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Review

Wheat rust evolution in Spain: an historical review

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Abstract. Rusts are important wheat diseases worldwide. The three rust diseases of wheat are yellow rust, leaf rust and stem rust, and each has characteristic features. The Guadalquivir valley in the south–west and Girona in the north–east are the areas Spain most affected by these diseases. Key factors for understanding the history of wheat rust epidemics in Spain are historical weather records in the rust–prone areas and characterization of rust resistance in historical varieties currently preserved in seed banks. These diseases in Spain have been of moderate importance, with stem rust being the most significant disease. During the second half of the 20th century several major epidemics occurred. In 1958 and 1978 severe outbreaks of yellow rust occurred in the Guadalquivir valley. These were probably associated with crop intensification, especially a large number of host landraces replaced by just a few cultivars, as well as immigration of external pathogen inoculum. From the early 1970s, CIMMYT elite cultivars arrived in Spain. These possessed good resistance to leaf and stem rust (*Sr2*), and had early heading dates. Subsequently, stem rust severity rapidly decreased in Spanish fields, but leaf rust epidemics became frequent during 1998–2008 on durum wheat in south–west Spain. In 2013, races virulent on *Lr14a* gene were first reported in Spain, but they did not result in disease epidemics. In 2012–16 yellow rust epidemics were recorded at many locations due to incursion of the 'Warrior' race. Despite the availability of effective fungicides and resistant cultivars to manage the three rust diseases, these diseases continue to threaten wheat production in Spain. In 2016, stem rust caused epidemics on durum wheat in Sicily (Italy), which has similar climatic conditions to those found in the south and east of Spain. Alert systems and international co-operation are needed to characterize the resistance of cultivars, and to monitor the movement and virulence of the wheat rust fungi.

Keywords. *Triticum aestivum*, *Triticum turgidum, Puccinia triticina*, *Puccinia striiformis, Puccinia graminis,* rust diseases.

INTRODUCTION

Wheat rusts are diseases caused by obligate biotrophic pathogenic fungi that belong to the division *Basidiomycota*, order *Pucciniales*, and genus *Puccinia*. The diseases are caused by three distinct species producing three different diseases. Yellow rust is caused by *Puccinia striiformis* West. f. sp.

tritici, leaf rust is caused by *P. triticina* Eriks., and stem rust is caused by *P. graminis* Pers. f. sp. *tritici* Eriks & E. Henn. Wheat rusts have complex life cycles (macrocyclic) that involve five types of spores, i.e., urediniospores, teliospores, basidiospores, pycniospores, and aeciospores. These pathogens are heteroecious, requiring alternate hosts to complete their life cycles (Kolmer, 2013). On wheat, uredioniospores are produced asexually from uredinia ("pustules") that develop on the leaves, and each pustule may produce up to 3,000 spores per day over a period of 20 days (Roelfs *et al*., 1992). Polycyclic infections occur in wheat field within growing seasons, when the newly formed urediniospores re–infect the same populations of wheat plants, and these infections have potential to develop into epidemics. Urediniospores are airborne and may travel as far as several thousand kilometres from their initial sources (Ordoñez *et al*., 2010).

CHARACTERISTICS OF WHEAT RUSTS

Yellow (or stripe) rust

Typical symptoms of *Puccinia striiformis* f. sp. *tritici* infections are yellow–orange pustules forming stripes on the leaves, and awns can also be affected. Since the discovery that barberry (*Berberis* spp.) are the alternate hosts, *P. striiformis* is now considered as a macrocyclic and heteroecious rust (Jin *et al*., 2010). Temperatures for infection and disease development are low (2–15°C), with an optimum temperature of approx. 10°C (Roelfs *et al*., 1992). Yellow rust is the prevailing rust at high altitudes or in places with moderate or cold winter, although new races with tolerance to warmer temperatures have been recently reported (Hovmøller *et al*., 2011). Yield losses can reach 24 to 39% in winter wheat cultivars in Central Asia (Sharma *et al.,* 2016). According to McIntosh *et al*. (2013), 67 yellow rust resistance genes (*Yr1* to *Yr67*), and 42 with temporary designations, have been discovered.

Leaf (or brown) rust

Leaf rust is the most common wheat rust worldwide. Pustules of *P. triticina* are reddish–brown in colour. Leaf rust is heteroecious, with *Thalictrum speciosissimum, Isopyrum fumaroides* and *Anchusa azurea* reported as alternate hosts (Anikster *et al*., 1997; Bolton *et al*., 2008). The disease progresses at temperatures from 10 to 30°C, with an optimum temperature of 20°C (Roelfs *et al*., 1992), and causes yield losses attributable mainly to reduced kernel weights (Saari and Prescott, 1985; Huerta–Espino *et al*., 2011). However, in environments conducive to leaf rust, losses can surpass 30% of potential yield (Cátedra and Solís, 2003). Cultivars resistant to leaf rust carry *Lr* genes. More than 100 of these genes and their alleles have been identified in wheat, and 71 of these are officially named (Singh *et al.,* 2013).

Stem (or black) rust

Stem rust is characterized by dark reddish–brown pustules. *Puccinia graminis* f. sp. *tritici* can cause disease at temperatures ranging from 15 to 35°C, with an optimum of approx. 25°C (Roelfs *et al*., 1992). In the past this was considered to be the most harmful wheat rust, causing yield losses of up to 50% (Leonard and Szabo, 2005). Stem rust is heteroecious with several species of barberry and *Mahonia* spp. as alternate hosts (Leonard and Szabo, 2005). Cultivars resistant to stem rust carry *Sr* genes, and at least 60 *Sr* genes are known (Chen *et al*., 2018).

CLIMATIC CONDITIONS AND HISTORIC WHEAT AREAS OF SPAIN

Spain has a prevailing Mediterranean climate, that is characterized by dry, hot summers and mild, wet winters, in the *Csa* 'Köppen–Geiger' classification (Kottek *et al*., 2006). In the north of Spain, where temperatures are generally less than in the south, most areas have *Csb* (Mediterranean climate with a warm summer) or *Cfb* classifications (temperate oceanic climate). It is also important to discriminate between the 'standard Mediterranean' climate of lowland regions with moderately–cool winters, and 'continentalized Mediterranean' climate of the interior with cold winters. The standard Mediterranean climate covers coastal areas (excluding the northern Atlantic coast), the Guadalquivir river basin, and the lower reaches of the Tagus and Guadiana basins to the west of the country (Figure 1). The continentalized Mediterranean climate predominates in Spain's plateau (*Meseta*) of the interior, at more than 600 m above sea level (AEMET, 2011).

Water deficits are the main constraints to high yields in Spanish field crops. Two thirds of the country receives less than 400 mm of annual rainfall, and the amount of solar radiation is high, especially in the south (Rivero, 2013). Winds coming from Morocco blowing from SW to NE are important for transport of rust inoculum from early to late maturing wheat varieties (Bout–Roumazeilles *et al*., 2007).

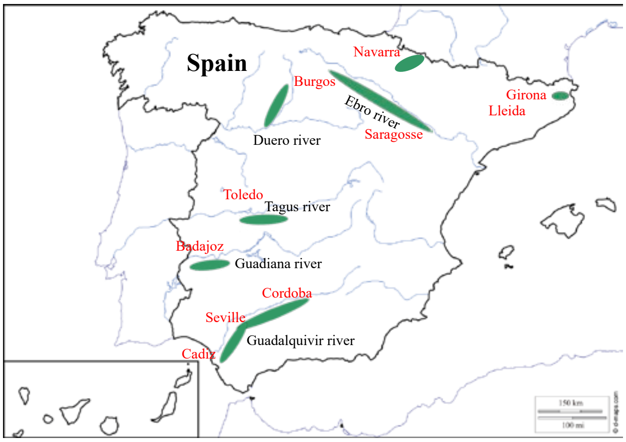

Figure 1. Main wheat growing regions (green) and provinces (red font) in Spain, that are prone to rust outbreaks.

Wheat has been, and continues to be, cultivated in the best dryland soils of Spain. These are located near the basins of the main Spanish rivers that are, from north to south, the Ebro, Duero, Tagus, Guadiana, and Guadalquivir (Figure 1). The deep clay soils of these areas are suitable for wheat production (Rivero, 2013). Sowing of wheat takes place during October through to December each year, while harvest dates range from late May (Guadalquivir basin) to mid–July (Ebro and Duero basin). Extreme heat in summer (especially in the south) prevents extended growing cycles. Winter and facultative wheat cultivars are planted in the Ebro, Duero, Tagus, and Guadiana basins. Spring wheat cultivars are winter–sown in southern Spain (Guadalquivir basin). Bread wheat is the main wheat class, with a current area of approx. 1.8 million ha in north and central Spain, while durum wheat is grown on approx. 0.3 million ha and is the prevailing class in southern Spain (AETC, 2018).

ORIGIN OF WHEAT RUSTS AND THEIR PRESENCE IN SPAIN

Wheat was domesticated as cereal grain approx. 8,000 years BCE, in the Fertile Crescent (Zohary *et al.*, 2012). The most important species of cultivated wheat are *Triticum aestivum* L. subsp. *aestivum* (bread wheat) and *Triticum turgidum* L. subsp. *durum* (Desf.) Husnot (durum wheat). Leaf rust first originated from rust infected *Aegilops speltoides* in Israel while rust isolates from durum wheat derive from virulent genotypes on bread wheat (Liu *et al.*, 2014). The putative centre of origin of yellow rust is reported to be near the Himalaya region (Ali *et al.*, 2014), while that of stem rust is Central Asia, which is also the origin of barberry (Leonard and Szabo, 2005).

Three rust diseases probably adapted quickly to domesticated wheat in a 'host tracking' manner (Stukenbrock and McDonald, 2008). Cultivated wheat spread eastward and westward at approx. 1 km per year (Zohary *et al.*, 2012). In the west, wheat reached Turkey and later spread to the entire Mediterranean Basin, first arriving in Spain approx. 5,600–5,700 years BCE when the 'Neolithic culture' entered Spain. The first two introductions were likely via maritime travel on the Mediterranean Sea from Italy to the Valencia region (east of Spain), and by land through the Pyrenees to northern Spain. Another route is recorded via Morocco to southern Spain approx. 200 years later (García–Martínez de Lagrán, 2015). The expansion of the Neolithic culture was rapid in the Iberian Peninsula (during less than 300 years), and was likely facilitated by the network of Mesolithic peoples. The rust diseases presumably spread along with the cultivation of wheat.

Wheat rusts were important diseases in ancient times. Aristotle (384–322 BCE) mentioned that humidity produced the 'rust disease', and Theophrastus (371–287 BCE) recorded that rust was caused by sunshine and dew (Arthur, 1929). Stem rust uredospores have been retrieved from excavations in Israel from sites established in the late Bronze Age (1,300 BCE) (Kislev, 1982).

In Roman times (8th BCE to 5th ACE centuries) a divinity dedicated to wheat rusts was created, i.e. the god *Robigus*. The celebration *Robigalia* was established on April 25, and was one of the many agricultural festivals celebrated in the month of April. A prayer was recited and a red dog puppy was sacrificed on an altar in a forest outside Rome, Italy (current Via Cassia–Via Sesto Miglio cross, coordinates; 41.967156 N, 12.439740 W). There is also evidence of the Robigalia celebration taking place in *Hispania* (Roman Spain). At the archaeological sites of Mas Castellar de Pontós (Girona) and La Huelga (Palencia), remains of sacrificed dogs have been found that could be connected to Robigalia ceremonies (Adroher *et al.*, 1993; Lettow–Vorbeck *et al.*, 2014). The Spanish word for rust, *roya* derives from the Latin *Robigus*.

Pope Gregory I declared in 590 ACE that April 25 was a day to pray for a good harvest, i.e. the (major) Rogation Day. In western Christianity, a rogation is a public supplication consisting of blessing the fields, and asking for God's mercy through prayers like the Litany of the Saints (Gozalo de Andrés, 2003; Wikipedia, Rogation days, 2018). The coincidence of Rogation Day with Saint Mark's day is chance. Saint Mark died on that day in 68 ACE as a martyr in Alexandria (Egypt). Saint Mark's day (*día de San Marcos*) is still celebrated as a feast day in many villages and small towns throughout Spain, and it is common that people gather and eat together in the countryside on April 25 (Table 1).

DESCRIPTIONS OF WHEAT RUSTS IN THE MIDDLE AND MODERN AGES (5TH TO 19TH CENTURIES ACE)

It is not known whether the occurrence of wheat rust increased in Spain in the Middle Ages compared to Roman times. The 'honeymoon' hypothesis suggests that the severity of grain, especially wheat, diseases was low in Roman times and increased in the Middle Ages in North Europe, as bread wheat became the prevalent cereal (Dark and Gent, 2001). It is possible that Spain also underwent this 'honeymoon' effect, but the scanty records of rust attacks does not allow corroboration of this hypothesis. In the Book of Agriculture of G. Alonso de Herrera (16th century) there is a mention of 'rust', but on barley, and it is not clear if this referred to rust or to any foliar disease favoured by fog (Alonso de Herrera, 1818).

Barberry (*Berberis vulgaris*) is present in Spain, and three subspecies are reported to occur, subsp. *vulgaris*, *seroi* and *australis*. Moors may have planted barberry bushes as thorny hedges to border fields and gardens of *Al–Andalus* (Muslim Spain), and they also produced good quality jam from the berries (Roelfs *et al.*, 1992). Andalusian botanist Abu'l–Khayr cited the presence of barberry bushes in his 'Book of Agriculture' in the 11th century (Harvey, 1993). The expansion of barberry plantings may have contributed to increases in rust outbreaks in Spain, since this these plants are alternate hosts for stem rust and, as recently reported by Jin *et al.* (2010), also for yellow rust. As barberry only grows at altitudes above 1,000 m in southern Spain, but in the north can grow at lower elevations (300 m and above; López, 2007), it is likely that rust outbreaks due to barberry proximity first occurred in wheat cultivated in northern Spain.

Drought, locusts, birds, and ants were frequently cited as the main constraints to Spanish wheat production in the Late Middle and Modern Ages (12th to 19th century) (Alberola–Romá, 2012; Zadoks, 2013; Páscoa *et al.*, 2017), but rusts were rarely mentioned. Throughout the Middle Ages there were periods of climatic instability. From 1645 to 1715, the 'minimum of Maunder' (a reduction of solar activity) led to global cooling resulting in the so–called 'Little Ice Age' (Barriendos, 1997; Alberola–Romá, 2014). In the 40 year period of 1760 to 1800 the 'Maldà Oscillation' produced a 'moody' climate throughout the Spanish Mediterranean area, with years of severe drought and others of heavy rains (Barriendos and Llasat, 2009). Rust epidemics were probably not frequent, but they may have occurred with some regularity, especially in years with heavy rains in winter and spring.

A possible consequence of increased rust severity during this period was the retrieval of ancient wheat hulled species, einkorn, emmer and spelt, which are considered to be more resistant to wheat rusts than non-hulled varieties (Campbell, 1997; Hussien *et al.*, 1998; Zapata *et al.*, 2004). These cereal types, dominant in the Neolithic Period but in declining production at the time of the Roman Empire, may have been re-introduced to some extent to many places in Spain and Europe in the Middle Ages, especially in humid and mountainous land as found in many places in northern Spain (e.g. Asturias). Their cultivation continued until recently in that region (Dugan, 2008).

In S. Clemente's supplement (*adición*) to the book *Libro de Agricultura General* from Alonso de Herrera, it is stated that "*chamorro* [awnless] wheat is more resistant to rust because dew droplets do not build up in their spikes", but *candeal velloso* is more infected by rust due to its awned heads. To quote Alonso de Herrera (1818), "*Chapado velloso* and *moruno velloso* wheat [two kinds of durum wheat] resist well the rust".

DESCRIPTIONS OF WHEAT RUSTS IN THE 19TH AND EARLY 20TH CENTURIES

Throughout the 19th century European scientists reported the presence of rusts in wheat fields, but severe epidemics were rarely noted. Epidemics that occurred were of only local or regional importance, probably because of low crop intensification, long rotation periods between wheat crops, and diversity of wheat landraces. Yellow rust was the first to appear in February–March each growing season, followed by leaf rust in March–April and stem rust, the most damaging, in May. In Castille, straw and other materials were commonly burned to avoid dew formation on the leaves, and dew was removed by ropes each held by two people walking along the crop furrows. In 1877 stem rust epidemics were reported in Navarra (Ruiz de Casaviella, 1878), and leaf rust was also recorded in Teruel, Castellón and Guadalajara (González–Fragoso, 1918).

In 1923, during a trip to northern Spain, American plant pathologist E.C. Stakman observed greater presence of stem rust in fields close to barberry bushes than in other areas (Stakman, 1923). A brochure by the Spanish Ministry of Agricuture (*Ministerio de Agricultura de España*) in 1932 described the state of wheat rusts in

Table 1. Selected locations in Spain where Saint Mark's day is a popular feast.

Location	Province	Population[1] (2017)	Characteristics
Adra	*Almería*	24,697	Celebration
El Ejido	*Almería*	88,096	Local pilgrimage
Noreña	*Asturias*	5,210	Gastronomic fair
El Barraco	*Ávila*	1,886	Local pilgrimage
Almendralejo	*Badajoz*	33,540	Local pilgrimage
Talayuela	*Cáceres*	7,338	Celebration
Puente Genil	*Córdoba*	30,173	Local pilgrimage
Arroyo del Ojanco	*Jaén*	2,353	Local pilgrimage
Beas de Segura	*Jaén*	5,275	Local pilgrimage, bullfighting festival
Noia	*La Coruña*	14,295	Horse, livestock and machinery fair
Oleiros	*La Coruña*	35,198	Celebration
San Martín de la Vega	*Madrid*	18,824	Celebration, procession, bullfighting festival
Valdemoro	*Madrid*	73,976	Meal on park, typical sweet (*hornazo*)
Benaoján	*Málaga*	1,497	Festival, local pilgrimage
Cuevas de San Marcos	*Málaga*	3,722	Local pilgrimage, own name village, typical sweet (*hornazos de San Marcos*)
Alfarnate	*Málaga*	1,113	Local pilgrimage
Bullas	*Murcia*	11,546	Local pilgrimage
Yecla	*Murcia*	34,092	Local pilgrimage
Palencia	*Palencia*	78,892	Local pilgrimage
Agulo	*S.C. Tenerife*	1,066	Bonfire jumping
Tegueste	*S.C. Tenerife*	11,108	Local pilgrimage
Numancia de la Sagra	*Toledo*	4,755	Celebration
Gatika	*Vizcaya*	1,672	Celebration

[1] Locations shown are those with populations of more than 1,000 inhabitants.

Spain. The most common rust was listed to be stem rust, and the main control measures suggested were removal of barberry bushes near wheat fields, hot water treatment of wheat seed to kill the spores, and use of resistant wheat varieties. Praying to God was still considered as a disease control measure at the time (*Ministerio de Agricultura*, 1932).

Unamuno Irigoyen (1943), in his reception speech to the *Real Academia de Ciencias Exactas, Físicas y Naturales*, stated that, "from all known rust fungi there is no doubt that wheat rusts are the most important from an agricultural economy point of view, because of the great losses they cause on harvest". He also confirmed the absence of published data about the importance of rust fungi in Spain.

DESCRIPTIONS OF WHEAT RUST EPIDEMICS, RACES, AND RESISTANCE BREEDING FROM THE SECOND HALF OF THE 20TH CENTURY

The most severe rust attacks from 1950 onwards were in areas where wheat crop areas were largest and most intensified, with the Guadalquivir basin region (western Andalusia, south–west Spain) having the greatest rust severity. There are also reports of rust attacks in Girona (Catalonia, north–east). Until the 1950s, there was no information about rust races in Spain, and on many occasions wheat rust diseases and their causal species were confounded, especially leaf and stem rust. The first scientific studies were carried out by M.J. Urríes after his stay in 1947 with W.Q. Loegering at the Minnesota Agricultural Experiment Station (Co-operative Rust Laboratory at St. Paul, Minnesota, USA) to study stem rust. He later collaborated with agronomists R. Cañamas and J. Salazar from INIA in Madrid (Fernández, 1964). J. Salazar continued his research at the *Centro de Cerealicultura* (Center for Cereal Research) in Madrid in the 1950s, 1960s, and 1970s. He surveyed the virulence of the main stem and leaf rust races in Spain. The main highlights relating to epidemics, race surveys, and breeding for resistance to the three wheat rust diseases are presented here.

YELLOW RUST

Yellow rust epidemics in Andalusia

Yellow rust rarely produced epidemics in Spain, but in 1957 and 1960 severe yellow rust outbreaks were reported on bread wheat in the Guadalquivir basin (Zadoks, 1960). Only a few years earlier, French (Florence Aurore) and Italian (Mara, Impeto) cultivars had been imported in an attempt to increase the low yields of typical older Spanish landrace varieties. Concurrently, changes in cultural practices such as increased seed rates and enhanced N fertilization were implemented for wheat crops. In 1978 another more severe yellow rust epidemic occurred in the Guadalquivir basin. According to Nagarajan *et al.* (1984), these epidemics were caused by a 'perfect storm' of conditions favourable to yellow rust, including:

1. Replacement of varieties. The cultivars Mahissa 1 and Siete Cerros (of CIMMYT origin) had replaced a multitude of landraces and varieties, but the replacements were highly susceptible to yellow rust. However, other new cultivars such as Cajeme, Yecora, Cocorit and Mexicale were resistant (Alvarado and Morillo, 1978).

2. Presence of yellow rust inoculum. In 1976 and 1977, severe yellow rust epidemics were recorded in many parts of the south–west Mediterranean Basin, such as Tunisia and Algeria. Those countries were also replacing old landraces with high yielding, semi–dwarf CIMMYT cultivars, and airborne spores could easily have reached Andalusia from these countries.

3. Favourable weather for the development of the disease. Heavy rains in the Guadalquivir basin were reported in the spring of 1978, with many cloudy days and mild temperatures.

However, Nagarajan *et al.* (1984) made *P. striiformis* isolate surveys, and ruled out the presence of a new virulent race. The main races were 40E008, 40E136 and 41E136 (Johnson *et al.*, 1972), which belonged to the 'French group' and the 'Levantine group'. At this time wheat cultural practices also intensified (increased plant density and fertilizer applications). The epidemics prompted the former *Instituto Nacional de Semillas y Plantas de Vivero* (National Institute of Seed and Nursery Plants) to demand resistance to yellow rust as a prerequisite to register a variety (Palmero *et al.*, 2008). Yellow rust severity rapidly decreased thereafter.

The 'Warrior' yellow rust race

From 1980 yellow rust did not cause significant damage in Spain, but in 2012 yellow rust epidemics were again reported on bread wheat at several Spanish locations. The newly created Global Rust Reference Center (GRRC) in Denmark (GRRC, 2018) surveyed Spanish yellow rust races, and all matched the 'Warrior' race. This race was first detected in 2011 in Denmark, France, Germany, Sweden, United Kingdom, and Spain, often at high frequencies. The race replaced previous populations, from which it was clearly different, since it originated from a population close to the Himalayas (Hovmøller *et al.*, 2016). The rapid spread of the 'Warrior' race from northern to southern Europe was due to its virulence on most bread wheat cultivars, including the British cultivar 'Warrior', from which the race takes its name. The race displays a high number of virulence alleles, including those for *Yr1, Yr2, Yr3, Yr4, Yr6, Yr7, Yr9, Yr17, Yr25*, *Yr32*, and *YrSp* (Table 2).

Previously, in 2008 and 2009, yellow rust was found on some bread wheat cultivars in Navarra (northern Spain). In 2011 yellow rust severity increased in Navarra, and in 2012 spread to other locations in northern Spain (Aragon, Castilla y León). In 2013 yellow rust spread south (Castilla La Mancha, Andalusia) and east-

Table 2. Races of *Puccinia striiformis* f. sp. *tritici* (yellow or stripe rust) in Spain during 2010–2016, according to the Global Rust Reference Center.

Pu. striiformis f. sp. *tritici*	Year						
	2010	2011	2012	2013	2014	2015	2016
Race name	PstS2v17v27	PstS2v27, PstS2v27v17, PstS3v2v25v27, Warrior	Warrior	Warrior	Warrior	Warrior, Warrior(-), Triticale 2006	Warrior(-)
Frequency (%)	100	29/14/43/14	100	100	100	44/44/12	100
No. isolates	2	8	6	8	6	9	5

[1] Virulence of race PstS2v27 (*Yr2,6,7,8,9,25,27*), PstS2v17v27 (*Yr2,6,7,8,9,17,25,27*), PstS3v2v25v27 (*Yr2,6,7,8,25,27*), Warrior (*Yr1,2,3,4,6,7,9,17,25,32,Sp,Amb*), Warrior (-) (*Yr1,2,3,4,6,7,9,17,25,32,Sp*), and Triticale2006 (*Yr2,6,7,8,10*).

wards (Catalonia). Farmers had to treat bread wheat crops with fungicides in many locations. The GENVCE (Spanish Group for Screening Field Crops New Varieties) field tests in 2013/14 found that the cultivars Artur Nick, Gazul, and Valbona were resistant (Gómez-Caño, 2016).

In 2014 yellow rust epidemics intensified. As an example, in 2013 variety Altamira was susceptible only in Navarra, but in 2014 it was also susceptible in Castilla y León, Aragón, and Madrid. As well, important cultivars in Spain such as CCB Ingenio, Artur Nick and Nogal became susceptible to yellow rust. In 2015, race Triticale 2015, first detected in Scandinavia and virulent on many triticale cultivars, was found in Spain by GRRC researchers (GRRC, 2018).

For durum wheat, in 2013 the cultivars Gigadur, Lecitur, Clovis and Massimo Meridio showed yellow rust symptoms in Andalusia and Extremadura. In 2014 yellow rust was also recorded in Castilla y León in durum wheat crops. Yellow rust severity on durum wheat increased and was similar to that on bread wheat in many regions in 2016. In research on yield losses in durum wheat due to yellow rust, performed at a field trial in Aranjuez (Madrid), Vergara–Diaz *et al.* (2015) reported a mean yield loss of 18%, while two cultivars suffered 57% losses. The numbers and weights of kernels decreased, but head numbers were not affected by the disease.

A new yellow rust race was detected in 2016 in Morocco and Sicily (Italy) by the GRRC. This race, named PstS14 and virulent on *Yr2, Yr3, Yr6, Yr7, Yr8, Yr9, Yr17, Yr25, Yr32,* and *YrSp* was detected in Spain in 2018 (GRRC, 2018). Yellow rust severity on the Avocet differential host set at three locations of Andalusia (2016–2017) is presented in Table 3. Resistance genes *Yr5, Yr10, Yr15* were effective in all locations, and Avocet lines with *Yr1* and *Yr8* genes showed resistance to most tested isolates. Yellow rust infections decreased slightly by 2017 in durum and bread wheat crops throughout Spain.

Table 3. Severity of yellow rust (*Puccinia striiformis*) on the Avocet bread wheat near–isogenic differential, set at three locations in the Guadalquivir basin of Andalusia during 2016 and 2017.

Differential genotype	Yellow rust severity		
	Escacena del campo (Huelva)	Écija (Sevilla)	Jerez de la Frontera (Cádiz)
Year	2016	2017	2017
Avocet S	70	-	15
Avocet (*YrA*)	30	20	30
Yr1/6*Avocet S	30	0	0
Yr5/6*Avocet S	0	0	0
Yr6/6*Avocet S	60	40	15
Yr7/6*Avocet S	60	40	20
Yr8/6*Avocet S	5	8	10
Yr9/6*Avocet S	50	80	10
Yr10/6*Avocet S	0	0	0
Yr15/6*Avocet S	0	0	0
Yr17/6*Avocet S	40	40	5
Yr18/6*Avocet S	40	80	20
Yr24/6*Avocet S	15	30	15
Yr26/6*Avocet S	15	20	5
Yr27/6*Avocet S	20	7	2
Yr32/6*Avocet S	50	40	15
YrSp/6*Avocet S	30	3	0

LEAF RUST

First race surveys (1968–1977)

J. Salazar initiated the first leaf rust surveys in Spain. In 1973 he published research on 159 rust samples collected from 1968 to 1971 (151 from bread wheat, seven from durum, and one from triticale) that were characterized for their virulence. He identified 31 races, using a differential set based on five varieties. The most common race was found in 23 isolates, and the five main races comprised 52% of total isolates (Salazar and Brañas, 1973b). In another study performed during 1972 to 1975, 178 samples were collected and 33 races identified. Rust samples were taken from Tortosa (Tarragona), Borjas Blancas (Lleida), La Alberca (Murcia), and La Coruña. None of the races were virulent on variety Malakoff (*Lr1*), and the prevailing races were similar to those found previously (Salazar and Brañas, 1977). These results were published as reports without details regarding methods, which makes it difficult to fully understand the study.

Leaf rust epidemics on durum wheat (1997–2004)

Durum wheat is a traditional crop in southern Spain with average crop areas of approx. 200,000 ha since the 19th century. In 1992, however, area of durum wheat increased when the European Union implemented a supplement subsidy (in the Common Agricultural Policy) for cultivation of this crop (Royo, 2005). Durum acrea reached a peak of 940,000 ha in 2003/04. Although durum wheat was generally considered more resistant to leaf rust than bread wheat, from 2001/02 leaf rust epidemics on durum wheat were recorded at many locations in the Guadalquivir basin. Most durum cultivars were susceptible. Only the Italian variety Colosseo (with *Lr14a* gene) was resistant. Other resistant Italian cultivars such as Italo, Vinci, and Virgilio were brought to Spain in the 2004 growing season (RAEA, 2004). However, most bread wheat cultivars were resistant to leaf rust during this period.

In 2001 a severe leaf rust epidemic was reported in Mexico where durum wheat variety Altar C84, resistant to leaf rust for almost 20 years, became susceptible. The new virulent race, designated as BBG/BN, caused losses valued at $US 32 million in Mexico over the course of 3 years (Singh *et al.*, 2004). Many durum cultivars from CIMMYT, including Altar, carried the *Lr72* gene that protected from many races, including leaf rust races from bread wheat (Herrera *et al.*, 2014). A mutation at the virulence locus corresponding to *Lr72* resulted in a race virulent to most durum wheat cultivars. The variety Gallareta, an Altar sibling, was one of the most cultivated cultivars at that time in Spain, and this displayed susceptibility. As most durum wheat cultivars sown in Spain had CIMMYT origins, many probably carried the *Lr72* gene.

In field trials on yield losses due to foliar diseases in durum wheat in the Guadalquivir basin during the 2000–2001 and 2001–2002 growing seasons, yield losses reached 28 to 30% in susceptible cultivars. Both seasons were characterized by high levels of leaf rust infections (Cátedra and Solís, 2003).

Martínez *et al.* (2005) studied the virulence of 56 single pustule leaf rust isolates from durum and bread wheat, collected from several Andalusian locations during 1998–2000 (Table 4). Thirty–five races were identified using the Thatcher near isogenic lines as differentials. No race was virulent to genes *Lr9* and *Lr24*. Bread wheat races were different from durum wheat races, and the bread wheat races were more variable than those from durum wheat (Kolmer *et al.*, 2013). None of the durum races were virulent to *Lr1, Lr3, Lr15, Lr16* and *Lr17* genes, whereas several bread wheat isolates were virulent to these genes.

A worldwide study of durum wheat leaf rust virulence performed by the Cereal Disease Laboratory (CDL) (Minnesota, USA) determined that Spanish and Italian races grouped together (Kolmer and Liu, 2000). The races were classified as DBBDML, having virulence/avirulence spectra of *Lr2c, 10, 14b, 20, 23 / Lr1, 2a, 2c, 3, 9, 16, 24, 26, 3ka, 11, 17, 30, B, 3bg, 14a, 15, 18, 28*. In a later study, seven isolates taken from durum wheat in Andalusia during the period 2000 to 2003 were found to be similar to isolates from Spain, France, and those from America, suggesting a common origin (Ordoñez and Kolmer, 2007).

Table 4. Frequency of *Puccinia triticina* (leaf or brown rust) isolates virulent on Thatcher near–isogenic lines, collected in Spain and Andalusia in different years.

Genes / locations[1]	Salazar 1972–75	Andalusia 1997	Andalusia 1998–2000	Andalusia 1998–2000 (durum)	Andalusia 2000–03 (durum)	Andalusia 2009–13 (durum)
Lr1	3	0	30	0	0	1.2
Lr2a	17	0	2	0	0	0
Lr2b	52	0	34	47		
Lr2c	88	100	73	100	0	100
Lr3	53	40	41	0	0	3.6
Lr3bg		40	41	0	0	3.6
Lr3ka		10	25	0	0	0
Lr9		0	0	0	0	0
Lr10		100	89	87	100	97.6
Lr11	73	0	96	100	0	0
Lr12			100	100		
Lr13			56	20		
Lr14a		20			0	13.2
Lr14b		100	98	93	14.3	98.8
Lr15		0	30	0	0	
Lr16		30	30	0	0	1.2
Lr17		20	32	0	0	0
Lr18		50	96	100	0	57.8
Lr19		0	0	0	0	
Lr20		60	71	93	100	100
Lr21		0	98	100		
Lr22			100	100	14.3	
Lr23		100	79	87	100	
Lr24		0	0	0	0	0
Lr25		0	0	0	0	
Lr26		0	7	7	0	0
Lr28		0	9	0	0	0
Lr30		10	13	0	0	0
Lr32		0	9	0	0	
Lr34			100	100		
Lr35			82	73		
Lr37			100	100		
LrB		60	64	47		
Thatcher		100	100	100	100	100
No. isolates	178	10	56	15	8	83

[1] Modified and here reproduced with the permission of the copyright holder from Martínez *et al.* (2005).

From 2004 onwards, rust attacks in Spain began to decrease. Farmers regularly applied fungicides to their crops, new durum cultivars from breeders were released in the Guadalquivir basin with resistance to leaf rust, and the environmental conditions of subsequent seasons (mainly low rainfall) were unfavourable to rust epidemic development.

Many of the recently released durum wheat resistant cultivars carried *Lr14a* located on chromosome 7BL. This gene, from the emmer cultivar Yaroslav, was transferred to bread wheat and then to durum wheat. The Italian cultivar Creso (released in 1974) carried this gene, and for more than 30 years was resistant to all leaf rust races. Many durum wheat cultivars worldwide inherited the *Lr14a* gene, including Italian variety Colosseo and Spanish variety Don Jaime (Martínez *et al.*, 2005).

New races virulent to Lr14a in Spain

Pustules of high infection type were observed on the cultivars Colosseo and Don Jaime in the Spring of 2013, at widely separated field trials at Conil de la Frontera (Cádiz, southern Spain) and La Tallada d'Empordà (Girona, north–east Spain). This confirmed that virulence to *Lr14a* gene was present in Spain (Table 5). Additionally, this race was different from the reported French races virulent to *Lr14a* that were avirulent to *Lr72*, while the Spanish races were also virulent to *Lr72* (Soleiman *et al.*, 2016).

Durum wheat breeding programmes are also using other genes for resistance to leaf rust. Herrera–Foessel *et al.* (2005) reported the presence of new genes in durum cultivars, such as the complementary genes *Lr27* + *Lr31* (present in CIMMYT variety Jupare or in Spanish Don Ricardo), *Lr61* (present in CIMMYT variety Guayacán), *LrCam* (present in Camayo) and *Lr3* (present in Storlom). At the same time a high level of partial resistance was found in some durum wheat cultivars (Herrera–Foessel *et al.*, 2008). Further research has identified novel resistance genes to be deployed in the near future in durum wheat from wild relatives but already in the bread wheat background, i.e. *Lr19* (from *Lophopyrum ponticum*), *Lr47* (from *Triticum speltoides*), and *Lr37* (from *Triticum ventricosum*). Other research has focused on selecting durum landraces, lines or old varieties with leaf rust resistance. Loladze *et al.* (2016) found usable resistance in the durum varieties Gaza, Amria, Geromtel_3, Geruftel_1, Tunsyr_2, and Biblos, of varied origins.

Table 5. Resistance responses of 20 near–isogenic lines and eight durum genotypes, each at the 5th leaf growth stage, to two races of *Puccinia triticina* (leaf or brown rust), from 2009–11 and the race of 2013.

Genotype	Race and infection type		
	Isolates 2009–11		Isolate 2013
	DBB/BN	DBB/CN	DBB/BS (Conil, Girona)
Thatcher	S	S	S
Lr1	R	R	R
Lr2a	R	R	R
Lr2c	S	S	S
Lr3	R	R	R
Lr3bg	R	R	R
Lr3ka	R	R	R
Lr9	R	R	R
Lr10	S	S	S
Lr11	R	R	R
Lr13	R	R	R
Lr14a	R	R	S
Lr15	R	R	R
Lr16	R	R	R
Lr17	R	R	R
Lr18	R	S	R
Lr23	S	S	S
Lr24	R	R	R
Lr26	R	R	R
Lr30	R	R	R
Jupare (*Lr27+31,Lr72*)	R	R	R
Gallareta (*Lr72*)	S	S	S
Somateria (*Lr14a+*)	R	R	S
Colosseo (*Lr14a+*)	R	R	S
Don Jaime (*Lr14a+*)	R	R	S
Storlom (*Lr3,Lr72*)	R	R	R
Guayacán (*Lr61*)	R	R	R
Camayo (*LrCam*)	R	R	R

[1] R indicates a resistance response and S a susceptible response. Modified and here reproduced with the permission of the copyright holder from Soleiman *et al.* (2016).

In a study of gene postulation in bread wheat, the presence of resistance genes *Lr1, Lr10, Lr13, Lr20, Lr26* and *Lr28* was confirmed (Martínez *et al.*, 2007). In durum wheat, the resistance responses of most cultivars when inoculated with several leaf rust isolates did not match with any of the *Lr* genes from the Thatcher differential series. Some cultivars also had some levels of partial resistance (Martínez *et al.*, 2007). Another study was performed by the same group to characterize leaf rust resistance in a collection of 917 accessions from the Spanish Center for Genetic Resources (CRF–INIA). Susceptible reactions were normal, and only 6% of total entries (4.8% in durum, 11.9% bread wheat) had severities less than 20% compared to the susceptible check (Figure 2). Seven susceptible accessions (six bread, one rivet wheat) were also identified with fair levels of partial resistance (Martínez *et al.*, 2001).

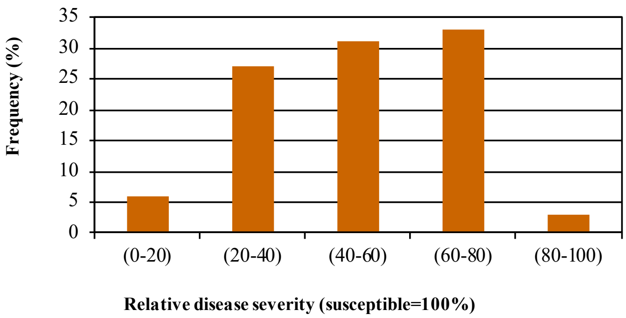

Figure 2. Relative leaf rust (*Puccinia triticina*) severity in a collection of 917 Spanish wheat landraces, planted at Cordoba, Spain in 1996/97. Here reproduced with the permission of the copyright holder from Martínez *et al.* (2001).

STEM RUST

Initial studies (1948–1971)

M.J. Urríes collected stem rust samples during 1948 to 1961 when this rust predominated, for identification of races using the Stakman differential set (Urríes and Arzoz, 1961). Subsequently, J. Salazar and M. Brañas monitored stem rust in the period 1968 to 1971, and reported only mild attacks in the field. From the 120 rust samples they collected, the majority were taken from bread wheat, although some were from barley and *Aegilops* spp. A total of 15 races were found, and their virulence profiles in samples from 1948, 1961 and 1968 to 1971 are displayed in Table 6. Samples collected near barberry bushes belonged to a group of races different from the isolate group collected at distance from barberry. The majority of races tested were avirulent to varieties Reliance (*Sr5*), Vernal (*Sr9e*) and Khapli (*Sr13*) (Salazar and Brañas, 1973a).

Stem rust vanishes by the mid–1970s

The first CIMMYT wheat cultivars were introduced to Spain in the early 1970s and these had earlier heading dates than most cultivars cultivated in Spain at that time. In Andalusia, harvest date was advanced by about a month, to May 25 to June 15. Stem rust did not appear on wheat leaves until the end of April each year, by which time it was too late to cause epidemics and the disease gradually disappeared from wheat fields. Furthermore, these new CIMMYT cultivars carried the *Sr2* gene that provided partial resistance and was effective worldwide (Singh and Rajaram, 2002). However, at present in off–season summer field trials under irrigation performed by some wheat breeding companies, pustules of stem rust can be seen at some locations, e.g. Conil de la Frontera (Cadiz) in southern Spain.

Table 6. Virulence of isolates of *Puccinia graminis* f. sp. *tritici* (stem rust) collected in Spain over several time periods and tested on a set of differentials wheat genotypes.

Differential	*Sr* gene	Year[1]		
		1948	1961	1968–71
Little Club	Susc.	100	100	100
Marquis	*Sr7b*	46.6	37.2	55.8
Reliance	*Sr5*	6.6	0.5	9.2
Kota	*Sr28*	22.6	33.3	32.5
Arnautka	*Sr9d*	86.6	47.6	51.7
Mindum	*Sr9d*	86.6	47.6	52.5
Spelmar	*Sr9d*	86.6	47.6	53.3
Kubanka	*Sr9g*	100	100	81.7
Acme	*Sr9g*	100	100	79.2
Einkorn CI2433	*Sr21*	65.3	21.9	40.0
Vernal	*Sr9e*	2.6	0.2	3.3
Khapli	*Sr13*	0	0	0
No. isolates		–	510	120

[1] Analyses performed in 1948 and 1961 by Urríes and Arzoz (1961). The 1968–71 analyses were performed by Salazar and Brañas (1973a).

The 'Sicily threat' of 2016

In 1999 a new virulent stem rust race, named Ug99, appeared in Uganda, and subsequently spread throughout East Africa (Wanyera *et al.*, 2006). In 2003 this race was found in Ethiopia and then crossed the Red Sea. In 2007 it was detected in Iran, but was controlled by releasing resistant cultivars led by international co-operation. No sign of stem rust was seen in Spain during this period.

In 2016 a severe stem rust epidemic was recorded in Sicily affecting 20,000 ha of durum wheat. The race involved was different from Ug99 and was virulent to genes *Sr9e* and *Sr13*. Both genes are common in durum cultivars (Bhattacharya, 2017). A risk analysis by the GRRC predicted the possibility that spores of the Sicilian stem rust race (TTRTF) were already in the eastern regions of the Iberian Peninsula (GRRC, 2018). However, to our knowledge stem rust race TTRFT has not yet been detected in Spain.

CONCLUSIONS

Wheat rust outbreaks occur from time to time but are difficult to predict. The main factors promoting epidemics are: 1) the presence of airborne inoculum that can be dispersed over very long distances, 2) novel pathogen races with virulence to the main *R*–genes, 3) deployment of susceptible host cultivars, 4) particular cultural practices, such as a high crop seed rates, monoculture, and irrigation, and 5) changing weather conditions. These factors are difficult to control, as continents and many countries are involved. International co-ordination is needed to monitor the movement of inoculum, identify prevailing races and their virulence, and gain knowledge of the rust resistance genes present in the cultivated wheat cultivars, in Spain and worldwide. As such, and emphatically, the monitoring and research carried out by the Borlaug Global Rust Initiative (BGRI, 2018), and the Global Rust Reference Center (GRRC, 2018) are crucial. Additionally, at the Spanish national level, it is important that disease alert systems such as RAIF in Andalusia (RAIF, 2018) are adequately maintained into the future.

The use of rust resistant cultivars is important, preferably deploying effective *R*–genes against the prevailing pathogen races prevailing in a region. Many plant breeding companies and institutions are attempting to combine the common type of resistance (monogenic, vertical and hypersensitive) with more difficult to manage partial resistance (polygenic, and horizontal), to enhance the durability of the resistance.

Diversification of crop genetics is also relevant. Rust epidemics in the second half of the 20th century were partly the result of crop intensification and reductions in the number of wheat cultivars grown, which were often genetically related and shared the same *R*–genes. Diversity solutions such as extended crop rotations, cultivar mixtures, segregating host populations, regional control to deploy cultivars with different *R*–genes, and genes for partial resistance, are all advisable rust management strategies (McDonald and Linde, 2002). The consequences of new cultural practices for wheat (including irrigation, new fertilizers, increased seeding rates, hybrid cultivars, and high–yielding susceptible cultivars) with respect to rust epidemics are yet to be seen. This may be controversial, as cultivars with *R*–genes normally have small yield penalties, and many farmers prefer to use high–yielding but susceptible cultivars, and apply fungicides to maximize their incomes. It is not always possible, however, to apply fungicides or do so in a timely manner. In addition, susceptible cultivars may act as inoculum reservoirs for any of the three wheat rust pathogens.

An array of fungicide classes (triazoles, strobilurins, carboxamides) are available for farmers. Fungicides are relatively affordable, effective, and they can control other foliar diseases as well as rusts. However, their application should be discouraged when resistant cultivars are available, as fungicide use will reduce farmer profitability and contribute to increased environmental footprints. Fungicides are certainly warranted when resistance is not available, or is not fully effective, particularly if rust outbreaks are forecasted to cause significant yield losses.

What may be expected of the three rusts in future

Yellow rust is the most unpredictable rust. The epidemics of 1958, 1978, and 2012 in Spain appeared suddenly and caused significant yield losses. Potential damage from epidemics decreased in importance when breeders released new resistant wheat cultivars and farmers applied fungicides. New races adapted to warm temperatures may become more prevalent and infect wheat for longer periods than expected.

Leaf rust is the most common rust in Spain, although it rarely causes major problems. Most of the durum and bread wheats grown contain effective *Lr* genes. However, virulence analyses of the prevailing races, and severity assessments in rust–prone regions, must continue to be carried out.

Stem rust has not been detected in Spain since the early 1970s although it may be present at low frequencies. It is important to carefully monitor this rust in view of the durum wheat stem rust outbreak of 2016 in Sicily.

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