밀 줄녹병 저항성 유전 육종 주요 연구 동향

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Research Advances in Wheat Breeding and Genetics for Stripe Rust Resistance

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Abstract Stripe rust (or yellow rust) caused by *Puccinia striiformis* f. sp. *tritici* is the major wheat disease responsible for deteriorating global wheat yield and quality. Although stripe rust appears to be prevalent mainly in temperate areas, new races adapting to high temperature have recently appeared in warmer areas, such as Australia, the Middle East, and Africa, increasing the threat to global food security. Among the approximately 80 reported genes for stripe rust resistance, six (*Yr5*, *Yr7*, *Yr15*, *Yr18*, *Yr36*, *Yr46*) have been cloned. Stripe rust resistance genes are generally classified into race-specific (or all-stage) and non-race-specific (or high temperature adult plant) resistance genes. While resistance conferred by most race-specific genes are overcome by the appearance of new pathogen races within few years, non-race-specific genes, such as *Yr18*, *Yr36*, and *Yr46*, provide more durable resistance and are often stable for several decades. *Yr18/Lr34/Sr57/Pm38* and *Yr46/Lr67/Sr55/Pm46* are especially useful in breeding as they confer resistance to leaf rust, stem rust, and powdery mildew as well as stripe rust. Unlike the extensive global research efforts, few studies have been conducted in Korea regarding breeding and genetics for stripe rust resistance. To prevent damage by stripe rust in advance, it is important to monitor the changes in major pathogen races in Korea, evaluate major wheat breeding lines and landraces for stripe rust resistance by establishing an efficient screening system, and introduce new germplasm with various resistance genes. Reinforcing wheat molecular genetics and genomics capacity is also important to enable identification of new stripe rust resistance genes and efficient transfer of the novel genes into elite wheat cultivars using molecular markers.

Keywords wheat, stripe rust, yellow rust, resistance, breeding

Received on May 6, 2020. Revised on May 6, 2020. Accepted on May 12, 2020.

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서 언

녹병은 전세계적으로 밀의 수량과 품질을 위협하는 대표적인 질병으로 잎녹병(leaf rust), 줄기녹병(stem rust 또는 black rust), 줄녹병(stripe rust 또는 yellow rust)으로 구분된다(Cummins & Hiratsuka 2004, Duplessis et al. 2011, Figueroa et al. 2018). 밀 줄녹병균인 *Puccinia striiformis* Westend. f. sp. *tritici* (*Pst*)는 서늘하고 습한 온대 지역에서 흔히 발생해서 지난 50년 동안 60개국 이상에서 보고되었지만, 2000년 이후에는 고온환경에 적응한 전염력이 강한 *Pst* 병원균 발생으로 점차 발생 지역과 빈도가 증가하는 추세이다(Chen 2005, Ali et al. 2014, Beddow

et al. 2015). 유럽, 호주 및 북미에서 발생하는 *Pst*는 대부분 다양성이 낮으나 중국 서부, 중앙아시아, 히말라야 근처에서 발병하는 *Pst*는 유전적 다양성이 상대적으로 높다고 보고되었다(Hovmoller et al. 2011, Ali et al. 2014, Chen et al. 2014). 2011~2013년과 2015년에 히말라야 근처에서 기원하는 *Pst* 병원균의 변이체는 유럽 전역에 발병하여 큰 피해를 초래하였다(Hovmoller et al. 2015, Hubbard et al. 2015).

Pst 병원균의 발병지역은 크게 10개의 역학 지역(epidemiological zones)으로 구별되는데, 최대 발병지역은 80% 이상의 수량 감소가 일어나고, 발병이 적은 지역은 5~10% 정도 수량이 감소하며, 평균적으로는 35% 이상의 수량 감소가 발생한다(Ali et al. 2014).

전세계 밀 품종의 88%는 *Pst*에 저항성이 없기 때문에 이로 인해 매년 약 10억 달러 정도의 경제적 손실이 일어나는데, 호주에서만 약 9천만 달러의 손실이 보고되고 있다(Murray & Brennan 2009, Beddow et al. 2015, Wellings 2011, Chen et al. 2014).

녹병균을 제어하는 방법은 화학적인 방법과 유전적인 방법이 있다. 병원균 매개체가 될 수 있는 녹색교량(green bridges)를 제거하는 경작적인 방법이 우선적인 방법이 될 수 있고, 다음으로는 살균제를 이용한 화학적 방법인데, 현재 승인된 녹병 살균제로는 quinone outside inhibitors (QoIs), 14 α -demethylation inhibitors (DMIs), succinate dehydrogenase inhibitors (SDHI) 등이 이용되고 있다(Oliver 2014). 그러나 많은 국가에서 적절한 살균제를 찾기가 쉽지 않고 부적절한 사용으로 인하여 인체와 환경에 심각한 피해가 발생하기도 하여 이로 인한 비용 증가가 문제점으로 대두되고 있다(Kolmer et al. 2007, Arduini et al. 2012, Kumar et al. 2013, Oliver 2014). 많은 지역에서는 녹병 방제를 위해서 초기 생육시기의 살균제를 통한 방제와 지속적인 포장 관리와 모니터링을 기본으로 하는 병해충 종합관리(integrated pest management, IPM)가 실질적인 방안으로 제시되고 있다(Jorgensen et al. 2008).

보다 효과적이고 경제적이면서 환경친화적인 방법은 저항성 품종 개발이지만 이를 위해서는 시간과 노력이 많이 요구된다

(Singh et al. 2000, Todorovska et al. 2009, Oliver 2014). 줄녹병은 현재까지 80여개의 저항성 유전자가 알려져 있는데(McIntosh et al. 1995, 2014, Chen 2005, Dakouri et al. 2013, Gessese et al. 2019), 이를 이용하여 저항성 품종을 효과적으로 육성하기 위해서는 목표 지역의 우점 균계를 파악하고 해당 균계에 효과적인 저항성 유전자를 우량 품종에 신속히 이전시켜야 하며, 다수의 유전자를 한 품종에 집적시킴으로써 균계 변화에도 대응해야 한다(Periannan et al. 2017, Mundt 2018). 본 논문은 국내 환경에 적합한 줄녹병 저항성 밀 품종 육성에 필요한 정보를 정리하였다.

본 론

줄녹병 생활사

녹병균은 숙주식물에 기생하여 성장과 번식을 하는데, 밀에서는 여름포자(urediniospores), 겨울포자(teliospores), 담자포자(basidiospores)를 형성하고 밀이 아닌 다른 대체숙주에서는 병포자(pycniospores)와 녹포자(aeciospores)를 형성한다(Cummins & Hiratsuka 2004, Bolton et al. 2008, McIntosh 2009, Jin et al. 2010, Duplessis et al. 2011). 줄녹병은 *P. striiformis* f. sp. *tritici* (*Pst*)에 의하여 발생하며 생활사는 Fig. 1과 같다(Zheng et al. 2013). 매자나무속(barberry)인 *Mahonia* spp.와 *Berberis*

Fig. 1. Life cycle of *Puccinia striiformis* (Zheng et al. 2013). This figure was imported from the open access article licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License (<http://creativecommons.org/licenses/by-nc-nd/3.0/>).

spp.이 줄녹병의 대체숙주로 알려져 있지만 잎녹병과는 달리 자연상태에서는 이들이 밀에 녹병을 퍼뜨리는 역할을 하지는 않는다(Chen et al. 2014).

줄녹병의 감염은 4°C에서 시작되어 7°C가 적정온도이며 잎녹병이나 줄기녹병과 달리 밀에 침투하기 위한 부착기(appressoria)를 형성하지 않고, 생식관이 잎의 기공을 직접 관통하여 흡입 모세포(haustorial mother cells)를 형성한 후에 긴 균사(hyphae)가 잎의 길이 방향으로 자라게 되어 잎에 노랑색 내지 주황색의 포자(uredospore pustules)가 직선의 줄무늬 모양으로 나타나게 된다(Moldenhauer et al. 2006, Chen et al. 2014, Fig. 2). 줄녹병 감염은 건물중, 뿌리 생장, 간장, 이삭 및 종실의 개수와 크기에 영향을 주며, 이러한 영향은 유묘기 감염이 가장 크지만 개화·수정기에 시작된 감염도 수량에 영향을 준다(Wellings 2011).

줄녹병 저항성 기작

줄녹병 저항성은 두 가지 형태가 존재한다. 첫번째 형태는 전단계 저항성(ASR, all-stage resistance)이라고 하는데, 이들은 잎녹병의 유묘기 저항성(SR, seedling resistance) 유전자처럼 생육 초기에 저항성을 나타내며, 같은 병원균에 대해서는 성체에서도 저항성을 유지하기 때문에 줄녹병에서는 ASR로 구분한다. 줄녹병의 ASR은 잎녹병의 유묘기 저항성과 마찬가지로 주동유전자(major gene)가 주로 관여한다(Chen & Line 1995a, 1995b).

Fig. 2. Symptoms of wheat stripe rust disease caused by *Puccinia striiformis* f. sp. *tritici*. Photo courtesy: Yue Jin, USDA Agricultural Research Service, Image Number D517-1 (<http://www.ars.usda.gov/is/graphics/photos/jun06/d517-1.htm>). As indicated in the copyright policy (<https://www.ars.usda.gov/oc/images/copyright/>), photos in the USDA-ARS Image Gallery are available free of charge and are copyright-free, public domain, images unless otherwise indicated.

두번째 형태는 고온성체저항성(HTAP, high temperature adult plant resistance)으로 구분되는데, HTAP는 생육 후기의 온도가 21°C 이상이 되면서 병원균이 쉽게 퍼지는 시기에 저항성을 보인다(Qayoum & Line 1985). 줄녹병의 HTAP 저항성 유전자는 유묘기에는 감수성을 나타내지만, 잎녹병의 성체 저항성(APR, adult plant resistance)처럼 성체가 되면 줄녹병에 대한 저항성을 나타낸다(Chen & Line 1995a, 1995b, Line & Chen 1995). 이러한 형태의 저항성 유전자로 대표되는 것들은 *Yr18*, *Yr36*과 *Yr46*이 있지만 이들의 정확한 저항성 기작에 대해서는 알려진 것이 적다(Ellis et al. 2014). 유전자 동정을 통하여 *Yr36*이 WKS (Wheat Kinase-START) 단백질을 코딩하는 것이 밝혀졌고, *Yr18*과 *Yr46*이 각각 ABC (ATP-binding cassette) transporter와 hexose transporter를 만든다는 정도만 밝혀졌다(Krattinger et al. 2009, Moore et al. 2015, Dodds & Lagudah 2016).

줄녹병 저항성 유전자

줄녹병 저항성 유전자는 *Yr*로 표기하며 주요 저항성 유전자의 정보는 Table 1에 정리하였다. 줄녹병균인 *Pst*의 높은 다양성과 빠른 변이로 인하여 새로운 병원균이 지속적으로 발생하는데, 이로 인해 기존 유전자가 무력화 되는 경우가 많이 발생한다. 1990년대에 *Yr2*와 *Yr9* 유전자가 무력화 되었고, *Yr17*과 *Yr27*이 각각 유럽과 인도에서 무력화 되면서 줄녹병이 대발생하였고, 2011년에도 유럽에서 병원성이 강한 새로운 균계의 발생으로 큰 피해가 초래되었다(Bahri et al. 2011, Hovmoller et al. 2015). 그러므로 균계 분화에 대응하기 위하여 종특이적 유전자와 종비특이적 유전자의 다양한 조합으로 줄녹병 저항성을 유지하는 것이 효과적이다(Singh et al. 2000, Herrera-Foessel et al. 2011). 예를 들어 종특이적 유전자인 *Yr5*이나 *Yr15*에 종비특이적 유전자인 *Yr18*, *Yr29*과 *Yr46*를 조합하는 것이 줄녹병 저항성 증진에 효과적임이 보고된 바 있다(Chen et al. 2014).

대부분의 줄녹병 저항성 유전자는 ASR에 속하며 주로 육배체 일반밀에서 유래하지만, 호밀(*Yr9*), 야생밀(*Yr5*, *Yr8*, *Yr15*, *Yr24*, *Yr26*, *Yr28*, *Yr35*, *Yr42*)에서 유래하기도 한다(Table 1). ASR의 경우 NBS-LRR 형태의 저항성 유전자에 의해 주로 조절될 것으로 추정되는 반면 HTAP 저항성은 보다 다양한 유전자나 환경인자에 영향을 받을 것으로 예측되고 있다(Hulbert et al. 2007, Chen 2013).

줄녹병의 HTAP 저항성 유전자는 대부분 다른 녹병이나 흰가루병 저항성과 연관이 되어있는데, *Yr17* (*Lr37/Sr38*), *Yr18* (*Lr34/Sr57/Pm38*), *Yr29* (*Lr46/Sr55/Pm46*), *Yr30* (*Lr27/Sr2*),

Table 1. Summary of major stripe rust (Yr) resistance genes.

Locus	Acc. ^z	Source	Chr. ^y	Type ^x	References ^w
<i>Yr1</i>	-	<i>T. aestivum</i>	2AL	ASR	Bansal et al. 2009, Hasancebi et al. 2014
<i>Yr4</i>	-	<i>T. aestivum</i>	3BS	ASR	Bansal et al. 2010
<i>Yr5 (YrSP)</i>	JN631792	<i>T. spelta album</i>	2BL	ASR	Chen et al. 2003, Yan et al. 2003, Smith et al. 2007, Murphy et al. 2009, Zhang et al. 2009, Naruoka et al. 2016, Marchal et al. 2018
<i>Yr6</i>	-	<i>T. aestivum</i>	7B	ASR	Li & Niu 2007
<i>Yr7</i>	MN273771	<i>T. aestivum</i>	2B	ASR	Yao et al. 2006, Marchal et al. 2018
<i>Yr8</i>	-	<i>T. comosa</i>	2D	ASR	Niu et al. 2004
<i>Yr9</i>	DQ167397	<i>S. cereale</i>	1BL	ASR	Mago et al. 2005
<i>Yr10</i>	AF149112	<i>T. aestivum</i>	1BS	ASR	Wang et al. 2002, Singh et al. 2009, Yuan et al. 2012, 2018, Liu et al. 2014
<i>Yr11</i>	-	<i>T. aestivum</i>	2D	HTAP	McIntosh et al. 2003, Nazari & Wellings 2008
<i>Yr12</i>	-	<i>T. aestivum</i>	2D	HTAP	McIntosh et al. 2003, Nazari & Wellings 2008
<i>Yr13</i>	-	<i>T. aestivum</i>	2D	HTAP	McIntosh et al. 2003, Nazari & Wellings 2008
<i>Yr14</i>	-	<i>T. aestivum</i>	2D	HTAP	McIntosh et al. 2003, Nazari & Wellings 2008
<i>Yr15 (Wtk1)</i>	MG649384	<i>T. dicoccoides G25</i>	1BS	ASR	Peng et al. 2000, Murphy et al. 2009, Yaniv et al. 2015, Klymiuk et al. 2018
<i>Yr16</i>	-	<i>T. aestivum</i>	2DL	HTAP	Agenbag et al. 2012
<i>Yr17</i>	GQ850586	<i>T. ventricosa</i>	2AS	HTAP	Helguera et al. 2003, Jia et al. 2011
<i>Yr18/Lr34/Sr57</i>	FJ436983	<i>T. aestivum</i>	7DS	HTAP	Lagudah et al. 2006, 2009, Krattinger et al. 2009
<i>Yr24/Yr26</i>	JX270677	<i>D. villosum</i>	1BS	ASR	Ma et al. 2001, Zhang et al. 2013, Zeng et al. 2014
<i>Yr28</i>	KX181569	<i>T. tauschii W-219</i>	4DS	ASR	Zhang et al. 2019
<i>Yr29</i>	-	<i>T. aestivum</i>	1BL	HTAP	Rosewarne et al. 2006
<i>Yr30</i>	-	<i>T. aestivum</i>	3BS	HTAP	Spielmeyer et al. 2003, Hayden et al. 2004
<i>Yr33</i>	-	<i>T. aestivum</i>	7D	-	Zahravi et al. 2003
<i>Yr34</i>	-	<i>T. aestivum</i>	5AL	HTAP	Qureshi et al. 2018
<i>Yr35</i>	-	<i>T. dicoccoides</i>	6BS	ASR	Dadkhodaie et al. 2011
<i>Yr36 (WKS1)</i>	EU835199	<i>T. dicoccoides</i>	6BS	HTAP	Fu et al. 2009
<i>Yr37</i>		<i>A. kotschy</i>	2DL	-	Marais et al. 2005
<i>Yr38</i>		<i>A. sharonensis</i>	6AL	-	Marais et al. 2010
<i>Yr39</i>	-	<i>T. aestivum</i>	1BS	HTAP	Lin & Chen 2007
<i>Yr40</i>	-	<i>A. geniculata</i>	5DS	-	Kuraparthi et al. 2009
<i>Yr41</i>	-	<i>T. aestivum</i>	2BS	-	Luo et al. 2008
<i>Yr42</i>	-	<i>A. neglecta</i>	6AS	ASR	Marais et al. 2009
<i>Yr43/Yr44</i>	-	<i>T. aestivum</i>	2BL	-	Sui et al. 2009
<i>Yr45</i>	-	<i>T. aestivum</i>	3DL	ASR	Li et al. 2011
<i>Yr46/Lr67/Sr55</i>	KR604818	<i>T. aestivum</i>	4DS	HTAP	Herrera-Foessel et al. 2011, Abdelbacki et al. 2014, Moore et al. 2015
<i>Yr47</i>	-	<i>T. aestivum</i>	5BS	HTAP	Obert et al. 2005, Bansal et al. 2011, Qureshi et al. 2017
<i>Yr48</i>	-	<i>T. aestivum</i>	5AL	HTAP	Lowe et al. 2011
<i>Yr50</i>	-	<i>T. intermedium</i>	4BL	HTAP	Liu et al. 2013
<i>Yr51</i>	-	<i>T. aestivum</i>	4AL	ASR	Randhawa et al. 2014
<i>Yr52</i>	-	<i>T. aestivum</i>	7BL	HTAP	Ren et al. 2012
<i>Yr53</i>	-	<i>T. aestivum</i>	2BL	ASR	Xu et al. 2013

Table 1. Continued

Locus	Acc. ^z	Source	Chr. ^y	Type ^x	References ^w
<i>Yr57</i>	-	<i>T. aestivum</i>	3BS	ASR	Randhawa et al. 2015
<i>Yr58</i>	-	<i>T. aestivum</i>	3BS	ASR	Chhetri et al. 2016
<i>Yr59</i>	-	<i>T. aestivum</i>	7BL	HTAP	Zhou et al. 2014a
<i>Yr60</i>	-	<i>T. aestivum</i>	4AL	ASR, HTAP	Herrera-Foessel et al. 2015
<i>Yr61</i>	-	<i>T. aestivum</i>	7AS	ASR	Zhou et al. 2014b
<i>Yr62</i>	-	<i>T. aestivum</i>	4BL	HTAP	Lu et al. 2014
<i>Yr64</i>	-	<i>T. durum</i>	1BS	-	Cheng et al. 2014, Qie et al. 2019
<i>Yr65</i>	-	<i>T. durum</i>	1BS	ASR	Cheng et al. 2014
<i>Yr67</i>	-	<i>T. aestivum</i>	7BL	-	Li et al. 2009
<i>Yr69</i>	-	<i>T. aestivum</i>	2AS	HTAP	Hou et al. 2016
<i>Yr71</i>	-	<i>T. aestivum</i>	3D	HTAP	Bariana et al. 2016
<i>Yr76</i>	-	<i>T. compactum</i>	3AS	-	Xiang et al. 2016
<i>Yr81</i>	-	<i>T. aestivum</i>	6A	HTAP	Gessese et al. 2019

^zWheat nucleotide accession registered at NCBI (National Center for Biotechnology Information)^yChromosomal location^xASR: all-stage resistance, HTAP: high temperature adult plant resistance, -: uncertain^wReference for gene cloning is underlined

Yr46 (*Lr67/Sr55/Pm46*)과 *Yr47* (*Lr52*)이 그 예로, *Yr18*, *Yr29*과 *Yr36*는 미국에서 HTAP 저항성 품종 육성에 많이 사용되고 있다(Table 1). 특히 6BS 염색체에 위치한 *Yr36*은 종실 단백질 함량에 영향하는 *Gpc-B1* 유전자에 근접해 있어 빵 품질향상을 위한 분자표지와 병행하여 이용되고 있다(Chen 2013). 위에서 언급한 *Yr5*, *Yr15*, *Yr17*, *Yr18*, *Yr29*, *Yr36*, *Yr46*를 비롯하여 주요 줄녹병 저항성 유전자의 도입을 위한 분자표지 관련 정보는 MAS Wheat 홈페이지(<https://maswheat.ucdavis.edu/>)에 잘 정리되어 있으므로 육종사업에 유용하게 활용할 수 있다.

결론

줄녹병은 온대지방에서 주로 발생하지만 최근 광범위한 기후에 적응하는 균계가 발생하면서 전세계적으로 밀의 생산성과 품질에 큰 위협이 되고 있다. 줄녹병 저항성 유전자는 약 80여개가 보고되었고 동정이 이루어진 것은 6개로 *Yr5*, *Yr7*, *Yr15*, *Yr18/Lr34/Sr57/Pm38*, *Yr36*, *Yr46/Lr67/Sr55/Pm46*이다(Table 1). 새로운 줄녹병 저항성 유전자를 발굴하고 다수의 저항성 유전자를 우수 품종에 집적시키기 위한 연구가 국제적으로 활발하게 이루어지고 있으나 우리나라의 줄녹병 저항성 유전육종 연구는 아직 초기단계이다. 국내 육성 밀 계통인 수원11호와 수원92호가 줄녹병 저항성 유전자인 *YrSu*, *YrSo*를 각각 보유하고 있다는 외국의 보고 사례가 있었으나(Wan et al. 2004, Mamun

et al. 2018) 이들 계통이 줄녹병 저항성 품종 개발을 위하여 국내에서 활용된 사례는 찾아보기 어렵다.

줄녹병은 저항성이 없는 품종에서 발병하는 경우 적게는 5~10%에서 많게는 80% 이상 밀 수량을 감소시키며 지속적인 균계 분화로 병원성 양상과 환경적응성이 빠르게 변화하므로 우리나라도 저항성 품종 육성을 통하여 발병피해를 선제적으로 예방해야 한다. 이를 위해서는 대량·정밀 검정체계를 구축하여 주요 줄녹병 균계에 대한 국내 밀 품종 및 육종계통, 재래종의 저항성을 판정해야 하며, 다양한 저항성 유전자를 보유한 유전자원을 적극적으로 도입하여 육종에 활용해야 한다.

보다 장기적으로는 밀 분자유전학 및 유전체 연구 강화를 통하여 국내에서도 새로운 녹병 저항성 유전자를 자체적으로 발굴해야 한다. 밀은 배수체이며 유전체의 크기가 벼의 40배 이상으로 매우 방대하여 유전연구가 까다로운 편이다. 그러나 최근 밀 표준유전체(IWGSC 2018)가 확립됨에 따라 전통적인 유전 지도기반 유전자분리(map-based cloning) 이외에도 다양한 유전분석 기술이 활용되고 있다. 목표 염색체만 선별(flow cytometry)하여 차세대염기서열분석(NGS)을 진행하는 MutChromSeq (Sanchez-Martin et al. 2016), 병 저항성 관련 부위만 선별하는 RenSeq (Steuernagel et al. 2016), 유전자 부위를 선별하는 ExomeSeq (Mo et al. 2018), 전유전체연관분석(GWAS)을 병 저항성 관련 부위에 집중하여 진행하는 AgRenSeq (Arora et al. 2019) 등이 그 사례이다. 따라서 신규 유전자원 탐색과 함께 유전체 기반

기술을 활용한 유전분석을 병행한다면 국내 고유의 녹병 저항성 유전자 및 분자표지를 개발하고 이를 녹병 저항성 밀 육종에 활용하는 것도 가능해질 것으로 기대한다.

적 요

Puccinia striiformis f. sp. *tritici*에 의하여 발생하는 줄녹병은 잎녹병, 줄기녹병과 함께 밀의 생산성과 품질을 떨어뜨리는 주요 질병이다. 줄녹병은 과거에 온대지역에 주로 발생하여 잎녹병에 비하여 피해가 적은 것으로 인식되어 왔으나, 최근 균계 분화로 호주, 중동, 아프리카를 포함한 고온지역으로도 피해가 확대되면서 위협이 커지고 있다. 줄녹병 저항성 유전자는 현재까지 80여개가 보고되었고 그 중 6개(*Yr5*, *Yr7*, *Yr15*, *Yr18*, *Yr36*, *Yr46*)가 동정되었다. 줄녹병 저항성은 크게 종특이적 저항성(전단계저항성)과 종비특이적 저항성(고온성체저항성)으로 구분되는데, 종특이적 저항성 유전자는 균계 분화로 인하여 저항성이 수년 안에 쉽게 무너지는 반면 *Yr18*, *Yr36*, *Yr46*을 비롯한 종비특이적 저항성 유전자는 저항성이 수십년 이상 유지되기도 한다. 특히 *Yr18/Lr34/Sr57/Pm38*과 *Yr46/Lr67/Sr55/Pm46* 유전자는 줄녹병뿐만 아니라 잎녹병, 줄기녹병, 흰가루병에도 저항성을 나타내므로 육종적으로 매우 유용하다. 우리나라는 줄녹병 저항성 유전자 중 연구가 아직 초기단계이므로 한반도 내 주요 균계의 분포와 변화, 저항성 검정체계 구축, 주요 밀 품종과 육성계통의 저항성 검정, 유망 유전자원 확보 및 활용 연구를 활성화하여 발병으로 인한 피해를 사전에 예방하는 것이 시급하다. 또한 장기적으로 분자유전학 및 유전체 분야의 연구를 강화하여 국내 고유의 줄녹병 저항성 유전자를 발굴하고 이를 밀 분자유종에 활용하기 위한 역량을 갖추어야 한다.

사 사

본 연구는 농촌진흥청 국립식량과학원 농업과학기술연구개발사업(과제명: 조기 육성 기술을 활용한 고품질 밀 우량 계통 육성 및 유전 분석, 과제번호: PJ014989032020)의 지원에 의해 이루어진 것으로 이에 감사드립니다.

REFERENCES

1. Abdelbacki AMM, Omara RI, Najeeb MA, Soliman NEK. 2014. Identification of leaf rust resistant genes *Lr9*, *Lr25*,

- Lr28*, *Lr29* & *Lr67* in ten Egyptian wheat cultivars using molecular markers. *Int J Biotech Res* 7: 89-96.
2. Agenbag GM, Pretorius ZA, Boyd LA, Bender CM, Prins R. 2012. Identification of adult plant resistance to stripe rust in the wheat cultivar Cappelle-Desprez. *Theor Appl Genet* 125: 109-120.
3. Ali S, Gladieux P, Leconte M, Gautier A, Justesen AF, Hovmöller MS, Enjalbert J, de Vallavieille-Pope C. 2014. Origin, migration routes and worldwide population genetic structure of the wheat yellow rust pathogen *Puccinia striiformis* f. sp. *tritici*. *PLoS Pathog* 10: e1003903.
4. Arduim GDS, Reis EM, Barcellos AL, Turra C. 2012. In vivo sensitivity reduction of *Puccinia triticina* races, causal agent of wheat leaf rust, to DMI and QoI fungicides. *Sum Phytopathol* 38: 306-311.
5. Arora S, Steuernagel B, Gaurav K, Chandramohan S, Long Y, Matny O, Hattam MAM. 2019. Resistance gene cloning from a wild crop relative by sequence capture and association genetics. *Nat Biotechnol* 37: 139-143.
6. Bahri B, Shah SJ, Hussain A, Leconte S, Enjalbert M, J. de Vallavieille-Pope C. 2011. Genetic diversity of wheat yellow rust population in Pakistan and its relationship with host resistance. *Plant Pathol* 60: 649-60.
7. Bansal UK, Hayden MJ, Keller B, Wellings CR, Park RF, Bariana HS. 2009. Relationship between wheat rust resistance genes *Yr1* and *Sr48* and a microsatellite marker. *Plant Pathol* 58: 1039-1043.
8. Bansal UK, Hayden MJ, Gill MB, Bariana HS. 2010. Chromosomal location of an uncharacterised stripe rust resistance gene in wheat. *Euphytica* 171: 121-127.
9. Bansal UK, Forrest KL, Hayden MJ, Miah H, Singh D, Bariana HS. 2011. Characterisation of a new stripe rust resistance gene *Yr47* and its genetic association with the leaf rust resistance gene *Lr52*. *Theor Appl Genet* 122: 1461-1466.
10. Bariana H, Forrest K, Qureshi N, Miah H, Hayden M, Bansal U. 2016. Adult plant stripe rust resistance gene *Yr71* maps close to *Lr24* in chromosome 3D of common wheat. *Mol Breeding* 36: 98.
11. Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ, Braun HJ, Park RF, Cuddy WS, Yonow T. 2015. Research investment implications of shifts in the global geography of wheat stripe rust. *Nat Plants* 1: 1-15.
12. Bolton MD, Kolmer JA, Garvin DF. 2008. Wheat leaf rust caused by *Puccinia triticina*. *Mol Plant Pathol* 9: 563-575.
13. Chen X, Soria MA, Yan G, Sun J, Dubcovsky J. 2003.

- Development of sequence tagged site and cleaved amplified polymorphic sequence markers for wheat stripe rust resistance gene *Yr5*. *Crop Sci* 43: 2058-2064.
14. Chen X. 2005. Epidemiology and control of stripe rust [*Puccinia striiformis* f. sp. *tritici*] on wheat. *Can J Plant Pathol* 27: 314-337.
 15. Chen X. 2013. Review article: High-temperature adult-plant resistance, key for sustainable control of stripe rust. *Am J Plant Sci* 4: 608-627.
 16. Chen XM, Line RF. 1995a. Gene action in wheat cultivars for durable high-temperature adult-plant resistance and interactions with race-specific, seedling resistance to stripe rust caused by *Puccinia striiformis*. *Phytopathology* 85: 567-572.
 17. Chen XM, Line RF. 1995b. Gene number and heritability of wheat cultivars with durable, high-temperature, adult-plant resistance and race-specific resistance to *Puccinia striiformis*. *Phytopathology* 85: 573-578.
 18. Chen W, Wellings C, Chen X, Kang Z, Liu T. 2014. Wheat stripe (yellow) rust caused by *Puccinia striiformis* f. sp. *tritici*. *Mol Plant Pathol* 15: 433-446.
 19. Cheng P, Xu LS, Wang MN, See DR, Chen XM. 2014. Molecular mapping of genes *Yr64* and *Yr65* for stripe rust resistance in hexaploid derivatives of durum wheat accessions PI 331260 and PI 480016. *Theor Appl Genet* 127: 2267-2277.
 20. Chhetri M, Bariana H, Kandiah P, Bansal U. 2016. *Yr58*: a new stripe rust resistance gene and its interaction with *Yr46* for enhanced resistance. *Phytopathology* 106: 1530-1534.
 21. Cummins GB, Hiratsuka Y. 2004. Illustrated genera of rust fungi. St. Paul. MN: APS Press.
 22. Dadkhodaie NA, Karaoglou H, Wellings CR, Park RF. 2011. Mapping genes *Lr53* and *Yr35* on the short arm of chromosome 6B of common wheat with microsatellite markers and studies of their association with *Lr36*. *Theor Appl Genet* 122: 479-487.
 23. Dakouri A, McCallum BD, Radovanovic N, Cloutier S. 2013. Molecular and phenotypic characterization of seedling and adult plant leaf rust resistance in a world wheat collection. *Mol Breeding* 32: 663-677.
 24. Dodds PN, Lagudah ES. 2016. Starving the enemy. *Science* 354: 1377-1378.
 25. Duplessis S, Cuomo CA, Lin YC, Aerts A, Tisserant E, Veneault-Fourrey C, Joly DL, Hacquard S, Amselem J, Cantarel BL, Chiu R, Coutinho PM, Feau N, Field M, Frey P, Gelhaye E, Goldberg J, Grabherr MG, Kodira CD, Kohler A, Kues U, Lindquist EA, Lucas SM, Mago R, Mauceli E, Morin E, Murat C, Pangilinan JL, Park R, Pearson M, Quesneville H, Rouhier N, Sakthikumar S, Salamov AA, Schmutz J, Selles B, Shapiro H, Tanguay P, Tuskan GA, Henrissat B, Van de Peer Y, Rouze P, Ellis JG, Dodds PN, Schein JE, Zhong S, Hamelin RC, Grigoriev IV, Szabo LJ, Martin F. 2011. Obligate biotrophy features unraveled by the genomic analysis of rust fungi. *Proc Natl Acad Sci USA* 108: 9166-9171.
 26. Ellis EG, Lagudah ES, Spielmeier W, Dodds PN. 2014. The past, present and future of breeding rust resistant wheat. *Front Plant Sci* 5: 641.
 27. Figueroa M, Hammond-Kosack KE, Solomon PS. 2018. A review of wheat diseases a field perspective. *Mol Plant Pathol* 6: 99-111.
 28. Fu D, Uauy C, Distelfeld A, Blechl A, Epstein L, Chen X, Dubcovsky J. 2009. A kinase-START gene confers temperature-dependent resistance to wheat stripe rust. *Science* 323: 1357-1360.
 29. Gessese M, Bariana H, Wong D, Hayden M, Bansal U. 2019. Molecular mapping of stripe rust resistance gene *Yr81* in a common wheat landrace Aus27430. *Plant Dis* 103: 1166-1171.
 30. Hasancebi S, Mert Z, Ertugrul F, Akan K, Aydin Y, Akfırat FS, Uncuoglu AA. 2014. An EST-SSR marker, bu099658, and its potential use in breeding for yellow rust resistance in wheat. *Czech J Genet Plant* 50: 11-18.
 31. Hayden MJ, Kuchel H, Chalmers KJ. 2004. Sequence tagged microsatellites for the *Xgwm533* locus provide new diagnostic markers to select for the presence of stem rust resistance gene *Sr2* in bread wheat (*Triticum aestivum* L.). *Theor Appl Genet* 109: 1641-1647.
 32. Helguera M, Khan IA, Kolmer J, Lijavetzky D, Zhong-Qi L, Dubcovsky J. 2003. PCR assays for the *Lr37-Yr17-Sr38* cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines. *Crop Sci* 43: 1839-1847.
 33. Herrera-Foessel SA, Lagudah ES, Huerta-Espino J, Hayden MJ, Bariana HS, Singh D, Singh RP. 2011. 'New slow-rusting leaf rust and stripe rust resistance genes *Lr67* and *Yr46* in wheat are pleiotropic or closely linked'. *Theor Appl Genet* 122: 239-249.
 34. Herrera-Foessel SA, Singh RP, Lan CX, Huerta-Espino J, Calvo-Salazar V, Bansal UK, Lagudah ES. 2015. *Yr60*, a gene conferring moderate resistance to stripe rust in wheat. *Plant Dis* 99: 508-511.

35. Hou L, Jia J, Zhang X, Li X, Yang Z, Ma J, Chang Z. 2016. Molecular mapping of the stripe rust resistance gene *Yr69* on wheat chromosome 2AS. *Plant Dis* 100: 1717-1724.
36. Hovmoller MS, Sorensen CK, Walter S, Justesen AF. 2011. Diversity of *Puccinia striiformis* on cereals and grasses. *Annu Rev Phytopathol* 49: 197-217.
37. Hovmoller MS, Walter S, Bayles RA, Hubbard A, Flath K, Sommerfeldt N, Leconte M, Czembor P, Rodriguez-Algaba J, Thach T, Hansen JG, Lassen P, Justesen AF, Ali S, De Vallavieille-Pope C. 2015. Replacement of the European wheat yellow rust population by new races from the centre of diversity in the near-Himalayan region. *Plant Pathol* 65: 402-411.
38. Hubbard A, Lewis CM, Yoshida K, Ramirez-Gonzalez RH, De Vallavieille-Pope C, Thomas J, Kamoun S, Bayles R, Uauy C, Saunders DGO. 2015. Field pathogenomics reveals the emergence of a diverse wheat yellow rust population. *Genome Biol* 16: 23.
39. Hulbert SH, Bai J, Fellers JP, Pacheco MG, Bowden RL. 2007. Gene expression patterns in near isogenic lines for wheat rust resistance gene *Lr34/Yr18*. *Phytopathol* 97: 1083-1093.
40. Jia J, Li G, Liu C, Lei M, Yang Z. 2011. Characterization of wheat yellow rust resistance gene *Yr17* using EST-SSR and rice syntenic region. *Cereal Res Commun* 39: 88-99.
41. Jin Y, Szabo LJ, Carson M. 2010. Century-old mystery of *Puccinia striiformis* life history solved with the identification of berberis as an alternate host. *Phytopathology* 100: 432-435.
42. Jorgensen LN, Nielsen GC, Orum JE, Jensen JE, Pinnschmidt HO. 2008. 'Integrating disease control in winter wheat - optimizing fungicide input'. *Outlooks on Pesticide Management* 19: 206-213.
43. Klymiuk V, Yaniv E, Huang L, Raats D, Fatiukha A, Chen S, Chang W. 2018. Cloning of the wheat *Yr15* resistance gene sheds light on the plant tandem kinase-pseudokinase family. *Nat Commun* 9: 1-12.
44. Kolmer J, Jin Y, Long D. 2007. Wheat leaf and stem rust in the United States. *Crop Pasture Sci* 58: 631-638.
45. Krattinger SG, Lagudah ES, Spielmeyer W, Singh RP, Huerta-Espino J, McFadden H, Bossolini E, Selter LL, Keller B. 2009. A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. *Science* 323: 1360-1363.
46. Kumar A, Chhuneja P, Jain S, Kaur S, Balyan HS, Gupta PK. 2013. Mapping main effect QTL and epistatic interactions for leaf rust and yellow rust using high density ITMI linkage map. *Aust J Crop Sci* 7: 492-499.
47. Kuraparthi V, Sood S, Gill BS. 2009. Molecular genetic description of the cryptic wheat-*Aegilops geniculata* introgression carrying rust resistance genes *Lr57* and *Yr40* using wheat ESTs and synteny with rice. *Genome* 52: 1025-1036.
48. Lagudah ES, McFadden H, Singh RP, Huerta-Espino J, Bariana HS, Spielmeyer W. 2006. Molecular genetic characterization of the *Lr34/Yr18* slow rusting resistance gene region in wheat. *Theor Appl Genet* 114: 21-30.
49. Lagudah ES, Krattinger SG, Herrera-Foessel S, Singh RP, Huerta-Espino J, Spielmeyer W, Brown-Guedira G, Selter LL, Keller B. 2009. Gene-specific markers for the wheat gene *Lr34/Yr18/Pm38* which confers resistance to multiple fungal pathogens. *Theor Appl Genet* 119: 889-898.
50. Li Q, Chen XM, Wang MN, Jing JX. 2011. *Yr45*, a new wheat gene for stripe rust resistance on the long arm of chromosome 3D. *Theor Appl Genet* 122: 189-197.
51. Li Y, Niu Y. 2007. Identification of molecular markers for wheat stripe rust resistance gene *Yr6*. *Europepmc* 189-192.
52. Li Y, Niu YC, Chen XM. 2009 Mapping a stripe rust resistance gene *YrC591* in wheat variety *C591* with SSR and AFLP markers. *Theor Appl Genet* 118: 339-346.
53. Lin F, Chen XM. 2007. Genetics and molecular mapping of genes for race-specific all-stage resistance and non-race-specific high-temperature adult-plant resistance to stripe rust in spring wheat cultivar Alpowa. *Theor Appl Genet* 114: 1277-1287.
54. Line RF, Chen XM. 1995. Successes in breeding for and managing durable resistance to wheat rusts. *Plant Dis* 79: 1254-1255
55. Liu J, Chang Z, Zhang X, Yang Z, Li X, Jia J, Wang J. 2013. Putative Thinopyrum intermedium-derived stripe rust resistance gene *Yr50* maps on wheat chromosome arm 4BL. *Theor Appl Genet* 126: 265-274.
56. Liu W, Frick M, Huel R, Nykiforuk CL, Wang X, Gaudet DA, Kang Z. 2014. The stripe rust resistance gene *Yr10* encodes an evolutionary-conserved and unique CC-NBS-LRR sequence in wheat. *Mol Plant* 7: 1740-1755.
57. Lowe I, Jankuloski L, Chao S, Chen X, See D, Dubcovsky J. 2011. Mapping and validation of QTL which confer partial resistance to broadly virulent post-2000 north american races of stripe rust in hexaploid wheat. *Theor Appl Genet* 123: 143-157.
58. Lu Y, Wang M, Chen X, See D, Chao S, Jing J. 2014. Mapping of *Yr62* and a small-effect QTL for high-temperature

- adult-plant resistance to stripe rust in spring wheat PI 192252. *Theor Appl Genet* 127: 1449-1459.
59. Luo PG, Hu XY, Ren ZL, Zhang HY, Shu K, Yang ZJ. 2008. Allelic analysis of stripe rust resistance genes on wheat chromosome 2BS. *Genome* 51: 922-927.
 60. Ma J, Zhou R, Dong Y, Wang L, Wang X, Jia J. 2001. Molecular mapping and detection of the yellow rust resistance gene *Yr26* in wheat transferred from *Triticum turgidum* L. using microsatellite markers. *Euphytica* 120: 219-226.
 61. Mago R, Miah H, Lawrence GJ, Wellings CR, Spielmeier W, Bariana HS, Ellis JG. 2005. High-resolution mapping and mutation analysis separate the rust resistance genes *Sr31*, *Lr26* and *Yr9* on the short arm of rye chromosome 1. *Theor Appl Genet* 112: 41-50.
 62. Mamun M, Tang C, Sun Y, Islam M, Liu P, Wang X, Kang Z. 2018. Wheat gene *TaATG8j* contributes to stripe rust resistance. *Int J Mol Sci* 19: 1666.
 63. Marais GF, McCallum B, Snyman JE, Pretorius ZA, Marais AS. 2005. Leaf rust and stripe rust resistance genes *Lr54* and *Yr37* transferred to wheat from *Aegilops kotschyi*. *Plant Breeding* 124: 538-541.
 64. Marais GF, Marais A, McCallum B, Pretorius Z. 2009. Transfer of leaf rust and stripe rust resistance genes *Lr62* and *Yr42* from *Aegilops neglecta* Req. ex Bertol. to common wheat. *Crop Sci* 49: 871-879.
 65. Marais GF, Badenhorst PE, Eksteen A, Pretorius ZA. 2010. Reduction of *Aegilops sharonensis* chromatin associated with resistance genes *Lr56* and *Yr38* in wheat. *Euphytica* 171: 15-22.
 66. Marchal C, Zhang J, Zhang P, Fenwick P, Steuernagel B, Adamski NM, Lagudah E. 2018. BED-domain-containing immune receptors confer diverse resistance spectra to yellow rust. *Nat Plants* 4: 662-668.
 67. McIntosh RA, Wellings CR, Park RF. 1995. Wheat Rusts: an atlas of resistance genes. Csiro Publishing.
 68. McIntosh RA, Yamazaki Y, Devos KM, Dubcovsky J, Rogers WJ, Appels R. 2003. Catalogue of gene symbols for wheat. *Wheat Inform Service* 97: 27-37.
 69. McIntosh R. 2009. The history and status of the wheat rusts. In: NGRI Technical Workshop. 11-24.
 70. McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, Xia XC. 2014. Catalogue of gene symbols for wheat. 2013-2014 Supplement. *Annual Wheat Newsletter*. 58.
 71. Mo Y, Howell T, Vasquez-Gross H, De Haro LA, Dubcovsky J, Pearce S. 2018. Mapping causal mutations by exome sequencing in a wheat TILLING population: a tall mutant case study. *Mol Genet Genomics* 293: 463-477.
 72. Moldenhauer J, Moerschbacher BM, Westhuizen AJ. 2006. Histological investigation of stripe rust (*Puccinia striiformis* f. sp. *tritici*) development in resistant and susceptible wheat cultivars. *Plant Pathol* 55: 469-74.
 73. Moore JW, Herrera-Foessel S, Lan C, Schnippenkoetter W, Ayliffe M, Huerta-Espino J, Lillemo M, Viccars L, Milne R, Periyannan S, Kong X, Spielmeier W, Talbot M, Bariana H, Patrick JW, Dodds P, Singh R, Lagudah E. 2015. A recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. *Nat Genet* 47: 1494-1500.
 74. Mundt CC. 2018. Pyramiding for Resistance Durability: Theory and Practice. *Phytopathol* 108: 792-802.
 75. Murphy LR, Santra D, Kidwell K, Yan G, Chen X, Campbell KG. 2009. Linkage maps of wheat stripe rust resistance genes *Yr5* and *Yr15* for use in marker-assisted selection. *Crop Sci* 49: 1786-1790.
 76. Murray GM and Brennan JP. 2009. Estimating disease losses to the Australian wheat industry. *Australas. Plant Pathol* 38: 558-570.
 77. Naruoka Y, Ando K, Bulli P, Muleta KT, Rynearson S, Pumphrey MO. 2016. Identification and validation of SNP markers linked to the stripe rust resistance gene *Yr5* in wheat. *Crop Sci* 56: 3055-3065.
 78. Nazari K, Wellings CR. 2008. Genetic analysis of seedling stripe rust resistance in the Australian wheat cultivar 'Batavia'. The International Wheat Symposium proceedings. Sydney University Press 1-3.
 79. Niu YC, Li SM, Li WF, Wu LR, Xu SC. 2004. Molecular markers assisted selection for the stripe rust (*Puccinia striiformis tritici*) resistance genes *Yr8* and *Yr10* in wheat breeding. In Plant protection towards the 21st century-proceedings of the XVth Int Plant Protection Congress, Beijing, China.
 80. Obert DE, Fritz AK, Moran JL, Singh S, Rudd JC, Menz MA. 2005. Identification and molecular tagging of a gene from PI 289824 conferring resistance to leaf rust (*Puccinia triticina*) in wheat. *Theor Appl Genet* 110: 1439-1444.
 81. Oliver RP. 2014. A reassessment of the risk of rust fungi developing resistance to fungicides. *Pest Manag Sci* 70: 1641-1645.
 82. Peng JH, Fahima T, Röder MS, Huang QY, Dahan A, Li YC, Nevo E. 2000. High-density molecular map of chromosome

- region harboring stripe-rust resistance genes *YrH52* and *Yr15* derived from wild emmer wheat, *Triticum dicoccoides*. *Genetica* 109: 199-210.
83. Periyannan S, Milne RJ, Figueroa M, Lagudah ES, Dodds PN. 2017. An overview of genetic rust resistance: from broad to specific mechanisms. *PLoS Pathog* 13: e1006380.
84. Qayoum A, Line RF. 1985. High-temperature, adult-plant resistance to stripe rust of wheat. *Phytopathology* 75: 1121-1125.
85. Qie Y, Liu Y, Wang M, Li X, See DR, An D, Chen X. 2019. Development, validation, and re-selection of wheat lines with pyramided genes *Yr64* and *Yr15* linked on the short arm of chromosome 1B for resistance to stripe rust. *Plant Dis* 103: 51-58.
86. Qureshi N, Bariana H, Forrest K, Hayden M, Keller B, Wicker T, Bansal U. 2017. Fine mapping of the chromosome 5B region carrying closely linked rust resistance genes *Yr47* and *Lr52* in wheat. *Theor Appl Genet* 130: 495-504.
87. Qureshi N, Bariana HS, Zhang P, McIntosh R, Bansal UK, Wong D, Shankar M. 2018. Genetic relationship of stripe rust resistance genes *Yr34* and *Yr48* in wheat and identification of linked KASP markers. *Plant Dis* 102: 413-420.
88. Randhawa MS, Bansal U, Valárik M, Klocová B, Doležel J, Bariana H. 2014. Molecular mapping of stripe rust resistance gene *Yr51* in chromosome 4AL of wheat. *Theor Appl Genet* 127: 317-324.
89. Randhawa MS, Bariana HS, Mago R, Bansal UK. 2015. Mapping of a new stripe rust resistance locus *Yr57* on chromosome 3BS of wheat. *Mol Breeding* 35: 65.
90. Ren RS, Wang MN, Chen XM, Zhang ZJ. 2012. Characterization and molecular mapping of *Yr52* for high-temperature adult-plant resistance to stripe rust in spring wheat germplasm PI 183527. *Theor Appl Genet* 125: 847-857.
91. Rosewarne GM, Singh RP, Huerta-Espino J, William HM, Bouchet S, Cloutier S, Lagudah ES. 2006. Leaf tip necrosis, molecular markers and β 1-proteasome subunits associated with the slow rusting resistance genes *Lr46/Yr29*. *Theor Appl Genet* 112: 500-508.
92. Sanchez-Martin J, Steuernagel B, Ghosh S, Herren G, Humi S, Adamski N, Dolezel J. 2016. Rapid gene isolation in barley and wheat by mutant chromosome sequencing. *Genome Biol* 17: 221.
93. Singh R, Datta D, Priyamvada Singh S, Tiwari R. 2009. A diagnostic PCR based assay for stripe rust resistance gene *Yr10* in wheat. *Acta Phytopa Thol Hun* 44: 11-18.
94. Singh RP, Huerta-Espino J, Rajaram S. 2000. Achieving near-immunity to leaf and stripe rusts in wheat by combining slow rusting resistance genes. *Acta Phytopa Thol Hun* 35: 133-139.
95. Smith PH, Hadfield J, Hart NJ, Koebner RMD, Boyd LA. 2007. STS markers for the wheat yellow rust resistance gene *Yr5* suggest a NBS-LRR-type resistance gene cluster. *Genome* 50: 259-265.
96. Spielmeier W, Lagudah E. 2003. Homoeologous set of NBS-LRR genes located at leaf and stripe rust resistance loci on short arms of chromosome 1 of wheat. *Funct Integr Genomic* 3: 86-90.
97. Steuernagel B, Periyannan SK, Hernandez-Pinzon I, Witek K, Rouse MN, Yu G, Lagudah ES. 2016. Rapid cloning of disease-resistance genes in plants using mutagenesis and sequence capture. *Nat Biotechnol* 34: 652.
98. Sui XX, Wang MN, Chen XM. 2009. Molecular mapping of a stripe rust resistance gene in spring wheat cultivar Zak. *Phytopathology* 99: 1209-1215.
99. Todorovska E, Christov N, Slavov S, Christova P, Vassilev D. 2009. Biotic stress resistance in wheat breeding and genomic selection implications. *Biotechnol Biotec Eq* 23: 417-426.
100. Wan A, Zhao Z, Chen X, He Z, Jin S, Jia Q, Bi Y. 2004. Wheat stripe rust epidemic and virulence of *Puccinia striiformis* f. sp. *tritici* in China in 2002. *Plant Dis* 88: 896-904.
101. Wang L, Ma J, Zhou R, Wang X, Jia J. 2002. Molecular tagging of the yellow rust resistance gene *Yr10* in common wheat, PI 178383 (*Triticum aestivum* L.). *Euphytica* 124: 71-73.
102. Wellings CR. 2011. Global status of stripe rust: a review of historical and current threats. *Euphytica* 179: 129-141.
103. Xiang C, Feng JY, Wang MN, Chen XM, See DR, Wan AM, Wang T. 2016. Molecular mapping of stripe rust resistance gene *Yr76* in winter club wheat cultivar Tyee. *Phytopathology* 106: 1186-1193.
104. Xu LS, Wang MN, Cheng P, Kang ZS, Hulbert SH, Chen XM. 2013. Molecular mapping of *Yr53*, a new gene for stripe rust resistance in durum wheat accession PI 480148 and its transfer to common wheat. *Theor Appl Genet* 126: 523-533.
105. Yan G, Chen X, Line R, Wellings C. 2003. Resistance gene-analog polymorphism markers co-segregating with

- the *Yr5* gene for resistance to wheat stripe rust. *Theor Appl Genet* 106: 636-643.
106. Yaniv E, Raats D, Ronin Y, Korol AB, Grama A, Bariana H, Dubcovsky J, Schulman AH. 2015. Evaluation of marker-assisted selection for the stripe rust resistance gene *Yr15*, introgressed from wild emmer wheat. *Mol Breeding* 35: 43.
 107. Yao ZJ, Lin RM, Xu SC, Li ZF, Wan AM, Ma ZY. 2006. The molecular tagging of the yellow rust resistance gene *Yr7* in wheat transferred from differential host Lee using microsatellite markers. *Scientia Agri Sinica* 39: 1146-1152.
 108. Yuan C, Jiang H, Wang H, Li K, Tang H, Li X, Fu D. 2012. Distribution, frequency and variation of stripe rust resistance loci *Yr10*, *Lr34/Yr18* and *Yr36* in Chinese wheat cultivars. *J Genet Genomics* 39: 587-592.
 109. Yuan C, Wu J, Yan B, Hao Q, Zhang C, Lyu B, Fu D. 2018. Remapping of the stripe rust resistance gene *Yr10* in common wheat. *Theor Appl Genet* 131: 1253-1262.
 110. Zahraoui M, Bariana HS, Shariflou MR, Balakrishna PV, Banks PM, Ghannadha MR, Pogna NE. 2003. Bulk segregant analysis of stripe rust resistance in wheat (*Triticum aestivum*) using microsatellite markers. In *Proceedings 10th Int Wheat Genet Symposium, Instituto Sperimentale per Cerealcoltura* 861-863.
 111. Zeng QD, Han DJ, Wang QL, Yuan FP, Wu JH, Zhang L, Kang ZS. 2014. Stripe rust resistance and genes in Chinese wheat cultivars and breeding lines. *Euphytica* 196: 271-284.
 112. Zhang R, Singh RP, Lillemo M, He X, Randhawa MS, Huerta-Espino J, Lan C. 2019. Two main stripe rust resistance genes identified in synthetic-derived wheat line Soru# 1. *Phytopathology* 109: 120-126.
 113. Zhang X, Han D, Zeng Q, Duan Y, Yuan F, Shi J, Wang Q, Wu J, Huang L, Kang Z. 2013. Fine mapping of wheat stripe rust resistance gene *Yr26* based on collinearity of wheat with *brachypodium distachyon* and rice. *PLoS ONE* 8: e57885.
 114. Zhang P, McIntosh RA, Hoxha S, Dong C. 2009. Wheat stripe rust resistance genes *Yr5* and *Yr7* are allelic. *Theor Appl Genetics* 120: 25-29.
 115. Zheng W, Huang L, Huang J, Wang X, Chen X, Zhao J, Liu H. 2013. High genome heterozygosity and endemic genetic recombination in the wheat stripe rust fungus. *Nat Commun* 4: 1-11.
 116. Zhou XL, Wang MN, Chen XM, Lu Y, Kang ZS, Jing JX. 2014a. Identification of *Yr59* conferring high-temperature adult-plant resistance to stripe rust in wheat germplasm PI 178759. *Theor Appl Genet* 127: 935-945.
 117. Zhou XL, Han DJ, Chen XM, Gou HL, Guo SJ, Rong L, Wang QL, Huang LL, Kang ZS. 2014b. Characterization and molecular mapping of stripe rust resistance gene *Yr61* in winter wheat cultivar Pindong 34. *Theor Appl Genet* 127: 2349-2358.