Types of Wheat Resistance to Leaf Rust

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Due to the global warming and dynamic changes in pathogenic virulence, leaf rust caused by *Puccinia triticina* has greatly expanded its epidermic region and become a severe threat to global wheat production. Leaf rust, caused by biotrophic fungal pathogen *Puccinia triticina* Erikss., is one of the most wide-spread and severe diseases in wheat all over the world.

Wheat Leaf Rust Resistance Genetics

1. Introduction

Leaf rust, caused by biotrophic fungal pathogen *Puccinia triticina* Erikss., is one of the most wide-spread and severe diseases in wheat all over the world [1]. The yield loss caused by leaf rust ranges from 5% to 20%, and reaches about 50% during epidemics [2]. Compared with other rust diseases such as stripe rust and stem rust, leaf rust adapts to a more moderate temperature (10–25 °C). However, due to the global warming, leaf rust has greatly expanded its epidermic region and advanced its occurrence period [3]. Generally, seedling plants of wheat are more vulnerable to rust diseases, and all of these changes have made leaf rust become a new threat to global wheat productions.

Rational application of genetic loci controlling wheat resistance to leaf rust in breeding practice is still the best choice for the disease control. Future application of wheat leaf rust resistance genes requires more efficient co-operations between wheat researchers and breeders. In recent years, many leaf rust resistance *(Lr)/quantitative trait locus (QLr)* have been identified and linked molecular markers have been developed. Knowledge regarding the sources and distribution of leaf rust resistance genes are important for developing new wheat cultivars with resistance. Wild wheat relatives are still valuable sources of novel genetic loci carrying *Lr/QLr*. Resistant germplasms including introgression lines generated from wheat relatives remain to be explored. With recent progresses of sequenced genomes of wheat relatives/progenitors, more resistance genes are expected to be cloned from these sources [4]. Previous issues such as long breeding periods and drawback from unwanted chromosome introgression will be solved by potential linkage drag with advanced techniques in speed breeding [5].

2. Pathogenic Profile

Leaf rust has a complicated life cycle including asexual stage on wheat and sexual stage on alternative hosts (**Figure 1**a,b) [1]. At the asexual stage, leaf rust infects wheat plant via its urediospores (**Figure 1**a). Urediospores can spread over long distances with air flow and re-infect wheat plants multiple times. Since leaf rust has a broad host range including wheat, barley, and their wild relatives, it can easily over-summer on grasses and volunteer crops. On the other hand, it normally over-winter on wheat as latent hypha or urediospores. At the sexual stage, leaf rust produces telia on wheat leaves in the late growing season (**Figure 1**a); teliospores from telia further infects alternative hosts including *Thalictrum* spp. or *Leptopyrum fumarioides*; pycnia/pycniospores and aecium/aeciospores can be formed on the alternative hosts; fertilization occur between pycniospores and receptive hyphae with opposite mating type combinations; aeciospores infect back to the host plants of wheat and produce uredium/urediospores to complete the life cycle (**Figure 1**b).

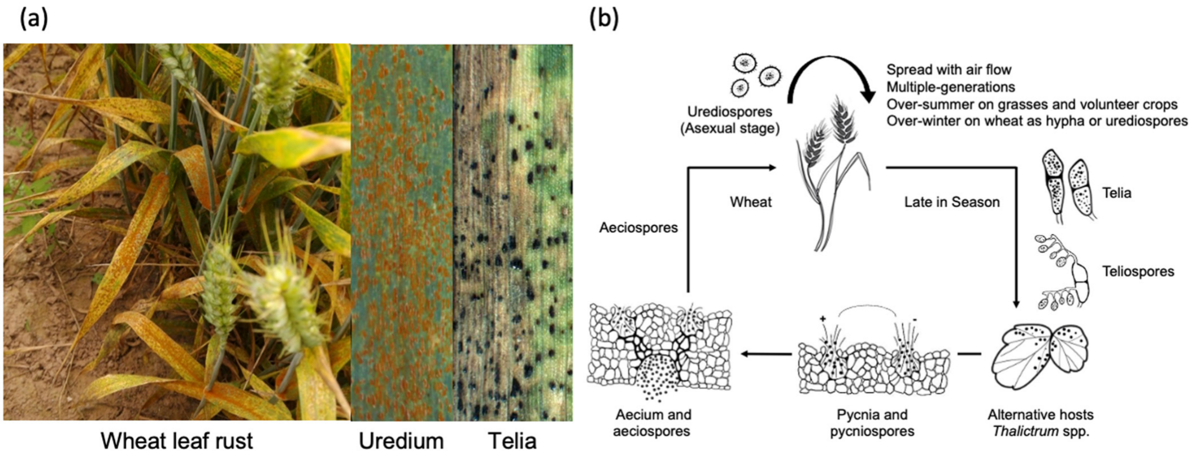

Figure 1. Pathogenic profile of *Puccinia triticina.* (**a**) Leaf rust infects wheat leaves via its urediospores at the asexual stage. Telia is produced on wheat leaves in the late growing season. (**b**) Life cycle of *P. triticina* can be divided into asexual stage on wheat and sexual stage on alternative hosts. Teliospores infect alternative hosts *Thalictrum* spp. and later produces pycnia and aecium. Aeciospores infect back to wheat plants to complete the life cycle.

3. Types of Wheat Resistance to Leaf Rust

Based on the physiological features, genetic determinations, and molecular mechanisms, wheat resistance to leaf rust can be classified into two types (**Table 1**): race-specific resistance and slow rusting resistance. The race-specific resistance follows the gene-for-gene theory. Currently, most of the cloned *Lr* genes controlling this type of resistance, including *Lr1*, *Lr10*, *Lr13*, *Lr21*, *Lr22a*, and *Lr42*, encode nucleotide binding site leucine-rich repeat (NBS-LRR) proteins [6][7][8][9][10][11]. As modeled in *Arabidopsis*, upon directly or indirectly recognition of avirulence (Avr) proteins secreted by phytopathogens, NBS-LRR proteins form a homo-pentamer called resistosome, which penetrates the cell membrane of the responsive cells and eventually results in the observed hypersensitive responses (HR) or necrosis on wheat leaves [12]. A recent protein crystallization study on wheat stem rust resistance protein Sr35 and its corresponding avirulent protein AvrSr35 revealed a similar resistosome structure [13]. Besides these NBS-LRR proteins, another race-specific resistance gene, *Lr14a*, encodes a membrane-localized protein containing multiple ankyrin repeats and Ca^{2+} channels [14]. The other recently cloned high-resistant gene *Lr9/Lr58* encodes a tandem kinase fusion protein [15]. Notably, certain race-specific resistance genes are functioning only at seedling stage but lost their resistance against multiple *Pt* pathotypes in the field at the adult plant stage. Others may keep their high resistance to leaf rust at the adult plant stage as hypersensitive adult plant resistance (APR) or all-stage (AS) race-specific resistance.

Table 1. Types of wheat resistance to leaf rust.

Type of Resistance	Resistance Stage	Resistant Features	Cloned Resistance Genes
Race-specific resistance	Seedling stage	Seedling resistance. Immune or hypersensitive response (cell death/necrosis) observed on the leaf surface. May be lost at adult plant stage against multiple *Pt* pathotypes in the field.	*Lr1, Lr10, Lr13, Lr21, Lr22a, Lr42* (NBS-LRR) [6][7][8][9][10][11] *Lr14a* (Ankyrin repeats and Ca^{2+} channels) [14] *Lr9/Lr58* (Tandem kinase) [15]
	Adult plant stage	Hypersensitive adult plant resistance (APR)/All-stage (AS) race-specific resistance. Immune or hypersensitive response (cell death/necrosis) observed on the leaf surface.	
Slow rusting	Adult plant stage	Non-race-specific resistance. A lower level but more durable resistance. Rust infection and sporulation can be accomplished in a much delayed and reduced manner.	*Lr34* (ATP-binding cassette transporter) [16] *Lr67* (Hexose transporter) [17]

Slow rusting resistance, also considered as APR in most cases, provides a lower level but more durable resistance in a non-race-specific manner only at the adult plant stage. Compare with the mentioned hypersensitive APR, rust infection and sporulation can be accomplished in a much delayed and reduced manner. It is normally controlled by quantitative trait loci (QTL) and provides broad-spectrum resistance to multiple pathogens. For instance, the first cloned leaf rust APR gene *Lr34* encoding an ATP-binding cassette (ABC) transporter controls resistance to stripe rust, stem rust, powdery mildew, and spot blotch [16]. The other cloned leaf rust APR gene *Lr67* encodes a hexose transporter that forms hetero dimer with other functional transporters to reduce the uptake of glucose [17].

With advances in techniques of genomic sequencing and molecular biology, cloning of *Lr* genes or leaf rust resistance QTL (*QLr*) has become a more feasible task. It can be accomplished following multiple strategies such as classical map-based positional cloning, or rapid gene-cloning approaches including MutChromSeq, MutRenSeq, AgRenSeq and MutIsoSeq, or even whole genome sequencing [18].

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