Epidemiology of *Puccinia graminis* f.sp. *tritici*-Ug99 in the Rift Valley “Flyway” from Uganda-Kenya to Yemen

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**Abstract**

Dispersal of a new virulence of *Puccinia graminis* f.sp. *tritici* (*Pgt*) -Ug99 from Uganda-Kenya to Yemen, over >1000 km, happened in four years. Geo-agro-ecology of wheat cultivation and the epidemiology of *Pgt* indicate that the Rift Valley is a natural conduit “flyway.” The widely prevalent “green bridges” favor survival and spread of *Pgt*. This part of the Rift Valley is one single epidemiological zone, and the annual *Pgt* build-up is from the endogenous inoculum.

**Introduction**

Photo-insensitive short-duration wheat (*Triticum*) is grown at high altitudes in equatorial East Africa. In a global perspective, the East African states are not the important wheat-growing areas but contribute to the evolution of *Puccinia graminis* f.sp. *tritici* (*Pgt*). Worldwide information on the origin, specificity, physiology, life cycle, collateral hosts, alternate hosts, epidemiology, and control of wheat rusts has been well documented (4,21). A new virulence of *Pgt*, designated as Ug99 (=PTKS) and reported from Uganda in 1999 (20), was virulent against stem rust (*Sr*) resistance genes *Sr*31, derived from rye (*Secale cereale*), and *Sr*38, from *T. ventricosum*. Some of the variants of *Pgt*-Ug99 have overcome most the useful resistance genes, such as *Sr*31, *Sr*38, and *Sr*24 derived from *Agropyron ponticum* (15,16).

**Agro-Ecology of Wheat Cultivation**

**Uganda.** Total wheat acreage in Uganda is only 5,000 ha. Two crops of bread wheat can be grown per year on the slopes of Mt. Elgon in Kapchorwa, Sironko, and Mbase. In Kapchorwa bread wheat is grown on large mechanized farms, whereas elsewhere, wheat is sown by small holders in plots of 0.2 to 2.0 ha size. The first cropping season is usually from March to July/August, and the second is from August/September to December/January. The bimodal rainfall pattern with two distinct rainy spells provides moisture for two crops of wheat. Though yields are poor, experimental new varieties such as UW 400, UW 300, and K. Chiriku yield 3.0 tons/ha (24).

**Kenya.** Wheat is the second most important cereal crop in Kenya after maize. Wheat is cultivated at elevations ranging from 1,700 to 2,800 m. There are two wet seasons per year, one from mid March to end of May/mid June, and the other during the short rainy season, from September to mid November (8). Kenya grows most of its 0.10 to 0.12 million ha of bread wheat during March to May/June. Total wheat production in Kenya is around 0.25 million tons. In the mechanized farms high-yielding, drought-resistant wheat varieties like Njoro BW1 and Njoro BW2 are cultivated in Narok, Nalvasha, Katumani, and Mogotio.
Njoro BW2 performs well on acidic soils prevalent in the Uasin Gishu and Nakuru districts. Other varieties like Kenya Heroe and Kenya Yombi, Duma, and Chozí are grown in dry areas. Because the cost of seed replacement is high, recycled seed is widely used and such recycling lasts for at least five years (18) before replacement. The two wheat growing seasons per year create a “green bridge” with self-sown (volunteer) seeds of the just-harvested wheat crop. This ensures a substrate for the perpetuation of the urediniospores. In Kenya, barley (Hordium vulgare) also is grown over 70,000 ha and historically Pgt is known to infect both bread wheat and barley (14).

**Ethiopia.** Ethiopia cultivates ~1.5 million ha wheat, mostly rainfed, two thirds of which is durum (T. durum), whereas the rest is bread wheat (T. aestivum) and Khapli (T. monococcum). Durum, native to Ethiopia, is widely cultivated by farmers, and land races of various kinds dominate. Ethiopia has an amazing wealth of genetic diversity in durum and is grown at altitudes of 1,800 to 2,700 m as a rain-fed crop. Durum is generally planted in August and matures in November/December. Wherever irrigation is available, an off-season second crop is grown. Bread wheat is a major crop in the medium and high altitude zones in southeastern, central, and northwestern agro-ecological zones (8). At higher elevations bread wheat is sown in November and matures by March/April in 150+ days. The pathogen survives on the “green bridge” and the local inoculum triggers stem rust development. As the dry season provides adequate dew, stem rust severity during this season is higher than that in other seasons. Durum grown at lower elevations (2,000-2,400 m) on less fertile and poorly drained vertisols tends to be more susceptible to Pgt and P. striiformis (Pst) damage than the bread wheat that is grown at higher elevations (>2,400 m) (2). The short rainy period called “belg” starts in March. Rainfall during belg is not so reliable and growing wheat during this season is risky. It also implies harvesting during meher (June), which often results in high grain moisture levels, and sprouting of the grain in the head (11) may promote more volunteer plants. In some highland regions, the belg and meher seasons merge into one extended growing period during which both long-cycle (sorghum and maize) and short-cycle cereals (wheat, barley, and teff) are grown. Bread wheat, durum wheat, Khapli wheat, barley, and hanfet (wheat-barley mixture) create enormous host diversity in comparison to the Kenya-Uganda region. Ethiopia has about 0.8 million ha under barley and harvests about 1.6 million tons. Wheat and barley areas are interchangeable according to elevation and moisture availability.

**Yemen.** In cool mountainous regions, wheat is grown as a rainfed crop over an area of 120,000 ha at altitudes >2,000 m. Land races of wheat dominate the area because access to improved varieties is highly limited. Despite 140+ days’ crop duration, the average yield of wheat is 1.2 tons/ha. Farmers prefer barley over wheat, because sheep and goat graze the crop and the rejuvenated grain crop is harvested by early May. Both barley and wheat are sown by November and harvested by April/ May. Yemen has about 40,000 ha of barley and depending on the soil moisture wheat availability area under the crops fluctuates. Area increase of wheat may influence the epidemiology of Pgt in Yemen as the probability of survival and perpetuation of the pathogen tends to increase.

**Evolution of the Ug99 Family**

During February 1999, a Sr31 virulence called “Ug99” (20) was identified in Uganda. Many bread wheat varieties carrying a 1B/1R translocation where gene Sr’31 is located became susceptible to Ug99. The Ug99 of Uganda was avirulent on Sr24 and was designated as PTKS. The Pgt-Ug99, sampled during 2003 and 2004 from Kenya, had additional virulence on Sr21 and was identified as TTKS (25). The Kenyan isolate collected in 2007 did not produce a uniform reaction on LcSr24Ag (Sr24 from Agropyron in Little Club background) (16). Depending on the isolate, lines with Sr24 produced an infection type (IT) varying from 2- to 3+. (15) and the Ug99 (TTKS) population was divided into two distinct groups, one producing IT 2 on Sr24 (named TTKSK) and the other with IT 3+ (indicated
as TTKST). The latter never produced a fully compatible reaction (IT 4) on Sr24. In Ethiopia, 152 field samples collected during 2006 and 2007 were analyzed and only TTKSR (1) that is avirulent on Sr24 was present. Because the fifth set of differentials used for samples from Ethiopia and Kenya were not identical (1,15), the nomenclature of the fifth letter varies. The Pgt-Ug99 spread further to Yemen in 2006 (7), but details of the virulence designation is not easily available in the literature. Now, Pgt-Ug99 has become a group name with several variants such as PTKS, TTKS, TTKSK, TTTSK, and TTKST.

Comparison of Long-term Weather at Two Locations in Kenya and Ethiopia

Monthly maximum and minimum temperatures and rainfall recorded at Nairobi and Nakuru in Kenya and Addis Ababa and Negheli in Ethiopia were examined. The altitude and geo-position of the sites in Kenya are: Nairobi, 1° 16’S, 36°49’E, 1,680 m alt.; and Nakuru, 0°10’S, 36°45’E, 2,032 m alt. The Ethiopian sites are: Addis Ababa, 9°01’N, 38°45’E, 2,300 m alt.; and Negheli, 7° 35’N, 38°42’E, 1,475 m alt. Suitability of the weather conditions for the survival of Pgt in the uredinial stage was inferred from the maximum temperature of the warm dry period. Seasonal rainfall in Kenya is driven mainly by the migration of the Inter-Tropical Convergence Zone (ITCZ), the relatively narrow belt of very low pressure and heavy precipitation that forms near the earth’s equator. The exact position of the ITCZ changes over the course of the year, migrating southward through Kenya in October to December, and returning northward in March, April, and May. This causes in Kenya two distinct wet periods – the “short” rains in October to December and the “long” rains in March to May. The central highland regions are substantially cooler than the coast, with the coolest (highest altitude) regions at 15°C. Temperatures vary little throughout the year (19) (Fig. 1). The rainfall pattern of Nagheli and Addis Ababa has a single monsoon-like spell from July to October, and a less conspicuous rainy season during March through May. Ethiopia experiences a monsoon-like rainfall period from June to October. The percentage of days having measurable rainfall (>1 mm) in western and central Ethiopia is 70 to 90%, whereas it is only 10 to 30% in the northeastern parts of the country (17).

In the Rift Valley, two wheat crops per year are grown and the green bridge is available for Pgt to survive in the uredinial stage (Table 1). The Rift Valley conduit interconnects the wheat-growing areas in the countries mentioned, thus making a single epidemiological zone (Fig. 2). The Pst also follows a similar pattern as was observed by Stubbs (23). Based on the available agro-ecological information on wheat/barley cultivation in Uganda-Kenya to Yemen, it can be inferred that Pgt survives in the uredinial stage throughout the year either on the main host or on a green bridge. This epidemiological advantage lends Pgt-Ug99 spatial and temporal leverage to spread in the Rift Valley, as illustrated in Table 1 and Fig. 2.
Fig. 1. Long-term mean monthly maximum temperature in °C (A); mean monthly minimum temperature in °C (B); and mean monthly rainfall in mm (C) for Nairobi and Nakuru in Kenya and Addis Ababa and Negheli in Ethiopia.
Fig. 2. The Rift Valley "flyway" (marked in red) supports the East African 'Puccinia pathway' and forms one large epidemiological zone. Blue blotches are the large lakes in the region.
Table 1. Information summary on the Ug99 spread in the Rift Valley.

<table>
<thead>
<tr>
<th>Country</th>
<th>Wheat area (1000 ha)</th>
<th>Wheat seasons</th>
<th>Pgt survival</th>
<th>Ug99 first recorded</th>
<th>Approx. dist. from Kenya (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uganda</td>
<td>5</td>
<td>Mar - Aug; Aug - Jan</td>
<td>Green bridge, crop overlap</td>
<td>1999</td>
<td>350</td>
</tr>
<tr>
<td>Kenya</td>
<td>120</td>
<td>mid Mar - mid Jun; Sep - Nov</td>
<td>Green bridge, crop overlap</td>
<td>2001</td>
<td>0</td>
</tr>
<tr>
<td>Tanzania</td>
<td>62</td>
<td>Same as Kenya</td>
<td>Green bridge</td>
<td>2001</td>
<td>100</td>
</tr>
<tr>
<td>Ethiopia</td>
<td>1500</td>
<td>Nov - Mar/ Apr; Aug - Nov/Dec</td>
<td>Green bridge; crop overlap</td>
<td>2003</td>
<td>1000</td>
</tr>
<tr>
<td>Eritrea</td>
<td>45</td>
<td>Jul - Nov; Mar - Jun</td>
<td>Green bridge, crop overlap</td>
<td>2010</td>
<td>1200</td>
</tr>
<tr>
<td>Yemen</td>
<td>120</td>
<td>Nov - Apr/May</td>
<td>Summer crop acts as green bridge</td>
<td>2006</td>
<td>1450</td>
</tr>
</tbody>
</table>

In Nairobi and Nakuru, the dry and warm period is during February and March and cooler months are July and August (Fig. 1). Nakuru, located on the western side of the mountain system, has a mean maximum temperature of 24°C and is cooler than Nairobi by at least by 2°C. Unlike Nairobi, Nakuru experiences a rather well distributed annual rainfall. Wheat is cultivated as a main season crop during the cooler part of the year when the monthly mean minimum temperatures are 10°C at Nairobi and 8°C at Nakuru. These temperature levels may not hinder the continuance of Pgt uredinia from sporulation (13). At both Nairobi and Nakuru, the maximum temperatures during November to March are 4-6°C higher than other months and the minimum temperature is lower by 1-2°C. This period favors severe stem rust development as the daily mean temperature stays around 18°C. Weather conditions at all these locations favor the year-round survival of Pgt on wheat or on a ‘green bridge.’ Addis Ababa and Negheli (Ethiopia) have comparable monthly mean maximum temperature except in July and August when Addis Ababa is 2°C cooler than Negheli. With a maximum of 20-22°C during July and August, the Ethiopian locations are cooler than the sites in Kenya by 2 to 4°C. In general, Ethiopia is cooler in comparison to the locations in Kenya by 4°C for the period October to March (Fig. 1).

**Uganda-Kenya to Ethiopia (Rift Valley) is One Epidemiological Zone**

The Rift Valley crops from Kenya to Yemen have experienced stem rust epidemics in 1972, 1977, and 1979 (22). The Rift Valley provides an ideal niche for the free flow of air-borne organisms, serving as a conduit connecting the east African mountains with the coastal mountain ranges in southern Yemen. Many spores and small insects are carried in wind currents (10) and the urediniospores of Pgt from the mountain slopes can conceivably be among them. The soaring air currents, deflected upwards by hills and mountains and the thermals formed over the land heated by the sun’s rays provide uplift for the spores so that they gain height. Where the lift ceases, spores glide slowly down, nearly until touch-down, and are uplifted by the next thermal, and so on. And by this method urediniospores can travel > 300 km in a day without losing viability. Spores wind-borne for over 48 h tend to lose their viability (10). The shortest aerial distance between wheat fields on Mount Kilimanjaro and the mountains near Addis Ababa, Ethiopia, is 1,000 km. The aerial distance from Addis Ababa to the wheat growing mountain region in Yemen is another 450 km. From Ethiopia to Yemen urediniospores can conceivably make this distance during favorable weather. The orographic features of the Rift Valley, and the continuous presence of wheat throughout the region, could have promoted the spread of Ug99 from Kenya to Yemen in four to five years. In this
epidemiological zone pathotypes of Pgt perpetuate year-round on susceptible hosts in the uredinial stage and the primary inoculum of Pgt is endemic; the pathogen need not migrate to distant locations each year because they survive on the off-season wheat and on the ‘green bridge.’ The Pgt races from Kenya to Ethiopia have been taken as an indicator for the frequent exchange of inoculum in the Rift Valley (12). Monthly overviews of observed rusts in Ethiopia by Ciccarone (5,6) indicate that Pst is prevalent year – round in the atmosphere between 2400 and 3000 m and Pgt between 2000 and 2400 m. Saari and Prescott (22) and Stubbs (23), using world-wide and multi-year virulence typing of Pst, surmised that the area from Uganda-Kenya to Yemen is also one Pst epidemiological zone. The present study confirms that for Pgt also Uganda-Kenya to Yemen is one stem rust epidemiological zone. Exchange of Pgt and Pst inoculum between Ethiopia and Kenya has been suggested by Burton (3), which is feasible as a reverse pathway. The underlying unifying factor is the role played by the Rift Valley. The Rift Valley acts as an efficient conduit serving as a “flyway” or as the East African “Puccinia pathway” (Fig. 2). Gene deployment along the pathway can be an efficient management strategy to contain Pgt.

Summary

A new virulence of Pgt designated as Ug99 (=PTKS), reported from Uganda in 1999, was virulent against stem rust (Sr) resistance genes Sr31 and Sr38, and this overcoming of the useful resistance genes was feared as a potential threat to wheat production around the world. The orographic features of the Rift Valley possibly enabled the spread of Ug99 from Kenya to Yemen in four to five years as there is a continuous presence of wheat throughout the region. In this tract, Pgt perpetuates year-round on susceptible hosts in the uredinial stage and since the Pgt inoculum is always there, the pathogen need not migrate to distant locations to survive on the off-season wheat and on the ‘green bridge.’ The underlying unifying factor is the role played by the Rift Valley. The Rift Valley acts as an efficient conduit serving as a “flyway” or as the East African “Puccinia pathway.” Gene deployment along the pathway can be an efficient management strategy to contain Pgt.

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