The threat to global food security from wheat rust: ethical and historical issues in fighting crop diseases and preserving genetic diversity

Abstract

Wheat rust can cause catastrophic crop failures. The Green Revolution succeeded in part thanks to the deployment of wheat with genetic resistance to stem rust. The appearance of a new strain of stem rust in Uganda (Ug99), first detected in 1998, raised the threat of global stem rust epidemics beyond its prevalence in Africa and the Middle East. Despite over twenty years of awareness campaigns, research, and breeding programmes, much of the wheat cultivated today still lacks resistance to Ug99, while races of the stripe and leaf rust present equal challenges to meeting market demands. Our article contributes a new assessment of ethical issues that emerge in our fight against stem rust. Specifically, the article explores how efforts to combat stem rust we employ today may threaten genetic diversity in wheat or impose a further bottleneck on choice of cultivars, thus directly impacting the ability of future generations to fight stem rust and also to find the genetic diversity needed to develop new varieties of wheat that are adapted to changes in climate.

Key Words

Wheat, Wheat Rust, Conservation, Genetic Diversity, Genetic Erosion, Crop Disease, Green Revolution

Highlights

- **Wheat rust poses a risk to global food security.**
- **The preservation of genetic diversity in wheat is crucial to ensure that future generations can continue to adapt wheat to evolving pathogens and to climate change.**
- **Preserving genetic diversity has historically involved both *ex situ* (storage) conservation practices and *in situ* (on-farm) conservation practices.**
- **Campaigns to eliminate susceptibility to rust and efforts to close yield gaps moving towards the nutrition requirements of 2050 risk eroding and eliminating efforts to preserve landraces through *in situ* conservation.**
- **Forecasting and monitoring programmes could provide opportunities to safely pursue *in situ* conservation of landraces that are susceptible to rust**
- **Identifying and including rare alleles in modern varieties can also ensure that cultivation continues to play a role in conservation.**

1. Introduction

1.1 Meeting the nutrition requirements of 2050

How, precisely, will we grow enough wheat in 2050? Global demand for wheat is expected to increase by 50% by 2050.[1] While at the same time farmers will face challenges from climate change, and increased pressure from pathogens like wheat rust.[2] Despite these challenges there will need to be marked increases in average yields if we are to meet this demand without clearing substantially more land for cultivation (Ray et al 2013; Hatfield et al 2019). Problems such as these influenced the CGIAR 2020 'Report Card' on food security, which determined that there is cause for grave concern that our food system is, across many areas, 'failing us' (Aguilar et al 2020: 10).

Rising populations during the twentieth century were accompanied by tremendous improvements in wheat yields and disease resistance, led in a great part by the breeding programmes of Norman Borlaug, principal architect of the Green Revolution. We may now be reaching the upper threshold of these improvements (Flavell 2017: 15; Fisher & Edmeades, 2010). However, the success of the Green Revolution had unintended consequences on genetic diversity in wheat. While saving the lives of millions, modern breeding techniques narrowed the genetic base of germplasm used to develop varieties for cultivation, and also led to imbalances in how genetic diversity in wheat is distributed globally (Reif et al 2005; Cavanagh et al 2013; Balfourier et al 2019). One of the great challenges to meeting the food requirements of future generations will be breeding new wheat cultivars adapted to changing environments (Ortiz et al 2008). We need to conserve genetic diversity in wheat in order to meet this challenge, but it is not the only challenge facing wheat cultivation that demands we work to conserve genetic diversity. Many of the great famines of the eighteenth and nineteenth centuries, with death tolls in the millions, began with outbreaks of pathogens that attacked staple crops (Alfani & O'Grada 2019). Rust fungi (taxonomized under the order *Pucciniales)* attack cereals, and have been devastating to wheat cultivation for millenia (Barnes et al 2020). Since the Green Revolution, crop losses to rust have been greatly reduced through campaigns to breed resistant varieties, the development of fungicides, and, earlier in the twentieth century, the removal of barberry shrubs from wheat-growing regions (barberry plays a role in some rust fungi life cycles). But rust evolves quickly, and there are, at present, numerous challenges posed to global food security by rust, particularly new virulent strains of *Puccinia graminis f.* sp. *tritici* (which causes stem rust), and *Puccinia striiformis f. sp. tritici* (which causes yellow or stripe rust).

1.2 Evolving pathogens and conservation of genetic diversity

The appearance of a new strain of stem rust in Uganda in 1998 (TTKSK, hereafter Ug99), reintroduced the threat of massive crop losses to a disease that all but disappeared from many continents as a result of numerous campaigns in the 20th century (Pretorius et al 2000).

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[1] Estimates of the increase in food production needed vary widely between 25% and 100%, while researchers largely anticipate demand for wheat to rise by 50% (Hunter et al 2017).

[2] Without adaptation measures to climate change, wheat yield losses globally will increase from 6% mean area-weighted global loss in the 2020s to 12-15% by the 2080s, with these losses predominantly occurring in low latitudes (Aggarwal et al 2019).

Stem rust is the most dangerous form of rust to wheat crops, and when attacking a variety that has no genetic resistance, losses to stem rust can be total (Soko et al 2018). Between 2005-2010, around 200,000 wheat varieties and germplasm materials were screened for resistance to Ug99, with less than 5-10% of the breeding materials demonstrating adequate resistance (Singh 2011: 471). As of 2017, roughly half of the stem rust (*Sr*) resistance loci identified and used in breeding were determined ineffective against Ug99 (Singh et al 2015; Zhang et al 2017). Presently restricted to Eastern Africa and the Middle East, geography does not provide as much protection as one might assume: studies have shown that rust spores can travel atmospherically for thousands of miles, including over oceans (Hovmøller et al 2008). Ravi Singh, who serves as the head of Global Wheat Improvement at the International Maize and Wheat Improvement Center (CIMMYT), warned in 2008 that since the Green Revolution, global wheat cultivation methods have heightened the risk of a stem rust pandemic from Ug99 or a similar pathogen. Increasing temperatures in the northern hemisphere, the loss of genetic diversity in wheat, the extension of wheat cultivation, the increased use of nitrogen fertilizers and irrigation, and over-reliance on a handful of genes that express resistance to races of stem rust all contribute to this increased risk (Singh et al 2008: 288). However, over a decade since issuing this warning, Ug99 remains a deadly threat of global food security, and while new resistance genes have been identified (Zhang et al 2017) efforts to develop durable, resistant varieties are resource-consuming and take time. Whether or not Ug99 spreads to other continents and becomes a pandemic, we now recognise that our present-day practices in wheat cultivation have not removed us from the so-called 'boom and bust cycle' where periods of disease-free cultivation are followed by epidemics and the threat of food insecurity (Wulff & Moscou 2014; Singh et al 2011).

If there is widespread scientific consensus that our vulnerability to rust is cyclical, determined in a great part by the genetic plasticity of rust fungi, then we have an ethical duty to ensure that future generations have available at least the same wealth of genetic resources to combat stem rust as we enjoy today. These resources are composed of: (a) the modern varieties of wheat cultivated today, (b) germplasm and breeding materials within *ex situ* collections, (c) wild wheat plants and species from which novel germplasm can be drawn on to develop new varieties, and (d) 'landraces', which are varieties of wheat developed prior to the widespread cultivated of so-called Green Revolution Wheats, (Warburton et al 2006; Mujeeb-Kazi et al 2013; Casañas et al 2017; Vincent et al 2019; Borrill et al 2019). Because many farmers the world over abandoned the cultivation of local landraces in preference for Green Revolution Wheats, many landraces were lost, inspiring the creation of numerous efforts to collect and store seeds and germplasm (*ex situ* conservation) and also to encourage farmers to continue to cultivate these older varieties (*in situ,* or on-farm conservation) (Curry 2017; Chaves et al 2013; Padulosi et al 2012). Despite efforts to preserve *in situ* cultivation of landraces and to use their germplasm to increase the genetic diversity in varieties bred and cultivated today, recent studies show a continued decline in genetic diversity in wheat varieties cultivated in many regions--Italy, Canada, America, and Australia, being sites where the loss is most noticeable (Kabbaj et al 2017). Historically, *ex situ* conservation measures have been complemented and aided by the continued *in situ* cultivation of landraces (Ford-Lloyd & Maxted 1993; Padulosi 2012), but the pressures placed on wheat production by rising demand, climate change, and the threat of rust epidemics, mean that the cultivation of landraces will continue to decline. This paper addresses the question of how we can maintain a balance between *ex situ* conservation of genetic diversity while recognising that in many cases, increased cultivation of landraces will not contribute to our need to raise yields and increase production.

2. Rust: a brief history

2.1 Before the appearance of Ug99

The campaign against wheat rust in the twentieth century was integral to meeting global nutrition requirements; and so again, mitigating the loss of crops to rust in the decades to come is necessary in order to avoid disaster. The first concerted efforts to breed wheat that would be immune to wheat rust date back to the early 1800s, after virulent attacks of wheat rust in Australia (Johnson 2010: 4). By the twentieth century, when the life-cycle of stem rust was understood to include barberry shrubs as a second host, large state-sponsored campaigns to eradicate barberry trees were undertaken in Europe and America (Barnes et al 2020; Peterson 2018). During the twentieth century, more than 500 million barberry bushes were destroyed in North America; but globally, wheat production during these decades was regularly punctuated by devastating losses from wheat rust (Ehrenberg 2010). The barberry eradication policies were partly successful; by the 1960s, stem rust had largely disappeared from the Great Plains in North America (Peterson 2018: 205). The legislation prohibiting the expansion of barberry shrubs has since lapsed, creating a dangerous environment in America, Europe, and Asia for future rust epidemics (Saunders et al 2019: 2; Barnes et al 2020). Still, while the elimination of barberry and the development of fungicides were both crucial to these improvements, these approaches have always been secondary; breeding for disease resistance remains preferable for numerous reasons (Byerlee 1996).

During the 1950s, an international seed exchange programme was initiated by the United States Department of Agriculture, which facilitated the open trade of seeds between breeding stations in different countries (Singh et al 2008). Seed exchange proved crucial to identifying resistance genes (*R* genes) in landraces, facilitating breeding programmes to develop varieties that offered both high yield and resistance to rust, and also as providing a means for diffusing these new varieties. Breeders in Germany succeeded in the 1930s in translocating the *R* gene *Sr*31 from 'Petkus' rye (Singh et al 2008: 278). In the 1960s, while working for a programme sponsored by the Rockefeller Foundation in Mexico, Norman Borlaug produced several semi-dwarf wheat varieties that were resistant to stem rust (Singh et al 2008: 278). CIMMYT grew out of this breeding programme, and CIMMYT wheats, bred initially for Mexico, proved popular in Asia, the Mediterranean, and South Africa—leading to a tremendous success in distributing CIMMYT wheats globally. During the 1970s, CIMMYT introduced *Sr31* to popular wheat varieties (alongside several other *R* genes) in the Americas, Europe, and Asia, leading to the near-disappearance of stem rust in the 1980s and 1990s (Villareal et al 1995; Singh et al 2008: 278). At its peak, *Sr*31 is estimated to have had a frequency of around 70% in CIMMYT germplasm, prior to 1999 (Singh et al 2008: 279). The success of the programme, and the increasing reliance on CIMMYT germplasm lead to growing fears of genetic uniformity (Warburton et al 2006: 298-9). It was during this same period that scientists became alarmed at the dangers involved in monoculture and reliance upon a handful of *R* genes as a bulwark against pathogens, particularly after the Southern Corn Leaf Blight of 1970 (Reif et al 2005). Borlaug and other scientists of his generation had always anticipated that the genes they discovered would not provide resistance to stem rust indefinitely (CIMMYT 2005: i). Still, the successes against stem rust from the 1970s onwards resulted in great international complacency. The Green Revolution persuaded many that hunger was only a distribution problem, leading to a decrease in attention and concern paid to evolving pathogens (Paarlberg 2009: 97). Thus, it was a shock for many when stem rust was observed on a wheat variety with the *R* gene *Sr*31 in a nursery stationed in Uganda in 1998.

2.1 Ug99 and its variants

Since the appearance of Ug99, careful monitoring has shown that there are increasingly more variants attached to the Ug99 lineage, which have been listed with their year of identification and geographical location on rustracker.cimmyt.org (Singh et al 2015; Bhavani et al 2019; Table 1). Many of the most popular varieties of wheat proved vulnerable to the pathogen. The mega-varieties PBW343 (cultivated in India), Inquilab 91 (cultivated in Pakistan), and most of the mega-varieties cultivated in China were all discovered to be susceptible to Ug99 (Singh et al 2011: 472).

In 2008, Mogens Hovmøller led a team of research looking at trans-oceanic spore dispersal of different varieties of wheat rust; they concluded that airborne transmission was most likely the culprit behind recent outbreaks of other variants of rust in the Americas and in Australia, although human transmission was also a very probable vector in international transmission—in either case, they argued that the appearance of Ug99 should be viewed as a global, and not a local threat (Hovmøller et al 2008). Other virulent stem rust races, such as 'Digalu' TKTTF (unrelated to Ug99), have also been observed to strike countries through airborne dispersion (Meyer et al 2017). International fears of the growing threat of rust led to the establishment of the Borlaug Global Rust Initiative (BGRI) (McIntosh & Pretorius 2011).

Ug99 could prove a threat to Europe in the future; but it is not the only threat. A study in 2018 showed that 80% of 57 varieties cultivated in the UK are highly susceptible to Digalu (Saunders et al 2019). Climate change and the spread of common barberry throughout Europe mean that stem rust will pose an increasing risk to European cultivation (Saunders et al 2019).

Figure 1 Ug99 and its Variants *(Singh et al 2015; updated by Bhavani et al 2019 and Rust Tracker)*

Race[3]	**Common Alias**	**Key Virulence (+) or Avirulence (-) ***	**Year of Identification**	**Confirmed Countries (year)**
TTKSK	Ug99	+*Sr*31 +*Sr*21 -*Sr*24 -*Sr*36 -*Sr*9h -*Sr*Tmp	1999	Uganda (1998/9), Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009), Eritrea (2012), Rwanda (2014), Egypt (2014)
TTKSF		+*Sr*21 -*Sr*31 -*Sr*24 -*Sr*36 -*Sr*9h -*Sr*Tmp	2000	South Africa (2000), Zimbabwe (2009), Uganda (2012)
TTKST	Ug99 + *Sr*24	.+*Sr*31, +*Sr*21 +*Sr*24 -*Sr*36 -*Sr*9h -*Sr*Tmp	2006	Kenya (2006), Tanzania (2009), Eritrea (2010), Uganda (2012), Egypt (2014), Rwanda (2014)
TTTSK	Ug99 + *Sr*36	+*Sr*31 +*Sr*21 +*Sr*36	2007	Kenya (2007), Tanzania (2009), Ethiopia (2010), Uganda (2012), Rwanda (2014)

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[3] The authors of the table note that: "Some uncertainty exists over the reaction of the *Sr21* gene (this influences the initial code letter being "T" (+*Sr21*) or "P" (-*Sr21*). Current table presents most plausible races."

		-*Sr*24 -*Sr*9h -*Sr*Tmp		
TTKSP		+*Sr*24 +*Sr*21 -*Sr*31 -*Sr*36 -*Sr*9h -*Sr*Tmp	2007	South Africa (2007)
PTKSK		.+Sr31, -Sr21 -Sr24 -Sr36 -Sr9h -SrTmp	2007	[Uganda (1998/9)?], Kenya (2009), Ethiopía (2007), Yemen (2009), South Africa (2017)
PTKST		.+Sr31, +Sr24 -Sr21 -Sr36 -Sr9h -SrTmp	2008	Ethiopia (2007), Kenya (2008), South Africa (2009), Eritrea (2010), Mozambique (2010), Zimbabwe (2010)
TTKSF+		+Sr21 +Sr9h -Sr31 -Sr24 -Sr36 -SrTmp	2012	South Africa (2010), Zimbabwe (2010)
TTKTT	**Ug99 + Sr24 + SrTmp**	.+Sr31 +Sr21 +Sr24, +SrTmp -Sr36 -Sr9h	2015	Kenya (2014)
TTKTK	**Ug99 + SrTmp**	.+Sr31 +Sr21 +SrTmp -Sr24 -Sr36 -Sr9h	2015	Kenya (2014), Egypt (2014), Eritrea (2014), Rwanda (2014), Uganda (2014)
TTHSK		+Sr31 +Sr21 -Sr24 -Sr36 -Sr9h -SrTmp	2015	Kenya (2014)
PTKTK		.+Sr31, -Sr21 -Sr24 -Sr36 -Sr9h -SrTmp	2015	Kenya (2014)
TTHST		. .+Sr31, +Sr21 +Sr24 -Sr36 -Sr9h -SrTmp	2015	Kenya (2013)

[Dataset: Bhavani et al 2019; Pathotype Tracker, Where is Ug99?]

As McIntosh & Pretorius cautioned in a summary of the first meetings of the BGRI, there were systemic contradictions in the approaches being adopted. By encouraging farmers to adopt resistant varieties, they encouraged at the same time 'genetic vulnerability created by the widespread adoption of widely adapted mega-varieties or situations where competing breeding organisations are exploiting the same limited set of resistance genes' (McIntosh & Pretorius 2011; Dodds & Rathjen 2010). These contradictions are being addressed, but still compromise our efforts to combat rust. In 2017, researchers discovered that *R* gene *Sr*13 confers resistance to Ug99, thus making it possible to clone the gene for stacking in future wheat varieties (Zhang et al 2017). In the same year, a great step was taken forward in host-pathogen interaction when researchers working on stem rust fungi separately identified the *AvrSr*35 effector and the *AvrSr50* effector (Moscou & van Esse 2017: 1542; Salcedo et al 2017; Chen et al 2017). Pathogen avirulence factors (*Avr*) secrete effector proteins that trigger *R* genes such as *Sr*35 and *Sr*50 to initiate an immune response at the site of infection (Salcedo et al 2017). When these effectors are absent or altered in the fungi, the all-stage resistance (*R*) genes that provide protection fail to recognise the pathogen. As variants of Ug99 emerge, the ability to monitor and identify changes in the pathogen will aid efforts to deploy resistance genes in new wheat varieties, potentially making us less dependent upon the deployment of *R* genes in the future (Moscou & van Esse 2017).

2.3 Gene stewardship, boom-and-bust cycles, and genetic diversity

Genetic resistance is the best means available to us to combat rust (Singh et al 2008; Ellis et al 2014). Over the decades we have identified numerous genes that provide resistance to rust. *R* genes confer all-stage resistance to a pathogen, and were relied upon heavily in the twentieth century to develop resistance against rust (Ellis et al 2014). After recognising the boom and bust cycle that reliance on *R* genes introduces, researchers at CIMMYT began to pivot towards breeding for Adult Plant Resistance (APR) instead, producing what were called 'slow rusting' varieties (Warburton et al 2006: 299; Evanega et al 2013).[4] APR genes don't place the same selective pressures on rust, and their effects are additive, meaning that stacking APR genes probably provides a better route to durable resistance (Mundt 2018). There are over 80 known *R* and APR genes that confer resistance to stripe rust, and approximately 60 known *R* / APR genes for stem rust (though many of these are ineffective for Ug99) (Chen et al 2017; Laroche et al 2019). A single gene can confer APR, and today APR genes have been used to produce breeding lines with near-immunity to rust diseases even in the absence of effective *R* genes (Ellis et al 2014).

When a variety relies upon one or two *R* genes for resistance, the chances that rust will evolve virulence in 3-5 years are increased; when more than three genes are stacked in a pyramid, the variety is more durable and the genes are protected for use by future generations (Ellis et al 2014; Stam & McDonald 2018). Breeding new rust resistant varieties is labour-intensive and, in the past, has taken between five to twelve years (Ehrenberg 2010: 25; Wulff & Moscou 2014). However, new technologies are making this process faster: diagnostic markers can identify resistance genes without field evaluations, and marker-assisted selection promises accurate selection of genes for inclusion in new cultivars (Bhavani et al 2019; Ellis et al 2014; Mago et al 2011; Heffner et al 2011). The breeding shuttle between Kenya and Mexico, initiated by CIMMYT, has quickened the timeline for breeding varieties with durable resistance to Ug99 (Singh et al 2014). Mapping quantitative trait loci (QTL) can help to identify both major and minor effect genes. In 2014, researchers were able to map stem rust resistance loci using these methods (Yu et al 2014), and this technique is currently being employed to identify stripe rust resistance loci in Canadian Spring Wheat varieties and in Indian wheat breeding lines (Bokore et al 2017; Rani et al 2019).

The current aim of CIMMYT is to take advantage of these advances and to end the boom and bust cycle through 'gene stewardship', a term that encompasses all efforts to preserve the genetic diversity needed to combat rust and breed for climate change, but which is focused particularly upon efforts to stack or form pyramids of resistant genes when deployed in modern varieties (Evanega et al 2013). This was difficult to do in the past as it was hard to determine how many genes might be providing resistance in a variety; gene marking has allowed us to identify multiple genes within one resistant variety (Aktar-Uz-Zaman et al 2017; Wessels & Botes 2014). However, these new technologies still leave us reliant upon having a

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[4] The distinction between *R* genes and APR genes is sometimes referred to as 'major' and 'minor' resistance (though there are also some genes that don't neatly fit these categories) (Mundt 2018).

large base of genetic diversity from which to identify and deploy resistance loci. The problems of conserving genetic diversity and developing durable resistance to rust are inextricably linked.

3. Balancing *in situ* and *ex situ* conservation

The value of the landraces we have lost since the Green Revolution isn't calculable. As Finckh observed, 'It is impossible now to gauge the extent to which the overall heterogeneity would have been useful as a buffer against the effects of diseases' (Finckh et al 2000: 814). The remaining question is how best to balance the conservation of surviving genetic diversity in wheat with the pressures from increased market demands, climate change, and pathogens. While anthropologists and cultural historians have argued that *ex situ* conservation threatens the loss of cultivation knowledge and culture (Curry 2017; Brush 1995; Brush 2004; Mooney 1980), most biologists are agreed that *ex situ* and *in situ* conservation methods are complementary and necessary (Lopes et al 2015: 3484). *Ex situ* is essential as a form of insurance and also in providing a funnel for germplasm to be used in plant breeding and improvement, while *in situ* conservation, besides also providing insurance, preserves biodiversity in the environment and ensures the opportunity for continued adaptation (Padulosi 2012; Brush 1995). When a pathogen such as Ug99 evolves, many landraces and older varieties of wheat will inevitably prove to be vulnerable. The efforts of CIMMYT to contain the spread of Ug99 and related stem rust pathogens rely upon work to identify genetic resistance in wild wheat plants and cultivated landraces, to develop durable resistance through stacking resistance loci, and also, to raise awareness that: "breeders and farmers should discourage growing stem rust susceptible varieties thereby reducing the inoculum build up" (Bhavani et al 2019: 220). Pressures on farmers to abandon the cultivation of landraces that are susceptible to emerging pathogens will upset the complementary roles played by *ex situ* and *in situ* methods.

The collection and study of landrace germplasm is ongoing. Turkey, for example, saw peak collection periods for *ex situ* collections in 1948, from 1970-1972, and again in 1984, but there hasn't been a systematic national survey of wheat varieties in Turkey since the 1930s (Morgounov et al 2016: 3113). Surveys in Tajikistan and Uzbekistan in 2015 identified new landraces (Baboev et al 2015; Husenov et al 2015), and there have been recent studies on continued cultivation of landraces in Morocco (Sahri et al 2014; Chentoufi et al 2014). Efforts to compare countries have shown that Ethiopia has the greatest surviving number of landraces (Mengistu et al 2016). Comparison of genetic diversity in durum wheat worldwide with Ethiopian landrace material has been used to confirm that genetic diversity has been partially depleted by modern breeding (Ren et al 2013; Mengistu et al 2016). All such studies emphasise the precarious traditions that ensure the continued use of these varieties, despite the values they possess.

Landraces provide a regular point of departure for researchers hoping to identify novel resistance loci, and have been used in the past as a point of focus for increasing the genetic diversity in CIMMYT germplasm (Warburton et al 2006). Researchers at CIMMYT in Turkey undertook work to phenotype landraces from central and western Asia in 2014-2015 to identify traits, currently unexploited, in resisting drought and heat (Lopes et al 2015). *Ex situ* collections are part of this process to rediscover genetic diversity in wheat. The A.E. Watkins collection, composed of 826 landrace cultivars collected by Watkins in the 1930s, has been shown to contain a high level of genetic diversity that hasn't been captured in present-day breeding programmes (Wingen et al 2014; Winfield et al 2018). In 2017, the National Small Grains Collection (NSGC) held by the United States Department of Agriculture was shown to hold potentially novel genes for resistance to stem rust (Chao et al 2017).

One difficulty in *ex situ* conservation of landraces comes in the fact that landraces are heterogeneous, and that individual spikes selected for conservation do not in themselves contain all the genetic diversity within the landrace. In a study on the durum wheat landrace 'Kyperounda', native to Cyprus, researchers showed that the heterogeneity and richness of the landrace would be missed by current *ex situ* conservation methods that either relied upon random selection of spikes to conserve ('bulking') or collecting spikes based on phenotypic differences (Kyratzis et al 2019). Thus, there's always a risk that *ex situ* conservation will miss the conservation of valuable germplasm. Mislabelling and the loss of accessions was a grave problem in early efforts to form seed banks and collections in the 1970s and 1980s, but it continues to turn up as a problem in research today. In a study on genetic diversity within durum wheat landraces, researchers found several cases where samples of landraces proved to be instead samples of modern varieties (Kabbaj et al 2017; Kyratzis et al 2019).

There are also diverse benefits to encouraging *in situ* conservation. The last twenty years have seen a rich plurality of small programmes and foundations emerge which enlist *in situ* conservation strategies, culminating in an international conference hosted by Biodiversity International in Frankfurt in 2011 (Padulosi et al: 2012). Here, it was affirmed that genetic erosion is necessarily accompanied by cultural erosion, as the cultivation practices that shaped the development of many landraces over generations fall out of practice (Padulosi et al: 2012). While the loss of cultivation practices doesn't appear impinge upon the ability to utilise deposits to *ex situ* collections (Ford-Lloyd & Maxted 1993), it is still a positive feature of *in situ* conservation that it contributes to cultural diversity and the preservation of cultivation practices.

To some extent, landraces can be protected by creating commercial markets. This approach has been successful in Canada with the rehabilitation of the landrace 'Red Fife', which nearly disappeared from cultivation before it was revitalized and marketed as a bread flour (Kucek et al 2014). The marketing approach has also been institutionalised within EU agricultural policy. At a meeting of the EU Committee on Conservation, Characterisation, Collection, and Utilisation of Genetic Resources in Agriculture in 2014, it was recognised that a more consistent approach was needed towards genetic resources in agriculture to prevent the disappearance of local landraces and varieties. One of the success stories of the committee was the preservation of Solina wheat, a landrace cultivated in Italy, which has been successfully marketed as a flour for seitan, cookies, and breadsticks (AGRI-2015-EVAL-09). Solina wheat, of course, is not valuable because the breadsticks are so much better when Solina wheat is used; rather, the value of the landrace lies in its utility as a future genetic resource. At the same time, the committee warned that market forces couldn't alone be relied upon—as the committee stated in their report, 'it cannot be expected that all genetic resources will become economically viable, or at least, not all in the present time' (Ref. Ares(2014)398686 - 18/02/2014). There are undoubtedly many wheat landraces that make for poor products, which have bad yield, and which may be poorly acclimatised to key wheat-growing regions. If we rely upon the market to preserve crop genetic diversity, we will find that it disappears swiftly.

There are breeding programmes that are seeking to occupy intermediary positions between *in situ* and *ex situ* methods. CIMMYT maintain a large *ex situ* seed collection, which is duplicated at the Svalbard seed bank, but this collection is used to increase the instance of rare alleles and overall diversity of its wheat varieties. Programmes such as Breedwheat in France (2011-2019, funded in part by 10 private companies) are working to collect and conserve landraces in nurseries, as part of their programme to create a genetic map for wheat and increase the genetic diversity in the wheat gene pool. During its operation, Breedwheat succeeded in amassing 4,506 accessions of wheat drawn from farmers around the world (Balfourier et al 2019), though these represented varieties both pre-dating 1960 and those bred after the Green Revolution. Breedwheat hopes to use these accessions to increase genetic diversity in modern varieties, in an effort to bring global cultivation back towards the germplasm diversity we believe to have obtained prior to the Green Revolution. Breedwheat was dependent upon accessions from seedbanks and from accessions taken from wheat that is presently cultivated—such a balance will not be possible in the future, and if *in situ* conservation continues to decline, programmes like Breedwheat will, by necessity, be entirely dependent upon seedbanks and collections for their programmes.

4. Farmer's Responses to Stripe and Stem Rust: Canada and Ethiopia

Farmers in rust-prone regions tend to increase cultivation of varieties with resistance after rust outbreaks (Jaleta et al 2019; Chaves et al 2013; Abro et al 2017), and by doing so they protect their yields and help prevent the spread of the pathogen in the short-term. In sections 4.1 and 4.2-4.3 we look at responses to recent stripe rust and stem rust epidemics in Canada and Ethiopia, in order to assess (a) to what extent farmers shift towards varieties marketed as resistant after experiencing epidemics and (b) to assess how these shifts may contribute to problems for gene stewardship. In the case of Ethiopia, we also consider how these shifts in market trends could affect the cultivation of landraces.

4.1 The 2011 Stripe rust epidemic in Western Canada

Rust has been a growing problem in Western Canada since 2000, when a variety of stripe rust *PstS1* was introduced from East Africa (Brar et al 2019) ; but a bad epidemic of stripe rust in 2010 / 2011 led to changes in how seed was marketed and bred, with a strong emphasis on discouraging farmers from continuing to use susceptible varieties (Brar and Kutcher 2016; Brar 2018). The impact was not geographically uniform, Alberta was particularly badly hit due to its proximity to a nearby rust hotspot in the United States, whereas Manitoba fared better (Brar 2018).

Seed in Western Canada is classed according to five degrees of resistance: S – susceptible, MS- mostly susceptible, I – intermittently susceptible, MR -- mostly resistant, R – resistant (SaskSeed Guide 2019).[5] [Figure 2] shows that between 2013 and 2019, farmers in Alberta reduced acreage of S, MS, and I varieties, increasing the cultivation of varieties that are at least moderately resistant. Manitoba, less affected by rust but still within an area of risk, had virtually no acreage dedicated to R varieties in 2013, but by 2019 this had expanded to 11%. This illustrates how farmers in rust prone regions tend to increase the cultivation of resistant varieties after an outbreak, but that resistance is only one of several aspects considered when choosing a variety.

These market trends have already resulted in some resistance genes losing their efficacy due to over-deployment. Between 2007 and 2013, farmers increased cultivation of two varieties, AC Radiant and Selkirk, marketed as resistant, resulting in the breakdown of the genes *Yr10* and *Yr37* (Brar and Kutcher 2016; Brar et al 2019). AC Radiant's popularity means that today *Yr*10 is counted as no longer effective in the region (Brar et al 2019). Other genes, critical to resistance, could face the same fate. As much as ~50% of the commercial wheat grown in Canada includes the APR gene *Yr18,* including many popular varieties marketed as R to stripe rust, such as Lilian (Brar et al 2019; Randhawa et al 2012).

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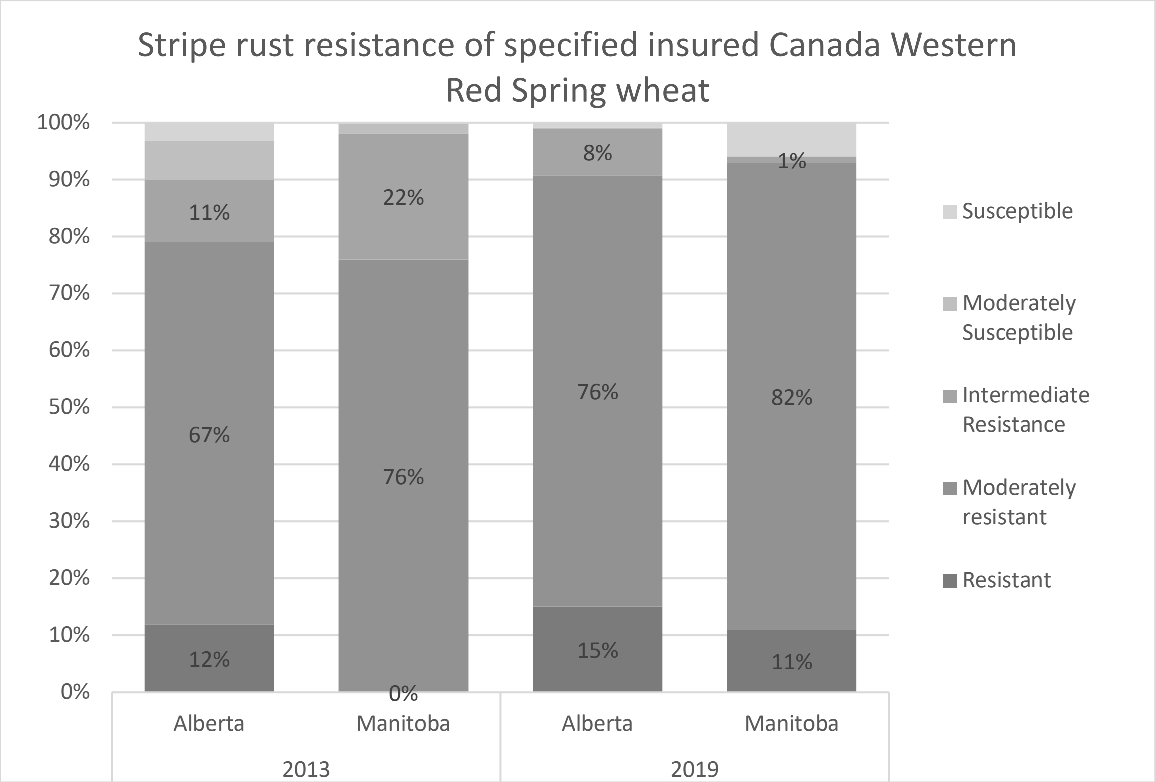
[5] It's important to note that the classification label "R" used by the seed guide is unrelated to the abbreviation *R* for all-stage resistance genes.

Much of these increases in acreage dedicated to R varieties from 2013-2019 were accounted for by farmers moving to a small number of wheat varieties, such as the variety AAC Viewfield. [Figure 3] shows how AAC Viewfield increased in popularity after coming to market in 2016. In 2019 it was the most cultivated variety in Alberta, due to its strong resistance to stripe rust and competitive yields (Cuthbert et al 2018). Plant breeders are just now working to develop durable resistance by stacking the resistance loci identified in Canadian wheat varieties, including Viewfield's parent variety, Stettler (Bokore et al 2017).

While Viewfield's resistance genes haven't been identified, Viewfield doesn't introduce novel resistance loci to the region. Given its parent lines, the resistance loci in Viewfield are already shared between different varieties in cultivation in Alberta (Bokore et al 2017), and while stacking these loci in future varieties will provide them durability, Viewfield itself isn't part of this future generation of durable varieties. Until varieties with stacked resistance loci from these varieties arrive on the market, there's not much else that farmers can do except follow the policies that encourage them towards resistant varieties. This is not ideal from the gene stewardship perspective, as pyramids function best when the resistance loci haven't already been relied upon heavily (Mundt 2018; Stam et al 2018). But once varieties with stacked resistance loci arrive on the market, the continued cultivation of varieties like Viewfield will threaten the durability of the pyramid. As plant pathologist Christ Mundt observed, "it seems unlikely that breeding programs would be willing to forgo use of resistance genes singly when present in an agronomically favourable variety." (Mundt 2018: 793).

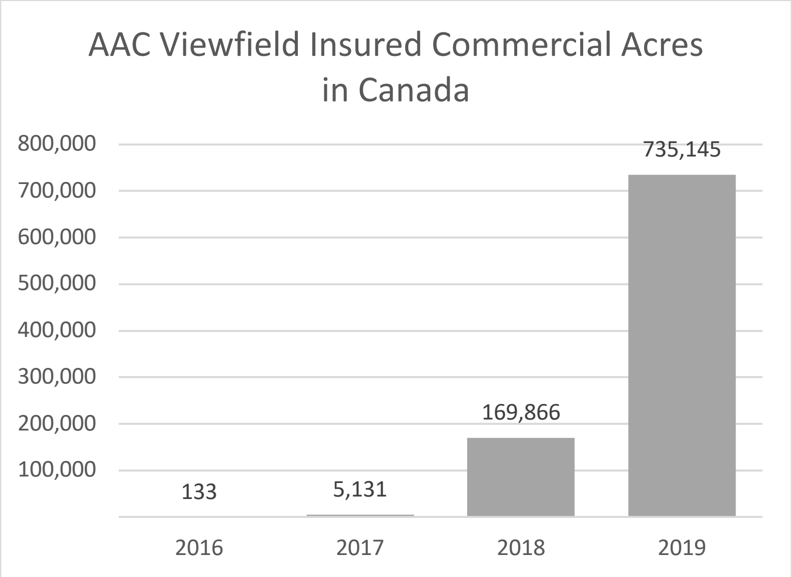
Policies, commercial seed producers, and necessity are moving farmers towards a narrow range of varieties classed as Resistant to stripe rust in Western Canada. This, in itself, is potentially reducing the amount of genetic diversity in cultivated wheat in the region. While it is unavoidable that increased pressure is placed on a handful of resistance loci presently, a further problem will emerge when 'agronomically favourable varieties' are still competing on a market with durable resistant varieties.

Figure 2



Source: *Canadian Western Red Spring varieties by acreage insured; Canadian Grain Commission 2013-2019.* [6] SaskSeed Guide 2013 and 2019.

Figure 3



Source: Canadian Western Red Spring varieties by acreage insured; Canadian Grain Commission. 2016-2019.

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[6] The most common class of wheat grown in western Canada is Canadian Western Red Spring (CWRS); roughly two-thirds of the wheat acreage grown in Alberta is dedicated to this class each year (totalling ~4,000,000 acres). While insurance data (covering ~90-95% of acreage) (Canadian Grains Commission 2019).

4.2 Recent stripe and stem rust epidemics in Ethiopia

Just as in Canada, farmers in Ethiopia also tend to shift (incrementally) towards varieties marketed as resistant in the wake of epidemics. After a bad year for stripe rust in Ethiopia in 2011 where 44% of farmers reported infection in their plots (Jaleta et al 2019), researchers in liaison with CIMMYT conducted a series of surveys where farmers were asked what they had grown before and after the epidemic. The total acreage cultivated for wheat varieties known to be at least moderately susceptible to stripe rust in the region studied fell by approximately 50% between 2009-10 and 2013-14 (table 4), while the total acreage for wheat varieties known to be at least moderately resistant to stripe rust roughly doubled. Table 5 shows that while farmers overall tend to prefer resistant varieties in the years following the bad epidemic, not all farmers directly affected chose to cultivate resistant varieties. In 2013-14, 21% of land was still used to cultivate varieties known to be susceptible to stripe rust [table 4]. The losses that farmers sustained (or that their neighbours sustained) to rust didn't result in a uniform adoption of resistant varieties; other factors were of equal or greater importance in informing their choices of which varieties to cultivate.

Table 4: Area share of popular improved wheat varieties from surveyed plots, Ethiopia.

			2009/2010 survey		2013/2014 survey	
	Resistance to stripe rust	**Year released**	**(ha)**	**%**	**(ha)**	**%**
Kubsa	Susceptible	1994	309	22.6	196.3	16.8
Galema	Susceptible	1995	101.8	7.4	16.7	1.4
Tusie	Resistant	1997	104.3	7.6	29.1	2.5
Dashen	Susceptible	1984	73.2	5.4	31.8	2.7
Mada Walabu	Resistant	1999	62.4	4.6	14.9	1.3
Pavon	Moderately resistant	1982	38	2.8	46.7	4
Digalu	Resistant	2005	30.7	2.2	321.5	27.5
ET-13	Resistant	1981	20.8	1.5	23	2
Enkoy	Resistant	1974	15.6	1.1	4.4	0.4
Millennium	Moderately resistant	2007	3.6	0.3	2.3	0.2
Danda'a	Moderately resistant	2010	0	0	67.2	5.8
Kakaba	Moderately resistant	2010	0	0	62	5.3
Other known improved varieties	Unknown		78.6	5.7	37.1	3.2
Known improved varieties but recycled for >5 seasons	Unknown		153.3	11.2	39.5	3.4
Local and unknown	Unknown		377.7	27.6	275.4	23.6
Total wheat area			**1,369**	**100**	**1,168**	**100**

Source: Dataset, Wheat Rust Coping Mechanisms, 2019, https://doi.org/10.3886/E110562V1

After the varieties Kubsa and Galema suffered great losses in the stripe rust epidemic of 2010 2011, the government worked with stakeholders to encourage farmers to use varieties with resistance to stripe rust, leading to the great increase in the cultivation of Digalu [table 4]. These responses are becoming more common in so-called 'disease feeder' areas (Grieve et al 2019:

118). The tenfold increase in the cultivation of Digalu helped to mitigate against losses to stripe rust, but in 2013, Digalu suffered badly from a stem rust outbreak, and then 2016-2017, Digalu became highly susceptible to a new race of stripe rust (Jaleta et al 2019). This reinforces the risks posed by the deployment of varieties dependent on one or two resistance loci.

Table 5: Change in wheat varieties cultivated from the surveyed plots, Ethiopia

	2009/2010 survey (ha)	2013/2014 survey (ha)	Percentage change in acreage
At least moderately susceptible to stripe rust	488	247	-49%
At least moderately resistant to stripe rust	272	569	109%
Other known improved varieties	79	37	-53%
Known improved varieties but recycled for >5 seasons	153	40	-74%
Local and unknown	378	275	-27%
Total wheat area	**1,369**	**1,168**	**-15%**

Source: [Dataset], Wheat Rust Coping Mechanisms, 2019, https://doi.org/10.3886/E110562V1

As [table 5] shows, the total acreage cultivated for local and unknown wheat varieties fell by 27% between 2009-10 and 2013-14. This does not mean that everything in this category was composed of landraces; but we are not in a position to know what was potentially lost. As Jaleta observes, this cycle of increasing reliance upon a smaller handful of varieties when epidemics occur is only heightening the risk of even worse epidemics, as they reduce varietal diversification. This raises a crucial question: ought farmers that are presently conserving landraces and older varieties of wheat (by intention or by accident of necessity) be encouraged or discouraged from abandoning older, susceptible varieties in the face of an epidemic? We don't have data on landraces that fell out of cultivation during the stripe rust epidemics, but cycles such as these make it clear that the rapid evolution of rust can undo the temporary good achieved by the widespread adoption of resistant varieties.

5. Practical solutions: monitoring, forecasting, and stewardship

Technological advances mean that we are on the cusp of a step change in our ability to survey, monitor and forecast rust epidemics. In 2011, monitoring was labour-intensive: assessments of stem rust in Australia and New Zealand relied on field surveys of commercial fields, with observations being made by field workers every 20-30 km (Park et al: 2011: 110). In 2013, CIMMYT launched a test pilot in Turkey of its SMS based system for surveillance of wheat rust (Dusunceli et al, 2015: 282). The system was viewed as essential on multiple fronts: it would aid epidemiology, it would serve as an 'early warning tool', and it would also identify the best tools for management (Dusunceli et al, 2015: 283). In 2017 and 2018, an early warning system (EWS) involving inoculum (or spore) forecasts, weather, surveillance, and mobile phone data was deployed in Ethiopia (Allen-Sader et al 2019). The results were positive: "The EWS successfully provided timely information to assist policy makers formulate decisions about allocation of limited stock of fungicide during the 2017 and 2018 wheat seasons." (Allen-Sader et al 2019).

How will this increase in information affect the decisions of individual farmers? Jaleta has shown that farmers in Ethiopia currently face choices on how to weigh the risk of rust infections by cultivating varieties with strong resistance, or by risking the chance of an outbreak and cultivating a variety expected to provide a higher yield which lacks adequate resistance (Jaleta 2019: 2). All else being equal, we would expect a forecast that suggested a low risk of rust to result in the majority of farmers to simply continue cultivating last year's varieties, irrespective of their resistance to rust (Jaleta 2019: 2). However, faced with a forecast that suggested a high risk of rust (as well as the likely governmental and NGO response) we would expect some farmers to switch to growing resistant varieties.

Forecasting and monitoring will change how farmers choose varieties, but these changes can be used to better inform the deployment of the emerging varieties with stacked resistance loci, and it will also offer an opportunity to identify regions in which the cultivation of landraces and older varieties are not at high risk.

No one desires a world where the genetic diversity in wheat is contained primarily in breeding material collections and *ex situ* storage programmes. However, there are numerous policies and programmes in place right now which we believe can help to ensure that wheat landrace cultivation isn't further diminished:

- Gene stewardship. Efforts to stack resistance loci and deploy varieties with durable resistance in high-risk regions will help to arrest the boom and bust cycle. This would remove the bottleneck in genetic diversity caused by farmers gravitating towards non-durable varieties marketed as resistant in the wake of epidemics.
- Extension of monitoring and forecasting programmes for rust. Landrace cultivation could, in high-risk areas, frustrate efforts to develop durable resistance. However, monitoring and forecasting will also increase trust in low-risk areas and regions where landrace cultivation can be safely encouraged.
- Modelling pre-Green Revolution genetic diversity. Programmes such as Breedwheat provide opportunities for rare alleles to be reintroduced in modern varieties. While the value of landraces is not exhausted by their rare alleles, the reintroduction of these rare alleles into modern cultivated varieties should be viewed as an adaptation of *in situ* cultivation.
- Commercial branding of landraces. While there are limits to the efficacy of these efforts, some landraces have enjoyed widespread resurgence due to marketing and branding.
- Increased efforts to identify landraces stored *ex situ* which have fallen out of cultivation. It is, at present, extremely difficult to gauge the ratio between landrace breeding materials held in collections and the *in situ* cultivation or deployment of those varieties.

No future generation will have available the same wealth of genetic diversity in wheat that existed while Norman Borlaug's generation were working to develop resistance to rust; however, existing germplasm and breeding material collections are continuing to produce new resistance loci and valuable traits for adapting varieties to climate change. The relationship between *ex situ* and *in situ* conservation will be put under immense pressure to meet the challenges posed by 2050: the cultivation of landraces may be part of closing the yield gap in some wheat-producing regions, but by and large, we will not have the space to cultivate varieties with lower yields or which lack the durable resistance gained through building pyramids of minor-effect genes.

Bibliography

AGRI-2015-EVAL-09. Preparatory action : EU plant and animal genetic resources in agriculture. Strategy for pre-project: Cultivation of the Solina wheat in its area of origin, for human and environmental health. Stable URL: https://www.geneticresources.eu/wp-content/uploads/2019/10/PrepActGR-II-Strategy-Solina-IT.pdf Accessed September 17th, 2020.

Ref. Ares(2014)398686 - 18/02/2014. Summary Report of the 27th Meeting of the Committee on the Conservation, Characterisation, Collection, and Utilisation of Genetic Resources in Agriculture. 2014. European Commission for Agriculture and Rural Development. Stable URL: https://ec.europa.eu/transparency/regcomitology/index.cfm?do=Search.getPDF&ds_id=32273&version=1&AttLang=en&db_number=1&docType=SUMMARY_RECORD Accessed September 17th, 2020.

Abro, Z.A., Jaleta, M., Qaim, M., et al. 2017. Yield Effects of rust-resistant wheat varieties in Ethiopia. Food Security, 9: 1343-1357. DOI: 10.1007/s12571-017-0735-6

Aggarwal, P., Vyas, S., Thornton, P., Campbell, B. 2019. How much does climate change add to the challenge of feeding the planet this century? Environ. Res. Lett. 14 : 043001. DOI : 10.1088/1748-9326/aafa3e

Aguilar, S., Bomba, B., Campbell, A., Echeverria, R., et al. 2020. Actions to transform food systems under climate change. Wageningen, The Netherlands: CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS).

Aktar-Uz-Zaman, Tuhina-Khatun, Hanafi M., Sahebi, M. 2017. Genetic analysis of rust resistance genes in global wheat cultivars: an overview, Biotechnology & Biotechnological Equipment, 31:3: 431-445. DOI: 10.1080/13102818.2017.1304180

Alfani, G., Ó Gráda, C., eds. 2017. Famine In European History. Cambridge: Cambridge University Press.

Allen-Sader, C., Thurston, W., Meyer, M., Nure, E., et al. 2019. An early warning system to predict and mitigate wheat rust diseases in Ethiopia, Environmental Research Letters, 14: 115004: 1-11. DOI: 10.1088/1748-9326/ab4034

Baboev, S., Morgounov, A. and Muminjanov, H. 2015. Wheat landraces in farmers' fields in Uzbekistan: National survey, collection, and conservation, 2010–2015. FAO, Ankara, Turkey.

Balfourier, F.,Bouchet, S., Robert, S., de Oliveira R., et al. 2019. Worldwide phylogeography and history of wheat genetic diversity. Science Advances. 5:5: eaav0536. DOI: 10.1126/sciadv.aav0536

Barnes, G, Saunders, DGO, Williamson, T. 2020. Banishing barberry: The history of Berberis vulgaris prevalence and wheat stem rust incidence across Britain. Plant Pathol., 69: 1193– 1202. DOI: 10.1111/ppa.13231

Bhavani S., Hodson D.P., Huerta-Espino J., Randhawa M.S., Singh R.P. 2019. Progress in breeding for resistance to Ug99 and other races of the stem rust fungus in CIMMYT wheat germplasm. Front. Agr. Sci. Eng. 6(3): 210–224. DOI: 10.15302/J-FASE-2019268

Bokore FE, Cuthbert RD, Knox RE, et al. 2017. Quantitative trait loci for resistance to stripe rust of wheat revealed using global field nurseries and opportunities for stacking resistance genes. Theor Appl Genet. 130:12:2617-2635. DOI: 10.1007/s00122-017-2980-7

Borrill, P., Harrington, S. A., & Uauy, C. 2019. Applying the latest advances in genomics and phenomics for trait discovery in polyploid wheat. *The Plant Journal : for cell and molecular biology*, *97*:1: 56–72. DOI: 10.1111/tpj.14150

Brar, G., Kutcher, H. 2016. Race characterization of Puccinia striiformis f. sp. Triciti. The cause of wheat stripe rust, in Saskatchewan and Southern Alberta, Canada and Virulence Comparison with races from the United States. Plant Disease, 100: 8. DOI: 10.1094/PDIS-12-15-1410-RE

Brar, G., Fetch, T., McCallum, B., Hucl, P., et al. 2019. Virulence Dynamics and Breeding for Resistance to Stripe, Stem, and Leaf Rust in Canada Since 2000. Plant Disease. 103:12. DOI: 10.1094/PDIS-04-19-0866-FE

Brush, S. B. 1995. In situ conservation of landraces in centers of crop diversity. Crop Science, 35: 346-354. DOI: 10.2135/cropsci1995.0011183X003500020009x

Byerlee, D. 1996. Modern Varieties, productivity and sustainability: recent experience and emerging challenges. *World Development* 24:4, 697-718. DOI: 10.1016/0305-750X(95)00162-6

[dataset] Canadian Grain Commission. 2013-2019. Grain Varieties by Acreage Insured. Stable URL: https://www.grainscanada.gc.ca/en/grain-research/statistics/varieties-by-acreage/ Accessed September 17th, 2020.

Casañas, F., Simo, J., Casals, J., Prohens, J. 2017. Toward an Evolved Concept of Landrace. Frontiers in plant science, 8:145. DOI: 10.3389/fpls.2017.00145

Cavanagh, C., Chao, S., Wang, S., Bevan, Huang, B., et al. 2013. Genome-wide comparative diversity uncovers multiple targets of selection for improvement in hexaploid wheat landraces and cultivars. PNAS, 110:20: 8057-8062. DOI: 10.1073/pnas.1217133110

Chao, S., Rouse, M.N., Acevedo, M., Szabo-Hever, A., et al. 2017, Evaluation of Genetic Diversity and Host Resistance to Stem Rust in USDA NSGC Durum Wheat Accessions. The Plant Genome, 10: 1-13. DOI:10.3835/plantgenome2016.07.0071

Chen, J., Upadhyaya, N., Ortiz, D., Sperschneider, J., et al. 2017. Loss of AvrSr50 by somatic exchange in stem rust leads to virulence for Sr50 resistance in wheat. Science. 358:6370: 1607-1610. DOI: 10.1126/science.aao4810

Chen, S., Guo, Y., Briggs, J. et al. 2018. Mapping and characterization of wheat stem rust resistance genes SrTm5 and Sr60 from Triticum monococcum . Theor Appl Genet 131: 625–635. DOI: 10.1007/s00122-017-3024-z

Chaves, M.S., Martinelli, J.A., Wesp-Guterres, C. et al. 2013. The importance for food security of maintaining rust resistance in wheat. Food Sec., 5 : 157–176. DOI : 10.1007/s12571-013-0248-x

Chentoufi, L., Sahri, A., Arbaoui, M. et al. 2014. Anchoring durum wheat diversity in the reality of traditional agricultural systems: varieties, seed management, and farmers' perception in two Moroccan regions. J Ethnobiology Ethnomedicine, 10:58. DOI: 10.1186/1746-4269-10-58

CIMMYT. 2005. Sounding the Alarm on Global Stem Rust. Stable URL: http://www.globalrust. org/uploads/documents/SoundingAlarmGlobalRust.pdf Accessed September 18th, 2020.

Curry, H.A. 2017. Breeding uniformity and banking diversity: The genescapes of industrial agriculture, 1935-1970. Global Environment, 10:1: 83-113. DOI: 10.3197/ge.2017.100104

Cuthbert, R., DePauw, R., Knox, R., Singh, A., et al. 2018. AAC Viewfield hard red spring wheat. Canadian Journal of Plant Science. 99:1: 102-110. DOI: 10.1139/cjps-2018-0147

Dodds, P. N., and Rathjen, J. P. 2010. Plant immunity: towards an integrated view of plant-pathogen interactions. Nat. Rev. Genet., 11 : 539–548. DOI: 10.1038/nrg2812

Dusunceli, F., Stocchi, A., Scaduto, C., Mancini, F., et al. 2015. An SMS based system for surveillance of wheat rust diseases: a pilot initiative in Central Anatolia region in Turkey Bulletin OEPP/EPPO, 45:2: 282-287. DOI: 10.1111/epp.12226

Ehrenberg, R. 2010. Rust never sleeps: A new flare-up in an age-old battle between wheat and a fungal killer. Science News, 178:7: 22-25.

Ellis JG, Lagudah ES, Spielmeyer W, Dodds PN. 2014. The past, present and future of breeding rust resistant wheat. Front Plant Sci. 5:641. DOI:10.3389/fpls.2014.00641

Evanega, S., Singh, R., Coffman, R., et al. 2013. The Borlaug Global Rust Initiative: Reducing the Genetic Vulnerability of Wheat to Rust. Genomics of Plant Genetic Resources: 317-331. DOI: 10.1007/978-94-007-7575-6_1

Finckh, M., Gacek, E. Goyeau, H., Lannou, C., Merz, U., et al. 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. Agronomie, EDP Sciences, 20: 7, 813-837. DOI: 10.1051/agro:2000177 . hal-00886081

Fisher, R.A., Edmeades, G.O. 2010. Breeding and cereal yield progress. Crop Sci. DOI:10.2135/cropsci 2009.10.0564

Flavell, R.B. 2017. Innovations continuously enhance crop breeding and demand new strategic planning, Global Food Security, 12:15-21. DOI: 10.1016/j.gfs.2016.10.001

Ford-Lloyd B, Maxted N. 1993. Preserving diversity. Nature. 361:579. DOI:10.1038/361579a0.

Grieve, B.D., Duckett, T., Collison, M., Boyd, L., West, J., et al. 2019. The challenges posed by global broadacre crops in delivering smart agri-robotic solutions: A fundamental rethink is required. Global Food Security, 23, 116-124. DOI: 10.1016/j.gfs.2019.04.011

Hatfield J. L., Beres B. L. 2019. Yield Gaps in Wheat: Path to Enhancing Productivity. Frontiers in Plant Science 10: 1603. DOI=10.3389/fpls.2019.01603

Heffner E L, Jannink J L, Sorrells M E. 2011. Genomic selection accuracy using multifamily prediction models in a wheat-breeding program. Plant Genome, 1: 65–75. DOI: 10.3835/plantgenome.2010.12.0029

Hovmøller, M.S., Yahyaoui, M.E.A., Justesen A.F., 2008. Rapid global spread of two aggressive strains of a wheat rust fungus, Molecular Ecology 17: 3818-3826. DOI: 10.1111/j.1365-294X.2008.03886.x

Hunter, M. Smith, R. Meagan E. Schipanski, Lesley W. et al. 2017. Agriculture in 2050: Recalibrating Targets for Sustainable Intensification, BioScience, 67:4: 386–391. DOI: 10.1093/biosci/bix010

Husenov, B., Otambekova, M., Morgounov, A. and Muminjanov, H. 2015. Wheat landraces in farmers' fields in Tajikistan: National survey, collection, and conservation, 2013–2015. FAO, Ankara, Turkey.

Jaleta, M., Hodson, D., Abeyo, B., Yirga, C., et al. 2019. 'Smallholders' coping mechanisms with wheat rust epidemics: Lessons from Ethiopia', PloS ONE, 14:7: e0219327. DOI: 10.1371/journal.pone.0219327

[dataset] Jaleta, M. Wheat rust coping mechanisms . Ann Arbor, MI: Inter-university Consortium for Political and Social Research [distributor], 2019-07-05. DOI: 10.3886/E110562V1

Johnson, G.I. 2010. Shield the young harvest from the devouring blight: Charles Darwin, Joseph Banks, Thomas Andrew Knight, and wheat rust: Discovery, adventure, and 'getting the message out.' Australasian Plant Pathology, 39: 1-22.

Kabbaj H., Sall A.T., Al-Abdallat A., Geleta M., Amri A., et al. 2017. Genetic Diversity within a Global Panel of Durum Wheat (Triticum durum) Landraces and Modern Germplasm Reveals the History of Alleles Exchange, Frontiers in Plant Science, 8. DOI=10.3389/fpls.2017.01277

Kucek, L., Dyck, E., Russell, J., Clark, L., Hamelman, J., et al. 2017. Evaluation of wheat and emmer varieties for artisanal baking, pasta making, and sensory quality. Journal of Cereal Science, 74: 19-27. DOI 10.1016/j.jcs.2016.12.010

Kyratzis AC, Nikoloudakis N, Katsiotis A. 2019. Genetic variability in landraces populations and the risk to lose genetic variation. The example of landrace 'Kyperounda' and its implications for *ex situ* conservation. PLoS ONE 14:10: e0224255. DOI: 10.1371/journal.pone.0224255

Laroche, A., Frick, M, Graf, R., Larsen, J., et al. 2019. Pyramiding disease resistance genes in elite winter wheat germplasm for Western Canada. The Crop Journal. 7 :6 :739-49. DOI 10.1016/j.cj.2019.08.005

Lopes, M., El-Basyoni, I., Baenziger, P., Singh, S., et al. 2015. Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. Journal of Experimental Botany, 66:12, 3477–3486. DOI: 10.1093/jxb/erv122

Mago R, Simkova H, Brown-Guedira G, Dreisigacker S, Breen J, et al. 2011. An accurate DNA marker assay for stem rust resistance gene Sr2 in wheat. Theoretical and Applied Genetics, 122:4: 735–744 DOI: 10.1007/s00122-010-1482-7

McIntosh, R.A., Pretorius, Z.A., 2011. Global Rust Initiative provides momentum for wheat rust research, Euphytica 179: 1-2, DOI 10.1007/s10681-011-0389-y

Mengistu, D.K., Kidane, Y.G., Catellani, M., Frascaroli, E., et al. 2016. High-density molecular characterization and association mapping in Ethiopian durum wheat landraces reveals high diversity and potential for wheat breeding. Plant Biotechnol J, 14: 1800-1812. DOI:10.1111/pbi.12538

Meyer, M., Burgin, L., Hort, M.C., Hodson, D.P., et al, 2017. Large-Scale Atmospheric Dispersal Simulations Identify Likely Airborne Incursion Routes of Wheat Stem Rust Into Ethiopia, *Phytopathology,* 107:10: 1175-1186. DOI: 10.1094/PHYTO-01-17-0035-FI

Mooney, P.R. 1980. Seeds of the Earth: A Private or Public Resources. Ottawa, ON: Inter Press.

Morgounov, A., Keser, M., Kan, M., et al. 2016. Wheat Landraces Currently Grown in Turkey: Distribution, Diversity, and Use. Crop Science : 56 :6 : 3112-3124. DOI : 10.2135/cropsci2016.03.0192

Moscou, M., van Esse, P. 2017. The quest for durable resistance. Science. 358:6370: 1541-1542. DOI: 10.1126/science.aar4797

Mujeeb-Kazi, A., Gul Kazi, A., Dundas, I, Rasheed, A., et al. 2013. Chapter Four - Genetic Diversity for Wheat Improvement as a Conduit to Food Security, Advances in Agronomy 122, 179-257. DOI: 10.1016/B978-0-12-417187-9.00004-8.

Mundt C. 2018. Pyramiding for Resistance Durability: Theory and Practice. Phytopathology. 108:7:792-802. DOI: 10.1094/PHYTO-12-17-0426-RVW

Ortiz, R., Sayre, K.D., Govaerts, B., Gupta, R., et al, 2008. Climate change: Can wheat beat the heat? Agriculture Ecosystems & Environment 126, 46-58. DOI: 10.1016/j.agee.2008.01.019

Paarlberg, R. 2009. Starved For Science: How Biotechnology is Being Kept out of Africa. Boston, Mass: Harvard University Press

Park, R., Fetch, T., Hodson, D., Jin, Y., et al, 2011. International surveillance of wheat rust pathogens: progress and challenges, Euphytica, 179:109-117. DOI 10.1007/s10681-011-0375-4

Padulosi S., Bergamini, N., Lawrence, T. (eds)., 2012. On-farm conservation of neglected and underutilized species: status, trends, and novel approaches to cope with climate change, Frankfurt: Biodiversity Headquarters.

Peterson, P.D. 2018. The Barberry Eradication, Program, in Minnesota, for Stem Rust Control: A Case Study, Annual Review of Phytopathology 56:203-23, DOI: 10.1146/annurev- phyto- 080417- 050133

Pretorius ZA, Singh RP, Wagoire WW & Payne TS. 2000. Detection of virulence to wheat stem rust resistance gene Sr31 in Puccinia graminis f. sp. tritici in Uganda. Plant Disease 84:2: 203. DOI: 10.1094/PDIS.2000.84.2.203B

[Dataset] RustTracker.org: *A Global Wheat Rust Monitoring System.* Updated January 2019. Stable URL: https://rusttracker.cimmyt.org/

Randhawa, H., Puchalski, M., Frick, A. Goyal, T., et al. 2012. Stripe rust resistance among western Canadian spring wheat and triticale varieties. Canadian Journal of Plant Science. 92: 713-722. DOI: 10.4141/CJPS2011-252

Rani, R., Singh, R., Yadav, N. 2019. Evaluating stripe rust resistance in Indian wheat genotypes and breeding lines using molecular markers. Comptes Rendus Biologiques. 342:5-6: 154-174. DOI: 10.1016/j.crvi.2019.04.002

Ray, D., Mueller, N., West, P., Foley, J. 2013. Yield Trends Are Insufficient to Double Global Crop Production by 2050. PLoS ONE. 8(6): e66428. DOI: 10.1371/journal.pone.0066428.

Reif JC, Zhang P, Dreisigacker S, et al. 2005. Wheat genetic diversity trends during domestication and breeding. Theor Appl Genet. 110:5:859-864. DOI:10.1007/s00122-004-1881-8

Ren, J., Sun, D., Chen, L., You, F.M., Wang, J., Peng, Y., Nevo, E. et al. 2013. Genetic diversity revealed by single nucleotide polymorphism markers in a worldwide germplasm collection of durum wheat. Int. J. Mol. Sci. 14, 7061– 7088. DOI: 10.3390/ijms14047061

Sahri, A., Chentoufi, L., Arbaoui, M. et al. 2014. Towards a comprehensive characterization of durum wheat landraces in Moroccan traditional agrosystems: analysing genetic diversity in the light of geography, farmers' taxonomy and tetraploid wheat domestication history. BMC Evol Biol 14 : 264 DOI : 10.1186/s12862-014-0264-2

Salcedo, A., Rutter, W., Wang, S., Akhunova, A., et al. 2017. Variation in the AvrSr35 gene determines Sr35 resistance against wheat stem rust race Ug99. Science. 358:6370: 1604-1606. DOI: 10.1126/science.aao7294

Saskatchewan Advisory Council on Grain Crops. 2019. Varieties of Grain Crops 2019. Stable URL: https://publications.saskatchewan.ca/api/v1/products/83696/formats/96889/download Accessed September 17th, 2020.

Singh,R., Hodson, D., Huerta-Espino, J., Jin, Y., et al. 2008. Will Stem Rust Destroy the World's Wheat Crop?, *Advances in Agronomy,* 98, 271-309. DOI: 10.1016/S0065-2113(08)00205-8

Singh,R., Hodson, D., Huerta-Espino, J., Jin, Y., et al. 2011. The Emergence of Ug99 Races of the Stem Rust Fungus is a Threat to World Wheat Production. The Annual Review of Phytopathology, 49, 465-81, DOI: 10.1146/annurev-phyto-072910-095423

Singh, R., Herrera-Fosel, S., Huerta-Espino, J., Singh, S., et al. 2014. Progress Towards Genetics and Breeding for Minor Genes Based Resistance to Ug99 and Other Rusts in CIMMYT High-Yielding Spring Wheat. Journal of Integrative Agriculture, 13:2: 255-261. DOI: 10.1016/S2095-3119(13)60649-8

Singh, R., Hodson, D., Huerta-Espino, J., Jin, Y., et al 2015. Emergence and Spread of New Races of Wheat Stem Rust Fungus: Continued Threat to Food Security and Prospects of Genetic Control, Phytopathology 105, 871- 884. DOI: 10.1094/PHYTO-01-15-0030-FI

Saunders, D., Pretorius, Z.A. Høvmoller, M., 2019. Tackling the re-emergence of wheat stem rust in Western Europe, Communications Biology, 2:51,1-3. DOI: 10.1038/s42003-019-0294-9

Soko., T. Bender., C.M., Pretorius, Z.A. 2018. Yield Loss Associated with Different Levels of Stem Rust Resistance in Bread Wheat, Plant Disease 102:12 DOI: 10.1094/PDIS-02-18-0307-RE

Stam, R., McDonald., B. 2018. When resistance gene pyramids are not durable—the role of pathogen diversity. Molecular Plant Pathology. 19:3: 521-524. DOI: 10.1111/mpp.12636

Villareal, R., Del Toro, E., Mujeeb-Kazi, A., Rajaram, S. 1995. The 1BL/1RS chromosome translocation effect on yield characteristics in a *Triticum aestivum* L. cross. Plant Breeding, 114: 497-500.

Vincent, H., Amri, A., Castañeda-Álvarez, N. P., Dempewolf, H., et al. 2019. Modelling of crop wild relative species identifies areas globally for in situ conservation. Communications Biology, *2*, 136. DOI: 10.1038/s42003-019-0372-z

Warburton, M.L., Crossa, J., Franco, J. et al. 2006. Bringing wild relatives back into the family: recovering genetic diversity in CIMMYT improved wheat germplasm. Euphytica 149, 289–301. DOI: 10.1007/s10681-005-9077-0

Wessels, E., & Botes, W. 2014. Accelerating resistance breeding in wheat by integrating marker-assisted selection and doubled haploid technology, South African Journal of Plant and Soil, 31:1: 35-43. DOI: 10.1080/02571862.2014.903434

Wingen LU, Orford S, Goram R, et al. 2014. Establishing the A. E. Watkins landrace cultivar collection as a resource for systematic gene discovery in bread wheat. *Theor Appl Genet*. 124:8:1831-1842. DOI:10.1007/s00122-014-2344-5

Winfield, M. O., Allen, A. M., Wilkinson, P. A., Burridge, et al. 2018. High-density genotyping of the A.E. Watkins Collection of hexaploid landraces identifies a large molecular diversity compared to elite bread wheat. Plant biotechnology journal, 16:1: 165–175. DOI: 10.1111/pbi.12757

Wulff, B.H. and Moscou, M.J., 2014.Strategies for transferring resistance into wheat: from crosses to GM casettes, Frontiers in Plant Science 5. DOI: 10.3389/fpls.2014.00692

Yu, L., Barbier, H., Rouse, M.N. et al. 2014. A consensus map for Ug99 stem rust resistance loci in wheat. Theor Appl Genet 127, 1561–1581 DOI: 10.1007/s00122-014-2326-7

Zhang, w. Shisheng, C., Zewdie, A., Jayaveeramuthu N., et al. 2017. Identification and characterization of Sr13, a tetraploid wheat gene that confers resistance to the Ug99 stem rust race group. Proceedings of the National Academy of Sciences 114:45, E9483-E9492, DOI: 10.1073/pnas.1706277114