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Genes and Loci Controlling the Resistance of Strawberry (*F. ananassa* Duch.) to Pathogens

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ABSTRACT

Strawberry (*F. ànanassa*) is one of the most popular and widespread berry crops in the world. Strawberry diseases are the main limiting factor that seriously affects the yield of plants and leads to economic losses. Most strawberry cultivars are very sensitive to pathogenic fungi and bacteria, such as *Colletotrichum acutatum* (anthracnose root), *Colletotrichum gloeo sporioides (crown rot), Fusarium oxysporum fragariae* (fusarium wilt), *Phytophthora fragariae* (red stele root rot), *Verticillium dahlia* (verticillium wilt), *Botrytis cinerea* (grey mould) and *Xanthomonas fragariae* (angular leaf spot). Currently, due to the rapid development of molecular genetics in general and in particular knowledge related to the organization of genomes of agricultural crops, the use of DNA technologies in strawberry breeding has become possible. To identify disease resistance loci, the most popular approach was to map the loci of quantitative traits (QTL). Accurate evaluation of heritability and the number, location and effects of loci controlling traits are the basis for strategic decisions in breeding programs. The purpose of this review is to present up-to-date data on known genes and quantitative trait loci (QTL) that control the resistance to the most common strawberry pathogens.

Key words: Bacterial diseases, DNA-markers, Fungal diseases, Resistance, Strawberry (*F. ananassa* Duch).

The first cultivars of octoploid (2 n = 8 × = 56) garden strawberries (*Fragaria ananassa* Duchesne ex Rozier) were found in France about 300 years ago (Stauct, 1989). According to modern concepts, the parent species were formed by merging and interacting the genomes of four diploid progenitor species - *F. vesca* L., *F. nipponica* Lindl., *F. iinumae* Makino and *F. viridis* Duch (Edger *et al*., 2019).

Currently, cultivated strawberries *F. ananassa* is the most important and most economically profitable berry crop in the world (Govorov and Govorova, 2015). It accounts for over 70% of global berry production (Liu *et al*., 2021).

Recently, due to the active exchange of planting material between countries, as well as climatic changes, there has been an expansion of the areas of fungal and bacterial diseases of strawberries and the prevalence of pathogens and their vectors in regions not characteristic of their habitat (Zavriev and Ignatov, 2020).

The fight against pathogens is quite difficult, since, on the one hand, there is no or limited range of chemical preparations for protection and on the other hand, there is the possibility of rapid spread of these microorganisms.

Therefore, the task of creating new cultivars of this crop resistant to pathogens is a key priority of genetic improvement programs, in connection with which the creation and selection of genotypes with complex resistance to diseases is carried out all over the world. One of the methods that allows such selection at the early stages of ontogenesis is the identification of genes that determine resistance and the subsequent use of targeted selection using DNA markers closely linked to these genes (Moose and Mumm, 2008).

One of the main problems in strawberry genetics is the availability of highly productive subgenome-specific markers.

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Since cultivated strawberries have four subgenomes, each locus can represent up to eight different alleles in one individual, which makes it difficult to analyze segregation accurately.

In this review, we consider currently known strawberry loci associated with resistance to fungal and bacterial pathogens and associated DNA markers.

Anthracnose root (*Colletotrichum acutatum*)

Colletotrichum species can cause significant losses in strawberry production worldwide (Parikka *et al*., 2014; Baroncelli *et al*., 2015; Wang *et al*., 2017). Symptoms include anthracnose black rot and crown rot (Freeman *et al*., 2001). These symptoms may be caused by *Colletotrichum acutatum, Colletotrichum fragariae* and *Colletotrichum gloeosporioides* (Freeman *et al*., 1998).

Anthracnose of strawberries, caused by *Colletotrichum acutatum*, is a disease of global importance (Nilsson *et al*., 2014; Yan *et al*., 2015).

The disease causes the death of up to 80% of plants in nurseries and crop losses of more than 50% in strawberry fields (Sreenivasaprasad and Talhinhas, 2005). Anthracnose has been a quarantine disease on the territory of the Eurasian Economic Community since 2016 (Bosshard ,1996; Tsvetkova and Kuznetsova, 2020). For the development of the disease, the temperature from +24 to +28°C (Smith, 1990) and a long period of humidity are favorable most of all (Forcelini *et al.*, 2017). Anthracnose affects almost all organs of the plant. At the beginning of the development of the disease, red-brown, gradually blackening spots are formed on young leaves and tendrils. Over time, ulcers are formed, which merge forming rings. Yellow-orange foci containing spores are formed on the black necrotic parts of plants. Spores are the primary source of infection (Govorova and Govorov, 2015).

As a result, the rosette or the whole plant withers and shrivels. Flowers and fruits are infected from the affected leaves and tendrils. The flowers at the same time look burnt and die. Through the stamens, the fungus penetrates into the receptacle of the ovary. Single or group indentations from dark brown to black occur on immature fruits. Drying out, they acquire a chocolate-brown color. On mature fruits, there are depressed, rounded bronze-brown spots with a distinct edge, then blackening spots of hard dry rot. In the presence of moisture, the affected areas of the berries are covered with scab, in dry weather, the berries dry up or mummify. The root system is also affected, acquiring a red-brown color on the cross sections (Mertely *et al.*, 2017).

Anthracnose rot of strawberry cones leads to sudden wilting and death of plants (Govorova and Govorov, 2015). The disease is insidious, since for a long time it may not manifest itself in any way (Freeman *et al.*,1998). Such hidden infections are the main reason for the spread of *C. acutatum*. Detection of the pathogen at this phase can significantly help in reducing its spread.

Phenotypic selection for disease resistance requires significant resources for testing with inoculated plants (Moose and Mumm, 2008). DNA tests for resistance to anthracnose should be widely applicable in connection with the global importance of anthracnose diseases.

Currently, a significant number of *C. acutatum* isolates, which belong to two pathogenicity groups have been identified (Denoyes and Baudry, 1995). Resistance to *C. acutatum* of the first group of pathogenicity is polygenic, while resistance to *C. acutatum* Simmonds of the second group of pathogenicity is monogenic, controlled by a dominant *Rca2* gene (Lerceteau-Kohler *et al.*, 2003; Denoyes-Rathan *et al.*, 2004).

Data have been published on population mapping from the crossing of the resistant Capitola cultivar and the susceptible Pajaro using AFLP markers. According to the results, 4 markers were linked to the *Rca2* gene, two of them were converted into SCAR markers (STS-Rca2_240 and STS-Rca2_417). The STS-Rca2_240 marker is localized at a distance of 2.8 cM from the *Rca2* gene, the STS-Rca2_417 marker is at 0.6 cM (Lerceteau-Kohler *et al.*, 2005). These markers are currently used to assess the allellic state of *Rca2* (Luk'yanchuk *et al.*, 2018; Lyzhin *et al.*, 2019; Lyzhin and Luk'yanchuk, 2021; Lyzhin and Luk'yanchuk, 2022).

A partially dominant allele has been identified at the main locus, named FaRCa1, which gives resistance to infection with isolates of the *C. acutatum* species complex from Florida. This locus appears to be part of the *Colletotrichum* resistance group of the first pathogenicity group, in contrast to *Rca2*, which is effective against *C. acutatum* Simmonds isolates (Salinas *et al.*, 2019; 2020). These results should become the basis for breeding tools that will lead to more effective selection for sustainability in strawberry breeding programs.

C. gloeosporioides (crown rot) has symptoms similar to *C. acutatum*; it is a polyphage, develops optimally in humid environmental conditions at temperatures above 25°C (MacKenzie *et al.,* 2007). Infection begins with the penetration of the fungus into the aboveground part, followed by colonization and reproduction, which causes a reddish-brown dense rot in the tissues. The amount of time required for penetration into the tissue before the appearance of infection symptoms varies in different cultivars (Sharma and Kulshrestha, 2015), which creates a problem of accurate phenotyping of resistance due to the complexity of monitoring the progression of the disease to wilting and destruction of plants.

Two complex multi-family populations were subjected to a pedigree-based QTL analysis to identify the *C. gloeosporioides* -resistant locus FaRCg1 on LG 6B in two different seasons. The complex structures of these population sets allowed evaluating the effects of FaRCg1 on many genetic backgrounds simultaneously. Both populations provided convincing evidence of QTL in a single subgenome using triple FlexQTL™ analysis, both for the entire genome and for chromosomes. Detection and characterization of the FaRCg1 locus and molecular tools developed on its basis will be used to achieve increased genetic resistance (Anciro *et al.*, 2018).

Red stele root rot (*Phytophthora fragariae* hickman)

Phytophthora (red stele root rot) of strawberries is caused by two species of pseudo fungi of the *Phytophthora* genus (Abd-El-Kareem *et al.*, 2020). The first one, *Phytophthora fragariae* Hickman, causes *Phytophthora* root rot or so-called « redness of the central root cylinder ». The second one, Phytophthora *cactorum* (Leb. Et Cohn) Schroet. causes the "late blight leathery rot" disease (Govorova and Govorov, 2015).

Late blight root rot can manifest itself in chronic and transient forms. With a chronic form in spring, the diseased bushes are delayed in development, the leaves that have appeared lose their luster, acquire a grayish color, the petioles shorten, the plates become smaller and become cup-shaped. Bushes lag behind in growth, old leaves on

them prematurely wilt and wither. Fruiting of diseased bushes sharply decreases or stops altogether, the formation of tendrils is weak. Individual plants during the period of mass fruiting may die, but more often death occurs 2-3 years after infection. With a transient form of the disease, the entire plant or its lower leaves and sometimes only the peduncles suddenly wither in spring. In plants, the fascicular roots die off and the larger ones become bare and narrow downwards, the central axial cylinder of the root acquires a red color (Govorova and Govorov, 2015).

In European breeding programs, resistance to late blight root rot is mainly associated with the presence of *Rpf1*, *Rpf2* and *Rpf3* genes. *Rpf1* controls resistance to at least 16 *P. fragariae* races (Nickerson and Murray, 1993; Sasnauskas *et al.*, 2007). One of the DNA markers used to assess the allelic state of *Rpf1* is SCAR-R1A (corresponding to the dominant allele of the gene) (Haymes *et al.*, 1997; 2000; Lyzhin and Lukyanchuk, 2020). RAPD markers OPO-16C438, OPO-8A1450, OPC-8D510, as well as SCAR marker R1B can also be used to determine the allelic state of *Rpf1* (Haymes *et al.*, 1997; 2000).

Other root rot resistance genes have been poorly studied. *Rpf2* is present in such cultivars as “Climax”, «Redgauntlet», «Siletz» and «Sparkle» (van de Weg, 1997) and as far as we know, it is not mapped. *Rpf3* and *Rpf6* in the resistant cultivar “Yalova4” were mapped using AFLP analysis and associated with markers E26M59H and E39M51B, respectively (Haymes *et al.*, 1998; Hokanson and Maas, 2010). However, the conversion of polymorphic AFLP fragments into markers for practical molecular screening was not carried out (Khrabrov *et al.*, 2019).

Crown root [*Phytophthora cactorum* (lebert and cohn)]

Crown root of strawberries (*F. ananassa* Duch.), cused by *Phytophthora cactorum* (Lebert and Cohn), is a devastating disease and is found all over the world (Santos *et al.*, 2002). *P. cactorum* causes leathery rot on fruits, as well as ulcers, wilting and leaf lesions. Leathery rot is the most common manifestation of the pathogen and leads to the death of plants (Stensvand *et al.,* 1999).

Data on the large effect of resistance of the FaRPc2 locus to phytophthora leathery rot have been published (Mangandi *et al.*, 2017). Four predominant single nucleotide polymorphisms (SNPs) of haplotypes (H1, H2, H3 and H4) were identified in the FaRPc2 region, covering approximately 1.5 Mb. Haplotypes H1 and H4 are closely related to susceptibility. The two haplotypes appear to originate from different lineages, indicating that they may represent two resistance-related genes or two alleles of the same resistance gene in FaRPc2. DNA markers have been developed for two haplotypes at the FaRPc2 locus associated with resistance - H2 and H3. One HRM marker, RPCHRM3, associated with H3, was transformed into a competitive allele-specific PCR marker (KASP) (Noh *et al.*, 2018).

Grey mould (*Sclerotinia fuckeliana* fuckel; conidial stage: *botrytis cinerea* pers. ex. Fr.)

Botrytis cinerea is a typical necrotrophic plant fungal pathogen that inflicts on over 1000 plant species, including almost all vegetable and fruit crops (Fillinger and Elad, 2016).

Grey mould caused by *Botrytis cinerea* Pers.ex. Fr., conidial stage of ascomycetes *Sclerotinia fuckeliana* Fuckel, is one of the most devastating diseases of strawberries worldwide (Sutton, 1998; Essghaier *et al.*, 2009). The fight against the pathogen using fungicides is difficult due to the long latency period, long and overlapping periods of flowering and fruiting, the mass development of fungi that occurs during harvest and the appearance of strains of fungi resistant to pesticides (Sutton,1990). The disease often affects strawberry inflorescences, causing the death of flowers, especially during long rainy periods, or causes asymptomatic infections in which the pathogen remains hidden until the fruit ripens. Light brown, fast-growing spots with a gray fluffy velvety coating of spores and mycelium of the pathogen appear on the berries on the surface - the conidial stage of the fungus. Detection of the pathogen in healthy organs takes a long time, can be misleading due to the presence of many competing fungi with a higher growth rate in culture and infection is not quantifiable.

An article by Rigotti *et al.* (2002) shows the usefulness of PCR-based technology for the detection of *B. cinerea* on strawberry plants. The pair of primers C 729+/- obtained by them was tested on 34 isolates of fungi by polymerase chain reaction (PCR). In all tested strains of *B. cinerea*, the primer amplified a fragment with a length of 750 pn, which allows it to be used for further studies to identify hidden strawberry infections. This molecular tool should improve the understanding of the epidemiology of *B. cinerea*.

Real-time PCR-analysis have been developed for the detection and quantification of *B. cinerea*, suitable for a wide range of different host plant species. In the TaqMan system, a fluorogenic probe specific to the target DNA is annealed between PCR primers; during amplification, the probe is cleaved by 5′-3′ exonuclease activity of Taq polymerase releasing fluorescence. The analysis developed for the IGS domain was the most sensitive and allowed reliable detection and quantification of only 20 mcg of *B. cinerea* DNA. The developed analysis was used to track the progression of *B. cinerea* infection in plant material and is suitable for detecting and quantifying the pathogen before symptoms develop (Suarez *et al.*, 2005).

Angular leaf spot *(Xanthomonas fragariae)*

Xanthomonas fragariae is a gram-negative bacterium that causes angular spotting of strawberry leaves and is listed in Europe as a quarantine pathogen in the EPPO A2 list (Puławska *et al.*, 2020). This is a potentially serious and insidious disease, first reported in the United States. The first symptoms of the infection are water-soaked angular lesions on the lower surface of the leaf, which appear

translucent when viewed in passing light. Eventually, these spots can merge and become visible on the upper surface of the leaf in the form of reddish-brown spots of irregular shape. This pathogen is also attributed to the blackening of sepals, rot and destruction of whole plants (Maas, 1984). The spread of the pathogen is facilitated by rains or overhead irrigation (Hildebrand *et al.,* 2005). Since the symptoms are easily confused with those of other pathogens, laboratory confirmation is required. In continental Europe, yield losses of 10-20% have been reported, although in systems where top watering is used to allow bacteria to spread and multiply on wet leaves, losses are believed to have been higher (Elphinstone *et al*., 2005).

To date, no strawberry cultivar has been registered as resistant to *X. fragariae*. Six stable offspring from families 14.100 and 14.101 were selected for observation in extended field trials. The FaRXf1 locus associated with resistance has been identified. The allelic diversity at the FaRXf1 locus is unknown. It is expected that the use of the new locus through the development of high-performance DNA markers will improve future breeding efforts and accelerate the commercialization of resistant strawberry cultivars (Roach *et al*., 2016).

Fusarium wilt (*Fusarium oxysporum schlechtend. ex fr. f. sp. Fragariae* winks et williams)

Fusarium oxysporum is an asexual ascomycete of soil origin that causes severe vascular wilt in many crops.

F. oxysporum f. sp. fragariae causes rapid wilting and death of strawberries, which leads to serious economic losses worldwide. The primary source of infection with fusarium wilt includes infected soil and plants with latent infection (Winks, 1965). According to Koike *et al.* (2009); symptoms include withering of leaves, drying and withering of old leaves, delayed plant growth, decreased fruiting, as a result of which the plants are finally destroyed and die. Fusarium wilt has not yet become a serious threat to production wherever strawberries are grown; however, there is a significant risk of the spread of virulent strains through global trade and the danger of the evolution and emergence of virulent pathogen races that affect known resistance genes (Henry *et al.,* 2021).

Molecular markers that identify *F. oxysporum* races will accelerate pathogen identification. TaqMan multiplex analysis was developed for *F. oxysporum f. sp*. (van Dam *et al.,* 2018). Random amplification of polymorphic DNA analysis followed by sequencing was used to develop primers for amplified regions characterized by sequence, or transposable elements. Primers have been developed that amplify the genomic region between two transposable elements, Han-Skippy (Suga *et al*., 2013). This area has also been used to develop a set of primers for quantitative real-time PCR. However, the PCR analysis developed by Suga and co-authors (Suga *et al*., 2013) failed to detect some pathogenic isolates of *F. oxysporum* from California, such as GL1270 and GL1385 (Henry *et al*., 2017).

Pincot and co-authors (Pincot *et al*., 2018) identified multiple sources of resistance to fusarium wilt in a closed breeding population developed at the University of California, Davis. The dominant gene (*Fw1*) on chromosome 2B has been identified, which confers resistance to the virulent isolate *F. oxysporum f. sp. fragariae* found in California. The isolate they used (AMP132) was subsequently classified as Race 1.

Further, studies (Pincot *et al*., 2022) revealed that resistance to pathogen races is widespread in populations and that resistance to race 1 is provided partially or completely by dominant alleles among loci (FW1, FW2, FW3, FW4 and FW5) found on three non-homologous chromosomes (1A, 2B and 6B). The main genes have not yet been cloned and functionally characterized; however, probable candidates have been identified that provide plant resistance to genes.

Verticillium wilt [*Verticillium dahliae* (Kleb.)]

Verticillium dahliae (Kleb.) is a soil pathogen of plants, which has a great harmful effect on the yield of strawberries (Maas, 1998). This ascomycete fungus is a particular problem due to the durability of the inoculate in the soil, in which dormant sprouts, called microsclerotia, persist for up to 14 years in the absence of the host plant. Strawberries of any age are affected by the disease. Symptoms vary mainly depending on the cultivar and type of soil. On light sandy soils, a “lightning-fast” form is noted - plants die in 3-4 days. On loamy and sandy loam soil, a longer course of the disease is observed.

The chronic form is characterized by a relatively slow increase in the symptoms of the disease, manifested in the form of chloroticity, lag in the growth of leaves and a decrease in their number. More often, in natural field conditions, dark spots appear on the leaves, gradually turning into interstitial necrosis. With all forms of verticillosis on strawberries, the conducting vessels of the root are brown on the cross section. As the disease develops, the root inside turns brown and dies, turning into dry rot (Govorova and Govorov, 2004).

The effective fight against the disease is hindered by the restriction of the use of fungicides (Colla *et al*., 2012).

The population from the crossing of two parents ‘Redgauntlet’ and ‘Hapil’ strawberries was screened in the field for three seasons. Average withering rates were significantly associated with multiple QTL, which were significant in all years (Antanaviciute *et al*., 2015).

As a result of molecular studies, four different loci represented by SNP markers were identified, which are located in the same coupling groups as four QTL using SSR marker analysis (Antanaviciute *et al*., 2015) and six new QTL of resistance. The initial SSR markers associated with withering resistance were all mapped to the same chromosome that was originally reported, however, different subgenomes were assigned when investigating the nomenclature of coupling groups given by van Dijk *et al.* (2014)

and Sargent *et al.* (2016). QTL RvD1 is mapped to coupling group 3B and is located 2.7 Mb from the FaRVd3B SNP marker. RVd3 is mapped to group 7A and is 6.4 Mb from FaVd7A2. RVd7 is mapped to the 2D coupling group and is 1.2 Mb away from FaRVd2D2. RVd4-M1 is mapped to coupling group 2B, however, it is believed that it does not represent the same QTL as FaRVd2B, since it was mapped at a distance of 12.6 Mb (Cockerton *et al.*, 2019).

Powdery mildew *(Sphaerotheca macularis f. sp. Fragariae)*

Strawberry powdery midew (*Podosphaera aphanis* Wallr., formely known as *Sphaerotheca macularis f.sp. fragariae)* causes significant losses of strawberry yield.

Powdery mildew affects all aboveground parts of the bush. First, an inconspicuous delicate white coating appears on the leaves on both sides, then an abundant flour coating forms on highly susceptible cultivars. The affected leaves stop growing, become coarse, the edges of the leaf lobes are twisted in the form of a boat, the lower part turns up and acquires a bronze or purple hue. With the development of the pathogen during flowering, normal pollination does not occur, so the berries form ugly, covered with coating, acquire a matte shade, mushroom flavor and smell (Govorova and Govorov, 2004).

In the works of Sargent and co-authors (Sargent *et al.*, 2016), three different, significant QTL for resistance to powdery mildew were identified: FxaPMR7A, FxaPMR7X2 and FxaPMR5b, two of them were identified in the field experiments and one in the experiments with greenhouse plants. The names of QTL reflect the coupling groups in which they are mapped, while the names of subgenomes (A, b, X1 and X2) are given in accordance with the map previously developed by this group of authors. The loci FxaPMR7A, FxaPMR7X2 and FxaPMR5b are associated with markers: 8082 (LOD= 9.74, the percentage of explained variance is 34.2%), AX-89800832 (LOD= 5.17, the percentage of explained variance is 19%) and AX-89836603 (LOD= 4.97, the percentage of explained variance is 18.3%), respectively, where LOD is Levels Of Detail. By comparing with previous studies and carefully examining the *F. vesca* genome sequence, candidate genes underlying the genetic control of this trait were identified. Thus, a cluster of genes belonging to the TIR-NBS-LRR class was identified in the region of chromosome 7A corresponding to the FxaPMR7A locus. To create resistant cultivars, further work on QTL verification and the development of markers for resistance screening will be required (Sargent *et al.*, 2019).

CONCLUSION

Thus, the search for resistance loci for those not yet identified and the development of markers for recently mapped loci, as well as the expansion of the number of markers for molecular screening, are the primary tasks of intensifying breeding research to create cultivars with a high level of resistance to the most dangerous strawberry pathogens.

Despite the fact that significant advances have been made in recent years in the study of the strawberry genome, in particular disease resistance, the use of molecular markers for screening in this crop is still limited.

In practice, a small number of markers are used - SCAR markers of the *Rca2* gene (resistance to anthracnose) and the *Rpf1* gene (resistance to late blight root rot). For *P. cactorum*, DNA markers have recently been identified for two haplotypes at the FaRPc2 locus associated with resistance. Resistance to *V. dahaliae* and *P. aphanis* seems to be quite complex and to date, several main loci have been identified that potentially control resistance. No genes of resistance to grey mould caused by *B. cinerea* have been registered.

Conflict of interest

All authors declare that they have no conflict of interest.

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