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Research on Advance of Rice False Smut *Ustilaginoidea virens* (Cooke) Takah Worldwide: *III. Infection Cycle and Invasion Mechanism of U. virens and Rice Resistance to RFS*

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Abstract

In this part, the infection cycle and invasion mechanism of RFS, including the primary and secondary source of RFS infection. The factors affecting the disease occurrence and epidemiology, including the infection time and pathway, different conditions affecting the incidence of RFS, for example, the type of rice varieties and morphological characteristic, meteorological factors, environmental conditions, cultivation management, and amount of *U. virens* in the field. The mechanism of rice varieties' resistance to RFS were also discussed, including morphological characteristics, and biochemical mechanism, resistance genes of rice.

Keywords: *U. virens*, Infection cycle and mechanism, affect factors, rice resistance and mechanism

1. Introduction

To understand the invasion mechanism and cycle of *U virens*, the resistance and the resistant mechanism of rice varieties to RFS, there are significance for further study of *U. virens* and effective prevention and control of RFS, as well as rice genetic breeding for disease resistance. There are different viewpoints on the source of infection in the early, but a more consistent view was that the overwintering sclerotia and chlamydospore are the main original resources of infection. There are many factors affect the occurrence and prevalence, for example, the climate conditions, temperature, humidity, hours of illumination, especially the "key growth stage of rice" (KGSR, *i.e.*, the late booting stage and begin heading to flowering period are the susceptible period of rice to RFS) encounter the local climatic conditions which suitable for the occurrence of RFS; The resistance of rice to RFS, fertilizer and water management, and amount of original *U. virens*. The mechanism of rice varieties' resistance to RFS was determined by itself genetic, for example, the morphological characteristics of rice variety, the content and activity of biochemical substances. However, the most essential factors are the resistance genes of rice varieties.

2. Disease Cycle of RFS and Factors Affecting the Disease Occurrence

Knowledge of the pathogen's life history and infection process in nature is critical for disease control (Tang et al., 2012b).

2.1 Primary Infection Source of RFS

U. virens can overwintering in the form of mycelium, chlamydospore, sclerotium and RFS balls. The overwintering sclerotia germinated and produced ascospores, which caused rice false smut in the coming year (Liao, 1994). Inoculation with chlamydospore, ascospores and thin-wall conidia can successfully induce RFS (Chen et al., 1995; Huang et al., 2002; Yao et al., 2012). Zuo et al. (1996) captured chlamydospores over the rice fields, suggesting that chlamydospores have the ability of air flow spreading. Therefore, it is deduced that there is a pathogen source base or intermediate host suitable for the dormancy of chlamydospore outside rice fields. However, there is a totally different point of view on this point. Chen et al. (1994c) believed that chlamydospores in soil germinated and produced conidia, and the conidia spreading by wind and rain and caused the primary infection; However, the sclerotia were not found in some areas of some provinces in China, but the rice was infected by *U. virens* every year, so it was really questionable that sclerotium was the major primary infection source (Wang, 1992; Chen et al., 1995). On the other hands, Liu et al. (2009b) demonstrated that the primary infection source of RFS mainly was the seeds with pathogen, followed by the overwintering pathogen in soil.

Most scholars abroad were consistent with the views that the pathogens overwintering in the form of sclerotium and chlamydospore were the major primary infection sources, and the chlamydospores played a decisive role in the secondary infection (Ikegami, 1963; Ou, 1985).

2.2 Secondary Source of RFS Infection

A more consistent view on the secondary infection source of false smut is chlamydospores. The chlamydospores in soil germinated and produced conidia, and the conidia caused primary infection by spreading through wind and rain. Many studies have reported that there was a severe incidence of RFS in late maturing varieties, and that the secondary infection may be the major factor (Chen et al., 1994c). A large number of chlamydospores could be captured over the rice field, and the number of spores was relatively increased with the arrival of the flowering period. Evidently, the secondary infection source of RFS is mainly chlamydospores and conidia by air spread (Ou, 1985).

2.3 Infection Time and Pathway

The infection periods and pathways of *U. virens* are not very clear. There are main views of the seedling stage system infection, or late booting to early heading stage infection (late stage infection), or systemic infection and late growing stage infection. However, more advanced inoculation and detection technology have been employed recently, indicating that RFS infection is mainly in the late stages.

2.3.1 Systematic Infection in Seedling Stage

The experimental results demonstrated that the infection of *U. virens* may be the seedling stage systematic infection. When rice seeds with pathogen germination, the pathogenic spores can successfully infect a large number of radicles and coleoptiles, and extend along the outer surface of the sieve tube of the phloem until reaching the middle and late stages of tillering (Ikegami, 1962, 1963; Schroud et al., 2005). It was subsequently found by histological observation and molecular techniques detected that the pathogen can attack the root at the seedling stage and lead to symptomless colonization of the entire plant (Ditmore et al., 2006; TeBeest, 2010). Dai et al. (2005) detected and found that the conidia of *U. virens* formed mycelium on the surface of the glume and extended into the inner hull, which provides evidence for the direct infection of conidia on rice grains.

A large number of comparative field studies regarding to whether the rice seeds with pathogen can lead to occurrence of RFS have conducted. Some results indicated that seeds with pathogens can cause RFS (Chen et al., 1994b; Liu et al., 2009b). Overwintered chlamydospores could infect seeds, seedling coleoptiles, leaves and roots of the early rice, and cause RFS during heading stage (Chen et al., 1995; Gao et al., 2011). Rice seeds contaminated by *U. virens* and treated with biocidal (pathogens-free) were sown and planted under sterile soil and isolated conditions, the rice seeds carrying pathogens could induce RFS, while the sterilized seeds could not induce diseases, indicating that the seeds could carry pathogens and caused RFS (Liao, 1993). By using spray or injection inoculation with chlamydospores at the rice seeds germination, seedling or booting stages, it could successful caused RFS (Ikegami, 1962, 1963; Miao, 1992).

2.3.2 Late Growth Stage Infection

Most researchers believed that the primary infection site was the floral organ of rice, and the infection period was between the middle and late booting stages to the early heading period (Xu et al., 2001; Wang et al., 2008; Chen et al., 2013). Liu et al. (2007) believed that the main infection period of *U. virens* was between the big belly stage to begin heading period, but not the seed germination stages. Strong evidences support that the infection occurred in flowering stage was that artificial inoculation in the late booting stage could increase the

diseased panicle rate substantially (Cai et al., 2009; Gao et al., 2011). At present, it was believed that 1-2 weeks before heading are the main invasion period of RFS (Li et al., 1986; Wang, 1992; Guo et al., 2000). Du et al. (1990) illustrated that seed treated with biocidal there was no effect of prevention and cure RFS, and inoculation with *U. virens* after germination of rice seeds also did not incur the disease, proving that *U. virens* is not systemic infection.

An experiment of bagging protection was conducted, the results have shown that there was no occurrence of RFS when rice plants were bagged in elongation stage and early booting stage, while RFS occurred in all of the treatments of bagging after the late booting stage (pollen mother cells (PMC) filling stage), indicating that the infection of RFS began early booting and late booting stage (Deng et al., 1990) (Table 1).

Table 1. Studies on the infection stage of RFS by bagging

Treatment	Rate of infected panicle%	Rate of diseased grain‰	Treatment	Rate of infected panicle%	Rate of diseased grain‰
Bagging at elongation stage	0	0	Inoculation at elongation stage	0	0
Bagging at early booting stage	0	0	Inoculation at early booting stage	0	0
Bagging at late booting stage	15.0	5.68	Inoculation at late booting stage	38.6	17.8
Bagging at begin heading stage	9.5	3.86	Inoculation at begin heading stage	18.5	8.24
Bagging at full heading stage	5.2	1.12	Inoculation at full heading stage	5.2	3.36

From the incidences of RFS of different period inoculation with *U. virens*, there was no RFS occurred during the elongation stage and the meiosis stage of PMC, while most serious occurred of RFS with inoculation during late booting stage and begin heading stage. Inoculation at begin heading and full heading stages of rice, there were a small amount of RFS balls appeared, suggesting that the infection of RFS mainly occurred after late booting stage (Hu et al., 2010; Liu et al., 2009b). The inoculation was performed at 6 to 9 d before heading, then the incidence were the highest either for resistant or susceptible rice varieties; in addition, the incidence was very low or there was no occurrence of RFS for the inoculation at 10 to 13 d before heading (Zhang et al., 2004).

Field observations and the results of inoculation experiments combined with histological studies, now suggest that the most likely route of *U. virens* infection is when rice plants are at the booting stage (Sonoda et al., 1997; Ashizawa et al., 2012). Furthermore, experiments using a mixture of conidia and hyphae of *U. virens* cultured demonstrated that serious cases of RFS could arise when the inoculation was made by injecting the panicles at the booting stage (Zhang et al., 2004; Sonoda et al., 1997; Ashizawa et al., 2011).

2.3.3 Systematic Infection + Late Stage Infection

There were also experiments supporting that RFS not only could infect systematically, but also infect at late stage (Liao, 1992). Artificial inoculation with chlamydospores at early and middle seedling stages of rice, it could induce RFS at adult periods. After three years and nine experiment replicates, it was proven that the *U. virens* could infect rice most easily from the formation of young panicle to the middle of the booting stage, and the rice was basically not be infected after begin heading (Chen et al., 1994a).

2.3.4 Infection Site and Infection Mechanism of *U. virens*

A recent cytological study indicated that the pathogen of *U. virens* infected the filaments intercellular and extended intercellular along the filament base (Tang et al., 2012b). It was found that the hyphae of *U. virens* are able to invade the spikelet apices, via a small gap between the lemma and palea.

Infection sites: Examination of serial semi-thin and ultrathin sections of infected spikelets showed that the primary infection sites of *U. virens* was upper parts of the three stamen filaments located between the ovary and the lodicules. The pathogen did not penetrate host cell walls directly and did not form typical appressoria structures and haustorium. The ovary remained alive in the RFS ball and was never infected (Tang et al., 2012b). *U. virens* did not kill the host cells, so it belongs to living nutrition type fungus (Hu et al., 2012a; Tang et al., 2012b).

In the booting stage, *U. virens* specifically infects the stamen filaments of rice, and thus it grows and develops into chlamydospores and finally formed smut ball. *U. virens* could not infect the ovary and anther, however, the secondary hyphae can occasionally infect the stigma and outer cells of lodicule (Dai et al., 2005). However,

Dodan et al. (1996) and Mandhare et al. (2008) found that conidiophore of *U. virens* could infect the ovary and single spikelet and then transformed into chlamydospores and false smut ball.

A recent study has indicated that *U. virens* follows a specific route, with the hyphae colonizing the outer surface of the spikelet, and then entering the inside of spikelet from the apex (Ashizawa et al., 2012). Consistent with a previous report (Tang et al., 2012b), *U. virens* initially attaches itself to the surface of the filaments, and then formed several discrete structures, including mycelial stroma and infection hyphae.

Mechanism of infection: The route of *U. virens* penetrates rice panicles has long been a question of debate. A recent study utilized a transgenic strain expressing green fluorescent protein gene (GFP) (Ashizawa et al., 2012) to observe the *U. virens*' initial infection of rice panicles before heading. The detection method of nested PCR to detect the *U. virens*, and found that there were attachment and infection in the early reproduction stage of rice (Zhou et al., 2003, 2006; Wang et al., 2005a). The GFP-labeled conidia of *U. virens* were injected into rice sheaths at booting stage, there were a lot of conidia present on spikelet surfaces 48 hour post-inoculation (hpi), hyphae had invaded spikelets through the apices, via the small gap between the lemma and palea and had already reached all floral organs 144 hpi (Ashizawa et al., 2012).

The primary site of *U. virens* colonization was at the base of the filaments with the inner spikelets becoming infected by hyphae at 24 hpi. The accumulation of hyphae reached its highest level at 168 hpi, before rice heading stage, as the infection extended upward from basal filaments to the anther apex, and then enclosed all the floral organs to produce a velvety smut ball (Hu et al., 2014).

2.4 Conditions Affecting the Incidence of RFS

The occurrence and epidemic of RFS was affected by many factors, for example, the amount of *U. virens* and its pathogenicity, resistance of rice varieties, climate factors, and cultivation management. The susceptible varieties and continuous rainfall for more than 5 d during rice booting and heading period are the two key factors to cause outbreak and epidemiology of RFS (Hu et al., 2010). Rice plants at late booting stage, and flowering to filling stage encounter a relatively low temperature (*i.e.*, 22-28 °C), rainy and humid climate or rainy weather exceed consecutive 5 d days, the degree of RFS incidence will be serious (Wang et al., 2005b; Liu et al., 2000).

Figure 1. Late maturing variety (left) was seriously infect by RFS but early maturing (right) no any infection

2.4.1 Resistance of Rice Varieties

The resistance difference of different rice varieties to RFS varies greatly (Chen et al., 1992, 1994c). Observation in the paddy fields combined with artificial inoculation in greenhouse and field natural infection have both proven that there was real resistance to RFS of different rice varieties (Ashizawa et al., 2011; Tang et al，2012a). Under natural conditions, the infected panicle rate and the disease index of different varieties vary greatly, and the values were in the ranges of 0.43-33.04% and 0.05-16.14%, respectively (Jin et al., 2005; Lu et al., 2008). The resistances of rice varieties were affected by the internal genetic mechanism (Xu et al., 2002; Fang et al., 2008) and external morphological characteristics.

Rice varieties types: The resistance difference of rice varieties has close relationships to types of rice varieties, plant types, and growth characteristics. In general, the waxy type varieties are more susceptible to RFS than that of the japonica varieties, and the *japonica* is more susceptible than *indica* varieties. Erect dense panicle varieties are more susceptible to RFS than that of general varieties, the incidence of RFS in hybrid rice was much more severe than that of the conventional rice varieties (Wang et al., 2004; Lv et al., 2007). The short-stalked, large panicle, wide leaf but small angle varieties are fertilizer tolerant and lodging-resistant, and they are suitable for high density planting, which are in favor of the occurrence of RFS. Varieties with long duration of tillering, booting and flowering stage, the incidence of RFS is also more serious. The RFS in the two-line hybrid rice was more serious than that of the three-line hybrid rice (Liu et al., 2009a; Tang et al., 2012a; Gan et al., 2013).

Rice plants morphology: The effects of rice plant types on the occurrence of RFS vary greatly (Hu et al., 2012b). The occurrence of RFS has a close relationship to the panicle traits, and the correlations are as follows: grain number per panicle > secondary branch grain number > secondary branch number > the seed density. The number of grains per panicle, especially the number of grains in the secondary branch, is the main causes of the high incidence of RFS (Wang et al., 2004).

2.4.2 Meteorological Factors: Temperature, Rainy Days and Rainfall, Humidity, Light, etc.

It was demonstrated with many years observation in the fields, the RFS incidence of the same rice variety in different years are quite different. If the resistant varieties of rice encounter rainy days during the booting period and begin heading stage, then the incidence of RFS will be aggravate; on the contrary, if the susceptible varieties encounter dryness and high temperature weather during these stages, then the incidence of RFS will decrease or even no be infected (Wang et al., 2004).

The climate factor that rice plants encounter in vulnerable period or KGSR is one of the key factors determining the degree of RFS incidence. If KGSR encounter more rainy days, abundant rainfall, a short sunshine duration, the relative humidity (RH) was high (above 85%), the temperature was suitable (22-28 °C), and a small temperature difference between day and night, then the degree of RFS incidence was severe. If these factors were contrary, then the degree of RFS incidence was low (Yashoda et al., 2000; Ye et al., 2005; Yang, 2007; Fei et al., 2010). It was found that the severity of RFS was closely related to the local accumulated sunshine hours and total rainfall in KGSR. If the number of sunshine hours was reduced and the rainfall was increased, then the morbidity of RFS was aggravated (Pan et al., 1997b).

The rain days and rainfall during the KGSR were positively correlated with the infected panicle rate, the correlation coefficient was r = 0.8342* and r = 0.8826*, and the related equation was Y = -6.7985 + 6.0538x and Y = -2.6963 + 0.3652x, respectively. RFS is negatively correlated with the daily mean temperature but positive correlated with humidity at the begin heading stage. When the daily mean temperature was 23-24 °C and RH 82%-87% during the begin heading period are conducive to the occurrence of RFS (Lv et al., 2007).

Shading and RFS: Rice plants were treated with two or three layers of gauze for shading, the number of infected hills, panicles and grains by RFS are 1.08-1.37, 1.19-1.66 and 2.53-3.94 times of those no-shading controls, respectively (Qian et al., 1993). The experimental results verified that cloudy and rainy weather was conducive to the occurrence of RFS (Table 1).

2.4.3 Environmental Conditions

The RFS incidences of the same rice varieties in the same year which planted in different areas are different. Occurrences of RFS are associated with altitude and ecological environment, and the incidence of high altitude was more severe than that of the low altitude; the incidence of RFS in temperate and highlands is low, while in tropical lowlands is high (Zhang et al., 2006a). Even in the same paddy field, the rice plants incidence of RFS on the edge was severe, while in the middle of the field was low (Jin et al., 2005; Chen et al., 2005).

2.4.4 Cultivation Management

The occurrence of RFS is also associated with rice cultivation and management, especially the management of fertilizer and water.

Fertilization: Different fertilizer, dosage of application and application time of fertilizer significantly affect the occurrence and severity of RFS. The incidence of RFS was higher if more nitrogen fertilizer was applied and the application time was late (Bhardwaj, 1990; Pan et al., 1993; Ye et al., 2005; Yang, 2007). Increasing the amount of nitrogen fertilizer significantly increased the rate of infected rice plants.

Fertilization habit of partial nitrogen, excess dosage of fertilizer and late fertilization will reduce the rice resistance ability to RFS (Zhao, 2008). The applied total quantity of nitrogen (X_1), amount of panicle fertilizer

(X_2) and application time of panicle fertilizer (X_3) were strongly affect the incidence of RFS (Y), the regression equation was $Y = -93.053 + 3.393X_1 + 9.265X_2 + 3.711X_3$, and the correlation coefficient $R = 0.8922^{**}$. Among all of these factors, the direct effect of the application amount of ammonia fertilizer on the RFS incidence was the highest, $P_{0.1} = 0.393$ (Pan et al., 1997a). If 600 kg/hectare of urea was used as panicle fertilizer, then the infected panicle rate was 17.5%, and increased by 34.6% and 48.9% compared with that of the 300 kg/hectare and no application of the panicle fertilizer (Chen et al., 2009a).

When 165.0, 225.0, 232.5, 240.0 and 300.0 kg of pure N was used as the topdressing fertilizer (urea) per hectare at heading period, the infected rice panicle rates of RFS were 1.33%, 1.97%, 2.13%, 2.33% and 3.13% (Chen et al., 2000), respectively. Reasonable amounts ratio of nitrogen, phosphorus and potassium fertilizer were beneficial to increasing rice yield and reducing the occurrence and harm degree of RFS (Wang et al., 2010; Hong et al., 2013; Qing et al., 2014).

Transplanting method and water management: The planting density and water management also affect the incidence of RFS. Close planting and long-term deep water irrigation can increase the incidence of RFS. Waterlogging paddy fields, especially long-term waterlogging in late stage of rice growing will lead to high humidity and result in serious occurrence of RFS (Zhang et al., 1997; Zhang et al., 2005; Yang, 2007; Wang et al., 2010).

Sowing and transplanting period. Generally speaking, the incidence of RFS of early transplanting rice groups were significantly lower than those of the late transplanting for each rice variety in the same area (Wang et al., 2010). The infected rate of the late maturing group and early maturing group varieties were investigated in 2005 and 2006, the infected rate of hill, panicle and grain were 76.3%, 26.6%, 4.6% and 16.8%, 5.4%, 4.7% for the same rice variety, respectively (Lu et al., 2006).

The sowing and transplanting time of rice will determine the time of KGSR, and affects the KGSR if encounter the local climatic conditions which suitable for the occurrence of RFS. It was reported that the reason for the severe incidence of RFS was that the heading stage met the most appropriate of the local meteorological conditions for the occurrence of RFS (Singh et al., 1981). The incidence rate of RFS of the early sowing was only 0-3.1%, while for the late sowing rice it was 48.5-56.1% (Ahonsi et al., 2000).

2.4.5 Amount of *U. virens* in the Field

The occurrence of RFS was positively correlated with the accumulation degree of *U. virens* in the fields. In general, the occurrence of RFS in the old disease areas and/or used to be serious occur areas then the RFS is high, due to the large number of *U. virens* left behind previous year was significantly higher than that of the field with little pathogen, and vice versa (Liao, 1994; Zhou et al., 2010).

3. Rice Resistance to RFS and Their Mechanism

Most researches did not find any rice varieties (materials) with immunity or high resistance to RFS (Guo et al., 2010; Jiang et al., 2010a, 2010b; Zheng et al., 2013), but there were some studies which found highly resistant and immune varieties (Huang et al., 2010). It was verified by natural infection or artificial inoculation that there were significant differences in resistance to RFS among rice varieties (Yang et al., 2008). Many research results and long-term field observation have both shown that the resistance of rice varieties to RFS was real subsistent. 198 rice varieties were identified by using artificial injection inoculation method of the conidia suspension liquid, there were 44 rice varieties with complete immunity to RFS, 34 varieties with high resistance (Chen et al., 2009b). The identification results of Pan et al. (2012) showed that the resistance of rice varieties to RFS were actual existence, for example, the most serious infected panicle rate reached up to 80%-90% of the susceptible rice variety, while for the resistant one, there was low infected panicle rate (Singh et al., 1987; Phatak et al., 1991; Lore et al., 2013). The incidence of 160 rice varieties were investigated under natural conditions, and demonstrated that there were 16 varieties with resistance (Urmila et al., 1999).

3.1 Morphological Characteristics and Rice Resistance to RFS

There are also differences in the resistances to RFS of rice varieties with different morphological characteristics (Hu et al., 2012b). RFS incidence was closely related to panicle traits, the following order affect the RFS severity from large to small, secondary branch number > secondary branch grain number > grain number per panicle > grain density. Grain density was the main factor affecting the incidence of RFS (Xu et al., 1987). The incidence was significantly and positively correlated with the flag leaf width, and extremely significantly negatively correlated with the number of panicles per unit area, flag leaf angle and plant height. The more number of grain per panicle was, the higher incidence of RFS. Large-panicle type, more grain numbers and high grain density of rice cultivars were more easily to be infected by RFS (Chen et al., 2011).

3.2 Biochemical Mechanism and Rice Resistance to RFS

The glume of resistance varieties had large amounts of lignin, while the susceptible varieties had less lignin; and the red fluorescent substances in the glume of the resistant cultivars were higher than those of the susceptible one. The endosperm cells of the resistance varieties had more polyphenols, but there was no polyphenols in the susceptible varieties (Dai et al., 2005). Rice plants were inoculated with conidia suspension of *U. virens*, the content of MDA was significantly increased in the susceptible varieties, and the content changes of resistant cultivars were smaller; the CAT activity of the resistant varieties was decreased, and that of the susceptible varieties was increased. The activities of POD, PAL and PPO of the resistant varieties increased, and the susceptible cultivars did not show significant changes when rice plants were inoculated with conidia suspension of *U. virens*; but the differences of SOD activity between the resistant and susceptible varieties were not significant (Jiang, 2010; Li et al., 2010). The activity of the CAT of the susceptible varieties decreased, while the PAL activity increased after inoculation (Lu, 2013). Gan et al. (2013) believed that there were no inevitable correlations between rice resistance and the activities of the defense enzymes POD and SOD. Brassinosteroids in rice plant may have more important roles than that of salicylic acid and ethylene in response to *U. virens* infection, the disturbance of other hormones such as auxin, gibberellins and jasmonates may also affect *U. virens* infection (Yang et al., 2014).

3.3 Resistance Genes of Rice

Hereditary resistance to RFS of rice was not only controlled by major gene, but also affected by multiple genes, which was consistent with the E-1-3 genetic model, namely two pairs of major genes plus the polygene mixed genetic model. The heritability of the major gene was 76.67%, and the polygene was 22.86% (Li et al., 2008). The resistance of rice varieties to RFS was affected by additive and non-additive effects, and the effect of the female parent had a critical influence (Wang et al., 2013). The dynamic expressions of RFS progression- related protein genes including *OsPR10a*, *OsPRla* and *OsPR1b* were analyzed by using RT-PCR. The expressions intensity of PRPG *OsPR10a*, *OsPR1a* and *OsPR1b* in incompatible interaction process were shown to be higher than those of the compatible interaction (Lu, 2013).

3.4 The Genes Location of Rice Resistance to RFS and Their Distribution

There were 146 molecular markers were selected from the recombinant inbred lines (RILs) of Lemont/Teqing. The total genetic distance of 146 markers was 2227.6 cM, covering 95.6% of the donor genomes, and the average adjacent marker distance was 15.2 cM. There were two anti-RFS of rice QTL (*QFsr10* and *QFsr12*) were located on the 10^{th} and 12^{th} chromosomes, the enhanced resistance alleles were from the parent Lemont, and the respective additive effects were 3.38 and 3.34 (Xu et al., 2002). Quantitative resistance loci (QRL) was identified using 213 introgression lines (ILs) from a cross between Teqing (recipient) and Lemont (donor). Ten QRL affecting percentages of infected hills, panicles and spikelets were detected and mapped to rice chromosomes 2, 3, 4, 6, 8, 10, 11 and 12. Four QRL of qFSR-6-7, qFSR-10-5, qFSR-10-2 and qFSR-11-2 had relatively larger and consistent effects (Zhou et al., 2014).

Seven QTLs of *qFsr1, qFsr2, qFsr4, qFsr8, qFsr10, qFsr11* and *qFsr12* were detected (Li et al., 2011), which were respectively located on the 1^{st}, 2^{nd}, 4^{th}, 8^{th}, 10^{th}, 11^{th} and 12^{th} chromosomes, and the contribution rate was 9.8%-22.5%. The explanation rate of the trait of *qFsr10* and *qFsr11* was between 18.0%-19.3% and the disease index of RFS was decreased by 8.0-16.3%.

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