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Wheat rust: The devastation and attempts to control over the years

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Abstract

Wheat, staple food of billions and one of the major crops in volume, is an excellent source of nutrition and income. However, its susceptibility to rust poses a constant threat to sustainable production and hence food security itself. Wheat rust is the most urgent problem regarding the production of this irrevocably important crop. While cultural measures could lower down the extent of the infection, it isn't a permanent solution. Breeding for durable resistance is by far the most dependable solution to the problem. However even this has had many setbacks of pathogen evolution, climate change and other factors. Linked DNA markers show promise for achieving race-specific resistance genes in combinations aimed at their longevity. However, a national deployment strategy is inevitable for its success. The most promising activity so far is breeding for cultivars carrying durable resistance genes based on both minor and additive gene effect. However, using genetic engineering still faces the sentimental opposition of the public against genetically modified organisms. A lot has been done and a lot is to be done in order to grow rust free wheat in our fields. The paper discusses in brief about the major milestones and ongoing attempts regarding wheat breeding for rust resistance.

Keywords: Breeding for resistance; climate change and rust; Puccinia; Wheat loss.

Introduction

Wheat is a source of food and staple diet for over 1 billion people in developing countries. Grown on more than 200 million hectares, world wheat production recently has exceeded 707 million tons. North and East Africa, the Near East and Central and South Asia account for some 37 percent of global wheat production where in most countries it is the staple food crop, providing on average some 40 percent of the per capita calorie supply (FAO, 2014). Today, wheat stands as the third largest food crop in volume exceeded only by rice and maize, marking an integral dependence of civilization on the crop. However, even wheat has benefited from this integral relationship with the human diet; namely distribution (making it the world's most area-occupying crop) and genetic structure fortification for improvement in regards to yield and performance.

Wheat Rusts

Rust are among the most important fungal disease in wheat owing to its wide distribution, easy transportation over miles, ability to form new races and infect the previously resistant varieties. The 'rust' fungus, *Puccinia* is the main causative pathogen for these diseases. All the rust fungi show similar disease symptoms on the host plants. They also have similar requirements for infection. The diseases get their name from their appearance on the plant; leaves and stems. Infection can occur on any above-ground plant part, leading to the production of pustules that contain thousands of dry yellow-orange to brownish red or blackish spores. These pustules give the rust appearance on the plant (Marsalis and Goldberg, 2014)

The causative agent of wheat rust are: *Puccinia recondita f. sp. tritici*—brown rust agent (McIntosh et al., 1995), *Puccinia striiformis*—yellow rust agent (McIntosh et al., 1995) and *Puccinia graminis f. sp. tritici*—black rust agent (Schumann and Leonard, 2000). Specific pustules make the identification of the fungus very easy. Pustules are the laceration of the epidermis, and the powder (orange, brown, brick red, dark brown or yellowish depending on the species) mainly are the spores of the fungus that are easily carried away through the wind. These rusts have species-specific symptoms (Ezzahiri, 2001): Brown rust (leaf rust): pustules are small in size, oval or circular,

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brownish or orange in color. Preferably they appear on the upper leaf surface of the leaf. Black rust (stem rust): pustules are longer than the brown rust, have brick-red to dark maroon color, grows on the stems and leaves. Its pustules produce spores on both surfaces of the leaf. The pustules found on stem are elongated vertically and have rough pieces of lacerated epidermis along the sides. However, reddishbrown powder spores are produced on both leaves and stems. Yellow rust (stripe rust): the pustules are yellowish, aligned along the leaf veins like streaks. Pustules are also found to develop at the lower surface of spikes and dusty yellow urediniospores leaves. The distinguish it from other rusts. The urediniospores are produced in lesions and grow systemically in leaves (Ekom et al., 2015). A brief list of hosts and symptoms of different kind of rust is mentioned in Table 1.

Losses due to wheat rust

The wheat rust pathogens are obligate parasites i.e. they need living tissue to grow and multiply, and require two hosts to complete their life cycle and it will overwinter in its alternate host. The pathogen completes its life cycle as 5 different types of spores which are formed during its sexual (primary host) and asexual stage (secondary host). Urediospores, teliospores and basidiospores foster on wheat plants while pycnidiospores and aeciospores grow on the alternate hosts in successive stage of reproduction. It affects a healthy vigorously growing plant and leads to complete crop failure if unchecked. Before sporulation, the wheat plant is generally asymptomatic. After the establishment spores on plant surface after some processes not fully understood, germ tube is used to germinate and penetrate the host cells to take nutrients (Rampitsch et al., 2006). A severely rust affected adult plant may

Disease	Pathogen	Primary hosts	Alternate	Symptoms
			hosts	
Leaf rust	Puccinia recondite	Bread and durum	Thalictrum,	Isolated uredinia on upper
	f. sp. tritici	wheats	Anchusa,	leaf surface and rarely on
			Isopyrum	leaf sheaths.
Stem	Pucciniagraminis f.	Bread and durum	Berberis	Isolated uredinia on upper
rust	sp. tritici	wheats, barley, and	vulgaris	and lower leaf surfaces,
		triticale		stem, and spikes.
Stripe	Pucciniastriiformis	Bread and durum	Unknown	Systemic uredinia on leaves
rust	f. sp. tritici	wheats, triticale, and		and spikes and rarely on
		a few barley cultivars		leaf sheaths.

Table 1. Types of rust, hosts and symptoms.

be chlorotic, stunted and/or discolored along with deformities like but not limited to witches' broom, gall formation, hypertrophy, stem canker etc. (Singh et al., 2002). This disease is also known as the "polio of agriculture". These diseases spread by releasing billions of spores in the wind, each of which have the capacity to start a new infection ultimately causing a great amount of crop failures. Under the favorable conditions, the infection by rust of seedling wheat can result in the death of tillers and even the entire plants (Roelfs and Bushnell, 1985). An adult wheat plant tiller, including leaf and stem tissue, has a surface area of about 150 cm². 100% disease severity (6.7 infections/cm²) destroys the tiller (Rowell and Roelfs, 1976). Severe disease can inhibit plant growth or can even cause death of the plant by decreasing the photosynthetic area, because of the loss of nutrients and water. It also disrupts the transportation system of the plant. The pathogen of the disease weakens the crops also by removing nutrients and sugars for its own consumption (Lim, 2014). Inhibited growth leads to small shriveled grain, weakened stems that lodge or break, and also the death of the plant in severe cases (Roelfs and Bushnell, 1985).

Source: Roelfs et al., 1992

Generally, most of the grain yield losses by stripe and leaf rusts are due to the infection of the flag leaf, which is responsible for greater than 70% of grain filling. If the flag leaf is heavily infected before flowering, significant yield losses can be seen. Highly susceptible varieties may incur as much as 75% reduction in the yield if the flag leaf is infected heavily in the early stages. Farmers should be very aware about the spread of infection from the lower leaves to upper leaves prior to the emergence of last leaf (Marsalis and Goldberg, 2016).The cost of a 10 percent loss in areas at risk is estimated to exceed USD 5.8 billion (FAO Global Programme, 2014-2017).

The loss in yield and harvest occurs due to the following mechanisms (Roelfs and Bushnell, 1985):

(a) Decrease in the photosynthetic area

The lesions of rust generally occupy a significant portion in host plant tissue. Flag leaf, glumes, peduncle and awn are most affected areas, and they are the very parts that are the major source of the nutrients that are allocated to the developing grain (Roelfs and Bushnell, 1985). Reduction in photosynthesis in those major parts, ultimately leads to the drastic reduction in the yield due to the small grain size and shriveled grains.

(b) Loss of water and nutrients from the lacerated lesions

In a diseased plant, the rupture in the plant epidermal cells by the rust fungus leads in the loss of water. The pathogen also consumes both the mineral nutrients and water from the host plant to produce a huge mass of urediospores. The daily continuation of this causes the plant to suffer the enhanced stress. Early stage infection leads in decreased availability and less production of nutrients for plants. Less root growth in the diseased plant also enhances the imbalance in normal water requirements. Thus, such plants become more susceptible to winterkill, produce less tillers, smaller heads, and have increased spikelet sterility (Roelfs and Bushnell, 1985).

(c) Blockage in the nutrient transportation

Stem rust leads to the production of uredia on leaf sheaths and peduncle tissue. The fungus often penetrates through the tissue of the true stem. This penetration of the plant tissue blocks the transport of food and nutrients to the roots and results to the death of the roots prematurely. (Bushnell and Rowell, 1968). Also, the blockage obstructs to the grain filling process by blocking the nutrient translocation to the grains which leads to shriveled kernels (Calpouzos et al., 1976).

(d) Lodging and breakage of stems

In extreme cases, the stem portion gets heavily infested, creating chances of stem breakage. The straw may also break, causing the plant spike to break over and fall to the ground causing loss in the yield. Also, while harvesting mechanically, broken and lodged plants often have the spike below the level of cutter bar, resulting uneconomical harvest of the grain (Roelfs and Bushnell, 1985).

Attempts so far Chemical control

Some very effective fungicides are now available for the control of rusts, especially for leaf and stripe rust. More importantly, effective control can be achieved with the timely application (McIntosh et al., 1995). Such fungicides include two main types of active ingredients i.e., triazoles (e.g., Folocur, Tilt, Propimax and Proline) and strobilurins (e.g., Headline and Quadris). Some fungicides even include both of these (e.g., Quuilt and Stratego) (Marsalis and Goldberg, 2016). Bayleton (Buchenauer, 1976) and Indar (Von Meyer et al., 1970) have proven to be effective in the control of the leaf rust of wheat (Line and Rakotondradona, 1980). They are of special interest since they can be applied as seed dressings. Indar is highly specific as it controls only wheat leaf rust, however, Bayleton controls the other wheat rusts as well. However, the use of these fungicide is ecologically unsafe and uneconomical (Chen, 2005) because of (Roelfs and Bushnell, 1985):

- (1) the effectiveness of the host resistance,
- (2) the high rate of disease increment for wheat stem rust under the ideal conditions, and
- (3) the relatively low economic return per hectare as compared to the cost of fungicide applications.

In large scale and high yielding situations, chemicals can be applied cautiously and repeatedly with the chances of returns on investment. However, in low scale and low yielding situations chemical use becomes very difficult to justify (McIntosh et al., 1995). The most effective time for fungicide application is between the emergence of last lead and complete heading. Application after flowering often is not economically feasible as considerable damage has already been occurred to the flag leaf by this point. The protection of flag leaf is of utmost significance. Application of fungicides are preventative measures, these are not able bring back healthy tissue once the tissues are infected. Fungicide applications after milk and into soft dough stages are considered to be too late and do not provide significant yield protection. For severe infection in the lower leaves at early stage, spraying before the emergence of last leaf may be warranted. Most damage is incurred due to infection at heading and flowering. In general, fungicides shelter around two to three weeks of protection from further infection. There are unlikely chances of profitable returns from more than one spraying, so it is must for one application at the optimal time (Marsalis and Goldberg, 2016).

While fungicides may be biologically effective, they are not economically and practically feasible for wheat rusts, especially considering that majority of farmers are smallholder producers in low-yielding environments. So, they are only recommended under epidemic conditions as an emergency measure. Also, their environmental side effects are considered far more hazardous than their effect on minimizing disease. There is also a high risk that pathogens may develop resistance to fungicides.

Cultural practices

Cultural practices come as another method for the control of wheat rust epidemics. There exists no single practice, which is effective under all situations, but using a series of cultural practices enhances the existing resistances (Singh et al., 2002). Practices such as changing planting dates, destroying alternate hosts, using early maturing varieties and multilines or varietal mixtures have also been done because they are effective in reducing the levels

of inoculum and in turn the disease pressure. These methods are good to partially reduce disease pressure in specific combinations under certain environment. Mexican farmers had shifted to sow wheat early to avoid stem rust before the use of resistant cultivars (Borlaug, 1984). Avoiding the excess application of nitrogen and frequent light irrigation water generally assist in controlling rust. In areas where the disease over summers, eradication of volunteer wheats and other susceptible grasses several weeks before planting also decreases the inoculum level, which delays initial infection. Where both winter and spring wheat are grown in the same area, separating these crops by either space or by another crop can delay the transfer of pathogen between the fields. Substantial benefits can be harvested from incorporation of diverse cultivars on the farm and spacing between fields of wheat (Roelfs and Bushnell, 1985).

Destruction of alternate host also has some major effects in the rust epidemics control as it delays disease onset, reduces number of pathogen races, decrease the initial inoculum level and brings stabilization of the pathogen phenotypes (Roelfs and Bushnell, 1985).

Zadoks and Bouwman (1985) focused the significance of the green-bridge in transporting the disease from one crop to the next. The green-bridge can be increased when some farmers plant late and some late. Removing the green-bridge with herbicides or tillage can also be taken as an effective control measure for the plant. In some areas, focus should be given to control volunteer plants several times during the season when wheat is not grown (Singh et al., 2002).

While the cultural method is environmentally sound and comprises enhanced effectiveness under particular situations, the application of cultural practices however requires extensive knowledge and can be depicted useless if large exogenous inoculum occurs (Roelfs et al., 1992).

Biological control

The hyper-parasite of rust, Darluca filum (Biv.) Cast., is very famous (Chester et al., 1951); however, it offers less effectiveness as the rust must be present to have a buildup of the hyperparasite. Another hyper-parasite, Aphanocladium album, is now tested on the field scale, but the potentials are unknown yet. Verticillium Though niveostratosum, V fungicola, and Cephalosporium acremonium were identified as greenhouse parasites of rust, they little potential as a practical means of the control (Chester, 1946). Of 24 species of fungi in 12 genera' screened for their hyper parasitic activity towards Puccinia coronata on oat seedlings, 7 Verticillium spp. and Acremonium implicatlim were able to colonize uredial sori (Leinhos and Buchenauer, 1992). Also, Erwinia spp., Trichoderma spp., and Bacillus spp. have been recommended for the control of rust (Rytter et al., 1989). Because of the high humidity requirements of hyper parasitic fungi, these methods are not effective in arid or temperate conditions (Grabski and Mendgen, 1986). Better results may be obtained in tropics (Saksiriat and Hoppe, 1990).

Adult Plant Resistance

Ever changing races of pathogens is a serious problem, which led the breeders to look for alternative forms of resistance. This resistance needs to be more durable such as partial resistance or slow rusting (Singh et al., 2000). The durable rust resistance is more likely to be of adult plant type than that of seedling type. It is not linked with the genes which produces hypersensitive reaction (McIntosh, 1992). Durable rust resistance is a mechanism granting resistance to a cultivar for long period of time during its wide cultivation in a suitable condition for a pathogen (Johnson, 1978, 1988). This resistance is mainly related with the minor genes, known as slow rusting genes (Rehman et al., 2013) and also based on additive effect of partial resistant minor genes. This resistance is usually polygenic in nature and found to be active in adult plant stage (Rehman et al., 2013).

Generally, adult plant resistance is not complete immunity, but delays infection and spore production, resulting to slow rusting phenotypes. By slowing the fungal life cycle with adult plant resistance genes, spore production and fungal population size are decreased. This decreases the genetic diversity and the potential to escape recognition mediated by the resistance genes through a single genetic variation, making it more durable (Ellis et al.. 2014). The durability of resistance genes is also described by the global genetic diversity of the pathogen, which is rendered during the asexual and sexual stages of the life cycle (Schwessinger, 2016). Adult plant resistance is observed more durable since a single genetic variation becomes insufficient to overcome such type of resistance in the asexual stage of Puccinia (Ellis et al., 2014).

This evaluation is commonly done in fields where disease intensity at the end are noted. Rust development is closely related to host's growth stage; slight differences of maturing days exposes the plant to different inoculum density (Roelfs et al., 1972). Less work has been carried out in this and in most studies, inoculation at a specific growth stage using single race is done. Normally, plants are inoculated with predetermined inoculum density and checked for rust development and resistance response. They are further replicated, including check varieties. The plants must be maintained disease-and pest-free and provided with adequate light and nutrition for normal growth. A wide range of isolates are used to minimize the probability of selecting race-specific resistances (Singh, 1992).

Breeding for resistance

Use of resistant cultivars has been considered to be the major mechanism for the control of the cereal rusts (Johnson, 1981). Planting such resistant wheat varieties was and still is considered to be the most effective for preventing the wheat rust diseases. After the discoveries of the genetic basis of resistance by Biffen (1905), Stakman and Levine's physiological specialization (1922) in the rust pathogens, and Flor's gene-for-gene interaction (1956), the utilization of the hypersensitive (race-specific) type of resistance has taken the domain of wheat improvement by storm for past few decades. In recent years, the use of DNA marker-assisted incorporation of multiple race-specific resistance genes had been suggested and is being attempted by a few breeding programs (McIntosh et al., 2003). However, rust control using resistant varieties has faced problems of limited durability in recent years. For decades, wheat rust resistance breeding followed by both national and international research centres has been based on the deployment of few genes that are sufficiently potent enough to suppress rust spore production even if the plant possesses only a single gene (FAO, 2009). These racespecific genes function only if the infecting rust population belongs to a patho-type that lacks virulence with reference to those specific genes. Studies have shown that at least 10-12 slow rusting genes are involved in the rust resistant behavior of CIMMYT wheat varieties (Singh et al., 2004). During 1965-1985, the CIMMYT wheat breeding program has succeeded to

incorporate diverse genes in wheat. Generally, the material distributed through the program during the period contained Sr2 and two to four additional genes for stem rust resistance. These additional genes include Sr5, Sr6, Sr7a, Sr7b, Sr8a, Sr9b, Sr9d, Sr9e, Sr9g, Sr10, Sr11, Sr12, Sr17, Sr24, Sr26, Sr30, Sr31 and Sr36 (Rajaram et al., 1988). The parallel strategy of this program was also followed by many national programs of the world (Rehman et al., 2013). Control of rust diseases is effectively best through co-ordinate achieved resistance breeding effort across the different epidemiological areas of the pathogen (McIntosh et al., 1995). Control by individual breeding organizations or countries within major geographic areas is very difficult in the absence of support and similar control strategies deployed in the neighboring countries and organizations. Resistance breeding strategy comprises the following (McIntosh et al., 1995):

- 1. monitoring pathogen variability by means of patho-type surveys
- searching for effective sources of resistance and understanding how to manipulate those sources in breeding programs
- 3. breeding and release of cultivars and
- 4. post release monitoring of resistant cultivar.

Given the rapid rate of change in the genetic make-up of rust populations, induced either by mutation or selection pressure, the increasingly narrow deployment of resistance (genes) in the field is easily overcome by the rust pathogen. As a result, such wheat varieties grown in many regions became vulnerable to new virulent wheat rust strains which has further been proven by the outbreak of the Ug99 strain (stem rust) in 1999 and Yr27 (yellow stripe rust) in 2010 (FAO, 2014). Significant advances have been made in characterizing genes that confer resistance to biotic stresses in several crops, thanks to the use of molecular markers. Up till now, more than 50 genes for stripe rust resistance have been identified and named while many other genes or quantitative trait loci (QTL) have been tentatively designed (McIntosh et al., 2008; Chen, 2013). The genes for resistance have been obtained primarily from cultivars of T. aestivum, but some are from other *Triticum* spp. as well as from Agropyronand secale. The durability of the resistance is not found to be linked with the genera or species of the donor (Singh et al., 2002). The continuous breeding effort at CIMMT which took about 30 years long time span, can be taken as a successful example of breeding for resistance mainly based on the minor genes resistance to leaf and stripe rusts. Three or four lines carrying different minor genes were crossed i.e. three way and four way crosses, to achieve the resistance. Selections were done for plants in large segregating populations, under artificially created rust epidemics condition. Races of pathogens that have virulence for racespecific resistance genes present in the parents were used. (Singh et al., 2000).

Genetic engineering to combat rust epidemic

Cloning of resistance genes, especially those with durable or broad-spectrum disease resistance, could open new possibilities in wheat improvement. Resistance genes, when cloned and used for transformation are presumed to show over-expression of resistance (Horvath et al., 2002). So genetically modified crops could serve the purpose. Risk et al., (2012) determined the effects of transgenic Lr34 with specific reference to how expression levels affect resistance. Transgenic Lr34 wheat lines were tested in two susceptible genetic backgrounds. They observed that the

introduction of the Lr34 resistance allele was enough to provide some enhanced levels of leaf rust resistance as Lr34 gene which was endogenous. And they observed the resistance in the seedlings after cold treatment and in flag leaves of adult plants as well as Lr34-associated leaf tip necrosis with the endogenous Lr34 gene (Ekom et al., 2015).But many of the research groups working on the problem of wheat rust are academic groups and hence unable to afford the huge regulatory expenses associated with developing of such genetically modified crops (Lim, 2014). Additionally, widespread anti-Genetically Modified Organisms (GMO) sentiments and movements need to be overcome. It is so because unlike most genetically modified corn or soy crops that are used as animal feed, wheat is directly consumed by human as bread and other products.

Climate change and rust epidemic

Much of the current debate of the world is on how agriculture and food security might be affected by shifting disease dynamics under climate change (Gregory et al., 2009; Mahmuti et al., 2009). The rising CO_2 levels, like everything else in the agriculture domain, influences the frequency and severity of disease epidemics as well and some studies so far also link the abundance of wheat pathogens to changing atmospheric composition (Shaw et al., 2008).

However, there has been no research on rust microevolution under rising temperatures and CO_2 levels which is why future appearance of new races under the influence of climate change cannot be predicted from current knowledge alone. No traces of potential effect of resistance of host plant, host-pathogen interaction and assessment of impacts on wheat rust due to climate change have been found on literature so far. The effects of

elevated CO₂ in studies regarding diseases varied with the host-pathogen combination (Karnosky et al., 2002; McElrone et al., 2005; Kobayashi et al., 2006; Eastburn et al., 2010; Melloy et al., 2010), but none of them addressed wheat rusts which is what makes it difficult to project 'generalized effects' of climate change on the rusts of wheat (Chakraborty et al., 2010). The effectiveness of resistance in wheat varieties could possibly alter under the changed climate and the resistance may get overcome quickly by new races, which evolve at a different rate in a changing climate. New races evolving faster with the changing climate may overcome resistance in wheat varieties. Temperature is an important factor that controls rate of reproduction and sporulation in rusts (Clifford and Harris, 1981; 1987). This may Dennis, change the geographical distribution of wheat rusts and their economic importance due to changes in host-pathogen interactions.

The physiology, biochemistry and molecular biology of host-pathogen interactions of wheat rusts have been extensively studied and reviewed in the past (Eversmeyer and Kramer, 2000; Line, 2002; Singh et al., 2002; Leonard and Szabo, 2005). The expression of many genes for resistance to leaf rust (P. triticina) (Kolmer, 1996), stem rust (Leonard and Szabo, 2005), and stripe rust (Singh et al., 2000; Datta et al., 2009) is influenced by temperature. For example, the reaction of wheat varieties with the stem rust resistance gene Sr15 can switch from resistant at 15°C to nearly fully-susceptible at 20°C (Roelfs, 1988). This suggests that rise in temperature and CO₂ levels could actually favor rust incidences. Rising atmospheric CO₂ and temperature will prolong the wheat growing season, enlarge crop canopy in turn to increase the amount of susceptible tissue making the canopy micro-climate more favorable to rust development. So according to a paper published by Chakraborty et al., 2010, research must expand beyond impact assessment to develop adaptation strategies, such as new varieties and other rust management options that will sustain their effectiveness under a changing climate.

Conclusion

Wheat Rust is the most urgent problem regarding the production of this irrevocably important crop. Its easy translocation through air makes almost every place in the world susceptible to the pathogen. Hence, just like the pathogen's biology, the techniques of preventing epidemics need to adapt both to climate change and changing durability of previously resistant crops. The ever-changing nature of wheat leaf, stripe and stem rusts poses a serious threat to future wheat production. Learning from wheat breeding history and epidemic losses by wheat rusts, breeders devised different ways to cope with the threat. Cultural methods, chemical methods, adult plant resistance; all have their own pros and cons. They have been tested and trailed in various field conditions. By far, the most successful one is the use of resistant variety. Creation of a resistant variety is not as it used to be before. Climate change, microgenes, loci of each gene, changing host-plant interaction and evolution of the pathogen need to be kept in regard. Institutions both national and international have launched programmes and attempts to minimize or find a solution for so long. Every now and then a new technique is trailed but is soon shadowed by either limited resources or limited expertise. Genetic solutions are narrowed down by people's anti-GMO sentiments and solutions brought about by organizations like the BGRI or FAO are

narrowed down by lack of proper connection between stakeholders and government.

The advances in preventing rust epidemics becomes outdated as soon as they arrive. A permanent durable solution is required for which further studies and researches in geneticengineering would be inevitable. Institutions such as Borlaug Global Rust Initiative, FAO have come up with ideas and projects to combat the problem but it's still a long way to go for rust free world. The projects require long chain of people working together for a common goal and absolutely specific conditions (according to the kind of rust in question).

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