MOLECULAR APPROACHES TO DISEASE RESISTANCE IN *FRAGARIA* SPP.

*Małgorzata U. Korbin**

Research Institute of Pomology and Floriculture
Pomologiczna 18, 96-100 Skierniewice, Poland

Received: October 25, 2010
Accepted: December 8, 2010

Abstract: Resistance to economically important diseases is one of the most desired traits to have in plant crops. The *Fragaria* genus including 21 wild and cultivated species (*Fragaria* x *ananassa*), contains genetic sources of diseases resistance that are quite rich but not fully exploited in breeding for resistance. Usefulness of different molecular techniques and high throughput technologies for the dissection of genetic resistance mechanisms and the explanation of plant diversity in relation to pathogens at the DNA level are described in this paper. The descriptions are based on the results of different studies on genome of *Fragaria* that were carried out in many research institutions in the world. The proposed model of comprehensive exploration of the strawberry genome, summarized with generating resistance markers and identification of genes involved with induction or regulation of plant response to pathogen attack, appear to be very useful in breeding strawberry for resistance.

Key words: genetic resources, molecular breeding, candidate genes, genome mapping, high throughput technologies

INTRODUCTION

The genus *Fragaria* L., a member of the family Rosaceae and sub-family Potentilloideae includes 21 species distinguished by their ploidy level (Staudt 1989). The species are distributed almost everywhere, from the arctic to the tropics. The diploid group is represented by *F. vesca*, *F. daltoniana, F. viridis* and *F. iinumae*, the tetraploids and hexaploids by *F. orientalis* and *F. moschata,* respectively, whereas *F. virginiana* and *F. chiloensis* dispose an octoploid chromosome set (Staudt 1989; Folta and Davis 2006).

Cultivated strawberry (*Fragaria* x *ananassa* Duch., 8n), an accidental hybrid of two native species *F. chiloensis* and *F. virginiana* (Darrow 1966) is one of the most important small fruit crops. Due to an attractive taste and relatively high content of bioactive compounds valuable for human health, strawberries are a part of the diet of millions of people (Maas *et al*. 1991, 1996; Tulipani *et al*. 2008). The annual world production of these fruits has increased in the last decade, from 3 to over 4 million tons. More than 70 countries are noted as significant strawberry producers (FAOStat 2009). Strawberry is strongly affected by many agrophages that cause significant losses in this spectacular fruit production (Zurawicz 2005). For this reason, the development of strawberry cultivars resistant to diseases that are economically important seems to be a promising strategy. Cultivars resistant to diseases offer an opportunity for long-term disease control. Economical and environmental benefits are also possible because pesticide application would be reduced. However, classical strawberry breeding is rather conservative due to difficulties in introgression of the resistance sources (Hancock and Bringhurst 1980; Hancock and Luby 1993). The creation of resistant cultivars needs new tools to act as assistance.

Molecular techniques and technologies that have been introduced into plant sciences since the late 1980s, make it possible to analyze the genome – from the simple dissection of plant genetic variability to structural and functional genomics, enhanced with bioinformatics. The results of the study on *Fragaria* genus lean towards a prediction, that in the future molecular investigations will play a key role in breeding for resistance. Consequently, efficient control methods for strawberry diseases will be elaborated.

Natural sources of strawberry resistance to diseases

Phenotypic variability of *Fragaria* plants in regard to strawberry diseases has been broadly investigated. Among wild species, resistance sources to *Verticillium* wilt, black root rot, powdery mildew and crown rot were found in *F. vesca* (Harland and King 1957; Gooding *et al.* 1981; Hancock and Luby 1993), immunity to powdery mildew in *F. moschata* (Maas 1998), while some clones of diversified *F. chiloensis* carry resistance to red stele, leaf spot and powdery mildew (Hancock *et al*. 1989). Potential resources of resistance in native octoploid species also include viral tolerance (Darrow 1966).

Many cultivated *F*. x *ananassa* varieties were also characterized as the phenotypes resistant or tolerant to respective strawberry diseases in field conditions (Maas and Smith 1978; Melville *et al*. 1980; Hancock *et al*. 1990;

*Corresponding address:
malgorzata.korbin@gmail.com

Wing *et al*. 1995; Nelson *et al*. 1996; Bell *et al*. 1997; Shaw and Gordon 2003; Mori *et al*. 2005; Particka and Hancock 2005; Zebrowska *et al*. 2006; Masny and Zurawicz 2008).

The inheritance of resistance

When considering the suitability of the resistance sources for breeding, four aspects have to be analyzed: the degree, the durability, the specificity and the inheritance of the resistance trait. Most commonly, plants with monogenically inherited resistance have been introduced to breeding programs. This type of resistance in plants is based on the activity of single R gene(s) that provide total protection against the pathogen, including hypersensitive reaction with cell death around the site of plant-pathogen interactions. On the other hand, polygenic resistance is correlated with the activity of many additive genes providing partial, more durable and non-race specific resistance. In consequence, the targeted selection is very desirable but time-consuming and troublesome. This is especially true, when race specific R genes, with partial resistance effect, are present. As nothing is simple in nature, it is possible for each type of resistance to be represented by numerous genetic mechanisms.

Two monogenically inherited resistances of *Fragaria* plants have been fully characterized. They are resistance to red stele root rot (red core) caused by soil-borne fungus, *Phytophthora fragariae,* and resistance to anthracnose caused by *Colletotrichum acutatum*. Mendelian segregation of resistance to red core in appropriate F_1 populations, and the analysis of phenotypic interactions between numerous strawberry cultivars and pathogen races from different geographical regions confirmed the existence of race specificity typical for monogenic resistance (van de Weg 1989a). The mechanism of resistance to red stele root rot is based on a gene-for-gene concept (Flor 1956), with five virulence and five resistance factors (van de Weg 1989a). The establishment of the GFG model has canceled out the previous theory of polygenic inheritance (Scott *et al*. 1984) and explained the phenomenon of the incomplete resistance. It was also a major step in the explanation of the genetics of strawberry resistance to *P. fragariae*, and identification of two highly effective and race specific R genes: *Rpf1* and *Rpf*2 (van de Weg 1997a, b). A key point for the elucidation of mechanism(s) of strawberry resistance to anthracnose was the distinction of two pathogenicity groups of *C. acutatum* (Denoyes-Rothan and Baundry 1995). Plants infected with *C. acutatum* isolates belonging to group 2 pathogenicity showed a high level of resistance controlled by a single dominant *Rca2* gene (Lerceteau-Kohler *et al*. 2002), at the same time, a polygenically inheritanced resistance was observed in plants infected with the isolates from group 1 pathogenicity. Strawberry resistance to black leaf spot also has a monogenic character. Black leaf spot is a disease caused by the fungus *Alternaria alternata*. The single locus of this trait was identified in a study on numerous strawberry cultivars and genetic mutants obtained in Japan (Takahashi *et al*. 1991; 1997).

Polygenic quantitative inheritance characterizes strawberry resistance to anthracnose (Denoyes-Rothan *et al*. 2005), *Cactorum* crown and leather rot (Denoyes-Rothan *et al*. 2004), grey mould (Barritt 1980; Popova *et al.* 1985), *Verticillium* wilt (Zebrowska *et al*. 2006) and bacterial angular leaf spot (Lewers *et al*. 2003) for which *C. acutatum* (group 1 pathogenicity), *Phytophthora cactorum*, *Botrytis cinerea*, *Verticillium dahliae*, and respectively, *Xanthomonas fragariae* are indicated as causative agents of the diseases. In all these cases, the study on identification of genome regions containing sets of genes that control resistance and called quantitative trait loci (QTL), have been undertaken.

No genetic and molecular dissections of host-pathogen interactions and inheritance character have been performed for other diseases that affect plants belonging to the *Fragaria* genus.

Strawberry markers linked to disease resistance

The term "molecular markers" is applied to a large number of different molecular techniques that detect plant variability at the DNA level. Properly prepared DNA markers tightly linked to the resistance genes can assist plant breeders to improve their breeding outcomes. This means improvement, from assessing genetic diversity of the germplasm used in breeding programs to marker assisted selection of progeny (MAS) (Charcosset and Moreau 2004). Particularly, markers of monogenic traits are readily available, easy to map on plant chromosomes and relatively easy to apply to breeding. The availability of polygenic trait markers is more limited and still controversial, due to the number of genes involved in the plant defense process and because of their quantitative character. Assuming that polygenic traits are controlled by a number of QTL that are inherited in a Mendelian fashion (Hospital and Charcosset 1997), the principles of MAS should be the same as for the R genes. However, due to the minor effects of QTL on the trait of interest, their map positions are less precise than for R genes. Therefore, well-chosen markers spanning the intervals defining map positions are recommended (Gimelfarb and Lande 1995).

The first markers linked to strawberry monogenic resistance were generated by Haymes and co-workers (1997) in regard to red stele. Using sixty plants from a segregating population, bulked segregant analysis (BSA) was carried out with almost six hundred RAPD primers. Seven RAPD-PCR markers had distinct presence or absence of polymorphisms between the bulks. The markers were mapped to within 1.7–13.9 cM of the *Rpf1* gene and some of them (*e.g.* M6) were converted into specific SCAR markers useful for marker-assisted breeding (Haymes *et al*. 2000). The next group of monogenic trait markers was described for strawberry resistance to anthracnose. The markers called mf1, mf2, mf3 and mf4 were generated as a result of the PCR-AFLP dissection of four bulks that represented two resistant and two susceptible progeny groups (Lerceteau-Kohler *et al*. 2002; Guerin *et al*. 2003). The mf4, that displayed well-isolated DNA band, was transformed into dominant SCAR marker with a length of 240 bp. This SCAR marker was present in all tested resistant cultivars except for 'Sequoia', for which crossover event between the mf4 and *Rca2* gene had probably taken place (Guerin *et al*. 2003). Development of the next generation of SCAR markers such as STS-Rca2-417, and their

location on 'Capitola' x 'Pajaro' linkage map have been continued (Lerceteau-Kohler *et al*. 2002; 2005).

The authors investigating polygenic resistance in strawberry have focused mainly on the characterization of QTL, linkage mapping, and further studies - for integrating this information with functional genomics. Previously, five QTL linked to plant resistance to anthracnose and five QTL linked to resistance to *Phytophthora* crown rot were identified and mapped (Lerceteau-Köhler *et al*. 2002; Denoyes-Rothan *et al*. 2004). None of the QTL markers of polygenic resistance to anthracnose correlate to the region of *Rca2* (monogenic anthracnose resistance). It was anticipated that the use of both types of markers, for R gene and for major QTLs, will enable pyramiding the resistance to provide a wider spectrum of *C. acutatum* control in strawberry (Denoyes-Rothan *et al*. 2005).

New strategies in *Fragaria* genotyping

In the last decade several new strategies, such as circumstantial study on candidate gene and QTL-based pedigree genotyping approach, bin mapping, and the use of genomics technology to sequence genome and screen expressed sequence tags (ESTs) through RNA assays, have been developed to increase the efficiency of plant variability detection.

First of all, the new technologies allowed for significant saturation of strawberry maps being a compendium of knowledge about plant diversity. The pioneering linked map based on random RAPD markers was constructed for *F. vesca* (Davis *et al* 1995). Using over two hundred progenies from cross 'Capitola' x CF1116 and over seven hundred AFLP, SSR and SCAR markers for anthracnose resistance, the French team constructed the linkage map for *F*. x *ananassa* (Lerceteau-Köhler *et al*. 2002; 2003; Denoyes-Rothan *et al*. 2004). The new generation of strawberry maps are enhanced by additional microsatellite, gene-specific intron polymorphism, cleaved-amplified polymorphic sequence (CAPS) markers (Cipriani *et al*. 2006; Sargent *et al*. 2006, 2007).

Huge progress in the strawberry genotyping area was assured by adaptation of new, high throughput nanotechnology, such as 454-sequencing and Illumina-Solexa sequencing, both based on sequencing by synthesis. At present, the available genomic sequence of *F. vesca* contains 1.75 Mb from 50 fosmid clones and is deposited in the GenBank under Acc. No. EU024823-EU024872. Fragaria Genome Sequencing Consortium works on sequencing of cosmids and BACs, and according to the plan, about 3 Gb of genome coverage will be generated (Sosinski *et al*. 2009). The sequenced genome as well as extensive EST database developed from strawberry in USA (Folta *et al*. 2005), constitute a powerful source a candidate genes potentially involved in induction and regulation of plant response to biotic factors. The EST collection was just utilized for identification of some candidate genes linked to resistance to anthracnose (Casado-Diaz *et al*. 2006). Based on published genome sequences of different plant species and degenerated oligonucleotide primers, Martinez-Zamora and co-workers (2004) isolated *Fragaria* resistance gene analogues (RGA) that belong to seven LRR and NBS families. The genes were identified in *F. vesca*, *F. chiloensis* and six *F.* x *ananassa* cultivars. A study conducted in the Research Institute of Pomology and Floriculture (RIPF), Skierniewice (Poland) in cooperation with Fasteris Co., Zurich (Switzerland) showed suitability of Illumina-Solexa high throughput sequencing for analysis of mechanism of strawberry resistance to *Verticillium* wilt. The sixty thousand out of 1.7 million sequences were recognized as differentially expressed on the first day after plant inoculation with *V. dahliae*, and over one hundred tags were chosen for further study on potential candidate genes in both, resistant and susceptible genotypes (Korbin, unpublished data).

Recombinant technology has been explored for improvement of disease resistance characteristics in strawberry since the 1990s. Transgenic strawberries transformed via *Agrobacterium tumefaciens* with a thaumatin II gene (Schestibratov and Dolgov 2005) and a pectate lyase gene (Jimenez-Bermundez *et al.* 2002) enhanced their resistance to grey mould. Resistance against the fungal pathogen *Sphaerotheca humuli* was enhanced in transgenic strawberry expressing a rice chitinase gene (Asao *et al*. 1997). Chalavi and co-workers (2003) observed enhanced strawberry resistance to *Verticillium* wilt after plant transformation with chitinase gene isolated from *Lycopersicon chilense*. Schart (2004) produced genetically modified strawberry which is less susceptible to grey mould, using cisgenic strategy that is based on plant modification with its own *F*. x *ananassa* genes. However, the results of these experiments stayed in the labs because of the rather negative public perception towards genetic modification of plants designed for consumption in fresh form. On the other hand, the elaboration of regeneration and transformation systems, including the choice of genotype, explants and proper media (James *et al*. 1990; Nehra *et al*. 1990; Gruchala *et al*. 2004, Landi and Mezzetti 2006), became fundamentals of GM-based strategy for confirmation of candidate gene role in respective plants.

CONCLUSION

Strawberry is susceptible to many diseases, with high costs in terms of yield losses and pesticide treatments. New EU regulations are headed towards the use of resistant plant material and sustainable crop management practices. Meanwhile, strawberry cultivars fully resistant to any disease have not been bred so far, nor have wild *Fragaria* species been extensively characterized as a source of resistance (Schwab *et al*. 2009). In this situation, the deep molecular-based characterization and wide exploitation of gene pools, and their introgression and pyramiding in new genotypes, can be a key strategy for generating strawberry with durable resistance, desirable for new horticulture. For further molecular dissection of the resistance sources within the *Fragaria* genus, developing collaborative research communities working on proper genetic systems (diploid inbred lines and large diversified germplasm) with precise genetic and physical maps, big genomics resources (EST database, cDNA libraries), with strong biochemical knowledge and bioinformatics support, are still necessary (Fig. 1).

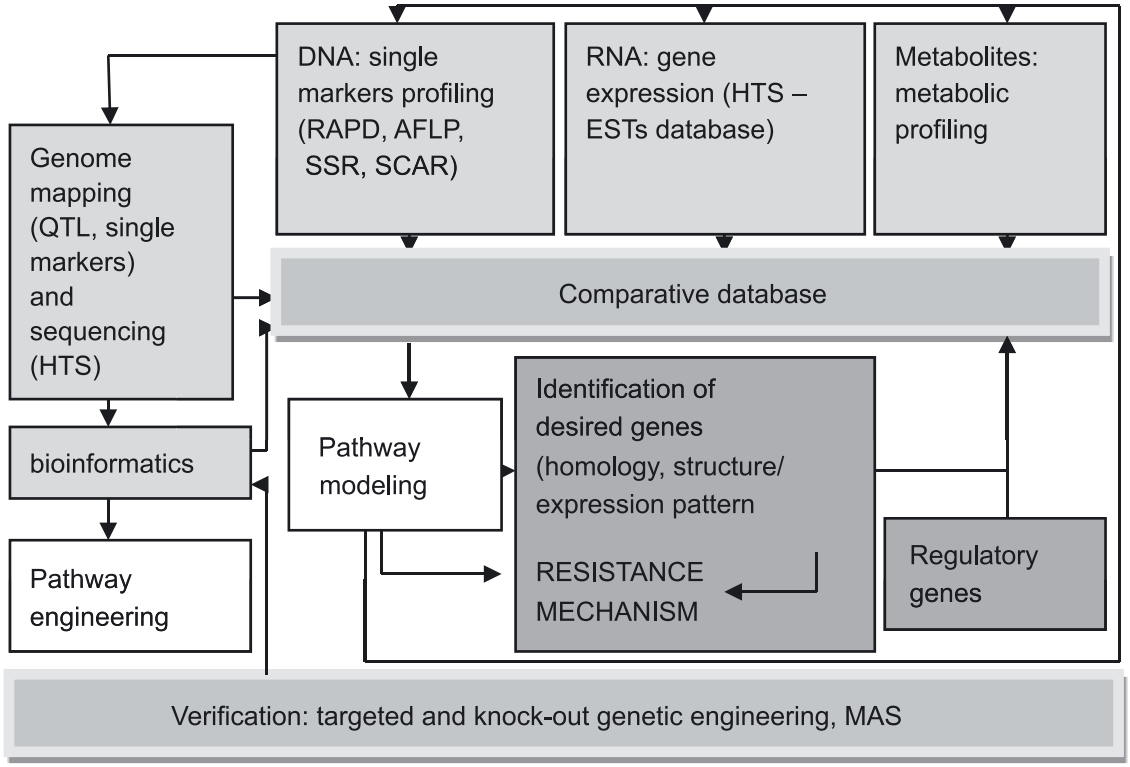

Fig. 1. Comprehensive study on plant response mechanism and molecular markers linked to strawberry disease resistance

REFERENCES

Asao G.H., Nishizawa Y., Arai S., Sato T., Hirai M., Yoshida K., Shinmyo A., Hibi T. 1997. Enhanced resistance against a fungal pathogen *Sphaerotheca humuli* in transgenic strawberry expressing a rice chitinase gene. Plant Biotechnol. 14 (3): 145–149.

Barritt B.H. 1980. Resistance of strawberry clones to *Botrytis* fruit rot. J. Am. Soc. Hort. Sci. 105 (2): 160–164.

Bell J.A., Simpson D.W., Harris D.C. 1997. Development of a method for screening strawberry germplasm for resistance to *Phytophthora cactorum*. Acta Hort. 439: 175–180.

Charcosset A., Moreau L. 2004. Use of molecular markers for the development of new cultivars and the evaluation of genetic diversity. Euphytica 137 (1): 81–94.

Cipriani G., Pinosa F., Bonoli M., Faedi W. 2006. A new set of microsatelite markers for *Fragaria* species and their application in linkage analysis. J. Hort. Sci. Biotechol. 81 (4): 668–675.

Casado-Diaz A., Encinas-Villarejo S., de los Santos B., Schiliro E., Yuber-Serrano E.M., Amil-Ruiz F., Pocovi M.I., Pliego-Alfaro F., Dorado G., Rey M., Romero F., Munoz-Blanco J., Caballero J.L. 2006. Analysis of strawberry genes differentially expressed in response to *Colletotrichum* infection. Physiol. Plantarum 128 (4): 633–650.

Chalavi V., Tabaeizadeh Z., Thibodeau O. 2003. Enhanced resistance to *Verticillium dahliae* in transgenic strawberry plant expressing a *Lycopersicon chilense* gene. J. Am. Soc. Hort. Sci. 128 (5): 747–753.

Darrow G.M. 1966. Strawberry. History, Breeding and Physiology. Holt, Rinehart and Winston, 1st ed. New York, 447 pp.

Davis T.M., Haigis K.M., McGowan P.J. 1995. Template mixing – a method of enhancing detection and interpretation of codominant RAPD markers. Theor. Appl. Genet. 91 (4): 582–588.

Denoyes-Rothan B., Baundry A. 1995. Species identification and pathogenicity study of French *Colletotrichum* strains isolated from strawberry using morphological, and cultural characteristics. Phytopathology 85 (1): 53–57.

Denoyes-Rothan B., Guerin G., Lerceteau-Kohler E., Risser G. 2005. Inheritance of a race-specific resistance to *Colletotrichum acutatum* in *Fragaria* x *ananassa*. Phytopathology 95 (4): 405–412.

Denoyes-Rothan B., Lerceteau-Kohler E., Guerin G., Bosseur S., Bariac J., Martin E., Roudeillac P. 2004. QTL analysis for resistance to *Colletotrichum acutatum* and *Phytophthora cactorum* in octoploid strawberry (*Fragaria* x *ananassa*). Acta Hort. 663: 147–151.

FAOStat 2009. Food and Agriculture. http://faostat.fao.org/site/567/default.asp#ancor

Flor H.H. 1956. The complementary genic systems in flax and flax rust. Adv. Genet. 8: 29–54.

Folta K.M., Davis T.M. 2006. Strawberry genes and genomics. Crit. Rev. Plant Sci. 25 (5): 399–413.

Folta K.M., Staton M., Stewart P.J, Jung S., Bies D.H., Jesdurai C., Main D. 2005. Expressed sequence (ESTs) and simple sequence repeat (SSR) markers from octoploid strawberry (*Fragaria* x *ananassa*). BMC Plant Biol. 5 Art. 12: 1–11.

Gimelfarb A., Lande R. 1995. Marker-assisted selection and marker-QTL associations in hybrid populations. Theor. Appl. Genet. 91 (3): 522–528.

Gooding H.J., McNicol R.J., MacIntyre D. 1981. Methods of screening strawberries for resistance to *Sphaerotheca macularis* and *Phytophthora cactorum*. J. Hort. Sci. 56 (3): 239–245.

Gruchala A., Korbin M., Zurawicz E. 2004. Conditions of transformation and regeneration of 'Induka' and 'Elista' strawberry plants. Plant Cell Tiss. Organ. Cult. 79 (2): 153–160.

Guerin G., Laigret F., Denoyes-Rothan B., Lerceteau-Kohler E., Roudeillac P. 2003. Development of a SCAR marker linked to dominant gene conferring resistance to *Colletotrichum acutatum* in strawberry (*Fragaria* x *ananassa*). Acta Hort. 636: 85–90.

Hancock J.F., Bringhust R.S. 1980. Sexual dimorphism in the strawberry *Fragaria chiloensis*. Evolution 34 (4): 762–768.

Hancock J.F., Flore J.A., Galletta G.J. 1989. Variation in leaf photosynthetic rates and yield in strawberries. J. Soc. Hortic. Sci. 64 (4): 449–454.

Hancock J.F., Luby J.J. 1993. Genetic resources in our doorstep: the wild strawberries. BioScience 43 (3): 141–147.

Hancock J.F., Maas J.L., Shans C.H., Breen P.J., Luby J.J. 1990. Strawberries (*Fragaria* spp.). p. 489–546. In: "Genetic Resources in Temperate Fruit and Nut Crops" (J. Moore, J. Ballington, eds.). ISHS, Wageningen Press, 980 pp.

Harland S.C., King E. 1957. Inheritance of mildew resistance in *Fragaria* with special reference to cytoplasmatic effects. Heredity 11, p. 257.

Haymes K.M., Henken B., Davis T.M., van de Weg W.E. 1997. Identification of RAPD markers linked to a *Phytophthora fragariae* resistance gene (*Rpf1*) in the cultivated strawberry. Theor. Appl. Genet. 94 (8): 1097–1101.

Haymes K.M., van de Weg W.E., Arens P., Maas J.L., Vosman B., denNijs A.P.M. 2000. Development of SCAR markers linked to a *Phytophthora fragariae* resistance gene and their assessment in European and North American strawberry genotypes. J. Am. Soc. Hort. Sci. 125 (3): 330–339.

Hospital F., Charcosset A. 1997. Marker-assisted introgression of quantitative trait loci. Genetics 147: 1469–1485.

James D.G., Passey A.J., Barbara D.J. 1990. *Agrobacterium*-mediated transformation of the cultivated strawberry (*Fragaria* x *ananassa*) using disarm binary vectors. Plant Sci. 69 (4): 79–94.

Jimenez-Bermundez S., Redondo-Nevado J., Munoz-Blanco J., Caballero J.L., Lopez-Aranda J.M., Valpuesta V., Pliego-Alfaro F., Quesanda M.A., Mercado J.A. 2002. Manipulation of strawberry fruit softening by antisense expression of a pectate lyase gene. Plant Physiol. 128 (2): 751–759.

Landi L., Mezzetti B. 2006. TDZ, auxin and genotype effects on leaf organogenesis on *Fragaria*. Plant Cell Rep. 25 (4): 281–288.

Lerceteau-Kohler E., Roudeillac P., Markocic M., Guerin G., Praud K., Denoyes-Rothan B. 2002. The use of molecular markers for durable resistance breeding in the cultivated strawberry (*Fragaria* x *ananassa*). Acta Hort. 567 (2): 615–618.

Lerceteau-Kohler E., Guerin G., Denoyes-Rothan B. 2005. Identification of SCAR markers linked to Rca2 anthracnose resistance gene and their assessment in strawberry germplasm. Theor. Appl. Genet. 111 (5): 862–870.

Lerceteau-Kohler E., Guerin G., Laigret F., Denoyes-Rothan B. 2003. Characterisation of mix disomic and polisomic inheritance in the octoploid strawberry (*Fragaria* x *ananassa*) using APLP mapping. Theor. Appl. Genet. 107 (4): 619–628.

Lewers K.S., Maas J.H., Hokanson S.C., Gouin C., Hartung J.S. 2003. Inheritance of resistance in strawberry to bacterial angular leaf spot disease caused by *Xanthomonas fragariae*. J. Am. Soc. Hortic. Sci. 128 (2): 209–212.

Maas J.L., Galletta G.J., Stoner G.D. 1991. Ellagic acid, an anticarcinogen in fruits, especially strawberry. HortScience 26 (1): 10–14.

Maas J.L, Smith W.L. 1978. Earliglow, a possible source of resistance to Botrytis fruit rot in strawberry. HortScience 13 (3): 275–276.

Maas J.L., Wang S.Y., Galletta G.J. 1996. Health enhancing properties of strawberry fruit. p. 11–18. In: Proc. IV North American Strawberry Conference. Orlando, USA. 15–17 February, 1996.

Maas J.L. 1998. Compendium of Strawberry Diseases. The APS Press, Beltsville, Maryland, 138 pp.

Masny A., Zurawicz E. 2008. Susceptibility of new dessert strawberry cultivars to *Verticillium* wilt. Zesz. Nauk. Inst. Sad. Kwiac. 16: 249–255.

Martínez-Zamora M.G., Castagnaro A.P., Díaz Ricci J.C. 2004. Isolation and diversity analysis of resistance gene analogues (RGAs) from cultivated and wild strawberries. Mol. Genet. Genomics 272 (4): 480–487.

Melville A.H., Draper A.D., Galletta G.J. 1980. Transmission of red stele resistance by inbred strawberry selection. J. Am. Soc. Hortic. Sci. 105 (5): 608–610.

Mori T., Kitamura H., Kuroda K. 2005. Varietal differences in *Fusarium* wilt-resistance in strawberry cultivars and the segregation of this trait in F_1 hybrids. J. Jap. Soc. Hortic. Sci. 74 (1): 57–59.

Nehra N.S., Chibbar R.N., Kartha K.K., Datla R.S.S., Crosby W.L., Stushoff C. 1990. Genetic transformation of strawberry by *Agrobacterium tumefaciens* using leaf disk regeneration system. Plant Cell Rep. 9 (6): 293–298.

Nelson M.D., Gubler W.D., Shaw D.W. 1996. Relative resistance of 47 strawberry cultivars to powdery mildew in California greenhouse and field environments. Plant Dis. 80 (3): 326–328.

Particka C., Hancock J.F. 2005. Field evaluation of strawberry genotypes for tolerance to black root rot on fumigated and nonfumigated soil. J. Am. Soc. Hortic. Sci. 130: 688–693.

Popova I.V., Konstantinova A.E., Zekalashvili A.U., Zhanov B.K. 1985. Features of breeding strawberries for resistance to berry molds. Sov. Agric. Sci. 3: 29–33.

Sargent D., Clarke J., Simpson D.W., Tobutt K.R., Arus P., Monfort A., Vilanova S., Denyes-Rothan B., Rousseau M., Folta K.M., Basil N.V., Battey N.H. 2006. An enhanced microsatellite map of diploid *Fragaria*. Theor. Appl. Genet. 112: 1349–1359.

Sargent D., Rys A., Nier S., Simpson D.W., Tobutt K.R. 2007. The development and mapping of functional markers in *Fragaria* and their transferability and potential for mapping in other genera. Theor. Appl. Genet. 114 (2): 373–384.

Schaart J.G. 2004. Towards consumer-friendly cisgenic strawberries which is less susceptible to *Botrytis cinerea*. Ph.D. thesis. Wageningen Universiteit, The Netherlands, 128 pp.

Schestibratov K.A., Dolgov S.V. 2005. Transgenic strawberry plants expressing a thaumatin II gene demonstrate enhanced resistance to *Botrytis cinerea*. Sci. Hort. 106 (2): 177–189.

Schwab W., Schaart J.G., Rosati C. 2009. Functional molecular biology research in *Rosaceae*. p. 457–486. In: "Genetics and Genomics of *Rosaceae*" (K. Folta, S.E. Gardiner, eds.). Springer, 636 pp.

Scott D.H., Draper A.D., Galletta G.J. 1984. Breeding strawberries for red stele resistance. Plant Breeding Rev. 2: 195–214.

Shaw D.V., Gordon T.R. 2003. Genetic response for reaction to *Verticillium* wilt in strawberry with two stage family and genotypic selection. HortScience 38: 432–434.

Sosinski B., Shulaev V., Dhingra A., Kalyanaraman A., Bumgarner R., Rokhsar D., Verde I., Velasco R., Abbott A.G. 2009. *Rosaceaous* genome sequencing: perspectives and progress. p. 601–615. In: "Genetics and Genomics of *Rosaceae*" (K. Folta, S.E. Gardiner, eds.). Springer, 636 pp.

Staudt G.S. 1989. The species of *Fragaria*, their taxonomy and geographical distribution. Acta Hort. 265: 23–34.

Takahashi H., Takai T., Matsumoto T. 1991. Susceptible strawberry cultivars to *Alternaria alternata* black spot of strawberry (*Alternaria alternata* strawberry pathotype) in Japan. J. Jap. Soc. Hort. Sci. 59: 539–544.

Takahashi H., Furuya H., Takai T., Matsumoto T. 1997. Characteristics of *Alternaria alternata* strawberry pathotype isolated in New Zealand and resistance of 'Akita Berry' strawberry to this fungus. J. Japan. Soc. Hort. Sci. 65 (1): 785–790.

Tulipani S., Mezzetti B., Capocasa F., Bompadre S., Beekwilder J., de Vos C.H., Capanoglu E., Bovy A., Battino M. 2008. Antioxidants, phenolic compounds, and nutritional quality of different strawberry genotypes. J. Agric. Food Chem. 56 (10): 3587–3592.

van de Weg W.E. 1989a. Genetics of resistance to *Phytophthora fragariae* Hickman in strawberry. Acta Hort. 265: 143–148.

van de Weg W.E. 1989b. Cultivar-race interactions of the strawberry-*Phytophthora fragariae* system with regard to a gene for gene model. Acta Hort. 265: 203–206.

van de Weg W.E., Wassenaar L.M., van de Lindeloof C.P.J. 1989. Inheritance of resistance to *Phytophthora fragariae* Hickman in strawberry. Euphytica 42: 25–30.

van de Weg W.E. 1997a. A gene for gene model to explain interactions between cultivars of strawberry and races *Phytophthora fragariae* var. *fragariae*. Theor. Appl. Genet. 94 (3–4): 445–451.

van de Weg W.E. 1997b. Resistance to *Phytophthora fragariae* var. *fragariae* in strawberry: the *Rpf2* gene. Theor. Appl. Genet. 94 (8): 1092–1096.

Wing K.B., Pritts M.P., Wilcox W.F. 1995. Field resistance of 20 strawberry cultivars to black root rot. Fruit Varieties J. 49 (2): 94–98.

Zebrowska J., Hortyński J., Cholewa T., Honcz K. 2006. Resistance to *Verticillium dahliae* (Kleb.) in the strawberry breeding lines. Commun. Agric. Appl. Biol. Sci. 71 (3): 1031–1036.

Zurawicz E. 2005. Truskawka i Poziomka. Praca zbiorowa. PWRiL, Warszawa, 294 pp.

POLISH SUMMARY

MOLEKULARNE PODEJŚCIE DO ZJAWISKA ODPORNOŚCI NA CHOROBY ROŚLIN Z RODZAJU *FRAGARIA*

Odporność na choroby jest jedną z najbardziej pożądanych cech roślin uprawnych. Rodzaj *Fragaria*, obejmujący 21 gatunków zarówno dzikich, jak i hodowlanych (*Fragaria* x *ananassa*), zawiera bogate, choć nie w pełni wykorzystane w hodowli odpornościowej, zasoby genowe. W oparciu o różne badania genomu *Fragaria*, prowadzone w wielu ośrodkach naukowych na świecie, opisano przydatność różnych technik molekularnych i technologii, wysokoprzepustowego sekwencjonowania dla analizy genetycznych mechanizmów odporności i wyjaśniono różnorodność roślin na poziomie DNA, w odniesieniu do patogenów. Zaproponowany model kompleksowej eksploracji genomu, zakończony wygenerowaniem markerów cechy odporności i identyfikacją genów zaangażowanych w indukowanie odpowiedzi rośliny na porażenie przez patogena, byłby niezwykle użyteczny dla hodowli odpornościowej truskawki, ale realizacja takiego programu wymaga współpracy wszystkich zainteresowanych zespołów badawczych.