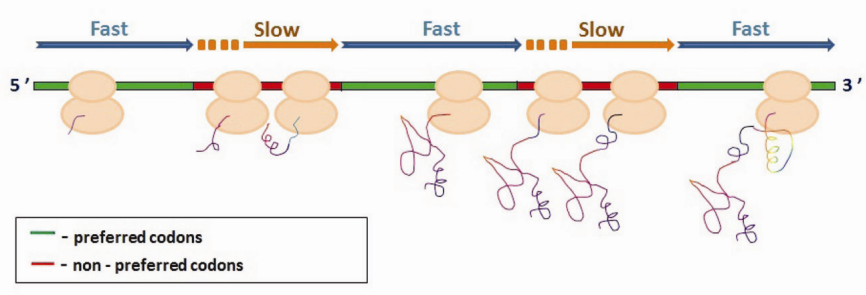

Figure 2. Schematic representation to show the relation between ribosome occupancy and different synonymous codons from ribosome profiling experiment. The green-red line represents an mRNA bound by a ribosome during translation. As the ribosome translates the regions of the mRNA, the difference in translation speed between the optimal and non-optimal codons can be observed. The green regions show sequences composed of preferred/optimal synonymous codons and the red regions show the non-preferred/non-optimal codons in the mRNA. More number of ribosome halting can be observed at the sequences containing non-preferred codons as it takes higher time to be decoded; consequently translation is slower at those sequences. However in the region composed of preferred codons, the translation speed is faster due to faster decoding of these codons leading to lesser number of ribosome to be associated with these codons.

codon and its preferred nature in the genome, in the ribosome profiling experiment carried out under *in vivo* and *in vitro* translation condition (Figure 2). The findings were same in both studies. Moreover, a change in concentration of mRNA had no impact on TFA, which was against the proposed balanced translation model. So the notion that ribosome retention in the preferred codon is less than that in the non-preferred codon was proved to be correct.

In conclusion, even though it was speculated earlier that synonymous codons are different with respect to the speed of translation elongation, there was no conclusive evidence. The findings by Yu *et al.*[9] support the fact that the speed of translation elongation due to preferred codons is higher than that of the non-preferred codons. It also explains well the reason behind the higher abundance of preferred codons in the high-expression genes. However, it does not eliminate the possible role of synonymous codons in accurate translation. In future, researchers will be looking forward to understanding the detailed mechanism of the fast and slow decoding processes of synonymous codons during translation.

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Suvendra Kumar Ray and Ishani Goswami are in the Department of Molecular Biology and Biotechnology, Tezpur University, Tezpur 784 028, India.*
**e-mail: suven@tezu.ernet.in*

Ug99: saga, reality and status

Pramod Prasad, S. C. Bhardwaj, Hanif Khan, O. P. Gangwar, Subodh Kumar and S. B. Singh

Wheat, the second most important cereal crop after rice, plays an important role in food and nutritional security worldwide. Wheat rusts, viz. black or stem rust (*Puccinia graminis* f. sp. *tritici*), brown or leaf rust (*P. triticina*) and yellow or stripe rust (*P. striiformis*), capable of spreading aerially over long distances, are highly variable and devastating pathogens. They evolve quickly to form new pathotypes/races, render resistant varieties susceptible and pose a serious threat to wheat production in different parts of the world[1]. Stem rust, also called 'polio of agriculture', has caused several severe epidemics in the past throughout the world. Developing rust-resistant varieties has been a continuous exercise over the years. One of the achievements of the green revolution of the 1960s was to reduce yield losses due to wheat rusts, as many resistance genes introduced in wheat during that period conferred resistance to most of the rust pathotypes of that time. A number of rust-resistant sources, including alien ones have been used to combat wheat stem rust. Introduction of rye (*Secale cereale* L.) gene (1B/1R translocation or substitution) into bread wheat[2,3], which carries *Lr26*/*Sr31*/*Yr9*, completely linked resistance gene has not only contributed 12–20% yield jump, but also imparted resistance to major biotic and abiotic stresses[4]. *Sr31* in combination with other stem rust resistance genes kept the stem rust fungus

under control for more than three decades. Stem rust of wheat was thought to be a disease of the past until 1998, when a new pathotype of *Pgt* was observed in Uganda. This new pathotype, designated as TTKSK in 1999, popularly known as Ug99, has the ability to overcome the resistance conferred by a majority of the stem rust resistance genes, including *Sr31*. Since then, ten variants in Ug99 lineage (also confirmed by molecular markers) have been detected in different countries. The emergence of Ug99 is considered as a highly significant event, having far-reaching consequences not only for Africa but also for the global wheat production due to susceptibility of most of the wheat cultivars to Ug99. The estimation advocates that 50 M ha of wheat grown globally is under the risk of Ug99, which is approximately 25% of the world's wheat area[5].

The variants in Ug99 lineage are designated as a five-letter code, a North American nomenclature system[6]. TTKSK is the earliest variant of Ug99 lineage, detected in 1999 with virulence to *Sr31* (ref. 5). TTKSK is now reported to spread to other countries like Kenya (2001), Ethiopia (2003), Sudan (2006), Yemen (2006), Iran (2007), Tanzania (2009) and Egypt (2014). Other variants, i.e. TTKSF (virulent to *Sr21*, but avirulent to *Sr31*) from South Africa (2000) and Zimbabwe (2009); TTKST (virulent to *Sr31*, *21* and *24*) from Kenya (2006), Tanzania (2009) and Eritrea (2010); TTTSK (virulent to *Sr31* and *36*) from Kenya (2007) and Tanzania (2009); TTKSP (virulent to *Sr21* and *24*) from South Africa (2007), PTKSK (virulent to *Sr31*, but avirulent to *Sr21*, *24* and *36*) from Ethiopia (2007) and Kenya (2007); PTKST (virulent to *Sr31* and *24*, but avirulent to *Sr21*) from Ethiopia (2007), Kenya (2008), South Africa (2009), Eritrea (2010), Mozambique (2010) and Zimbabwe (2010), and TTKSF (virulent to *Sr21*, but avirulent to *Sr31*) have been reported from South Africa (2000) and Zimbabwe (2009)[7]. Till date, 11 variants (Figure 1) have been documented as the members of the Ug99 pathotype lineage[8].

The Ug99 variants with combined virulence to *Sr31* and *Sr24* have been detected throughout Africa and their further spread in near future to other countries is expected[9]. Resistance contributed by *SrTmp* gene has now been broken down by the latest variants, i.e. TTKTT and TTKTK detected in Kenya. The confirmed detection of TTKTK from Kenya, Egypt, Eritrea, Rwanda and Uganda during 2014, suggests its rapid spread in Africa[8]. Ethiopia experienced severe stem rust epidemics in the southern wheat production region during 2013 and 2014 (ref. 9). This epidemic was caused by a non-Ug99 group pathotype of *Pgt*, designated as TKTTF. Pathotype TKTTF is virulent to Digalu variety in Ethiopia carrying resistance gene *SrTmp* that was effective to the known variants of the Ug99 group in Ethiopia. TKTTF was first detected from Ethiopia in August 2012, but remained at a low frequency until October 2013 when it caused grain loss up to 100% in more than 10,000 ha area[9].

The stem rust pathogen is known to produce millions of uredospores and these spores become airborne and disperse from one plant to another, or from one area to another and cause infection in susceptible varieties at a fast rate. The long distance dispersal of rust spores through the agency of air and human interventions is a well-documented means of pathogen spread across countries or continents. Ug99 has the parallel story of its dispersal and has been confirmed in Uganda, Kenya, Ethiopia, Sudan, Yemen and Egypt (2014)[10]. The recent detection of Ug99 in Egypt is being considered particularly important, as its dispersal route provides strong indication that Ug99 is moving towards the important wheat areas of the Middle East and South Asia. It is not just dispersing, but mutating at a fast rate to overcome stem rust resistance genes. If somehow the Ug99 reaches these regions, it would affect an estimated one billion people living in these parts of the world. One of the best strategies to avoid such a catastrophe is to identify and deploy resistant wheat genotypes that are suitable for Ug99-prone regions. Extensive screening across the Ug99 hotspots is needed for identification of the area-specific wheat genotypes with resistance to Ug99.

Responding to the call of Noble laureate, Norman Borlaug, the entire world came to one platform to combat the Ug99 threat. The Borlaug Global Rust Initiative (BGRI) (earlier Global Rust Initiative) came into being on 9 September 2005 at Nairobi, Kenya. BGRI initiated joint efforts by involving different nations and organizations to monitor the spread of wheat stem rust pathotype Ug99, screen the released varieties and germplasm for resistance to Ug99, distribute the sources of rust resistance worldwide, and breeding to incorporate diverse resistance genes and adult plant resistance genes into high-yielding adapted varieties. Global Cereal Rust Monitoring System (GCRMS), working under the umbrella of BGRI, Consultative Group on International Agricultural Research (CGIAR) centres, advanced research laboratories, national agricultural programmes and UN–FAO, have resulted in the emergence of strong, rapidly expanding, coordinated international rust surveillance network. It has helped in disseminating the updated information on survey and surveillance of wheat rusts.

Over 300,000 wheat germplasm from wheat-producing countries of Asia, Africa and other parts of the world, have been screened for resistance to virulent stem rust pathotypes belonging to the Ug99 lineage at Njoro (Kenya), Kulumsa and Debre Zeit (Ethiopia) during 2005–2014, to combat the risk of stem rust epidemics. Of these, about 15% of materials from various countries was found resistant to the pathotypes of Ug99 group. These germplasms can be used in the Ug99-infected and bordering areas, so that further multiplication and spread of the pathotypes could be minimized. Robin (*SrTmp*), a wheat cultivar in Kenya was popular due to its high yield potential and resistance to the then known pathotypes of Ug99 lineage. But during the 2014 crop season, it faced severe damage in some farmers' fields. The pathotype infecting this variety was identified as a new variant in the Ug99 group with virulence to stem rust resistance gene *SrTmp*[10].

It is predicted that most of the wheat-growing regions of the world will suffer more and more in the future because of existing favourable environmental conditions for stem rust outbreak and unavailability of suitable resistant wheat germplasm to Ug99 pathotypes, which could lead to an epidemic build-up. Pathotypes of Ug99 group have not been reported in India and Pakistan so far. Stem rust-prone areas in India are limited (about 25% of total area). Hence, it may not be a threat in the main wheat belt[11]; yet the vigil is being kept on the possible implications of entry of Ug99 pathotype into the country or independent mutation for *Sr31* (ref. 5). Among more than 1000 Indian germplasms screened against the pathotypes of Ug99 group in Kenya and Ethiopia, wheat variety HW 1085,

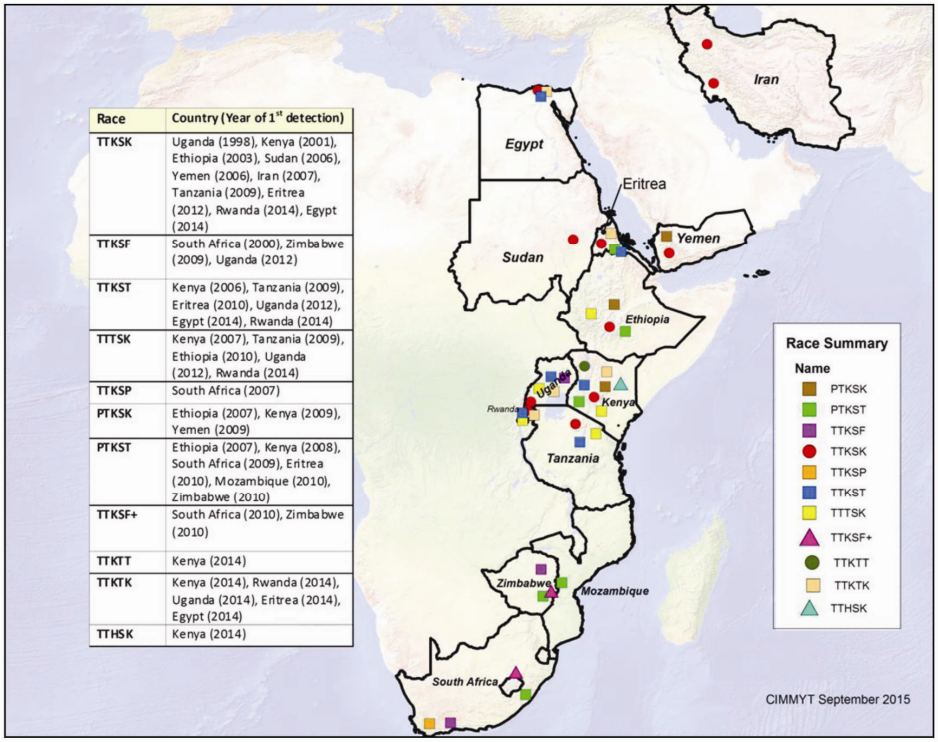

Figure 1. Variants in Ug99 group of *Puccinia graminis tritici* (source: Ravi P. Singh, CIMMYT, Mexico).

developed by ICAR-Indian Agricultural Research Institute, Regional Station, Wellington for Southern Hill Zone and three genetic stocks, i.e. FLW 2 (PBW 343 + *Sr24*), FLW 6 (HP 1633 + *Sr24*) and FLW 8 (HI 1077 + *Sr25*), developed at ICAR-Indian Institute of Wheat and Barley Research, Regional Station, Shimla, India were found resistant against the pathotypes under natural conditions in Kenya. The available data suggest that varieties like Lok 1, HI 9498, WH 147, GW 322, HI 1531, HI 8627, HD 4672, MACS 2846, NI 5439, DL 788-2, MPO 1215, NIDW 295, HI 8663, UAS 321 and UAS 431, which are under cultivation in Central and Peninsular India, possess considerable resistance to Ug99 variants[5]. Recently, Sharma *et al.*[12] found that wheat lines, viz. A-9-30-1, AKDW 4021, DDK 1037, DDK 1038, DDW 14, DL 153-2, GW 1250, HD 2781, HD 3014, HD 4720, HDR 77, HI 8381, HI 8498, HUW 234, HW 5211, K 9107, MACS 1967, MACS 2846, MACS 2988, MACS 2998, MACS 3742, MACS 5009, MPO 1215, NI 5439, NIDW 295, PBW 315, PBW 612, PDW 274, PDW 316, PDW 317, WH 147, *Sr22*, *Sr32*, *Sr35*, *Sr39*, *Sr42* and triticale varieties TL 2942, TL 2963 and TL 2966 were resistant to Ug99 and its variants on evaluation in Kenya and Ethiopia during 2006–2011.

As a follow-up of the detection of Ug99 (TTKSK) in Egypt during 2014 season along with the possibility of long-term dispersal of uredospores, thorough surveillance and monitoring is needed for stem rust in Israel, Lebanon, Jordan, Eastern Syria, Southern Turkey and South Asian countries, so that the possible stem rust outbreak due to variants of Ug99 group of *P. graminis tritici* in these areas could be avoided.

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Pramod Prasad, S. C. Bhardwaj, Hanif Khan, O. P. Gangwar, Subodh Kumar and S. B. Singh are in the Regional Station, ICAR-Indian Institute of Wheat and Barley Research, Shimla 171 002, India.*
**e-mail: scbfdl@hotmail.com*