ORIGINAL PAPER

The importance for food security of maintaining rust resistance in wheat

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Received: 9 May 2012 / Accepted: 30 January 2013 / Published online: 2 March 2013 © Springer Science+Business Media Dordrecht and International Society for Plant Pathology 2013

Abstract Wheat is one of the main sources of calories and protein of the world's population and therefore the pathogens that cause rust diseases of the crop are a real threat to food security. Besides the continuous evolution of rust pathogens which repeatedly results in overcoming the resistance of commercial varieties throughout the world, plant breeders are also now challenged by the impacts of global climatic changes. Agricultural practices will need to keep pace with the intensification of sustainable food production in order to face the challenge of feeding a world population estimated to reach about nine billion by 2050. Contemporary wheat breeding has

increasingly focused on the future, culminating in the emergence of a global partnership for breeding new wheat varieties with resistance to rust pathogens. Plant breeding now employs a wide range of both long-established and frontier technologies aimed at achieving the United Nations Millennium Development Goals of ending hunger and extreme poverty (MDG1), while concurrently promoting environmental sustainability (MDG7) through global partnerships for development (MDG8).

Keywords Breeding · Food production · Genetics · *Puccinia graminis tritici* Ug99 · Sustainable development · United Nations Millenium Development Goals

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Introduction

Concern with present and future global food security has begun to reemerge in the last few decades because the global population more than doubled between 1961 and 2007, and is projected to increase from 6.8 billion in 2010 to around 9 billion in 2050 (FAO 2010a). The global number of undernourished people in 2010 has been estimated to be about one billion, an unacceptably high number despite a small decline compared with the number in 2009 (FAO 2010b). To guarantee global food security for future generations the estimated yearly increase in agricultural productivity needs to be raised from the current 2 % per year to 3 % per year (Von Braun 2010).

Although the current global investment in agricultural research is increasing, principally in emerging economies such as Brazil, China and India (Butler 2010), the increase is much slower than during the 'Green Revolution' of the 1970s (Butler and Spencer 2010). To face the challenge of meeting urgent human needs such as the United Nations Millennium Development Goal of ending hunger and extreme poverty (United Nations 2000) the Food and Agricultural Agency of



the United Nations has estimated that the annual investment in the agricultural food production chain in developing countries needs to double to US\$83 billion (Nature Editorial 2010). These topics have gained such political importance that food security was widely discussed in the 2008 G8 and 2009 G20 meetings and at the World Economic Forum and G20 meetings in 2010 (Von Braun 2010). The issue of food price volatility was addressed in 2011 at the first-ever meeting of the G20 Agriculture Ministers with the ultimate objective of improving food security (Ministère de l'Agriculture 2011). Following this meeting, an action plan in this framework was adopted which includes the launch of an International Research Initiative for Wheat Improvement (http://www.wheatinitiative.org/).

In this paper we discuss the issue of food security focusing on wheat (*Triticum aestivum* L.) and the threat posed by rust pathogens. We start with descriptive statistical data on grain production and wheat consumption which illustrates the importance of the crop for global food security. Next, we describe how the pathogens causing diseases known as "rusts" can be real threats to food security because they are a constraint to the stability of global grain production. Later, we discuss the potential of combining traditional and modern technologies to breed new high-yielding wheat varieties with stable forms of rust resistance. The role of emerging global multidisciplinary collaborative research programs for achieving sustainable wheat production based on rust-resistant varieties is also discussed.

Wheat production and world food security

In the past 50 years, global food production has increased almost linearly at a mean rate of 32 million metric tonnes per year (Mt y⁻¹), rising from 887 Mt y⁻¹ in 1961 to 2.351 Mt y⁻¹ in 2007, of which 80 % was wheat, rice or maize (Tester and Langridge 2010). Even so, it has been estimated that to meet the projected demand in 2050 there would have to be a mean yearly increase of 44 Mt, 38 % more than the historic mean yearly increase (Tester and Langridge 2010). Furthermore, it has been estimated that in the next 40 years developing countries will be responsible for 95 % of the increased demand for cereal crops (Rosengrant and Cline 2003).

Food security currently depends on the increased production of three cereals: wheat, with 217 million hectares (M ha) currently planted, rice (*Oryza sativa* L.) with 159 Mha under cultivation and maize (*Zea mays* L.) with 161 Mha planted, which are at present the most abundant plants on the planet (FAOSTAT 2012a). Original data from the FAO (2011) and estimated data from the United Nations (2009) show that wheat is a key cereal crop for global food security as it constitutes an important source of calories and the main

source of protein in more than 80 countries. In terms of calories, about 30 % of the world population is dependent on wheat and its derivatives as primary sources of dietary energy, wheat being responsible for 13 % to 57 % of calorie intake depending on the country. Furthermore, wheat is the second principal source of calories in highly populated countries such as China and India as well as in 26 other countries, while in a further 16 countries it is the third principal calorie source. In total about 85 % of the global population depends on wheat as a basic calorie source (Table 1). Regarding protein, wheat is the primary source for more than 60 % of the global population, with its contribution to total dietary protein intake varying from 14 % to 60 % depending on the country. If we also consider the countries where wheat is the secondary and tertiary protein source, the percentage of the world population depending on wheat as a basic protein source rises to 82 % (Table 2).

During the last five decades, global wheat production has increased from 222 Mt in 1961 to 653 Mt in 2010, which represented 30 % of global grain production (FAOSTAT 2012b). The European Union, China, India, the United States of America and Russia are the principal wheat producers, with these countries being responsible for 67 % of the projected global wheat production for 2012. Wheat is now the most important cereal in terms of commercialized tonnage, estimated to be 135 Mt in 2012/13, with the major importing countries being projected to be in Asia and Africa (FAO 2012). It is expected that the demand for wheat in developing countries will continue to increase and will be about 400 Mt in 2015 and about 480 Mt in 2030 (FAO 2002).

Although estimates indicate that the 2010 wheat harvest was the third greatest so far registered (FAO 2010c), sudden interruptions in supply unsettled the markets and produced economic and social instability. This was highlighted by recent events resulting from the worst drought recorded in at least 50 years in the Black Sea Region (Kolesnikova 2010), principally Russia, Ukraine and Kazakhstan. This region not only produces roughly 30 % of globally commercialized wheat but satisfies the major part of world wheat demand (MacFarquhar 2010). In August 2010, Russia announced that it had lost about 30 % of its wheat harvest due to elevated temperatures and drought (Kramer 2010), and imposed export restrictions which extended to the 1st of July, 2011 (Gorst and Blas 2011). Unfavorable environmental conditions were also responsible for reductions in wheat production in the USA and Canada, as well as in various importing countries, including some in North Africa (FAO 2010d). According to the FAO, global food prices rose 5 % in August 2010, in the main stimulated by the price of wheat, which was 60 % to 80 % higher in September than in July. This was a factor in disturbances



Table 1 Calorie intake from wheat for countries where wheat is the primary, secondary or tertiary calorie source

| | Country | Calorie intake | Population in 2010 ^b | |
|--|---|-----------------------------|---------------------------------|-------|
| | | from wheat (%) ^a | (thousands) | (%) |
| Countries where wheat is the primary calorie source ^a | Azerbaijan, Turkmenistan, Tajikistan, Uzbekistan Tunisia, Algeria, Islamic Republic of Iran, Mongolia, Turkey, Morocco, Georgia, Libyan Arab Jamahiriya, Kyrgyzstan, Occupied Palestinian Territory, Armenia | 53–57 40–48 | 2,071,546 | 29.98 |
| | Syrian Arab Republic, Yemen, Kazakhstan, Jordan, Pakistan, Albania, Egypt, Djibouti, Russian Federation, Malta, Uruguay, Chile, Bulgaria, Lebanon, Mauritania | 30–39 | | |
| | Ukraine, Romania, United Arab Emirates, Italy, Slovakia, Mauritius, Saudi Arabia, Croatia, Lithuania, Poland, Greece, The Former Yugoslav Republic of Macedonia, Argentina, Czech Republic, Israel, Trinidad and Tobago, Fiji, Hungary, Norway, New Caledonia, Netherlands Antilles, Ireland, Kuwait, Saint Lucia, United Kingdom, Slovenia, France, Portugal, Belgium, Saint Vincent and the Grenadines, Bermuda | 20–29 | | |
| | Spain, Bolivia, Sweden, Austria, Finland, New Zealand, Jamaica, Estonia, Cyprus, Antigua and Barbuda, Dominica, Germany, Canada, Switzerland, Denmark, Luxembourg, Iceland, Maldives, Belize, French Polynesia, Australia, Netherlands, Serbia, Belarus, Seychelles, United States of America, Latvia, Grenada, Sao Tome and Principe, Gabon, Brazil | 13–19 | | |
| Countries where wheat is the secondary calorie | Eritrea, India, Bosnia and Herzegovina, China (Mainland, Hong Kong SAR, Macao SAR and Taiwan Province) | 20–29 | 3,149,753 | 45.59 |
| source ^a | Republic of Moldova, Congo, South Africa, Malaysia, Swaziland, Guyana, Barbados, Saint Kitts and Nevis, Peru, Sri Lanka, Lesotho, Brunei Darussalam, Samoa, Japan, Republic of Korea, Ecuador, Botswana, Cape Verde, Haiti, Panama, Bahamas, Senegal | 10–19 | | |
| | Bangladesh, Kenya | 6–9 | | |
| Countries where wheat is the tertiary calorie source ^a | Suriname, Sudan, Nepal, Venezuela, Angola, Namibia, Guatemala, Cuba, Honduras, Zimbabwe, Costa Rica | 10–16 | 662,672 | 9.59 |
| | Mozambique, Dominican Republic, El Salvador, Mexico, Dem. People's Republic of Korea, Zambia, Indonesia, Thailand | 5–9 | | |
| Total global population dependent on wheat as their primary, secondary or tertiary calorie source ^{a,b} | | | 5,883,972 | 85.16 |
| World population in 2010 ^b | | | 6,908,688 | |

^a Estimated based on original data from the FAO (2011)

in Mozambique in which demonstrations occurred which were in part due to a 30 % increase in the price of bread. After 2 days of unrest in Maputo, the Mozambique government reversed the increase in the price of bread, but about 10 people had already been killed and 300 wounded. This unfortunate situation evoked the words of Lord John Boyd Orr, first Director General of the FAO and 1949 Nobel Peace Prize Laureate who said that 'you cannot build peace on empty stomachs' (Reynolds and Borlaug 2006a).

The present situation, where only three crops are responsible for a high proportion of world grain supply and foods, indicates a potential instability in the global strategy for grain production. Not only climatic changes, such as the long drought in Russia, but also epidemic diseases in wheat, rice and maize represent hazards to the global stability of food production. The vulnerability of these crops, especially to foliar diseases, is a consequence of the establishment of environments containing high densities of genetically

uniform plants as, according to basic epidemiological principals, both the incidence and severity of disease are proportional to the density of the host (Duveiller et al. 2007; Tilman et al. 2002).

Wheat rusts: an ever-present threat to food security

There are three types of wheat rust, stem rust (*Puccinia graminis* f. sp. *tritici*), leaf rust (*Puccinia triticina*) and stripe or yellow rust (*Puccinia striiformis* f. sp. *tritici*), all of which are highly specialized biotrophic plant pathogenic fungi belonging to the Basidiomycota (Figs. 1, 2 and 3). Isolates of these pathogens can differentially infect wheat genotypes carrying specific resistance genes which characterize them as physiological races, as first noted for *P. graminis* f. sp. *tritici* by Stakman and Piemeisel (1917).



^b Estimated based on original data from the United Nations (2009)

Table 2 Protein intake from wheat for countries where wheat is the primary, secondary or tertiary protein source

| | Country | Protein intake from wheat (%) ^a | Population in 2010 ^b | |
|--|---|--|---------------------------------|-------|
| | | | (thousands) | (%) |
| Countries where wheat is the primary protein source ^a | Tajikistan, Azerbaijan, Uzbekistan, Tunisia, Turkmenistan Algeria, Islamic Republic of Iran, Turkey, Morocco, Georgia, Syrian Arab Republic, Jordan, Libyan Arab Jamahiriya, Occupied Palestinian Territory, Yemen | 52–60 43–50 | 4,437,277 | 64.23 |
| | Djibouti, Kyrgyzstan, Armenia, Pakistan, Egypt, Kazakhstan, Albania, Bulgaria, Slovakia, Mongolia, Russian Federation, Ukraine | 31–39 | | |
| | Hungary, Lebanon, Malta, Mauritania, Romania, The former Yugoslav Republic of Macedonia, Croatia, Italy, Saudi Arabia, Uruguay, Chile, Mauritius, Fiji, India, Poland Trinidad and Tobago, Greece, United Arab Emirates, Congo, Czech Republic, Israel, Lithuania, Norway, United Kingdom, Belgium, China (Mainland, Hong Kong SAR, Macao SAR and Taiwan Province), France, Ireland, Jamaica, Moldova, Netherlands Antilles, New Caledonia, Switzerland, Austria, Bosnia and Herzegovina, Germany | 21–30 | | |
| | Canada, Finland, Portugal, Sao Tome and Principe, Slovenia, Australia, Belize, Bolivia, Estonia, New Zealand, Spain, Denmark, Dominica, Sweden, Cyprus, Iceland, Latvia, Netherlands, United States of America, Bolivarian Republic of Venezuela, Belarus, Bermuda, Gabon | 14–20 | | |
| Countries where wheat is | Eritrea, Kuwait, Argentina | 21-29 | 623,361 | 9.02 |
| the secondary protein source ^a | Saint Vincent and Grenadines, Saint Lucia, South Africa, Sri Lanka, Suriname, Angola, Liberia, Serbia and Montenegro, Haiti, Guyana, Malaysia, Swaziland, Antigua and Barbuda, Kiribati, Lesotho, Peru, Saint Kitts and Nevis, Samoa, Barbados, Guatemala, Namibia, Botswana, Grenada, Republic of Korea, Seychelles, Senegal, Zimbabwe, Japan | 11–20 | , | |
| | Bangladesh, Zambia | 8–9 | | |
| Countries where wheat is the tertiary protein source ^a | Nepal, Ecuador, Luxembourg, Mozambique, Sudan, Cape Verde, Cuba, French Polynesia, Brazil, Brunei Darussalam, Dominican Republic, Panama, Solomon Islands | 11–17 | 640,201 | 9.27 |
| | Bahamas, Costa Rica, Gambia, Maldives, Indonesia, Democratic Republic of Congo | 7–10 | | |
| Total global population dependent on wheat as their primary, secondary or tertiary protein source ^{a,b} World population in 2010 ^b | | | 5,700,840 6,908,688 | 82.52 |

^a Estimated based on original data from the FAO (2011)

Rusts are by far the most damaging diseases of cereals and, ever since antiquity, have had a great impact on human civilizations. The damage caused by the cereal rusts were well-document by Greek and Egyptian writers centuries before the birth of Christ (Carefoot and Sprott 1967). Further evidence comes from archeological artifacts, such as a storage jar dated to the Late Bronze Age (circa 1,300 BC) found in Israel containing plant fragments contaminated with charred, but well preserved, spores and hyphae of the wheat stem rust fungus (Kislev 1982). Estimation of losses in yield caused by wheat rusts began only in the twentieth century due to a better understanding of disease biology and the increasing need to assess financial investment in control programs (McIntosh et al. 1995). Since then, yield losses and the economic impact of wheat rusts has been comprehensively assessed and shown, in the worst

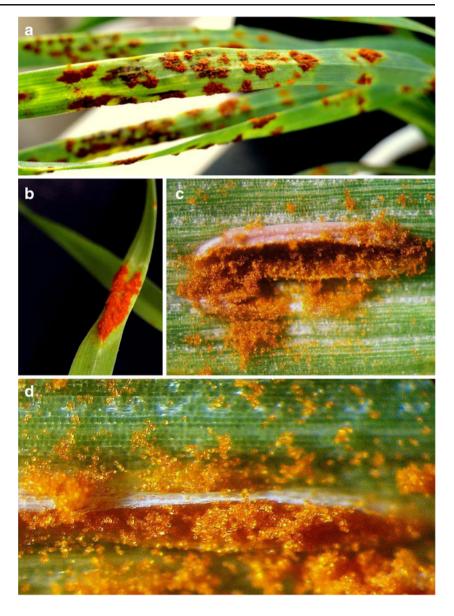
cases, to have resulted in losses measured in the millions in regard to both tonnage and monetary value measured in US dollars (Table 3).

Rust populations are generally very diverse in relation to the combinations and complexity of virulences (Kolmer and Liu 2000), even at locations where sexual recombination is not observed (German et al. 2007, 2009; Hovmøller and Justesen 2007). Such populations are essentially clones originating from dikaryotic uredospores and can evolve very quickly, probably due to mutations, co-adaptations and somatic recombination which can bring critical selective advantages to dikaryotic basidiomycetes (Clark and Anderson 2004). Furthermore, rust populations readily disseminate over great distances, moving thousands of kilometers over oceans and continents to reach regions very far away



^b Estimated based on original data from the United Nations (2009)

Fig. 1 Wheat stem rust caused by Puccinia graminis f. sp. tritici: a Severely infected leaves of a susceptible wheat genotype at seedling stage, b Photomicrograph of a pustule corresponding to the infection type 4, the most susceptible reaction of wheat stem rust (Leica MZ-12 10× magnification), c and d Photomicrograph of stem rust pustules on wheat leaves exposing urediniospores through ruptured epidermis (Leica MZ-12 80× and 100× magnification, respectively). All images by M. S. Chaves



from the location in which they were first detected (Brown and Hovmøller 2002; Kolmer 2005).

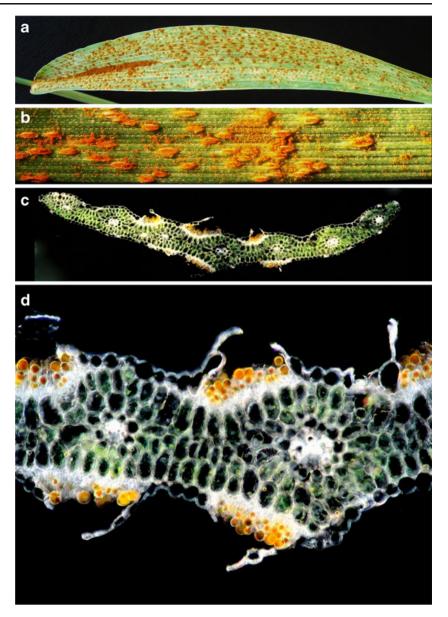
The genetic plasticity, constant evolution and easy dispersion of rust populations are global reasons for concern in wheat genetic improvement programs. During the last decades, there were some well-documented examples in which new or highly aggressive races of wheat rusts emerged and spread rapidly on a continental scale. For *P. striiformis* f. sp. *tritici* there were three independent events in North America, Australia and Africa/South Asia. Another recent event was the detection of a race of *P. graminis* f. sp. *tritici* in East Africa, which overcame the resistance conferred on wheat by the *Sr31* gene which is present in a large proportion of wheat grown throughout the world (Expert Panel 2005; Fig. 4). Since its detection in 1999 (Pretorius et al. 2000), race Ug99 has been confirmed in another eight countries in Africa and Asia (Hodson 2010). Another 26 countries are in areas of risk,

and among them are some of the largest wheat producers such as Australia, India and Pakistan (Stokstad 2007; The Economist 2010). During its migratory pathway, in addition to originally overcoming various resistance genes present in global wheat cultivars (Wanyera et al. 2006) race Ug99 accumulated virulence to the widely-used genes *Sr24* (Jin et al. 2008), and *Sr36* (Jin et al. 2009), and thus further increased the vulnerability of the global wheat crop. The variants so far detected are now called 'races of the Ug99 lineage'. Even though there is a global alert regarding the risk of dissemination of Ug99 races, until 2010 Kenya was the only country that had suffered significant losses (Hodson 2010), which reached 25 % of the wheat harvest in 2007 because of epidemics on four-fifths of all wheat-producing farms (BGRI 2010; The Economist 2010).

Due to the emergence of race Ug99 and the effects of the epidemics caused by this organism some analysts have



Fig. 2 Wheat leaf rust caused by Puccinia triticina: a Symptoms on flag leaf of susceptible cultivar severely infected, b Photomicrograph of a susceptible cultivar at seedling stage showing pustules on the adaxial leaf surface (Leica MZ-12 20× magnification), c and d Photomicrograph under dark field microscopy (Olympus BX-41) of a hand-cut transversal section of an infected wheat leaf showing pustules on both adaxial and abaxial leaf surfaces and urediniospores released through ruptured epidermis (100× magnification), d Photomicrograph with light and focus adjusted to enhance the view of intercellular hyphae spreading around living mesophyll cells (200× magnification). All images by M. S. Chaves



considered this race to be the 'polio of agriculture', in other words, a devastating disease which has almost been forgotten (The Economist 2010). Inevitably, the effects of race Ug99 on the global wheat crop have been compared with plant disease episodes of great impact in the past, such as the nineteenth century potato famine in Ireland, caused by the late blight organism, Phytophthora infestans, and the great Bengal rice famine of 1942–43 associated with a devastating epidemic of brown spot caused by the fungus, Bipolaris oryzae (Flood 2010). Currently, the migration of race Ug99 to other regions of the world is recognized as a real risk to global food security. It has been projected that just in the region of greatest risk (Africa, the Middle East and South Asia), depending on whether the scenario is a 10 % or 20 % loss of production, wheat losses may reach from 8.5 Mt to 59.6 Mt, representing monetary losses of between 1.1

billion and 8.3 billion US dollars (Hodson et al. 2005). This would affect the estimated 1 billion people living within these wheat-producing areas, representing about 25 % of the global area planted with wheat and about 19 % of global wheat production (Reynolds and Borlaug 2006b). It should be noted that these estimates were made without accounting for random, long-distance and accidental transfer of rusts, so the potential global wheat losses could be higher.

Schmidhuber and Tubiello (2007) analyzed the potential impact of climate change on food security. They concluded that such changes could affect all four dimensions of food security: food availability, that is the capacity of the global agricultural system to satisfy the demand for food; food stability, which refers to continuous availability of sufficient food for an adequate diet; access to food, which covers key





Fig. 3 Wheat stripe rust caused by *Puccinia striiformi* f. sp. *tritici*. Images by Silvia German, INIA La Estanzuela, Uruguay

elements of entitlement such as consumer purchasing power; and food usage, covering all aspects of food quality and safety, including sanitary conditions throughout the food chain. Following their line of thought it can be inferred that the potential impacts of wheat rust epidemics also represent a threat to all four dimensions of food security.

Breeding rust-resistant wheat varieties

Financial inputs into agricultural research and development are among the most effective investments for promoting growth and reducing poverty. From 1990 to 2002, for example, the annual global gains attributed to the wheat breeding program of CIMMYT have been estimated to be about US\$ 304 million in 2002 dollar value, with a benefit-cost ratio of around 50:1 (Nalley and Barkley 2007). Enhanced disease resistance is one of the most important traits of modern wheat varieties, permitting a reduction in the use of pesticides and promoting greater stability of yields (Byerlee 1996). During the last few decades the impact of improvements in genetic resistance of wheat to rusts has generated a large proportion of the return on global economic investment in international wheat research (Byerlee and Traxler 1995; Reynolds and Borlaug 2006a). For example, from 1970 to 1990 the incorporation of non-specific resistance to races of wheat leaf rust into modern bread wheat cultivars has been estimated, on the most pessimistic scenario, to have generated at least US\$ 17 million gross in 1994 dollar value (Smale et al. 1998). The International Maize and Wheat Improvement Center (CIMMYT) has estimated that from 1967 to 2007 their internal rate of return on research investment into leaf rust resistance in spring wheat breeding has been 41 %. Considering a discounted interest rate of 5 %, this equates to a net value of US\$ 5.36 billion (1990 dollar value) and a benefit-cost ratio of 27:1 (Marasas et al. 2003). In addition, non-specific resistance to wheat rusts has proved to be durable for long periods (Johnson 1984; Ribeiro do Vale et al. 2001), which is highly relevant to newly-developing countries where cultivar substitution is generally not rapid (Trethowan et al. 2005).

Despite the undeniable success in wheat breeding over the past century, plant breeders still face new challenges such as the impact of global climatic change, continuous pathogen evolution and, to some extent, the narrowing of available genetic diversity within elite germplasm. Wheat breeding for disease control will only be complete if it covers all aspects of the existing and potential global pathogen variability, including pathogen epidemiology, resistance discovery and genetic characterization, germplasm development and the fixation of resistance in wheat varieties which show high yields and quality along with satisfactory adaptability for adoption in agriculture (McIntosh and Pretorius 2011). Under the current scenario, plant breeding is undergoing changes towards a broader and deeper multidisciplinary collaborative effort in global research programs (Ortiz et al. 2007). This emerging plant breeding approach will employ a wide range of long-established and frontier technologies to produce valuable solutions to the urgent needs of humanity, thus contributing to the achievement of MDG1, MDG7 and MDG8 (United Nations 2000). The Global Rust Initiative (www.globalrust.org) was launched in 2005 as an outcome of the 2005 Expert Panel report (Expert Panel 2005) of race Ug99 in Kenya and Ethiopia and the potential for impact in neighboring regions and beyond. This landmark program was later renamed as the Borlaug Global Rust Initiative (BGRI) in honor to its founder, the 1970 Nobel Peace Prize Laureate Norman Borlaug. The initiative has the principal objectives of systematically reducing global vulnerability to wheat stem, yellow and leaf rusts and of advocating and facilitating the development of a sustainable international system to contain the threat of wheat rusts and continue the enhancements in productivity required to withstand future global threats to wheat production. Wheat genotypes combining high resistance and high potential productivity have been identified, although rigorous field-testing is still needed to determine the adaptation of these genotypes to areas of risk (Duveiller et al. 2007; Singh et al. 2008).

It has been affirmed that during this critical point in human development "...the policy decisions we make and the science we choose to carry out over the next few decades



Table 3 Estimated losses caused by wheat rusts worldwide

| Disease | Region | Period | Estimated losses | Reference |
|-------------|------------------------------|-----------|-----------------------|-------------------------|
| Leaf rust | Pakistan | 1978 | US\$ 86 million | Hussein et al. 1980 |
| | Mexico | 2000-2003 | US\$ 32 million | Singh et al. 2004 |
| | South America | 1996-2003 | US\$ 170 million | German et al. 2004 |
| | Australia | 2009 | AUD\$ 12 million | Murray and Brennan 2009 |
| Stem rust | Australia | 1973 | AUD\$ 100-200 million | McIntosh et al. 1995 |
| | United States (North Dakota) | 1919-1923 | 1.95 million tons | Roelfs 1978 |
| | United States (North Dakota) | 1950-1955 | 3.74 million tons | Roelfs 1978 |
| | Kenya | 2007 | US\$ 32 million | Hodson 2009b |
| Stripe rust | United States | 1960-1964 | US\$ 15-30 million | Line 2002 |
| | China | 1954 | 6 million tons | Chen et al. 2009 |
| | China | 2002 | 1.4 million tons | Wan et al. 2004 |
| | Pakistan | 2005 | US\$ 100 million | Duveiller et al. 2007 |

will determine whether all the people living in the world have access to adequate food..." (Godfray et al. 2010a). With respect to science, substantial advances can be achieved by the combined application of existing technologies (Godfray et al. (2010b), of which genetics seems to be the most promising. This is because, historically, it has been largely responsible for increased food production and continues to be the principal tool for increasing productivity by creating new varieties based upon marker assisted selection, genetic engineering or classic crop improvement methods (Butler 2010). Research into resistance to pests and diseases is also a very important and highly promising existing genetic-based technology, as it may lead to a reduction in the large number of health problems accruing to pesticide use in developing countries (Butler 2010). Concomitant with increases in plant resistance and productivity, there will be environmental gains due to the more rational use of land and natural resources along with the preservation of soil integrity and biodiversity (Reynolds and Borlaug 2006a).

Many traditional and cutting-edge tools are immediately available to help researchers breed new, high-yielding wheat varieties with stable forms of rust resistance. In the following sections we discuss how some of the most promising of these tools can be used in an integrated manner within the context of the emerging global breeding system to improve stability of wheat production by reducing rust pressure.

Present technologies for generating future wheat varieties

Shuttle breeding

The "shuttle breeding" strategy was created in 1945 by Norman Borlaug, the future 1970 Nobel Peace Laureate, and involves continuously developing improved wheat plants by planting seeds in different Mexican environments using two experiment stations. One is the "Norman E. Borlaug Experiment Station" (Formerly, "The Yaqui Valley Experiment Station", renamed since 25 March 2010), located in a dry sea level site at Obregón City (Ciudad Obregón) in northwest Mexico, while the other is "Toluca", a cool highland experiment station located near Mexico City. As climatic and plant disease conditions differ radically between the two sites, which are 10° apart in latitude and 2,600 m in altitude, wheat lines which prove to be outstanding at both sites are automatically adapted to a variety of environments. The shuttle breeding method, which involves using locations contrasting in regard to latitude, altitude and rainfall, has proved to be a most efficient way to introduce and select genes for photoperiod insensitivity (Rajaram et al. 2002). A further advantage of this approach is that by shuttling seeds between the two sites it is possible to have two growing seasons and hence produce two generations per year, thus halving the time required to develop a new variety. Shuttle breeding remains an important approach, especially in the early stages of breeding, and should be complemented by selection of specific lines in target areas (CIMMYT 2005). A shuttle breeding scheme has been established between the Mexican field stations at Ciudad Obregón during the winter, and Toluca or El Batan during summer. Also a Kenyan station at Njoro was started in 2006 to generate modern semi-dwarf wheat plants carrying adult plant resistance (APR) to rusts. Two crop seasons per year in both Mexico and Kenya halve the number of years required to generate and test advanced breeding lines (Singh et al. 2011).

Surveillance of wheat rust pathogens

Epidemiological studies and the creation of resistant wheat varieties have been greatly facilitated by the systematic





Fig. 4 Wheat stem rust caused by *Puccinia graminis* f. sp. *tritici*. Field plot in Kenya severely infected by race Ug99. Images by Silvia German, INIA La Estanzuela, Uruguay

surveys of rust races carried out by research institutes worldwide (Singh 1991; Kolmer 1999, 2001; Kolmer and Liu 2000; Hovmøller 2001; Park et al. 2001; Chen 2005; Martínez et al. 2005; Manninger 2006; Kolmer and Ordoñez 2007; Lind and Gultyaeva 2007; German et al. 2009). These studies have shown great diversity regarding wheat rust race complexity and combinations of virulence, even in locations where sexual recombination has not yet been observed, such as South America (German et al. 2007) and Northwest Europe (Hovmøller and Justesen 2007). Virulence evolves so rapidly in wheat rust races that the host race-specific resistance genes generally exploited in plant breeding are usually overcome within five years of introducing a resistant cultivar (Singh and Huerta-Spino 2001). Information on the incidence and geographic and temporal distribution of wheat rust races, along with the occurrence of new races and the effectiveness of resistance genes, is fundamental in formulating and adopting appropriate national and international policies, investments and strategies in plant protection, plant breeding, seed production systems and rust pathogen research (Park et al. 2011). Since there can be inconsistency between the differential genotypes or in the race nomenclature systems used by laboratories around the world, DNA markers such as simple sequence repeats (SSRs) and amplified fragment length polymorphism (AFLP) are very useful in confirming the genetic relatedness of rust isolates as well as for achieving insights on migration paths and gene flow in populations of rust pathogens (Duan et al. 2003; Szabo and Kolmer 2007; Visser et al. 2009, 2011; Park et al. 2011).

Due to the events concerning the emergence and spread of the highly virulent wheat stem rust race Ug99 (Pretorius et al. 2000) a Global Cereal Rust Monitoring System (GCRMS) has been established as part of the Borlaug Global Rust Initiative (BGRI). Technology based on Geographic Information Systems (GIS) has been used as the backbone of the GCRMS, with an increasing amount of standardized geo-referenced field survey data, the routine use of wind models and web-based visualization tools delivering information in near real-time being incorporated into the system (Hodson et al. 2009a). Although the priority focus is Ug99, data on other cereal rusts can also be included. The global status of cereal rusts can be freely tracked using the networked Google Earth application Rustmapper (http://apps.cimmyt.org/gis/rustmapper/index.htm) developed by CIMMYT (Park et al. 2011). Other tools, including a pathotype tracker and smart PDF maps, have been incorporated and regularly updated situation reports are now routinely included in the system. Since April 2010, all available information can be accessed in three UN languages (Arabic, English, and Russian) via the "Rust SPORE" web portal at http://www.fao.org/agriculture/ crops/rust/stem/en/ (Hodson 2011).

A further important advance in unifying and intensifying wheat rust surveillance and training was the establishment of a Global Rust Reference Center (GRRC) as proposed by the International Center for Agricultural Research in Dry Areas (ICARDA), the International Maize and Wheat Improvement Center (CIMMYT) and Aarhus University (Denmark) (Hovmøller et al. 2010). The GRRC quarantine greenhouse and laboratory facilities are ready at any time to receive live samples of wheat rusts from any country for race diagnosis in a secure environment (http://wheatrust.org/).

Marker-assisted selection

Marker-assisted selection (MAS) provides opportunities for enhancing selection because molecular markers allow the identification of desirable recessive alleles, or multiple alleles related to a single trait, when the alleles do not individually exert detectable effects on the expression of the trait. They can also provide a significant advantage in identifying traits that can only be screened in certain seasons or geographical locations and to identify traits with low heritability. In addition, the early detection of individual plants carrying target genes improves selection efficiency (Suenaga et al. 2003; William et al. 2007). Specific polymerase chain reaction (PCR) markers have already been developed for twenty-nine Lr leaf rust genes, ten Sr stem rust genes and four Yr stripe rust genes. Some of these markers are associated with the gene Lr34, which confers durable APR to leaf rust, (Lagudah et al. 2006, 2009) and the Sr2-complex conferring durable APR to stem rust (McNeil et al. 2008; Hayden et al. 2004; Spielmeyer et al. 2003). Markers are also known for the seedling resistance gene SrCad (Hiebert et al. 2011), which confers high levels



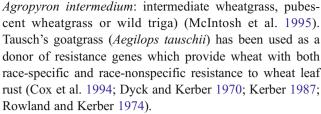
of resistance to stem rust when combined with the leaf rust resistance gene Lr34 and SrWeb (Hiebert et al. 2010), both of these genes being effective against race Ug99 and its variants. Examples in which MAS has been successfully applied to practical breeding are the wheat rust resistance genes Lr34 and Yr36 (Miedaner and Korzun 2012).

Haplodiploidization

The production of in vitro haploid plants via haplodiploidization is among the technologies which are of particular interest to plant breeders, as this technology allows them to develop completely homozygous true-breeding lines in just one generation. This is important, because in traditional breeding programs the development of true-breeding lines requires several backcrossing and self-pollination cycles. Doubled-haploid techniques not only reduce the time required to develop a new variety by about 3 to 4 years (Barnabás et al. 2001) but also increases many-fold the selection efficiency of crop breeding (Choo et al. 1985). In wheat rust research, double-haploids have been particularly important for the development of mapping populations used to identify markers closely associated with quantitative trait loci conferring durable resistance to stem, leaf and stripe rust (Suenaga et al. 2003; Brammer et al. 2004; Moldenhauer et al. 2008; Chu et al. 2008, 2009; Lan et al. 2010; Mago et al. 2011; Prins et al. 2011). Faced with the disturbing outbreaks of stem rust in Africa and neighboring regions, double-haploid wheat populations have also been increasingly used as a tool for the genetic analyses, mapping and stacking of seedling and adult plant resistance genes such as Sr2, effective against race Ug99, (McNeil et al. 2008) and Sr26 and SrR (Mago et al. 2011) plus the gene temporarily designated SrCad (Hiebert et al. 2011). Characterization of parental genotypes and the monitoring of auto-fecundation of F₁ plants using wheat gliadin analysis can be employed to minimize segregation distortions (Scagliusi et al. 2010).

Wheat relatives

Wheat improvement also depends on a continued supply of genetic variability; however, cultivated wheats have been found to exhibit only limited intraspecific variability (Smale 1996). Wild relatives of cultivated wheat are valuable for breeding programs because they can be used to increase the gene pool, which is of particular relevance to breeding rust resistant genotypes as most of the species in the tribe Triticeae carry wheat leaf rust resistance genes (Skovmand et al. 2002; Jones et al. 1995; Stepién et al. 2003; Zaharieva et al. 2001). Many leaf rust and stem rust resistance genes have been introgressed into cultivated wheat from *Thinopyrum ponticum* (syn. *Agropyron elongatum*: commonly known as tall wheatgrass, rush wheatgrass or Eurasian quackgrass) and *Thinopyrum intermedium* (syn.



Many of the rust resistance genes introgressed from wheat relatives have already been overcome by the pathogen. However, as the majority of the major genes currently effective against race Ug99 have been derived from relatives of Triticum aestivum (common, or bread, wheat) and Triticum durum (durum wheat), the search for new resistance mechanisms within these gene pools is one of the goals targeted by current research. Preliminary experiments at the Cereal Disease Laboratory of the Agricultural Research Service of the United Stated Department of Agriculture (ARS-USDA) have shown that resistance to Ug99 in Aegilops speltoides, Triticum timopheevi and Aegilops sharonensis is common, with many accessions exhibiting near-immune reactions (DRRW 2012). Recently, previously uncharacterized resistance genes effective against race Ug99 have been identified in accessions of Triticum monococcum and Triticum urartu (Rouse and Jin 2011). Since T. urartu is the A-genome progenitor of the modern allohexaploid wheat T. aestivum, and T. monococcum is closely related to T. urartu, introgressions from these species to allohexaploid wheat can be made with relative ease (Kerber and Dyck 1973).

Histopathology

Histological studies regarding interactions between plants and rusts can help to distinguish diverse resistance mechanisms and combine them in one genotype in an attempt to increase the durability of resistance (Rubiales and Niks 2000). Detailed analyses of plant germplasm may result in the discovery of alternative plant defense mechanisms unrelated to hypersensitivity and which might be more durable (Niks and Rubiales 2002). Correctly interpreted cytological data can provide important information regarding resistance and the most promising processes to investigate biochemically and physiologically (Heath 1981). High-resolution light microscopy and electron microscopy are useful tools for examining microphenotypes associated with resistance in plant pathogen interactions. Such studies have the potential to detect connections between genetic control and the phenotypic expression of resistance, as shown for the spring wheat cultivar Kariega, which possesses complete adult plant resistance to stripe rust. (Moldenhauer et al. 2008). Characterization of the biochemical and



physiological metabolic processes involved in plant defense reactions to wheat rusts can provide useful data for studies on the identification and characterization of differentially expressed genes in susceptible and partially resistant plant genotypes (Melichar et al. 2008; Ma and Shang 2009). The combined use of techniques such as histopathology, transcriptome and proteome analyses allied to the double-haploid technique in producing mapping populations may allow optimization of the identification of genetic sequences which are, de facto, involved in plant defense reactions. Data from studies using combinations of these techniques may lead to the identification of highly efficient markers closely associated with the target quantitative loci.

Transcriptome analysis

Transcriptome analysis is the study of changes in host and pathogen gene expression during compatible and incompatible interactions. An understanding of such interactions can be of great value for implementing efficient pathogen control measures if the fundamental knowledge gained in such studies is translated into durable disease control mechanisms, and while this is often the most difficult challenge, recent reports have shown that this goal can be achieved (Talbot 2003). The importance of identifying plant defense genes has been reinforced by recent findings, including the fact that many genes activated in response to biotic stress are also activated in response to abiotic stress (Glombitza et al. 2004) and the discovery that the expression of defense genes in resistant plants is faster and more intense than in susceptible plants (Martinez de Ilarduya et al. 2003; Li et al. 2006). These findings suggest that probably the specificity of the response lies in the genes first activated during plant-pathogen interaction (Lu et al. 2005).

Concerning the wheat rusts *P. triticina* and *P. striiformis* f. sp. tritici, many studies have been undertaken to assess the changes in host gene expression for both race-specific resistance (Danna et al. 2002; Fofana et al. 2007; Mallard et al. 2008; Coram et al. 2008b; Wang et al. 2010; Yu et al. 2010) and race non-specific resistance (Mallard et al. 2008; Liu et al. 2008; Bolton et al. 2008; Coram et al. 2008a) as well as non-host resistance (Neu et al. 2003). Some studies have also been made to identify genes presumed to be important in the parasitism of *P. triticina* (Thara et al. 2003; Hu et al. 2007) and P. striiformis f. sp. tritici (Zhang et al. 2008; Yin et al. 2009). The assessment of the quantity of rust biomass inside infected wheat leaves at different times has also been helpful in tracing the transcriptional changes in host tissues expressing different types of leaf and stripe rust reactions for Lr34mediated APR (Bolton et al. 2008) and *Yr39*-mediated high-temperature adult-plant (HTAP) resistance (Coram et al. 2008a).

Proteome analysis

The successful identification of gene interactions involving signal cascades depends on the integration of knowledge from genomics, transcriptomics and proteomics. Proteomics is the best tool available for the identification of proteins and post-translational modifications (PTMs) in protein structure which may give an indication of the final function of a protein (Rossignol et al. 2006). Since PTMs cannot be detected using nucleic acid-based approaches, proteomics can be a valuable tool not only for achieving a more comprehensive understanding of the molecular basis of plant-pathogen interactions but also for elucidating the role of some key metabolic processes, especially phosphorylation, in the defense reaction puzzle (Rampitsch et al. 2006).

Proteomics has been useful in detecting major PTM changes, mainly due to rust proteins, on the sixth day of infection in a compatible interaction between the wheat leaf rust fungus and its host (Rampitsch et al. 2006). This approach has also been used to identify a putative transporter protein, LR34, conferring durable resistance to multiple fungal wheat pathogens (Krattinger et al. 2009). It has also been shown that the barley (Hordeum vulgare L.) gene Rpg1 encodes a protein which has conferred durable resistance against many P. graminis f. sp. tritici races for over 60 years, this protein being rapidly phosphorylated in response to avirulent, but not virulent rust fungus spores, and that phosphorylation is required for disease resistance (Nirmala et al. 2010). An investigation of more than 260 haustorial proteins extracted from wheat leaf tissue infected with the leaf rust P. triticina detected many ribosomal structural proteins as well as many proteins involved in transport, energy production and general metabolism, it being interesting to note that 16 of these proteins corresponded to peptides from the stem rust P. graminis f. sp. tritici (Song et al. 2011).

The unequivocal identification of important peptides is the principal limiting factor inhibiting proteomics from attaining its full potential as a research tool for investigating pathosystems such the wheat leaf rust system (Rampitsch et al. 2006). For plant-pathogen interactions in general, better knowledge of the complete genomic system of both the host and the pathogen are needed for these challenges to be overcome. However, over the last few years there have been significant advances regarding the interactions between wheat varieties and rust pathogens, as will be discussed in the next section on genome sequencing.



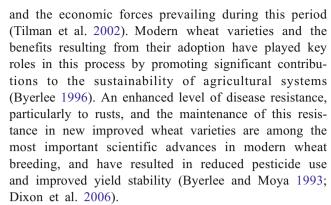
Genome sequencing

Genomics can offer innovative tools for understanding the molecular basis of phenotypic variation, accelerating gene cloning and marker-assisted selection, and for improving the efficiency of exploiting genetic diversity (Eversole 2012). The International Wheat Genome Sequencing Consortium (IWGSC) was launched in 2005 with the overall aim of producing significant results for wheat breeders and the wheat industry at large, in parallel with continued advances in basic research on the wheat genome such as sequencing the hexaploid wheat genome (Feuillet and Eversole 2007; Moolhuijzen et al. 2007). Gaining enhanced knowledge regarding the structure and function of the wheat genome and the biology of agronomically important traits through the deployment of advanced molecular tools are two of the IWGSC Consortium goals (IWGSC 2012). The IWGSC Consortium is also committed to ensuring the open use of the information generated so that breeders may have access to a complete and ordered gene catalogue and an almost unlimited number of molecular markers that can be used for marker-assisted selection and precision breeding approaches (Eversole 2012). The significant progress made since the initiative was launched has recently been reported (Eversole 2012), with current information on the various component projects and associated data being available at http:// www.wheatgenome.org. In addition, the IWGSC sequence repository has been established and can be accessed at http:// urgi.versailles.inra.fr/Species/Wheat/Sequence-Repository.

Regarding the pathogen, it is important to understand the factors related to pathogenicity, virulence and of their evolution, such knowledge being critical to shorten the overall time needed to ascertain the molecular genetic information necessary for functional and translational studies (Cantu et al. 2011). Significant advances have been made in the sequencing of rust genomes. The genome sequence of the wheat stem rust, P. graminis f. sp. tritici, and of stripe rust P. striiformis have recently been published (Duplessis et al. 2011; Cantu et al. 2011), and the genome of the wheat leaf rust P. triticina is currently being fully sequenced and annotated http://www.broadinstitute.org/annotation/genome/ puccinia group/Info.html. Decoding the genomic information of the entire sequenced host and pathogen genomes may provide key information as to how interactions between these organisms take place. Such pooled information may then be used in a rational and directed manner by geneticists and plant breeders for obtaining rust resistance.

Concluding remarks

Food availability has increased over the past 50 years, especially due to the development of technological innovation



It has been suggested that the next 50 years are expected to be the final period of rapidly expanding global human environmental impact, which may, without intervention, result in irreversible changes to the biosphere due to agricultural practices. To assure equitable, secure, sufficient and stable flows of food and ecosystem services for the predicted nine billion world population it is a necessity that humanity developes methods for sustainable food production (Tilman et al. 2002).

Contemporary wheat breeding has increasingly become focused on the future and represents a prime example of the traditional system of international collaboration which has proved to be extremely productive in the past. In the future, a wide range of longestablished and frontier technologies will invigorate research and produce valuable solutions to the urgent need for sustaining food production. Furthermore, such research will encompass at least three of the eight UN Millennium Development Goals, of ending hunger and extreme poverty (MDG1) while concurrently promoting environmental sustainability (MDG7) through a global partnership for development (MDG8). This scenario suggests that there is every reason to be optimistic about the future and for expecting that the development and adoption of new generations of modern wheat varieties will continue to be essential for promoting both increased food production and the sustainability of agroecosystems (Byerlee 1996).

Acknowledgments The Brazilian Agricultural Research Corporation (Empresa Brasileira de Pesquisa Agropecuária-Embrapa), The National Council for Cientific and Technological development (Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq), the Brazillian Ministry of Agriculture, Livestock and Supply (Ministério da Agricultura, Pecuária e Abastecimento-MAPA) and the Research Support Foundation for Brazilian State of Rio Grande do Sul (Fundação de Amparo à Pesquisa do Rio Grande do Sul-FAPERGS) receive our thanks for help and finance regarding our research on the genetic improvement of wheat in respect to rust resistance in Brazil.

Conflict of Interest The authors declare that they have no conflict of interest.



References

- Barnabás, B., Szakács, E., Karsai, I., & Bedö, Z. (2001). In vitro androgenesis of wheat: from fundamentals to practical application. *Euphytica*, 119, 211–216.
- BGRI (2010). Borlaug Global Rust Initiative. http://globalrust.org/traction. Accessed 20 September 2010.
- Bolton, M. D., Kolmer, J. A., Xu, W. W., & Garvin, D. F. (2008). Lr34-mediated leaf rust resistance in wheat: transcript profiling reveals a high energetic demand supported by transient recruitment of multiple metabolic pathways. Molecular Plant-Microbe Interactions, 21, 1515–1527.
- Brammer, S. P., Moraes-Fernandes, M. I. B., Barcellos, A. L., & Milach, S. C. K. (2004). Genetic analysis of adult-plant resistance to leaf rust in a double haploid wheat (*Triticum aestivum* L. em Thell) population. *Genetics and Molecular Biology*, 27, 432–436.
- Brown, J. K. M., & Hovmøller, M. S. (2002). Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science*, 297, 537–541.
- Butler, D. (2010). Q&A: what it will take to feed the world. *Nature*, 464, 969.Butler, D., & Spencer, N. (2010). The growing problem. *Nature*, 466(29), 546–547.
- Byerlee, D. (1996). Modern varieties, productivity and sustainability: recent experience and emerging challenges. *World Development*, 24(4), 697–718.
- Byerlee, D., & Moya, P. (1993). *Impacts of international wheat breeding Research in the developing World*, 1966–90. Mexico: CIMMYT.
- Byerlee, D., & Traxler, G. (1995). National and international wheat improvement research in the post-Green Revolution period: Evolution and impacts. American Journal of Agricultural Economics, 77, 268–278.
- Cantu, D., Govindarajulu, M., Kozik, A., Wang, M., Chen, X., Kojima, K. K., et al. (2011). Next generation sequencing provides rapid access to the genome of *Puccinia striiformis* f. sp. *tritici*, the causal agent of wheat stripe rust. *PLoS One*, 6(8), e24230. doi:10.1371/journal.pone.0024230.
- Carefoot, G. L., & Sprott, E. R. (1967). Famine on the Wind. Chicago: Rand McNally.
- Chen, X. M. (2005). Epidemiology and control of stripe rust [Puccinia striiformis f. sp. tritici] on wheat. Canadian Journal of Plant Pathology, 27, 314–337.
- Chen, W. Q., Wu, L. R., Liu, T. G., & Xu, S. C. (2009). Race dynamics, diversity and virulence evolution in *Puccinia striifor-mis* f. sp. *tritici*, the causal agent of wheat stripe rust in China from 2003 to 2007. *Plant Disease*, 93, 1093–1101.
- Choo, T. M., Reinbergs, E., & Kasha, K. J. (1985). Use of haploids in breeding barley. *Plant Breeding Reviews*, 3, 219–261.
- Chu, C. G., Xu, S. S., Friesen, T. L., & Faris, J. D. (2008). Whole genome mapping in a wheat doubled haploid population using SSRs and TRAPs and the identification of QTL for agronomic traits. *Molecular Breeding*, 22, 251–266.
- Chu, C.-G., Friesen, T. L., Xu, S. S., Faris, J. D., & Kolmer, J. A. (2009). Identification of novel QTLs for seedling and adult plant leaf rust resistance in a wheat doubled haploid population. *Theoretical and Applied Genetics*. doi:10.1007/s00122-009-1035-0.
- CIMMYT (2005). Wheat Shuttle Cleared for Flight, with Minor Course Corrections... CIMMYT e-Newsletter.http://www.cimmyt.org/en/about-us/media-resources/newsletter/previous-issues/86-2005/292-wheat-shuttle-cleared-for-flight-with-minor-course-corrections. Acessed 20 December 2010.
- Clark, T. A., & Anderson, J. B. (2004). Dikaryons of the basidiomycete fungus schizophyllum commune: evolution in long-term culture. *Genetics*, 167, 1663–1675.
- Coram, T. E., Settles, M., & Chen, X. (2008). Transcriptome analysis of high-temperature adult-plant resistance conditioned by *Yr39*

- during the wheat– *Puccinia striiformis* f. sp. *tritici* interaction. *Molecular Plant Pathology*, 9, 479–493.
- Coram, T. E., Wang, M., & Chen, X. (2008). Transcriptome analysis of the wheat-Puccinia striiformis f. sp. tritici interaction. Molecular Plant Pathology, 9, 157–169.
- Cox, T. S., Raupp, W. J., & Gill, B. S. (1994). Leaf rust-resistance genes Lr41, Lr42 and Lr43 transferred from Triticum tauschii to common wheat. Crop Science, 34, 339–343.
- Danna, C. H., Sacco, F., Ingala, L. R., Saione, H. A., & Ugalde, R. A. (2002). Cloning and mapping of genes involved in wheat-leaf rust interaction through gene-expression analysis using chromosome-deleted near-isogenic wheat lines. *Theoretical and Applied Genetics*. doi:10.1007/s00122-002-0990-5.
- Dixon, J., Nalley, L., Kosina, P., La Rovere, R., Hellin, J., & Aquino, P. (2006). Adoption and economic impact of improved wheat varieties in the developing world. *Journal of Agricultural Science*, 144, 489–502.
- DRRW (2012). The durable rust resistance in wheat project. http://www.wheatrust.cornell.edu/about/objective08.cfm. Acessed 22 Ocotber 2012.
- Duan, X., Enjalbert, J., Vautrin, D., Solignac, M., & Giraud, T. (2003). Isolation of 12 microsatellite loci, using an enrichment protocol, in the phytopathogenic fungus "Puccinia triticina". Molecular Ecology Notes. 3(1), 65–67.
- Duplessis, S., Cuomo, C. A., Lin, Y. C., Aerts, A., Tisserant, E., et al. (2011). Obligate biotrophy features unraveled by the genomic analysis of rust fungi. *Proceedings of the National Academy of Sciences* of USA, 108(22), 9166–9171. doi:10.1073/pnas.1019315108.
- Duveiller, E., Singh, R. P., & Nicol, J. M. (2007). The challenges of maintaining wheat productivity: pests, diseases, and potential epidemics. *Euphytica*, 157, 417–430.
- Dyck, P. L., & Kerber, E. R. (1970). Inheritance in hexaploid wheat of adult plant leaf rust resistance derived from *Aegilops squarrosa*. *Canadian Journal of Genetics and Cytology*, 12, 175–180.
- Eversole, K. (2012). The International Wheat Genome Sequencing Consortium (IWGSC): Building the foundation for a paradigm shift in wheat breeding. In: Börner, A. & Kobijlski, B (Ed.) European Cereals Genetics Co-operative Newsletter 2012, Proceedings of the 15th International EWAC Conference, Serbia, Novi Sad, 2011. http://www.ewac.eu/docs/proceedings2012.pdf. Accessed 26 October 2012
- Expert Panel on Stem Rust Outbreak in Eastern Africa. (2005). Sounding the alarm on global stem rust: An assessment of race Ug99 in Kenya and Ethiopia and the potential for impact in neighboring regions and beyond. Mexico: CIMMYT. http://www.cimmyt.org/english/wps/news/2005/aug/pdf/Expert_Panel_Report.pdf. Accessed 18 September 2008.
- FAO. (2002). World agriculture: towards 2015/2030 Summary report.

 Rome: Food and Agriculture Organization of The United Nations.

 http://www.fao.org/docrep/004/y3557e/y3557e00.htm. Accessed
 18 September 2008.
- FAO. (2010a). The State of Food Insecurity in the World Addressing food insecurity in protracted crises. Rome: Food and Agriculture Organization of The United Nations. http://www.fao.org/docrep/013/i1683e/i1683e.pdf Accessed 8 March 2011.
- FAO. (2010b). Global hunger declining, but still unacceptably high. Rome: Food and Agriculture Organization of The United Nations, Economic and Social Development Department. www.fao.org/docrep/012/al390e/al390e00.pdf. Accessed 8 March 2011.
- FAO. (2010c). Crop prospects and food situation, No. 3, September 2010. Rome: Food and Agriculture Organization of The United Nations. http://www.fao.org/docrep/012/ak354e/ak354e00.pdf Accessed 8 March 2011.
- FAO (2011). Economic and Social Development Department> Food Security Statistics> Data> Food security data and definitions> Diet composition> Food consumption pattern of main food items



http://www.fao.org/economic/ess/ess-fs/fs-data/ess-fadata/en/. Accessed 15 June 2011.

- FAO. (2012). Food outlook: global market analysis, May 2012. Rome: Food and Agriculture Organization of The United Nations. http://www.fao.org/fileadmin/user_upload/newsroom/docs/Final%20web%20version%202%20May%20(2).pdf. Accessed 10 October 2012.
- FAOSTAT (2012a). http://faostat.fao.org/site/567/DesktopDefault.aspx? PageID=567#ancor. Accessed 10 October 2012.
- FAOSTAT (2012b). http://faostat3.fao.org/home/index.html#VISUALIZE TOP 20. Accessed 22 October 2012.
- Feuillet, C., & Eversole, K. (2007). Physical mapping of the wheat genome: a coordinated effort to lay the foundation for genome sequencing and develop tools for breeders. *Israel Journal of Plant Sciences*, 55, 307–313.
- Flood, J. (2010). The importance of plant health to food security. Food Security, 2, 215–231.
- Fofana, B., Banks, T. W., McCallum, B., Strelkov, S. E., & Cloutier, S. (2007). Temporal gene expression profiling of the wheat leaf rust pathosystem using cDNA microarray reveals differences in compatible and incompatible defence pathways. *International Journal of Plant Genomics*. doi:10.1155/2007/17542.
- German, S., Kohli, M., Chaves, M., Barcellos, A., Nisi, J., Annone, J., Madariaga, R. & de Viedma, L. (2004). Breakdown of resistance of wheat cultivars and estimated losses caused by recent changes in the leaf rust population in South America. In: Proceedings of 11th international cereal rusts and powdery mildews conference abstract. John Innes Centre, Norwich, England, UK, pp A2.21.
- German, S., Barcellos, A., Chaves, M., Kohli, M., Campos, P., & Viedma, L. (2007). The situation of common wheat rusts in the Southern Cone of America and perspectives for control. Australian Journal of Agricultural Research, 58, 620–630.
- German, S; Chaves, M., Campos, P., Viedma, L. & Madariaga, R. (2009).
 Are rust pathogens under control in the Southern Cone of South America? Full Papers and Abstracts for the Presented Talks.
 Borlaug Global Rust Initiative (BGRI) 2009 Technical Workshop. http://www.globalrust.org/db/attachments/resources/879/3/Full%20papers%20and%20abstracts%20for%20presented%20talk-s.pdf. Accessed 10 December 2010.
- Glombitza, S., Dubuis, P. H., Thulke, O., Welzl, G., Bovet, L., Gotz, M., et al. (2004). Crosstalk and differential response to abiotic and biotic stressors reflected at the transcriptional level of effector genes from secondary metabolism. *Plant Molecular Biology*, 54, 1–19.
- Godfray, H. C. J., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Nisbett, N., et al. (2010). The future of the global food system. Philosophical Transactions of the Royal Society B Biological Sciences, 365, 2769–2777.
- Godfray, H. C. J., Beddington, J. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., et al. (2010). Food security: the challenge of feeding 9 Billion people. *Science*, 327, 812–817.
- Gorst, I. & Blas, J. (2011). Russia announces plans to lift grain export ban. Financial Times, Published online May 28 2011 http://www.ft.com/intl/cms/s/0/6b2bb096-8925-11e0-b342-00144feab49a.html#axzz1ToBMJ6Ro. Accessed 15 July 2011.
- Hayden, M. J., Kuchel, H., & Chalmers, K. J. (2004). Sequence tagged microsatellites for the Xgwm533 locus provide new diagnostic markers to select for the presence of stem rust resistance gene Sr2 in bread wheat (Triticum aestivum L.). Theoretical and Applied Genetics, 109, 1641–1647.
- Heath, M. C. (1981). Resistance of plants to rust infection. Phytopathology, 77, 971–974.
- Hiebert, C. W., Fetch, T. G., & Zegeye, T. (2010). Genetics and mapping of stem rust resistance to Ug99 in the wheat cultivar Webster. *Theoretical and Applied Genetics*. doi:10.1007/s00122-010-1291-z.

- Hiebert, C. W., Fetch, T. G., Zegeye, T., Thomas, J. B., Somers, D. J., Humphreys, D. G., et al. (2011). Genetics and mapping of seedling resistance to Ug99 stem rust in Canadian wheat cultivars 'Peace' and 'AC Cadillac'. *Theoretical and Applied Genetics*. doi:10.1007/s00122-010-1291-z.
- Hodson, D. P. (2009b). The Global Cereal Rust Monitoring System. Borlaug Global Rust Initiative 2009 Technical Workshop, Ciudad Obregón, Mexico, 2009. http://www.globalrust.org/db/attachments/resources/843/4/Obregon_ppt_Hodson.pdf. Acessed 05 November 2012.
- Hodson, D. P. (2010). Wheat rust: A growing threat to world food security. In: Food Outlook, Global Market Analysis, Special features (pp. 61–63). Rome: Food and Agriculture Organization of The United Nations.
- Hodson, D. P. (2011). Shifting boundaries: challenges for rust monitoring. *Euphytica*, 179, 93–104.
- Hodson, D. P., Singh, R. P., & Dixon, J. M. (2005). An initial assessment of the potential impact of stem rust (race Ug99) on wheat producing regions of Africa and Asia using GIS. In: Abstracts of the 7th International Wheat Conference, Mar del Plata, Argentina (p. 142) http://apps.cimmyt.org/gis/pdf/UG99postH.pdf. Accessed 02 December 2010.
- Hodson, D. P., Cressman, K., Nazari, K., Park, R.F. & Yahyaoui, A. (2009a). The Global Cereal Rust Monitoring System. Full Papers and Abstracts for the Presented Talks. Borlaug Global Rust Initiative (BGRI) 2009 Technical Workshop. http://www.globalrust.org/db/attachments/resources/879/3/Full%20papers%20and%20abstracts%20for%20presented%20-talks.pdf. Accessed 10 December 2010.
- Hovmøller, M. S. (2001). Disease severity and pathotype dynamics of Puccinia striiformis f. sp. tritici in Denmark. Plant Pathology, 50, 181–189.
- Hovmøller, M. S., & Justesen, A. F. (2007). Rates of evolution of avirulence phenotypes and DNA markers in a northwest European population of *Puccinia striiformis* f. sp. tritici. Molecular Ecology, 16, 4637–4647.
- Hovmøller, M. S., Walter, S., & Justesen, A. F. (2010). Escalating threat of wheat rusts. *Science*, 329(5990), 369.
- http://ageconsearch.umn.edu/bitstream/9778/1/sp07na01.pdf. Accessed 12 January 2010. Nature Editorial (2010). How to feed a hungry world. *Nature*, 466(7306), 531–532.
- Hu, G., Linning, R., Mccallum, B., Banks, T., Cloutier, S., Butterfield, Y., et al. (2007). Generation of a wheat leaf rust, Puccinia triticina, EST database from stage-specific cDNA libraries. *Molecular Plant Pathology*, 8, 451–467.
- Hussain, M., Hassan, S. F. & Kirmani, M. A. S. (1980). Virulence in Puccinia recondita Rob. ex. Desm. f. sp. tritici in Pakistan during 1978 and 1979. Proceedings of 5th European and Mediterranean cereal rust conference, Bari, Italy, 179–184.
- IWGSC (2012). The International Wheat Genome Sequencing Consortium. http://www.wheatgenome.org/. Accesed 22 October 2012.
- Jin, Y., Szabo, L. J., Pretorius, Z. A., Singh, R. P., Ward, R., & Fetch, T., Jr. (2008). Detection of virulence to resistance gene Sr24 within race TTKS of Puccinia graminis f. sp. tritici. Plant Disease, 92, 923–926.
- Jin, Y., Szabo, L. J., Rouse, M., Fetch, T., Pretorius, Z. A., Wanyera, R., et al. (2009). Detection of virulence to resistance gene Sr36 within race TTKS lineage of Puccinia graminis f. sp. tritici. Plant Disease, 93, 367–370.
- Johnson, R. (1984). A critical analysis of durable resistance. *Annual Review of Phytopathology*, 22, 309–330.
- Jones, S. S., Murray, T. D., & Allen, R. E. (1995). Use of alien genes for the development of disease resistance in wheat. *Annual Review of Phytopathology*, 33, 429–443.



Kerber, E. R. (1987). Resistance to leaf rust in hexaploid wheat: Lr32 a third gene derived from Triticum tauschii. Crop Science, 27, 204– 206

- Kerber, E. R., & Dyck, P. L. (1973). Inheritance of stem rust resistance transferred from diploid wheat (*Triticum monococcum*) to tetraploid and hexaploid wheat and chromosome location of the gene involved. *Canadian Journal of Genetics and Cytology*, 15, 397– 409
- Kislev, M. E. (1982). Stem rust of wheat 3300 years old found in Israel. Science. 216, 993–994.
- Kolesnikova, M. (2010). Worst Russian drought in 50 years threatens next crop. Bloomberg, Published August 27, 2010. http:// www.bloomberg.com/news/2010-08-03/worst-russian-droughtin-50-years-threatens-more-crops-grain-sowing-plans.html. Accessed 10 September 2010.
- Kolmer, J. A. (1999). Virulence dynamics, phenotypic diversity, and virulence complexity in two populations of *Puccinia* triticina in Canada from 1987 to 1997. Canadian Journal of Botany, 77, 333–338.
- Kolmer, J. A. (2001). Molecular polymorphism and virulence phenotypes of the wheat leaf rust fungus *Puccinia triticina* in Canada. *Canadian Journal of Botany*, 79, 917–926.
- Kolmer, J. A. (2005). Tracking wheat rust on a continental scale. *Current Opinion in Plant Biology*, 8, 441–449.
- Kolmer, J. A., & Liu, J. Q. (2000). Virulence and molecular polymorphism in international collections of the wheat leaf rust fungus Puccinia triticina. Phytopathology, 90, 427–436.
- Kolmer, J. A., & Ordoñez, M. E. (2007). Genetic differentiation of Puccinia triticina populations in Central Asia and the Caucasus. Population Biology. doi:10.1094/PHYTO-97-9-1141.
- Kramer, A. E. (2010). Drought in Russia ripples beyond the wheat fields. The New York Times, Published August 27, 2010. http:// www.nytimes.com/2010/08/28/business/global/28wheat.html. Accessed 10 September 2010.
- Krattinger, S. G., Lagudah, E. S., Spielmeyer, W., Singh, R. P., Huerta-Espino, J., McFadden, H., et al. (2009). A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. *Science*, 323, 1360–1363.
- Lagudah, E. S., McFadden, H., Singh, R. P., Huerta-Espino, J., Bariana, H. S., & Spielmeyer, W. (2006). Molecular genetics characterization of the *Lr34/Yr18* slow rusting resistance gene region in wheat. *Theoretical and Applied Genetics*, 114, 21–30.
- Lagudah, E. S., Krattinger, S. G., Herrera-Foessel, S., Singh, R. P., Huerta-Espino, J., Spielmeyer, W., et al. (2009). Gene-specific markers for the wheat gene Lr34/Yr18/Pm38 which confers resistance to multiple fungal pathogens. *Theoretical and Applied Genetics*. doi:10.1007/s00122-009-1097-z.
- Lan, C. X., Liang, S. S., Zhou, X. C., Zhou, G., Lu, Q. L., Xia, X. C., et al. (2010). Identification of genomic regions controlling adult-plant stripe rust resistance in Chinese landrace Pingyuan 50 through bulked segregant analysis. *Phytopathology*, 100, 313–318.
- Li, C., Bai, Y., Jacobsen, E., Visser, R., Lindhout, P., & Bonnema, G. (2006). Tomato defense to the powdery mildew fungus: differences in expression of genes in susceptible, monogenic and polygenic resistance responses are mainly in timing. *Plant Molecular Biology*, 62, 127–140.
- Lind, V., & Gultyaeva, E. (2007). Virulence frequences of *Puccinia triticina* in Germany and the European regions of the Russian Federation. *Journal of Phytopathology*, 155, 13–21.
- Line, R. F. (2002). Stripe rust of wheat and barley in North America: a retrospective historical review. Annual Review of Phytopathology, 40, 75–118.
- Liu, D., Xia, X.-C., He, Z.-H., & Xu, S.-C. (2008). A novel homeobox-like gene associated with reaction to stripe rust and powdery mildew in common wheat. *Phytopathology*, 98, 1291–1296.

Lu, Z. X., Gaudet, D. A., Frick, M., Puchalski, B., Genswein, B., & Laroche, A. (2005). Identification and characterization of genes differentially expressed in the resistance reaction in wheat infected with *Tilletia tritici*, the common bunt pathogen. *Journal* of *Biochemistry and Molecular Biology*, 38, 420–431.

- Ma, Q., & Shang, H. S. (2009). Ultrastructure of stripe rust (*Puccinia striiformis* f. sp *tritici*) interacting with slow-rusting, highly resistant, and susceptible wheat cultivars. *Journal of Plant Pathology*, 91, 597–606.
- MacFarquhar, N. (2010). U.N. Raises Concerns as Global Food Prices Jump. The New York Times Online, New York, Published September 03, 2010. http://www.nytimes.com/2010/09/04/world/ 04food.html. Accessed 10 September 2010.
- Mago, R., Lawrence, G. J., & Ellis, J. G. (2011). The application of DNA marker and doubled-haploid technology for stacking multiple stem rust resistance genes in wheat. *Molecular Breeding*. doi:10.1007/s11032-010-9434-0.
- Mallard, S., Nègre, S., Pouya, S., Gaudet, D., Lu, Z.-X., & Dedryver, F. (2008). Adult plant resistance-related gene expression in 'Camp Remy' wheat inoculated with *Puccinia striiformis*. *Molecular Plant Pathology*, 9, 213–225.
- Manninger, K. (2006). Physiological specialization of *Puccinia triticina* on wheat and triticale in Hungary in 2004. *Acta Phytopathologica et Entomologica Hungarica*, 41, 1588–2691.
- Marasas, C. N., Smale, M., & Singh, R. P. (2003). The economic impact of productivity maintenance research: breeding for leaf rust resistance in modern wheat. *Agricultural Economics*, 29, 253–263.
- Martinez de Ilarduya, O. M., Xie, Q. G., & Kaloshian, I. (2003). Aphid-induced defence responses in *Mi-1*-mediated compatible and incompatible tomato interactions. *Molecular Plant-Microbe Interactions*, 16, 699–708.
- Martínez, F., Sillero, J. C., & Rubiales, D. (2005). Pathogenic specialization of *Puccinia triticina* in Andalusia from 1998 to 2000. *Journal of Phytopathology*, 153, 344–349.
- McIntosh, R., & Pretorius, Z. (2011). Borlaug Global Rust Initiative provides momentum for wheat rust research. *Euphytica*, 179, 1–2.
- McIntosh, R. A., Wellings, C. R., & Park, R. F. (1995). Wheat rusts: An atlas of resistance genes. East Melbourne: CSIRO.
- McNeil, M. D., Kota, R., Paux, E., Dunn, D., McLean, R., Feuillet, C., et al. (2008). BAC-derived markers for assaying the stem rust resistance gene, *Sr2*, in wheat breeding programs. *Molecular Breeding*. doi:10.1007/s11032-007-9152-4.
- Melichar, J. P. E., Berry, S., Newell, C., MacCormack, R., & Boyd, L. A. (2008). QTL identification and microphenotype characterisation of the developmentally regulated yellow rust resistance in the UK wheat cultivar Guardian. *Theoretical and Applied Genetics*, 117, 391–399. doi:10.1007/s00122-008-0783-6.
- Miedaner, T., & Korzun, V. (2012). Marker-assisted selection for disease resistance in wheat and barley breeding. *Phytopathology*, 102, 560–566.
- Ministère de l'Agriculture, de l'Alimentation, de la Pêche, de la Ruralité et de l'Aménagement du territoire (2011). *Ministerial declaration Action plan on food price volatility and agriculture*. http://agriculture.gouv.fr/G20-agriculture. Accessed 12 July 2011
- Moldenhauer, J., Pretorius, Z. A., Moerschbacher, B. M., Prins, R., & Van der Westhuizen, A. J. (2008). Histopathology and PR-protein markers provide insight into adult plant resistance to stripe rust of wheat. *Molecular Plant Pathology*, 9, 137–145.
- Moolhuijzen, P., Dunn, D. S., Bellgard, M., Carter, M., Jia, J., Kong, X., et al. (2007). Wheat genome structure and function: genome sequence data and the International Wheat Genome Sequencing Consortium. *Australian Journal of Agricultural Research*, 58, 470–475.
- Murray, G. M & Brennan, J. P. (2009). The current and potential costs from diseases of wheat in Australia. Grains Research and



Development Corporation, Canberra. p. 25. http://www.grdc.com.au/uploads/documents/GRDC_WheatDiseaseLoss_Report_final.pdf Accessed 05 November 2012.

- Nalley, L. L. & Barkley, A. (2007). The Impact of the CIMMYT Wheat Breeding Program on Wheat Yields in Mexico's Yaqui Valley, 1990–2002: Implications for the Future of Public Wheat Breeding. Selected Paper prepared for presentation at the American Agricultural Economics Association Annual Meeting, Portland, OR, July 29-August 1, 2007.
- Neu, C., Keller, B., & Feuillet, C. (2003). Cytological and molecular analysis of the Hordeum vulgare-Puccinia triticina nonhost interaction Molecular Plant-Microbe Interactions, 16, 626–633.
- Niks, R., & Rubiales, D. (2002). Potentially durable resistance mechanisms in plants to specialized fungal pathogens. *Euphytica*, 124, 201–216
- Nirmala, J., Drader, T., Chen, X., Steffenson, B., & Kleinhofs, A. (2010). Stem rust spores elicit rapid RPG1 phosphorylation. *Molecular Plant-Microbe Interactions*, 23(12), 1635–1642. doi:10.1094/MPMI-06-10-0136.
- Ortiz, R., Trethowan, R., Ortiz Ferrara, G., Iwanaga, M., Dodds, J. H., Crouch, J. H., et al. (2007). High yield potential, shuttle breeding, genetic diversity, and a new international wheat improvement strategy. *Euphytica*, 157, 365–384.
- Park, R. F., Goyeau, H., Felsenstein, F. G., Bartos, P., & Zeller, F. J. (2001). Regional phenotypic diversity of *Puccinia triticina* and wheat host resistance in western Europe, 1995. *Euphytica*, 122, 113–127.
- Park, R., Fetch, T., Hodson, D., Jin, Y., Nazari, K., Prashar, M., et al. (2011). International surveillance of wheat rust pathogens: progress and challenges. *Euphytica*, 179, 109–117.
- Pretorius, Z. A., Singh, R. P., Wagoire, W. W., & Payne, T. S. (2000).
 Detection of virulence to wheat stem rust resistance gene Sr31 in Puccinia graminis f. sp. tritici in Uganda. Plant Disease, 84, 203.
- Prins, R., Pretorius, Z. A., Bender, C. M., & Lehmensiek, A. (2011).
 QTL mapping of stripe, leaf and stem rust resistance genes in a Kariega x Avocet S doubled haploid wheat population. *Molecular Breeding*. doi:10.1007/s11032-010-9428-y.
- Rajaram, S., Borlaug, N. E., & van Ginkel, M. (2002). CIMMYT international wheat breeding. In B. C. Curtis et al. (Eds.), *Bread wheat: Improvement and production*. FAO: Rome. http://www.fao.org/docrep/006/y4011e/y4011e09.htm#bm9. Accessed 17 October 2012.
- Rampitsch, C., Bykova, N. V., McCallum, B., Beimcik, E., & Ens, W. (2006). Analysis of the wheat and *Puccinia triticina* (leaf rust) proteomes during a susceptible host-pathogen interaction. *Proteomics*. doi:10.1002/pmic.200500351.
- Reynolds, M. P., & Borlaug, N. E. (2006a). Impacts of breeding on international collaborative wheat improvement. *Journal of Agricultural Science*, 144, 3–17.
- Reynolds, M. P., & Borlaug, N. E. (2006b). Applying innovations and new technologies from international collaborative wheat improvement. *Journal of Agricultural Science*, 144, 95–110.
- Ribeiro do Vale, F. X., Parlevliet, J. E., & Zambolim, L. (2001). Concepts in plant disease resistance. *Fitopatologia Brasileira*, 26, 577–589.
- Roelfs, A. P. (1978). Estimated losses caused by rust in small grains cereals in the United States – 1918–76. United States Department of Agriculture: Agricultural Research Service. 89 p.
- Rosengrant, M. W., & Cline, S. A. (2003). Global food security: challenges and policies. *Science*, *302*, 1917–1919.
- Rossignol, M., Peltier, J.-B., Mock, H.-P., Matros, A., Maldonado, A. M., & Jorrin, J. V. (2006). Plant proteome analysis: A 2004–2006 update. *Proteomics*, 6, 5529–5548.
- Rouse, M. N., & Jin, Y. (2011). Stem rust resistance in A-genome diploid relatives of wheat. *Plant Disease*, 95, 941–944. doi:10.1094/PDIS-04-10-0260.

- Rowland, G. G., & Kerber, E. R. (1974). Telocentric mapping in hexaploid wheat of genes for leaf rust resistance and other characters derived from *Aegilops squarrosa*. Canadian Journal of Genetics and Cytology, 16, 137–144.
- Rubiales, D. & Niks, R. E. (2000). Combination of mechanisms of resistance to rust fungi as a strategy to increase durability. In: C. Royo, M. M. Nachit, N. Di Fonzo & J. L. Araus (Eds.) *Durum wheat improvement in Mediterraneous region: new* challenges (p. 333–339). Options Mediterraneennes, Series A, 40.
- Scagliusi, S. M. M., Torres, G. A. M., Chaves, M. S. & Simioni, A. (2010). Use of high molecular weight glutenin analyses as a tool to avoid self-pollinated seeds when developing double haploid populations. In: Abstracts of the 8th International Wheat Conference (p. 470). Saint Petersburg: Vavilov Research Institute of Plant Industry.
- Schmidhuber, J., & Tubiello, F. N. (2007). Global food security under climate change. *Proceedings of the National Academy of Sciences*, 104(50), 19703–19708. www.pnas.org/cgi/doi/ 10.1073/pnas.0701976104. Accessed 22 October 2010.
- Singh, R. P. (1991). Pathogenicity variations of *Puccinia recondita* f. sp. *tritici* and *P. graminis* f. sp. *tritici* in wheat-growing areas of Mexico during 1988 and 1989. *Plant Disease*, 75, 790–794.
- Singh, R. P. & Huerta-Spino, J. (2001). Global monitoring of wheat rusts, and assessment of genetic diversity and vulnerability of popular cultivars. *Research Highlights of the CIMMYT wheat* program, 1999–2000. CIMMYT: Mexico, D.F.
- Singh, R. P., Huerta-Espino, J., Pfeiffer, W., & Figueroa-Lopez, P. (2004). Occurrence and impact of a new leaf rust race on durum wheat in northwestern Mexico from 2001 to 2003. *Plant Disease*, 88, 703–708.
- Singh, R. P., Hodson, D. P., Huerta-Espino, J., Jin, Y., Njau, P., Wanyera, R., et al. (2008). Will stem rust destroy the world's wheat crop? Advances in Agronomy, 98, 271–309.
- Singh, R. P., Huerta-Espino, J., Bhavani, S., Herrera-Foessel, S. A., Singh, D., Singh, P. K., et al. (2011). Race non-specific resistance to rust diseases in CIMMYT spring wheats. *Euphytica*, 179, 175–186.
- Skovmand, B., Rajaram, S., Ribaut, J. M., & Hede, A. R. (2002). Wheat genetic resources. In B. C. Curtis et al. (Eds.), *Bread wheat: Improvement and production*. FAO: Rome. www.fao.org/docrep/006/y4011e/y4011e08.htm. Accessed 08 December 2011.
- Smale, M. (1996) Understanding global trends in the use of wheat diversity and international flows of wheat genetic resources. *Economics Working Paper 96–02*. Mexico, D.F.:CIMMYT.
- Smale, M., Singh, R. P., Sayre, K., Pingali, S., Rajaram, S., & Dubin, H. J. (1998). Estimating the economic impact of breeding nospecific resistance to leaf rust in modern bread wheats. *Plant Disease*, 82, 1055–1061.
- Song, X., Rampitsch, C., Soltani, B., Mauthe, W., Linning, R., Banks, T., et al. (2011). Proteome analysis of wheat leaf rust fungus, *Puccinia triticina*, infection structures enriched for haustoria. *Proteomics*. doi:10.1002/pmic.201000014.
- Spielmeyer, W., Sharp, P. J., & Lagudah, E. S. (2003). Identification and validation of markers linked to broad-spectrum stem rust resistance gene Sr2 in wheat (Triticum aestivum L.). Crop Science, 43, 333–336.
- Stakman, E. C., & Piemeisel, F. J. (1917). Biologic forms of Puccinia graminis on cereals and grasses. *Journal of Agricultural Research*, 10, 429–495.
- Stepién, L., Golka, L., & Chelkowski, J. (2003). Leaf rust resistance genes of wheat: identification in cultivars and resistance sources. *Journal of Applied Genetics*, 44, 139–149.
- Stokstad, E. (2007). Deadly wheat fungus threatens world's breadbaskets. Science, 315, 1786–1787.
- Suenaga, K., Singh, R. P., Huerta-Espino, J., & William, H. M. (2003). Microsatellite markers for genes Lr34/Yr18 and other quantitative trait loci for leaf rust and stripe rust resistance in bread wheat. Phytopathology, 93, 881–890.



Szabo, L. J., & Kolmer, J. A. (2007). Development of simple sequence repeat markers for the plant pathogenic rust fungus "Puccinia triticina". Molecular Ecology Notes, 7, 708–710.

- Talbot, N. (2003). On the trail of a serial killer: Exploring the biology of Magnaporthe grisea. Annual Review of Microbiology, 57, 177–202.
- Tester, M., & Langridge, P. (2010). Breeding technologies to increase crop production in a changing world. *Science*, 327, 818–822.
- Thara, V. K., Fellers, J. P., & Zhou, J. M. (2003). In plant induced genes of *Puccinia triticina*. Molecular Plant Pathology, 4, 51–56.
- The Economist online (2010) A crop-killing fungus is spreading out of Africa towards the world's great wheat-growing areas. July, 1st 2010. http://www.economist.com/node/16481593. Accessed 22 August 2010.
- Tilman, D., Cassman, K. G., Matson, P. A., Naylor, R., & Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature*, 418, 671–677.
- Trethowan, R. M., Reynolds, M., Sayre, K., & Ortiz-Monasterio, I. (2005). Adapting wheat cultivars to resource conserving farming practices and human nutritional needs. *Annals of Applied Biology*, 146, 405–413.
- United Nations (2000). United Nations Millennium Declaration. United Nations General Assembly Fifty-fifth session, Agenda item 60 (b), 18 September 2000. http://www.un.org/millennium/declaration/ares552e.pdf. Acessed 18 October 2010.
- United Nations. (2009). World Population Prospects: The 2008 Revision. Department of Economic and Social Affairs. CD-ROM Edition: Population Division.
- Visser, B., Herselman, L., & Pretorius, Z. A. (2009). Genetic comparison of Ug99 with selected South African races of *Puccinia graminis* f. sp. tritici. Molecular Plant Patholpgy, 10, 213–222.
- Visser, B., Herselman, L., Park, R. F., Karaoglu, H., Bender, C. M., & Pretorius, Z. A. (2011). Characterization of two new wheat stem rust races within the Ug99 lineage in South Africa. *Euphytica*. doi:10.1007/S10681-010-0269-X.
- Von Braun, J. (2010). Strategic body needed to beat food crises. *Nature*, 465, 548–549.
- Wan, A., Zhao, Z., Chen, X., He, Z., Jin, S., Jia, Q., et al. (2004).
 Wheat stripe rust epidemic and virulence of *Puccinia striiformis* f. sp. *tritici* in China in 2002. *Plant Disease*, 88, 896–904.
- Wang, X., Liu, W., Chen, X., Tang, C., Dong, Y., Ma, J., et al. (2010). Differential gene expression in incompatible interaction between wheat and stripe rust fungus revealed by cDNA-AFLP and comparison to compatible interaction. *BMC Plant Biology*. doi:10.1186/1471-2229-10-9.
- Wanyera, R., Kinyua, M. G., Jin, Y., & Singh, R. P. (2006). The spread of stem rust caused by *Puccinia graminis* f. sp. *tritici*, with virulence on *Sr31* in wheat in Eastern Africa. *Plant Disease*, *90*, 113.
- William, H. M., Trethowan, R., & Crosby-Galvan, E. M. (2007). Wheat breeding assisted by markers: CIMMYT's experience. *Euphytica*, 157, 307–319.
- Yin, C., Chen, X., Wang, X., Han, Q., Kang, Z., & Hulbert, S. H. (2009). Generation and analysis of expression sequence tags from haustoria of the wheat stripe rust fungus *Puccinia striiformis* f. sp. *tritici*. *BMC Genomics*. doi:10.1186/1471-2164-10-626.
- Yu, X., Wang, X., Wang, C., Chen, X., Qu, Z., Yu, X., et al. (2010). Wheat defense genes in fungal (*Puccinia striiformis*) infection. Functional & Integrative Genomics, 10, 227–239.
- Zaharieva, M., Monneveux, P., Henry, M., Rioval, R., & Valkoun, J. (2001). Evaluation of a collection of wild wheat relative *Aegilops geniculata* Roth and identification of potential sources for useful traits. *Euphytica*, 119, 33–38.
- Zhang, Y., Qu, Z., Zheng, W., Liu, B., Wang, X., Xue, X., Xu, L., Huang, L., Han, Q., Zhao, J. & Kang, Z. (2008). Stage-specific gene expression during urediniospore germination in *Puccinia striiformis* f. sp *tritici*. *BMC Genomics*, 9 (203) doi:10.1186/1471-2164-9-203.



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Dr. Felipe André Sganzerla Graichen is an agronomist and gained his PhD in Plant Pathology from the Federal University of Rio Grande do Sul, Brazil. During a postdoc year at the same University he studied the resistance responses at the histopathological level in host and nonhost pathosystems involving small grain cereals and rusts. Currently he is an Adjunct Professor at the State University of Mato Grosso do Sul, located at Aquidauana, in Central Brazil.

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Dr. Sandra Patussi Brammer is a biologist specializing in cell biology. She obtained her Masters Degree in Genetics at the Federal University of Rio Grande do Sul, followed by her PhD in Genetics and Molecular Biology at the same University. In 2000, she went to Canada for training at the Agriculture and Agri-Food Canada/Cereal Research Centre located in Winnipeg. At present, she is a research scientist at the National Wheat

Research Center of the Brazilian Agricultural Research Corporation (EMBRAPA), located at Passo Fundo, in southern Brazil. Her current research activities are focused on plant genetics with emphasis on the molecular cytogenetics of winter cereals and related species. She has been a collaborator at the University of Passo Fundo, advising students for master and doctoral courses in the agronomy area as well as offering courses such as Molecular Biology and Agricultural Biotechnology, or as an invited professor in specialist course of Genetics and Evolutionary Biology. She also supervises post-doctoral workers and undergraduate students as a collaborator at other Brazilian Universities.



Dr. Sandra Mansur Scagliusi is a biologist specializing in plant virology at both the Agronomic Institute located at Campinas, in 1988, and at the University of São Paulo, in 1989. She holds a Masters Degree and a PhD in Plant Biology from the University of Campinas. Part of her PhD work was conducted at the University of Minnesota (USA), as a sandwich course. During her Masters training she also served as a research

scientist at the Agronomic Institute working in the Electron Microscopy Laboratory of the Virology Department. Currently she is a research scientist at the National Wheat Research Center of the Brazilian Agricultural Research Corporation (EMBRAPA), located in Passo Fundo, in southern Brazil. Her work is focused on tissue culture, with emphasis on the production of double-haploid plants of wheat and barley. In August 2007 Dr. Scagliusi received training in the technique of isolated microspore culture at the Lethbridge Research Centre of Agriculture and Agri-Food Canada. Under the supervision of Dr. François Eudes she acquired the skills to achieve the successful establishment of this technique for the very first time in Brazil, and since then she has been leading initiatives in order to broaden its use both in wheat and barley breeding programs and in basic research.





Dr. Paulo Roberto da Silva is a Brazilian national and holds a PhD degree in Molecular Biology from the Federal University of Rio Grande do Sul (Brazil), with specialization in molecular markers and gene expression as applied to plant breeding. Currently he is a professor and scientific researcher at the Midwestern State University of Paraná (UNICENTRO), located in Guarapuava, in southern Brazil. At UNICENTRO he is also Scientific Director and member of the advisory board of the Postgraduate

Program in Evolutionary Biology. He is a member of the board of scientific advisors of the Araucaria Foundation for the Support of Scientific and Technological Development of Paraná and an associate collaborator in research projects led by the EMBRAPA National Wheat Research Center. He is a reviewer for several scientific journals and has authored or co-authored scientific publications in biotechnology applied to cereal crops (molecular marker development, gene mapping and tagging and gene expression) mostly focusing on the leaf rust resistance genes of wheat.



Dr. Paula Wiethölter is a biologist and received her PhD in Plant Science from the Federal University of Rio Grande do Sul (Brazil) in 2008. During a postdoc year, she conducted studies aimed at the identification and characterization of genes differentially expressed in response to *Puccinia triticina* infection in wheat plants showing adult plant resistance to leaf rust. Currently she is a research fellow at the National Wheat Research Center of the Brazilian

Agricultural Research Corporation (EMBRAPA) and her research activities are now focused on transcriptome analysis in wheat plants showing adult plant resistance to leaf rust. She also works as professor at Meridional College, located in Passo Fundo, in southern Brazil.



Dr. Gisele Abigail Montan Torres is an agronomist and holds a PhD degree in Genetics and Molecular Biology from Université de Paris XI (Paris-Sud, France), where she worked on differentially expressed genes in response to water deficit. In 1997 she joined Michel Dron's team and started to investigate molecular plant-pathogen interactions. Currently she is a research scientist at the National Wheat Research Center

of the Brazilian Agricultural Research Corporation (EMBRAPA), from where she leads the Brazilian Network for Research on Wheat Blast Disease. Her current activities are focused on understanding the responses in the Magnaporthe oryzae x wheat pathosystem, especially at the adult-plant stage. Her team has adopted a holistic approach in which the phenotyping under controlled conditions is assisted by molecular biology tools such as genotyping, transcriptomics and proteomics. Since 2010 she has been responsible for the first ever successfully established network of trap nurseries in Brazil for collecting samples of the wheat blast pathogen and for characterizing genotype reactions to the disease. At EMBRAPA's National Wheat Research Center she is also in charge of research activities including the analysis of wheat storage proteins and prospecting for genes related to enduse quality and tolerance to drought in wheat. Before joining EMBRAPA's staff, she had a two-vear research experience in the Agronomic Institute, a public research center located at Campinas, which is linked to the government of São Paulo State (Brazil). For further information please access http://lattes.cnpq.br/1681035279707004



Dr. Elene Yamazaki Lau is an expert in plant genetic transformation and earned her PhD from the Federal University of Viçosa, in south-east Brazil. Currently she is a research scientist at the National Wheat Research Center of the Brazilian Agricultural Research Corporation (EMBRAPA) located in Passo Fundo, in Southern Brazil. Since joining EMBRAPA in 2009 she has been leading initiatives to deploy the genetic transformation technique in wheat with the main focus on

drought tolerance. During her eclectic training at the undergraduate and master's levels she acquired skills in various fields of knowledge ranging from the study of plant-pathogen interactions and molecular biology to the genetic transformation of plants, which enables her to play a versatile role in many research activities at EMBRAPA.





Dr. Luciano Consoli has been a scientific researcher at the National Wheat Research Center of the Brazilian Agricultural Research Corporation (EMBRAPA) since November 2006. At EMBRAPA he carries out wheat pre-breeding activities mainly related to abiotic stress, such as resistance to aluminum toxicity and pre-harvest sprouting using proteomic and association genetics approaches. At the College of Agriculture "Luiz de Queiroz" of the University of São Paulo (ESALQ/USP), Brazil,

he completed his undergraduate studies in Agronomic Engineering in 1992 and in 1995 received his MSc Degree in Genetics and Plant Breeding. In 2000 he earned his PhD in Genetics and Molecular Biology from the University of Paris XI/Orsay, France. From 2000 to 2004 he served as scientific researcher at the European plant biotechnology company Biogemma, based in France, where he worked with proteomics and molecular marker development for association genetics studies in plants. Before joining EMBRAPA he contributed to the achievement of saturated genetic maps and QTLs studies related to biotic stress during a postdoc year at the Department of Genetics of ESALQ (USP).



Dr. Ana Lúcia Soares Chaves is an agronomist and received her PhD in Plant Molecular and Cellular Biology from the Institut National Polytechnique de Toulouse (ENSAT), France. Under the supervision of Dr. Jean-Claude Pech and Dr. Alain Latché she studied the functional characterization of an elongation factor in mitochondrial translation, expressed during the ripening of tomato. Currently she is an Adjunct Professor at the Federal University of Pelotas, Brazil, where she teaches Bio-

chemistry on several undergraduate courses. She has experience in genomics, proteomics and biotechnology and works on research projects prospecting for and characterizing gene function in crops of economic importance. She also conducts studies on the molecular mechanisms involved in fruit ripening and in climatic adaptations in temperate zone fruit crops. More recently she started to investigate the molecular mechanisms involved in plant-pathogen interactions as an associate collaborator in research projects led by the EMBRAPA National Wheat Research Center. For further information please access http://www.ufpel.edu.br/iqg/db/ana chaves.htm

