotic stress responses and their genetic underpinnings, rye's self-incompatibility systems that enable efficient hybrid breeding, and the enigmatic supernumerary “B” chromosomes—researchers of which have used rye as an important model organism since 1924.

We are greatly indebted to the many authors and collaborators who contributed their expertise and efforts to make this book possible, and we extend our gratitude also to the expert reviewers who were indispensable in ensuring the quality and accuracy of each chapter. It has been a true privilege to work with the rye research community on this book, which we hope serves as a valuable resource for both experts and initiates.

Seeland, Germany

Nils Stein
M. Timothy Rabanus-Wallace

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Economic and Academic Importance of Rye

1

Viktor Korzun, Mira L. Ponomareva,
and Mark E. Sorrells

Abstract

Rye has been playing an important agronomic, nutritional and social role throughout human civilization. In the last 50 years, rye grain yields have increased but not enough to offset the decrease in cropping area to maintain production. In this context, hybrid rye has great potential due to high yield performance and greater resilience to climate variability. The production area of hybrid rye has been increasing for several years and is expected to continue increasing. In the last decade, uses, such as biogas as well as greening, are potential new markets for rye biomass production. Although rye genomics has lagged behind other cereal crops, it has made significant contributions to understanding the evo-

lution of the grass family through comparative genomics analyses. Rye genomics and breeding have made great strides in the past 50 years and led to exciting new areas of research, in particular, hybrid varieties of rye that out-yield conventional synthetic varieties by 20–30% for both biomass and grain. While rye may be considered a minor crop in terms of production, contributions to cereal genomics have been substantial.

1.1 Background

Rye (*Secale cereale* L.) has the remarkable capability to grow in a wide range of environments, and more specifically performs well in low input environments where other cereals fail. The most widely grown type of rye is winter rye, also called fall rye. Rye grain has considerable value for functional and healthy humans' food. Rye is climate resilient and able to survive cold temperatures, semi-arid and high-altitude zones, and marginal soils. Until now, most of the rye production uses population or synthetic rye varieties.

Nevertheless, rye was the first small grain cereal to be successfully bred to produce hybrid varieties with the first hybrids launched in 1984. The importance of rye has continued to increase due to high yield, resilient agronomic performance, and stable, good grain quality.

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1.2 World Rye Production

According to the FAOSTAT (statistical platform of the Food and Agriculture Organization of the United Nations) in 2018 around 11.27 million tonnes (Mt) of rye grain were harvested worldwide, of which 9.13 Mt were grown on the European continent (Table 1.1). Thus, the contribution of Europe to world rye production was 81.0% while other continents contributed much less with Asia—13.0%, Africa—0.9%, North America—4.0%, and Australia—0.9%.

Average world production of rye from 2009 to 2018 amounted to 14.2 million tonnes per year. Rye production in the last decade declined slightly at an average annual rate of 0.2% due to the increasing availability of high performing wheat varieties and low prices for rye grain. The maximum rate of decline was recorded in 2008 at 19%. The peak of global rye production was in

2009 at the level of 18.3 Mt. Although it is slowly declining, rye production has been stable relative to other cereals with moderate peaks and valleys.

Around the world, the area of cultivated land dedicated to growing rye (Bushuk 2001) has decreased substantially since the 1970s. In 1996, 17 Mha were harvested, but this dropped by 61% to 6.7 Mha by 2008. This negative trend has continued in the last decade (2009–2018). During this period, the harvested world area decreased by 2.2 Mha or 31%. In 2018, the cultivated area of rye in the world amounted to 4.12 Mha. The decrease in cultivated area has been largely offset by an increase in yield. This significant yield increase was achieved through improvement of agronomic practices, especially in the use of chemical fertilizers and crop rotation, decline in the use of less fertile land, and development of high-yielding varieties, especially hybrids.

Table 1.1 Rye production per continent and Top 10 countries and regions Data from FAOSTAT (2020)

Region/Country	Area (Million ha, Mha)	Yield level (Tonnes per ha)	
Production (Million tonnes, Mt)			
<i>World</i>	4.12	2.74	11.27
<i>Europa</i>	3.32	2.75	9.13
Belarus	0.25	2.00	0.50
Denmark	0.09	5.20	0.48
Germany	0.52	4.21	2.20
Poland	0.89	2.42	2.17
Russian Federation	0.96	2.00	1.92
Spain	0.14	2.85	0.39
Ukraine	0.15	2.65	0.39
<i>Asia</i>	0.46	3.21	1.46
China	0.27	3.90	1.04
Turkey	0.11	2.89	0.32
<i>North America</i>	0.23	2.64	0.60
United States of America	0.12	2.15	0.27
Canada	0.08	2.99	0.24
<i>Australia</i>	0.04	0.70	0.03
<i>Africa</i>	0.05	1.88	0.10
<i>South America</i>	0.05	1.93	0.10

Climate change is a global driver of farmers' interest in growing hybrid rye varieties. In Europe, the increasingly stringent regulations on the use of fertilizers and chemicals for plant protection are incentives for farmers to grow hybrids because of their tolerance to marginal soils and diseases.

Winter rye is of great importance in the world economy and food traditions of those seven countries, where the crop is grown on more than 90 thousand hectares (Belarus, Denmark, Germany, Poland, Russian Federation, Spain, and Ukraine) (Table 1.1). The Russian Federation leads in the area of cultivation of winter rye since this cereal crop has traditionally been grown in a country where the conditions for growing crops are tough. In recent years, China, Canada, and the United States have begun to cultivate increasing amounts of rye.

Retrospective analysis showed that on average for the period 1994–2018, the Russian Federation contributed most to the world production of rye followed by Poland and Germany. In recent years, production of rye has changed significantly. In total, the Russian Federation, Germany, and Poland produced between 6 and 8 Mt of rye that accounted for more than 70% of European rye and about 57% of the total world grain harvest of this crop. In 2018, Germany and Poland became the leaders in the production of rye. The top 10 countries include Belarus, Ukraine, China, Denmark, Canada, Turkey, and Spain.

Rye production in Germany shifted over the last 25 years from population to hybrid varieties. Despite a smaller cropping area of 0.52 Mha in Germany, winter rye grain production in Germany increased due to higher yield (4.2 t per hectare) resulting from the strong yield performance of hybrid rye varieties. At the same time, winter rye in Poland was harvested on 0.89 Mha at a yield of only 2.4 tonnes per hectare because of a lower level of agrotechnology use and limited use of hybrid rye varieties.

Traditionally, the cultivation of Russian rye grain was the most economically beneficial practice, especially since the agro-climatic conditions of Russia are optimal for rye. Rye is relatively undemanding crop, is resistant to severe winter

conditions, and grows well even in less fertile soils (including sandy). Therefore, the expenditures for fertilizers and plant protection chemicals on rye cultivation are lower than for other cereals. In 2018, rye grain production dropped from 2.4 to 1.92 Mt. The large reduction can be explained by reduced demand for rye and severe damage to winter rye by snow mold disease caused by several types of fungal pathogens like *Microdochium nivale*, *M. majus*, *Typhula ishikariensis*, *T. incarnata*, *Myriosclerotinia borealis* and *Pythium iwayami*, *P. okanoganense* (Gorskov et al. 2020; Ponomareva et al. 2020) Significant producers of rye are also China (1.04 Mt), Denmark (0.48 Mt), Belarus (0.50 Mt), and Ukraine (0.39 Mt).

Rye yields over the past six decades have increased in European countries and worldwide (Fig. 1.1). This can be explained by the expansion of the hybrid rye growing area and increased hybrid rye breeding efforts. Especially in Europe (Germany and Denmark), this has led to increased yield (Table 1.1).

The average rye yield was about 2.8 t/ha between 2008 and 2018. The lowest rye yield was in 2010 at less than 2.4 t/ha due to extremely unfavorable weather conditions with severe frost in winter and drought in summer. The highest yield of rye in Europe and on a global scale was recorded in 2017 with more than 3.0 t/ha.

From 1961 to 1978, rye and wheat yield in the world were very similar with about 2 t/ha, but since 1978 wheat yields were usually higher than rye by about 0.6 t/ha, and in Germany even 2.0 t/ha. This difference can be explained by the much higher investment in wheat breeding and the fact that rye is usually cultivated on poor soils. Nevertheless, yield potential of winter rye was much higher. For example, in 2001 and 2014 yield in Germany was above 6.1 t/ha on a total harvested area of 0.84 and 0.63 Mha, respectively. Breeding progress in Germany, especially hybrid breeding, prevented an even greater negative trend of area reduction (Fig. 1.2) due to increasing the yield per hectare with modern hybrids now delivering grain yields more than 12 t/ha.

Since early 2000, hybrid rye breeding investments have been increased resulting in

Fig. 1.1 Worldwide rye harvest area (blue, in Mha), production (green, in Mt), and yield (red, dt/ha) during 1961–2018. Data from FAOSTAT (2020)

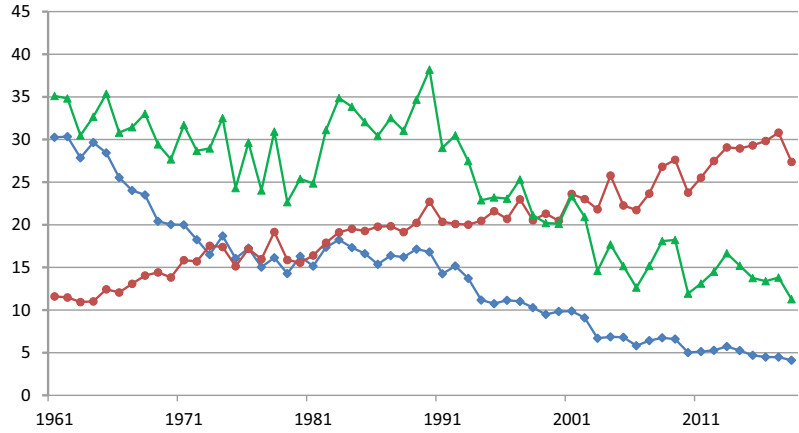
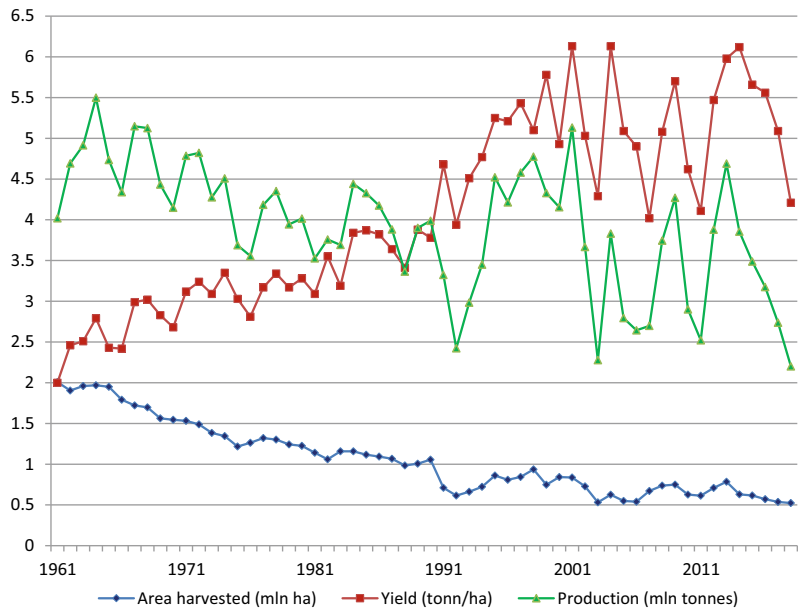


Fig. 1.2 Rye harvest area (blue, in mha), production (green, in million tonnes), and yield (red, in t/ha) in Germany during 1961–2018. Data from FAOSTAT (2020)



growing yield increases combined with strong agronomic performance and improved grain quality (*cf.* Wilde and Miedaner, Chap. 2 of this volume). Miedaner and Huebner (2011) reported that hybrids out-yielded population varieties by 20–25%.

In terms of global production, rye is a minor cereal (Table 1.2), since its production is less than 50% that of oats, ~8% that of barley, and 1.5% that of wheat.

1.3 Rye End Uses

Rye grain is used to bake bread and other products through the sour dough process that confers a unique taste with specific nutritional benefits and market opportunities. Rye-derived products benefit from reduced gluten compared to wheat. Rye is favored because its grain is rich in dietary fiber, carbohydrates, proteins, and several key

Table 1.2 Rye production compared to other cereals in the world in 2018. Data from FAOSTAT (2020)

Crop	Area (Mha)	Yield level (t per ha)	Production (Mt)
Maize	193.73	5.92	1147.62
Wheat	214.29	3.43	734.05
Rice	167.13	4.68	782.00
Barley	47.93	2.95	141.42
Sorghum	42.14	1.41	59.34
Oats	9.85	2.34	23.05
Triticale	3.81	3.36	12.80
Rye	4.12	2.74	11.27

minerals and nutrients. Trends in rye end use include an increase in rye being fed to animals and a decrease in human consumption. In recent years, rye has been well established as a feed component rich in energy for livestock, especially cattle and pigs, and for use in industry, distillery, and energy production.

According to Goncharenko (2014) potential consumption of winter rye is high. From 100 kg of winter rye grain, it is possible to make 160 kg of rye bread, 50 kg of pork meat, 230 l of milk, 36 l of ethanol, 60,000 l of biogas, or 450 kWh of energy.

The highest consumption on a country basis belongs to the Russian Federation. Russia consumed 2.55 Mt of rye in 2017, followed by Belarus (approximately 0.8 Mt), the USA (0.5 Mt), and Ukraine (0.38 Mt). Russian rye consumption is distributed as follows: 60% of grain is used in baking, about a third of the gross harvest is for animal feed, and 10% for other needs (Ponomareva and Ponomarev 2019).

According to the European Commission in 2020, the EU total supply of rye was 9.76 Mt of which 7.5 Mt were for domestic use. Most of domestic rye was used as food (2.96 Mt, 39%) and 2.70 Mt (36%) of domestic rye was used as animal feed (Fig. 1.3). For industrial processing, 0.60 Mt of rye (approximately 12%) were used for bioenergy (Cereals Supply and Demand 2020). The remaining part is represented by seed, stocks, and export.

Statistics show that in the European Union, rye produced for bread making has decreased or

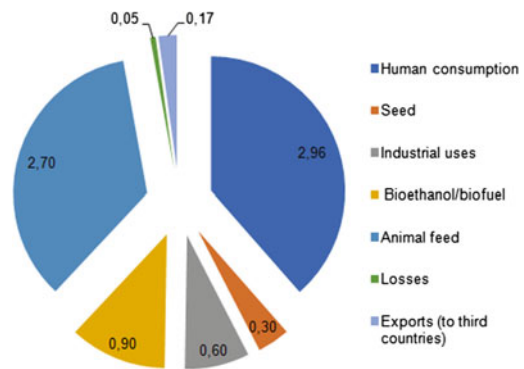


Fig. 1.3 Total supply of rye in EU (domestic use in Mt), 2020/2021 Projection (data from <https://data.europa.eu/euodp/en/data/dataset/cereals-supply-and-demand>)

stagnated, but other market segments such as feed are increasing. Since the 1990s, rye has been increasingly used to produce alcohol and plastics, as well as for the generation of renewable energy (Schlegel 2013).

Rye is mainly consumed in the countries of Northern and Eastern Europe, which exceed the European average of 5.4 kg/year per capita (2017; Table 1.3). Rye consumption is highest in Belarus consumption at an annual consumption per capita of 31.9 kg/year, although this value has decreased by 41% compared with 1995. In the EU, Poland ranks second in rye consumption at 25.7 kg/capita/year. Denmark ranks third in annual rye consumption per person for food production (23.5 kg/capita/year) with a strong increase in comparison with 1995. Rye has always been the national crop, most important

Table 1.3 Annual rye food consumption in the world and in selected countries (in kg/capita/year, data from FAOSTAT 2020)

Country/Year	1995	2005	2017
<i>World</i>	<i>1.4</i>	<i>0.9</i>	<i>0.6</i>
Europa	7.1	6.8	5.4
Belarus	78.0	33.4	31.9
Canada	0.5	0.6	0.6
China	0.5	0.1	0.2
Denmark	15.5	13.0	23.5
Estonia	21.5	18.9	20.8
Finland	15.8	15.4	18.4
Germany	12.0	9.9	9.3
Latvia	19.2	18.9	21.5
Lithuania	44.8	17.1	10.6
Norway	7.3	6.9	7.7
Poland	32.0	31.1	25.7
Russian Federation	11.9	8.9	5.3
Sweden	9.0	12.0	9.3
Turkey	2.4	3.4	2.4
Ukraine	12.8	8.2	8.1
USA	0.3	0.3	0.7

food product, and bread for Denmark. In Denmark, rye culture, eating and cultivation traditions have been passed down from generation to generation, with love and respect for rye and rye bread and increasing attention to health aspects of rye bread.

Among the Nordic and Baltic countries, Norway has the lowest consumption of rye at 7.7 kg/capita/year and the highest is Latvia and Estonia (21.5 and 20.8 kg/capita/year, respectively). The largest decline in 2017 compared to 1995 from the Baltic countries occurred in Lithuania. Rye consumption per capita has decreased over the last 20 years both in European countries and globally (Table 1.3). Worldwide, per capita consumption of rye decreased from 1.4 (1995) to 0.6 kg/capita/year (2017). In Europe consumption of rye has been quite stable and is about 9 times higher than worldwide consumption.

More than 3.2 Mt of rye produced in the EU is used for diversification. In Europe, rye is mostly used for feed, ethanol processing, and

biogas. In Germany, 66% of rye was used for animal feeding and 15% for human nutrition, mainly for bread making (StatJ 2015).

Rye is an ideal crop for agricultural biogas production in regions with low fertility and sandy soils. Rye biomass is increasingly being used as a renewable raw material for biogas production (Geiger and Miedaner 2009). Bioethanol and biogas production may be a growing market for rye. Maximum methane yield per hectare is the main goal for the farmer. According to Huebner et al. (2011), mean rye methane yield was 4424 m³/ha.

The European Biodiesel Board estimated that in 2017, Germany was the biggest producer of biofuel in Europe (more than 4 Mt) (<http://www.ebb-eu.org/stats.php> 2017). In 2007, 25% of Germany's rye harvest was used for bioenergy production. Rye as raw material for bioethanol can produce up to 5.4 t/ha fresh matter biomass yield, 420 l/t biomass, or 2268 l/ha of bioethanol yield, with 2.4 kg/l required biomass per liter of fuel (FNR, BDBe, harvest report of BMEL 2015).

In some countries, including Russia, rye is used as an early feed for green mass and as a cover crop. In the United States, rye is primarily grown as forage. The sowing of rye for green forage is expanding worldwide. This is the first culture to form a green conveyor, giving a high yield of biomass (up to 15 t/ha), suitable for all types of livestock and birds in spring and summer. Farms have additional opportunities to produce early fodder for silage, grass, flour, and hay (Sysuev et al. 2014). Forage is used in the form of green chop, pasture, haylage, or hay. Rye makes excellent forage, especially when combined with red clover and ryegrass. For best quality, rye should be cut between early heading and the milk stage of seed growth. Rye matures earlier and has higher crude protein levels than wheat and triticale. Although rye forage is less palatable than other forages, rye has greater cold tolerance, quicker growth at low temperatures, and more uniform seasonal forage production compared to wheat (*Triticum*), oats (*Avena*), barley (*Hordeum*), or triticale (*Triticosecale*) (Bruckner and Raymer 1990). Rye cultivars used for green fodder and hay in spring and summer grow fast and have thick foliage. They can regrow after being mown or grazed and their herbage is very nourishing (Schlegel 2013).

Rye is the most common and reliable cover crop in the Midwest and Northeast of the United States and in Canada, as it is one of the few cover crops that can be successfully established when planting in autumn after harvesting corn or soybeans. It is winter hardy throughout the region and accumulates significant amounts of biomass before spring planting of other crops (Snapp et al. 2005). As a cover crop, rye is multifunctional in no-till agroecosystems. This is the most effective way to reduce nitrogen and phosphorus losses. The deep root system of rye, especially rye hybrids, captures excess nitrogen and prevents it from entering groundwater or leaching. These nutrients are stored and then made available in the residual biomass for the next harvest. In general, fertilizer costs are decreased and labor is distributed evenly throughout the year.

1.4 Academic Importance of Rye

Our search in the Scopus international database, as per January 2021, revealed only 15,411 publications included rye as a keyword in contrast to over 150,000 publications on wheat. Most often the term rye is mentioned in publications with titles Agricultural and Biological Sciences, Biochemistry, Genetics, and Molecular Biology, Medicine, and Environmental Science and Chemistry (Fig. 1.4).

The aim of agricultural and biological research on rye has mainly focused on the study of economic traits such as grain yield, biomass, nutritional factors, early maturity, and grain quality (see Chap. 9 of this volume). The agronomic advantages and improved end use properties of rye grains achieved by research and development efforts make rye an attractive option for increasing global food production, particularly, for marginal land and stress-prone growing conditions.

As the only outcrossing Triticeae species, rye is of considerable interest both from an evolutionary and a genetic perspective, especially in comparative genomic studies with other grains species.

Genome sequences of Triticeae species are critical resources for understanding the biology and evolution of these species through comparative genomic approaches and for associating phenotypic traits with underlying genes. Rye was the last of the Triticeae species to be sequenced (see Chap. 7), thus closing a major gap in Triticeae genome research. Bauer et al. (2017), using comparative genome analyses, reported genomic diversity in ten rye inbred lines and one accession of the wild relative *Secale vavilovii*, revealing more than 90 million single nucleotide variants and insertions/deletions in the rye genome. These genomic resources have facilitated map-based cloning and functional characterization of genes underlying agronomic traits and advanced Triticeae genomics. Earlier, Hackauf et al. (2009) used marker sequences to construct a comparative map between rice and rye.

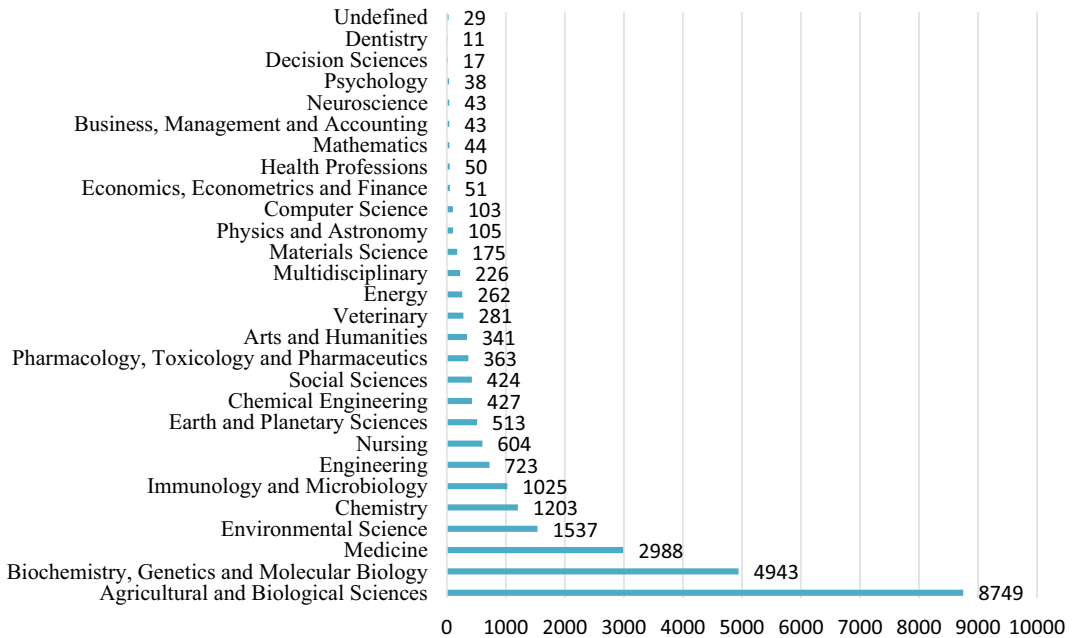


Fig. 1.4 Heading of publications using ‘rye’ as a string for database search. Scopus [Electronic resource]. Accessed: 09.01.2021

Genome wide sequence-based comparisons revealed many more chromosomal rearrangements between the grass genomes than previously reported based on RFLP analyses, thus exposing more complexity to the orthologous relationships between *Triticeae* genomes.

1.4.1 Rye as Genetic Resource for Wheat Improvement

Rye, a close relative of wheat (*Triticum aestivum* L.), which is the economically most important cereal (Feldman and Levy 2015), is providing a vast and largely untapped reservoir of genetic variation for traits such as stress tolerance, biomass, yield, and photosynthetic potential, not only for the commercial crop triticale (x *Triticosecale* Wittmack), but also for wheat (Lukaszewski 2015).

Rye chromosomes or their segments can be introgressed into wheat in the creation of substitution or translocation lines (Ren et al. 2017).

There have been numerous reports on the introgression of rye for wheat improvement dating back to the 1800s (Franke 1991; Driscoll and Anderson 1967). Rye can be crossed with wheat and its agronomic traits can be transferred via classic pre-breeding from wheat/rye hybrids into the wheat genome. Therefore, this crop had a major impact on plant breeding strategies both through the production of the synthetic hybrid triticale as well as through the introgression of rye chromatin in wheat varieties, particularly by the short arm of chromosome 1R (1RS), as a source of genes for agronomic traits and disease resistance (Baum and Appels 1991).

Rye has proven to be a useful source of genes for improving important traits and diversity in wheat breeding (Saulescu et al. 2011; Johansson et al. 2020), especially for disease resistance genes. The short arm of rye chromosome 1R carries resistance genes for leaf rust (*Lr26*), stem rust (*Sr31*), stripe rust (*Yr9*), and powdery mildew (*Pm8*) (McIntosh et al. 2011; Crespo-Herrera et al. 2017), therefore it was

incorporated into tetraploid and hexaploid wheats. The most prominent has been the widely used 1BL.1RS or 1AL.1RS translocations where the short arm of rye chromosome 1R from Petkus rye has replaced the short arm of wheat chromosome 1B or 1A. The 1BL.1RS wheat-rye translocation has contributed immensely to global wheat production as a source of resistance genes (*Sr31/Yr9/Lr26/Pm9*) to wheat fungal diseases (Schlegel 2020). This translocation has been used extensively in wheat breeding by CIMMYT and other breeding programs globally resulting in hundreds of wheat varieties with the rye chromosome arm (Crespo-Herrera et al. 2017) or segments of it (Lukaszewski 2000). It was reported to be present in about 1050 wheat cultivars (Schlegel and Korzun, 1997). This introgression was also found to increase root biomass leading to drought tolerance (Howell et al. 2019). Furthermore, new disease resistance genes from other rye chromosomes have been introgressed into wheat (Driscoll and Jensen 1965; Rabinovich 1998; An et al. 2019; <http://www.rye-gene-map.de/rye-introgression/>). Rye is one of the most winter hardy crops (Erath et al. 2017). While rye quality/utility does not compare to wheat, however, it can be reliably grown in harsher environments. As such, it has always been viewed with much envy by wheat breeders and many efforts have been made to utilize its gene pool for wheat improvement.

With a full reference genome sequence, inexpensive low-density high throughput sequencing (HTS) of a wheat panel proved sufficient to identify the positions of rye introgressions. Crop improvement in rye, as well as in wheat and triticale, will profit from investigations of rye gene families implicated in pathogen resistance, low temperature tolerance, and fertility control systems for hybrid breeding. Consortium scientists (Rabanus-Wallace et al. 2021) showed that rye introgressions in wheat breeding panels can be characterized at high throughput to predict the yield effects and trade-offs of rye chromatin (see Chap. 7 of this volume).

1.4.2 Rye Grain as a Source for Human Health Benefit

A healthy diet and lifestyle are currently in the spotlight, and the demand for healthy foods is growing. Rye was an essential part of the daily diet in northern and eastern parts of Europe because of its high energy value and beneficial agricultural properties (Liukkonen et al. 2007). Scientific evidence shows that rye contains a mixture of biologically active substances and possesses a wide range of protective properties in the prevention and treatment of metabolic syndrome, including cardiovascular diseases and type 2 diabetes as well as intestinal health and certain types of cancer (Jonsson et al. 2018). Their studies have shown that rye helps reduce development of childhood asthma, promotes weight loss, helps to prevent ulcers and stones in the gallbladder, and can improve the metabolic parameters of cells.

The main chemical constituents of the rye grain are the same as in other cereals: starch, dietary fiber (DF), protein, and mineral matter. Some of these key components include manganese, copper, magnesium, phosphorous, B-complex vitamins, and phenolic antioxidant compounds. Barley, oat, and rye grains are all rich sources of (1,3;1,4)-b-D-glucan, whereas wheat, rice, and maize have much lower concentrations. The benefits of DF in human nutrition, enhanced health, and lifestyle-related non-communicable disease prevention are well known and cereals play an important role. Rye flour mixed with wheat flour in various proportions up to 40%, has been shown to increase DF in whole meal rye bread without reducing the acceptability of certain types of bread or pastry products (Kołodziejczyk et al. 2020; Angioloni and Collar 2011; Ragaei and Abdel-Aal 2006). 73% of the diet art fiber in rye is insoluble and 27% soluble (Feng 2019). However, the health effects of rye can be associated not only with fiber content, but also with the so-called “rye fiber complex”, which is a mixture of various