Theoretical Bases and Sources for Breeding Wheat for Combined Disease Resistance

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Abstract: Achievements and prospects of wheat breeding for disease resistance in the world and in the Czech Republic are discussed. Attention was paid to possibilities of increasing resistance to rusts, powdery mildew, Fusarium head blight, leaf blotch, glume blotch, tan spot, common bunt and barley yellow dwarf virus on wheat. Methodical approaches adopted in national ring infection tests were outlined. New sources of resistance to the above-mentioned diseases were detected and described on the basis of three-year results of field infection tests.

Keywords: wheat; *Triticum aestivum* L.; sources of resistance; resistance genes; fungal diseases; virus diseases; Czech Republic

Wheat breeding for disease resistance is linked with low input farming. It has its beginnings in the USA, Canada and Australia when wheat was a major crop grown on large areas often as monoculture and therefore rather endangered by diseases and pests. Resistance against rusts was achieved first, particularly against stem rust, with typical boom and bust cycles, when effective resistance was suddenly rendered ineffective due to the occurrence of new races. Disease resistance was an important breeding aim also in the countries with high input wheat growing, e.g. in Western Europe. Susceptible cultivars required more and more pesticides that markedly increased production costs and were too risky due to toxic residues.

Soon it was experienced that cultivars resistant to one disease, e.g. stem rust, started to seriously suffer from another disease, e.g. leaf rust. Diseases that were defeated by resistance breeding were superseded by other diseases. However, the importance of single diseases varies with climatic conditions and crop management, e.g. application of fertilisers (particularly nitrogen), reduced or no tillage, etc. Other factors affecting the strategy of resistance breeding are pathogen variability, speed of development of new virulent races and availability of suitable sources of resistance for breeding. McIntosh (1998) listed 23 fungal wheat diseases, 5 virus diseases, 4 bacterial diseases and 4 nematode species attacking wheat on the global scale and pointed out that sources of resistance were available against all pests except two of them. As for the most important wheat diseases in the Czech Republic, only sources of resistance to wheat dwarf virus are not available. Availability of effective fungicides can also influence the importance of

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resistance breeding (e.g. difficult chemical control of Fusarium head blight enhances the importance of resistance breeding). Orientation at specific resistance (conditioned by major genes), adult plant resistance (governed by major or minor genes) or partial resistance (regulated by minor genes) also depends on the above-mentioned factors. The higher is the diversity of the genetic system governing resistance (pyramiding of major resistance genes, polygenic minor gene resistance), the lower is the vulnerability of resistance (loss of resistance due to the virulence of pathogen).

Breeding for combined resistance to diseases has become the perspective strategy of disease resistance breeding. At present this trend is supported by requirements for reduced production costs resulting from lower inputs, by the demand for organic farming as well as by requirements for reduced application of pesticides to protect environment and agricultural products from the risk of contaminants.

The aim of modern resistance breeding is sufficient resistance to all most important diseases rather than high resistance to one disease only, while the cost of resistance is also considered. Brown (2002) characterised the present trend as follows: "… if resistance is indeed costly, a breeder's most effective strategy may not be to select for excellent resistance (if that means sacrificing yield or quality) but to select for at least moderate resistance while eliminating very susceptible lines which might not only become heavily diseased themselves but also spread inoculum to other cultivars. The entire genotype of a cultivar rather than any single gene, no matter how important, determines its value to farmers and consumers, and therefore its commercial success or failure".

Empiric breeding for resistance was based on field selection and depended upon the natural incidence of tested diseases. Greenhouse seedling tests for resistance can speed up the breeding, however their value is limited to the resistance expressed both at the seedling and adult plant stage. Nowadays the application of molecular markers and other methods of molecular genetics becomes a powerful tool for selection in resistance breeding. However, it should not be overestimated as pointed out by Koebner and Summers (2003): "Laboratory-based breeding should remain the servant of the field breeder and not its master…. Wheat breeding will continue to be driven primarily by selection in breeder's plots, rather than by detection in microtitre plates".

Field tests remain the most useful tool for selection particularly when natural infection is supported by artificial inoculation of plants or with the use of infection spreaders. International tests for disease resistance (field disease nurseries) enable to compare the reactions of tested cultivars/lines under various climatic and soil conditions, as well as under various spectra of pathogen races. They can serve both ways: for determination of resistance (e.g. CIMMYT – Mexico Disease Nurseries) on the one hand and for determination of virulence in the pathogen population on the other hand (e.g. ring tests in the framework of COST Action 217 in the last decade). Results obtained in international ring tests inspired the initiation of Czech national ring tests.

This aim of this paper is to bring actual information about the methods used and results obtained in Czech national ring tests, paying attention to a majority of the most important wheat diseases, and to discuss possibilities of improving disease resistance.

Establishment of national ring tests

Being conscious of the high importance of breeding for combined resistance, in 2002 Czech wheat breeders and researchers initiated the establishment of national ring tests in which now all breeding stations specialised in wheat breeding, Research Institute of Crop Production in Prague-Ruzyně (RICP) and Agricultural Research Institute in Kroměříž participate. Verified methods are available for the field testing of resistance to stem rust, yellow rust and leaf rust, powdery mildew, Fusarium head blight and brown leaf spot diseases (caused by *Septoria tritici, Stagonospora nodorum* and *Pyrenophora tritici-repentis*) at 3–5 sites; to barley yellow dwarf virus at 2 sites (Prague-Ruzyně and Stupice) and to common bunt at Prague–Ruzyně. The sets of tested materials include available sources of resistance, grown cultivars and advanced breeding lines, together with checks. At present more than 70 materials are tested each year. Promising materials with detected resistance to a certain disease are tested repeatedly (at least for three years) and examined for resistance to other important diseases, because combined resistance is the major objective. With the exception of powdery mildew, where infection is natural, all other tests are performed under a high infection pressure using inoculations with the pathogens. Disease severity is usually scored on the 9-point scale basis.

Genetic aspects and results of disease resistance testing

Rust diseases

Stem rust *(Puccinia graminis* Pers. f.sp. *tritici)*. Breeding for resistance to stem rust was initiated by epidemics of this disease in the last century. In Central Europe stem rust on wheat lost its importance in the last decades. This was probably due to the successful resistance breeding in the countries of Southeastern Europe from where the airborne inoculum was usually transferred to Central Europe. The last stem rust epidemic in Czechoslovakia and in Southeastern Europe was recorded in 1972. Though there is no imminent threat of stem rust, several cultivars registered in Czechoslovakia and in the Czech Republic possess stem rust resistance based on genes *Sr31*, *Sr11*, *Sr29* and *Sr37*. Older Czechoslovak wheat cultivars carried gene *Sr5* derived from Eastern European cultivars (Bartoš *et al.* 1970). Gene *Sr2* played an important role in the American breeding for stem rust resistance. The long-lasting successful use of the 1BL.1RS translocation with *Sr31,* effective against all stem rust pathotypes worldwide, has been endangered since 1999 by the discovery of race Ug99 with virulence for *Sr31* and other important *Sr* genes in Uganda. From Uganda (and perhaps earlier from Kenya) race Ug99 started to spread. At present race Ug99 is the most serious threat to stem rust resistance all over the world where T1BL.1RS is carried by the grown cultivars. For this reason a "Global Rust Initiative" is being organised by CIMMYT (Anonym 2005). Breeding for combined rust resistance is simplified when sources of resistance carrying linked resistance genes are used in the breeding. It is the case of the translocation 1BL.1RS from Petkuser rye possessing in addition to stem rust resistance gene *Sr31* the leaf rust resistance gene *Lr 26*, yellow rust resistance gene *Yr9* and also the gene *Pm8* for powdery mildew resistance. In the eighties of the last century a half of cultivars registered in the former Czechoslovakia possessed that translocation; at present the number of cultivars with T1BL.1RS is limited and its resistance genes, except *Sr31*, are mostly ineffective. Other important translocations are those from *Aegilops ventricosa*. The line VPM1 (from a cross betweeen *Aegilops ventricosa, Triticum persicum* and cv. Marne) was primarily used to transfer eye spot resistance. Many cultivars derived from that source contain linked genes *Yr17*, *Lr37* and *Sr38* as well as a gene for resistance to cereal cyst nematode *Cre5*. Foreign cultivars registered in the Czech Republic Apache, Corsaire, Clever, Clarus, Rapsodia and the Czech cultivar Rheia possess translocation from *Aegilops ventricosa* with the above-mentioned genes.

Yellow rust *(Puccinia striiformis* West.*)*. Yellow rust is an important disease particularly in Western Europe, where novel races often cause problems in resistance breeding (recently it was virulence to *Yr17*, a still important gene in Western European cultivars). However, after the breakdown of resistance based on *Yr17* many cultivars possessing *Yr17* remained resistant due to the presence of other yellow rust resistance genes (Robert *et al*. 2000a, b). Some Western European cultivars displayed remarkably durable resistance (e.g. Cappelle Desprez). Field resistance showed a good effectiveness and also proved to be durable, e.g. in cultivar Alcedo (Meinel 1997). In Czechoslovakia and later in the Czech Republic field resistance to yellow rust was obligatory for registered cultivars since the sixties of the last century. This regulation substantially helped to avoid losses caused by yellow rust until recently. In the last years also yellow rust susceptible cultivars were registered and for this reason yellow rust can find its hosts easier again. This contributed to a new wave of its spread. In 1999–2001 yellow rust occurred more frequently also in other countries of Eastern Europe. The main topic of the 2001 Workshop of the Association of the Breeders and Seed Dealers of Austria in Gumpenstein (November 20–22) was motivated by such a high incidence of yellow rust. Experience of the yellow rust outbreak in the U.K., Denmark, Germany, Austria, Czech Republic, Slovakia and Hungary was summarised in the Proceedings (Bericht über die Arbeitstagung 2001 der Vereinigung der Pflanzenzüchter und Saatgutkaufleute Österreichs gehalten vom 20. bis 22. November 2001 in Österreich). Attention to yellow rust was also paid in the framework of COST Action 817 (1996–1999) when virulence of the rust and variety resistance were studied in ring tests organised in the U.K., Switzerland, Germany, Denmark, Portugal and in the Czech Republic. International ring tests have continued since then. Differences in virulence of different rust samples were observed, lines/cultivars with *Yr5, Yr10* and *Yr15* being resistant to all isolates.

Leaf rust (*Puccinia triticina* = *Puccinia persistens* Plow. subsp. *triticina* = *Puccinia recondita* Rob. ex Desm. f.sp. *tritici)*. Leaf rust causes losses particularly in warm dry summers. Its economic importance has increased. Resistance breeding in the world was particularly successful when partial field or adult plant resistance was exploited, e.g. gene *Lr34* in the CIMMYT wheat breeding. Gene *Lr34* is linked with *Yr18, Byd1* and *Ltn*. Leaf tip necrosis can be utilised as a marker of *Lr34*. In Europe cv. Trémie displayed very good field resistance. In our genetic study the presence of genes *Lr10* and *Lr13* in Trémie was verified and postulated, respectively. In addition a gene governing resistance in the field was determined, independent of *Lr10* and *Lr13*. It is effective in adult plants also to isolates virulent to *Lr10* and *Lr13*. The modern strategy of resistance breeding described by Winzeler *et al.* (1995) combines greenhouse and field tests. Recent ring tests organised by Winzeler *et al.* (2000), rust race surveys (Mesterházy *et al.* 2000; Bartoš *et al.* 2001) and analyses of *Lr* genes in cultivars grown in the U.K. (Singh *et al.* 2001) and in France (Goyeau & Park 1997) contributed to the knowledge of types of leaf rust resistance and resistance genes in cultivars grown in Europe. The following specific genes for leaf rust resistance in European cultivars were postulated: *Lr1, Lr3a, Lr3ka, Lr10, Lr13, Lr14a, Lr17b, Lr20, Lr26* and *Lr37* (Winzeler *et al.* 2000; Singh *et al.* 2001). Almost all of them were also postulated in cultivars registered in the Czech Republic, namely *Lr1, Lr3a, Lr3ka, Lr10, Lr13, Lr14a, Lr17b, Lr26* and *Lr37*. Listed specific genes are only partially effective or ineffective to the prevailing races. Specific resistance genes *Lr1* (+*Lr13* and *Lr3* in cultivar Vlada) or the combination of *Lr10* and *Lr13* (in cultivars Siria and Alka) offer a relatively good protection. Important was also field resistance of cultivar Viginta used in the breeding of many Czech and Slovak cultivars. In Eastern European cultivars that were frequently used in our breeding, gene *Lr3* was common and therefore it is present in many Czech cultivars but no more effective (Bartoš *et al.* 1969). In recent international race surveys genes *Lr9, Lr19* and *Lr24* showed a high effectiveness to leaf rust (Mesterházy *et al.* 2000). However, virulence to *Lr24* was already found in the race survey (Hanzalová unpubl.).

In Czechoslovakia race surveys of rusts on wheat started in the sixties of the last century. Results obtained till 1995 were analysed by Bartoš *et al.* (1996). Of the molecular markers for the determination of *Lr* genes, markers for *Lr10* (Schachermayr *et al*. 1997) and *Lr37* (Robert *et al.* 1999; Seah *et al*. 2001) were used in the RICP. The presence of *Lr10* in the Czech cultivars Siria and Alka was determined by a molecular marker and verified in several foreign cultivars (Blažková & Bartoš 2002). Similarly, the presence of *Lr37* was determined in several foreign cultivars (Ambrozková *et al.* 2002) as well as in the Czech cultivar Rheia (Bartoš *et al*. 2004). The latter authors compared the results of a phytopathological estimation of the presence of *Lr37* and the results obtained by a molecular marker in F_3 progenies of various crosses with the cv. Renan, which possesses the gene cluster *Lr37, Sr38* and *Yr17* (Bartoš *et al.* 2004). Differences between the phytopathological and molecular marker tests were found only in 4 out of the 98 tested progenies. The objective of the crosses with Renan was to combine resistances, e.g. cross with the cultivar Arina aimed at the combination of rust resistance with resistance to leaf blotch and tan spot.

In the ring tests resistance to rusts was tested in field trials where the spreader cultivars were inoculated with an urediospore water suspension of leaf or stem rust with syringe needle in April–May, with yellow rust a month earlier. A mixture of rust isolates was applied. Classification of the disease severity was carried out at the time of the highest rust incidence. Cultivars and lines with detected combined resistance to all three rust species are listed in Table 1.

Powdery mildew (*Blumeria graminis* (DC.) Speer = *Erysiphe graminis* de Condolle)

Although powdery mildew can now be effectively controlled by fungicides, this disease may be a serious problem in some regions and years because continuous protection, increasing the costs, cannot often be provided. The tests at the Humpolec location (potato growing region) with every year high occurrence of powdery mildew showed that the level of resistance to powdery mildew in presently grown wheat cultivars was not mostly satisfactory and, therefore, an increase in the resistance level by breeding became highly desirable. McIntosh *et al.* (2003) listed 31 *Pm* genes, but their effects on resistance in the field were highly variable and only partial. Huang and Roder (2004) reported that by that time 48 genes/alleles for resistance to powdery mildew at 32 loci were identified and located on 16 different chromosomes, out of which 21 resistance genes/alleles were tagged. Therefore, the pyramiding of resistance genes, desirable for

Table 1. Winter wheat cultivars resistant to rusts (1–9; 9 – without symptoms) in comparison with the check cultivars Samanta and Estica – average of 3–5 locations and four years (2002–2005)

Cultivar/line	Leaf rust	Stem rust	Yellow rust
CWW93/58	8.61	8.62	8.79
CH111.12772	8.54	8.58	8.65
SG-S 1066-01	8.58	8.27	8.50
NIC 97-4135A	8.05	8.00	8.75
SG-U 2007D	8.48	8.24	8.91
SG-U 3010t	8.34	8.44	9.00
01ST2032	8.65	8.83	8.80
Caphorn	8.49	8.83	8.88
PBIS 98/77	8.45	8.50	8.83
NORD 2879	8.45	8.33	8.58
Titlis	7.08	7.60	8.73
Ornicar	7.91	7.80	8.23
Samanta	5.00	5.45	4.60
Estica	3.40	4.72	8.54

sufficient protection, is now enabled also with the use of molecular methods.

Partial or field resistance to such a variable pathogen as powdery mildew is undoubtedly of great importance (Bartoš *et al.* 2002). It was described e.g. in cv. Mironovskaya 808, from which German cultivars Miras and Mikon were derived. Among Czech cultivars the best powdery mildew resistance was registered in cv. Vlasta of the cross Brimstone/Š13//Hana (Šíp *et al.* 1999). Powdery mildew resistance of Š13 was derived from *Triticum monococcum* and the responsible gene was designated as *Pm1b* (Zeller & Hsam 1998). However, in the cv. Vlasta genes *Pm2* and *Pm6* were postulated (obviously derived from Brimstone), but *Pm1b* was not found there (Zeller, person. commun.). Further studies are going on because the mere presence of *Pm2* and *Pm6* cannot explain the high resistance of cv. Vlasta in the field when compared with other cultivars carrying *Pm2* and *Pm6*.

Three-year (2003–2005) assessments of resistance to powdery mildew on a 1–9 scale at the Humpolec location showed the average symptom score of all included cultivars or breeding lines over 3–5 dates during vegetation 5.23. On the last reading date this score was much lower (only 3.8). Besides Vlasta with average symptom score 7.70, the three-year tests showed a relatively high level of resistance in the cultivars Abunda (7.02), Habicht (6.49), Ohio (6.46), Senat (6.15; data from two years) or Savannah (6.02). New advanced breeding lines (e.g. SG-S 1875-01, SG-U 5125A or SG-S 110-03) were developed showing a relatively higher resistance level (approaching to 7) which can be utilised in breeding for resistance to powdery mildew.

Fusarium head blight (*Fusarium* spp.)

Fusarium head blight (FHB), predominantly caused by *Fusarium graminearum* and *Fusarium culmorum,* belongs to the most damaging diseases of wheat in many parts of the world. It is encouraging that the genetic variation for resistance to head blight was found to be very large and valuable sources of resistance have been detected among both spring and winter wheat cultivars. However, resistance to FHB has different components (Mesterházy 1995; Wiśniewska *et al.* 2002) and there is a strong influence of environmental conditions on the response of wheat to FHB. Evaluation of disease incidence in practice and breeding may be complicated because multi-environment tests and many characters are needed to fully describe the state. Besides the exploitation of highly resistant, but genetically very distant sources (e.g. Sumai 3, Nobeoka Bozu, Beijing 8), there was given evidence (Ittu *et al.* 2002) that substantial progress in FHB resistance might be achieved through the cumulation of resistance genes from different sources that were better adapted to European conditions.

In Czech wheat breeding programs a major accent is laid on the utilisation of different better-adapted wheat cultivars and breeding lines possessing medium resistance. Nowadays, especially the resistant cultivars (lines) from neighbouring countries, together with resistant lines of Czech origin are deliberately used in our breeding programs. Besides this, resistance to FHB is selected for also in other crosses that do not have a resistant parent in their pedigree. Marker-assisted selection based on QTL loci that were found responsible for quantitative FHB resistance of Sumai 3 (Anderson *et al.* 1998; Bai & Shaner 2004) is also intended to apply in the breeding program of SELGEN Company.

In the RICP Prague-Ruzyně field inoculation experiments have been performed each year since 1992. The results of evaluating the response of selected winter wheat cultivars to artificial infection with *Fusarium culmorum* in field conditions over the 1992–1999 period are available in a publication of Šíp *et al.* (2002a). Besides resistance to FHB infection subsequent experiments (conducted till the present time) took into consideration also cultivar resistance to the accumulation of mycotoxins and effects of different fungal isolates and techniques of inoculation (Šíp *et al.* 2002b, 2003a; Chrpová *et al.* 2004). The following characters are considered as decisive in experiments with the spraying of inoculum onto flowering spikes within a hill plot, which is a technique used in national ring tests under study: visual symptom scores, percentage of *Fusarium* damaged grains and DON content. Symptom scoring on a 0–9 scale, based on estimates of percentage of infected spikelets, provides initial information about the superficial disease spread. Useful information about the pathogen colonisation in grain can be obtained by determining the percentage of *Fusarium* damaged grains. This trait was found closely related not only to DON content but also to other disease severity parameters (Sýkorová *et al.* 2004; Mesterházy *et al.* 2005). Field infection tests still rely on infections with *F. culmorum*, though it is now evident that *F. graminearum* has become a prevalent species. This

Table 2. Average data (2002–2004) on symptomatic reaction (VSS: 0–9; 9 – without symptoms), % of *Fusarium* damaged grains (FDG) and DON content from national tests of resistance to *Fusarium* head blight – 15 best performing materials and 3 check cultivars

	Cultivar /line	Origin	VSS (0–9)	FDG (%)	DON (mg/kg)
1	Petrus	DEU	7.0	25.2	17.5
2	Arina	CHE	6.7	22.1	14.3
3	Bizel	FRA	6.7	27.9	16.3
4	Kooperatorka	RUS	7.3	18.1	9.8
5	F 201R	ROM	7.8	19.5	14.5
6	SG-U 513	CZE	6.8	19.6	14.0
7	Szeged 219	HUN	6.3	17.6	12.2
8	Szeged 222	HUN	5.7	32.8	21.3
9	Szeged 231	HUN	6.3	19.6	11.5
10	SG-V NB x MM SUM 3	HUN	7.3	9.2	6.1
11	SG-S 1800-01	CZE	6.0	27.5	12.2
12	SG-S 1875-01 (Simila)*	CZE	6.6	22.4	9.7
13	SG-U 7029	CZE	6.3	19.3	12.3
14	SG-U 947-a (SW)	CZE	5.6	27.3	15.5
15	SG-U 143-4 (SW)	CZE	5.0	10.9	5.5
16	Sumai 3 – resistant (SW)	CHN	8.0	3.8	2.5
17	Samanta – moderately susceptible	CZE	5.3	35.3	26.9
18	Corso – susceptible (SW)	DEU	5.0	79.2	66.9

SW = spring wheat; *two-year tests

fact should be taken into consideration as early as possible, however, previous and also the latest studies (Mesterházy *et al*. 2005) provide evidence that there is a strong relation between resistance to *F. culmorum* and resistance to the other *Fusarium* species including *F. graminearum*.

Table 2 shows average data (2002–2004) on symptomatic reaction, % of *Fusarium* damaged grains and DON content for three groups of cultivars (lines): (1) examined resistance sources (1–6), (2) resistant lines derived from crossing with highly resistant parents (Sumai 3 or Nobeoka Bozu – 7–10) and (3) the most resistant lines obtained in breeding programs of SELGEN company (11–15). For the purposes of comparison data on the average performance of these characters are available for resistant Sumai 3, moderately susceptible Samanta and susceptible Corso. It is shown that the highest resistance to DON accumulation, connected with favourable performance in the other examined resistance traits, was detected in Sumai 3 and in the line SG-V NB × MM Sum 3 from Szeged (Hungary), which comprises Sumai 3 and Nobeoca Bozu in its pedigree. Unfortunately, this line has poor agronomic parameters. The other examined Szeged lines derived from the program that exploits resistance of Sumai 3 and Nobeoca Bozu (obtained from Dr. Á. Mesterházy) that are agronomically more suitable (above all line 222) showed moderate resistance to FHB. To combine FHB resistance with resistance to other diseases, yielding ability and quality traits is undoubtedly a serious problem. Until now Czech breeders have succeeded in combining different desirable traits with moderate resistance to FHB, which was recently detected in winter wheat advanced lines SG-S 1800-01 (Hana/Estica), SG-S 1875-01 (Simila) and SG-U 7029 (Hubertus/Dněstrjanka). In spring wheat the line SG-U143-4 (Greina/Tinos) was highly resistant and the line SG-U 947-a (Nandu/ 6182-c//Nandu/ BR-1522) moderately resistant to the accumulation of DON. These materials are agronomically suitable and their acquisition is another proof that the desirable resistance level can be reached by cumulating resistant genes from different sources possessing lower or medium resistance to FHB.

Brown leaf spot diseases

The analysis of pathogen spectra in infected wheat leaves showed growing importance of *Septoria tritici* and *Pyrenophora tritici-repentis*, besides *Stagonospora nodorum*, in the territory of the Czech Republic (Šíp *et al.* 2003b). Therefore, attention of wheat breeders is mainly paid to these three pathogens and selected wheat cultivars and lines are examined in ring tests (now at 4 locations) for resistance to each pathogen separately. To avoid the contamination of artificially inoculated experimental plots with other pathogens, protective belts (stand of triticale) or appropriate chemical treatment was needed. So as to minimize year/location effects, disease development was supported by mist irrigation of plots. In experiments under study the evaluation of symptomatic reaction was usually performed on three dates on a 0–9 scale (9 – without symptoms), paying attention to both the disease progress and the infected leaf area. This evaluation could supply for the expression of symptoms by the coefficient of infection (Beuningen & Kohli 1990; Šíp *et al*. 2001), derived by multiplying both digits of a two-digit scale recommended by Eyal *et al*. (1987). Besides this, at the Humpolec location a more precise analysis was based on evaluation of the sum of % of infected leaf area (three uppermost leaves of the plant) on three dates (Šíp *et al*. 2003c). The determination of a reduction of grain yield components showed the highest average reduction of thousand grain weight after infection with *Stagonospora nodorum* (16.9%), evidently due to the affection of both leaves and spikes by the disease. For infection with *Septoria tritici* and *Pyrenophora tritici-repentis* the respective reductions of thousand grain weight were 13.7% and 10.3%. In the conditions of Central Europe Horčička *et al.* (2001) estimated the average reduction of grain weight per spike due to infection with *Septoria* and *Pyrenophora* diseases to be 16%.

Genes and QTL loci responsible for resistance to these foliar pathogens have been identified, but genetic relations between pathogen and host plant are complicated due to high genetic diversity of pathogen populations. Resistance may often be found isolate specific or quantitative (Chartrain *et al.* 2004). Though marker-assisted selection is at disposal, Czech breeders still rely mainly on the results of field infection tests. Inoculation with pathogen populations prevalently occurring in the examined territory is undoubtedly an important prerequisite of success.

Another problem lies in obtaining combined resistance to all the three most important pathogens causing brown leaf spots. Based on evolutionary, taxonomic and genetic studies, systems of genetic

Table 3. Coefficients of correlation between % areas of leaves infected with *Septoria tritici* (ST), *Stagonospora nodorum* (SNL) and *Pyrenophora tritici-repentis* (PTR), and % areas of spikes infected with *Stagonospora nodorum* (SNS) in three years

	2002 ($n = 37$)	2003 ($n = 45$)	2004 ($n = 75$)
ST/SNL	0.24	0.46***	0.19
ST/PTR	0.41**	0.08	0.10
ST/SNS	0.19	0.35**	0.38***
SNL/PTR	0.05	0.08	0.01
SNL/SNS	0.70***	0.56***	0.58***
PTR/SNS	0.08	0.17	0.05

**$P < 0.01$; ***$P < 0.001$

control are evidently different. Correlation analysis (Table 3) showed that it was particularly difficult to obtain combined resistance to *Septorias* and *Pyrenophora tritici-repentis* (Šíp *et al.* 2003c) while the differential cultivar response to infections with *Septoria tritici* and *Stagonospora nodorum* was not exceptional either (Table 4). Therefore, the detection of sources of combined resistance to all pathogens causing brown leaf spots is highly valuable.

Leaf blotch (*Mycosphaerella graminicola* (Fuckel) Schröter, anamorph *Septoria tritici* Rob. ex Desm.)

Leaf blotch or Septoria tritici blotch (STB) is considered as currently the most important foliar disease of wheat in many regions of the world (Chartrain *et al.* 2004). Eight genes (*Stb*) have been identified for resistance to STB, but resistance was found isolate specific to a large extent (Brown *et al.* 2001; McCartney *et al.* 2002). Laboratory methods are now available for the detection of isolate specific reactions to infections with *Septoria tritici* (Arriano

Table 4. Average symptom scores (0–9; 9 – without symptoms) for 17 selected winter wheat resistance sources and two susceptible checks obtained in a three-year period (2003–2005) at three locations (Ruzyně, Stupice, Úhřetice) after infection with *Septoria tritici* (ST), *Stagonospora nodorum* (SN) and *Pyrenophora tritici-repentis* (PTR)

Cultivar/line	ST	SN	PTR	Average
NSL 9257-19	8.15	8.64	7.65	8.15
SG-U 7029I	7.85	7.61	8.12	7.86
Senat*	8.30	7.32	7.82	7.82
Reaper	7.39	7.03	6.89	7.10
Shamrock	6.78	7.59	6.83	7.07
NIC97-4135A	8.25	6.77	6.06	7.03
Ordeal	6.92	7.14	6.84	6.97
Milan*	7.93	7.68	4.37	6.66
Ornicar	7.63	4.05	8.16	6.61
Batis	7.35	6.75	5.43	6.51
SG-U 7068A-c*	5.68	5.29	8.35	6.44
Hereward	7.31	6.17	5.33	6.27
CWW 93/58	6.36	7.82	4.28	6.15
CH111.12772	6.80	5.65	5.87	6.11
Arina	7.20	4.14	6.85	6.06
Estica	5.68	7.20	4.80	5.90
Gene	6.83	1.95	4.65	4.47
Susceptible checks				
Galaxie	1.64	4.11	4.26	3.34
MV Marsall	1.71	2.42	2.53	2.22

*results of two years (2004–2005)

et al. 2001; Věchet & Vojáčková 2005) and testing the resistance in the juvenile plant stage.

Results of several genetic studies indicate that resistance is oligogenic (Bartoš et al. 2002). Chartrain et al. (2004) suggested that the pyramiding of several resistance genes might be an effective, durable strategy of breeding for resistance to STB. In their experiments the cultivars Arina, Milan and Senat were found to have high levels of partial resistance to a majority of the tested isolates as well as isolate specific resistances. Methodological approaches used in field tests in the Czech Republic were summarised by Šíp et al. (2003c). So as to be in accordance with disease development under natural conditions, artificial inoculations now start in growth stages preceding the flag leaf appearance. A high average level of resistance to STB was detected in cultivars (lines) Senat (Eriksen et al. 2003), NSL 9257-19, NIC97-4135A, Milan and also in the advanced breeding line SG-U 7029I (derived from the cross Hubertus/Dněstrjanka) (Table 4). It is highly advantageous from breeding aspects that this line, similarly like Senat and NSL 9257-19, was found to possess combined resistance to all important pathogens causing brown leaf spots. However, in our tests the Swiss cultivar Arina, considered as one of the most resistant materials in the field (Brown et al. 2001), showed a highly variable response to STB and susceptibility to glume blotch. The cultivar Milan, used as a source of resistance by CIMMYT (Gilchrist et al. 1999), showed relatively high resistance to leaf and glume blotch, but a low level of resistance to tan spot. In accordance with the results of Chartrain et al. (2004), it is not probably possible to rely on the resistance of the US cultivar Gene, which became ineffective 5 years after its release (Mundt et al. 1999). This cultivar showed the highest susceptibility to glume blotch. To obtain satisfactory, durable resistance, genetically diverse materials should undoubtedly be utilised. Brown et al. (2001) suggested that progress in improving resistance to STB might be made by the intercrossing of lines from different European breeding programmes.

Glume blotch (*Phaeosphaeria nodorum* (E. Müller) Hedjaroude, anamorph *Stagonospora nodorum* (Berk.) Cast. & Germ. = *Septoria nodorum* (Berk.) Berk.)

Glume blotch or Stagonospora nodorum blotch (SNB) remains an important disease particularly at higher altitudes with frequent rainfalls. The inheritance of resistance in bread wheat appears to be quantitative and additive gene effects are the most important (Bostwick et al. 1993). Four resistance genes (*Snb*) for glume blotch (one with provisional designation) were registered (McIntosh et al. 2003) and QTL loci associated with resistance were identified (Czembor et al. 2003; Toubia-Rahme & Buerstmayr 2003). As resistance sources, e.g. cultivars Atlas 66, Blueboy II, Frondoso, Fronthatch and Oasis were earlier described by Ginkel and Rajaram (1999). In previous field inoculation experiments carried out in the Research Institute of Crop Production in Prague-Ruzyně relatively good resistance to SNB was found in the cultivars Senta, Siria, Regina and Simona (Bartoš et al. 2002).

In the field experiments under study, besides the cultivars mentioned earlier (possessing resistance to STB) relatively high resistance to SNB was detected in CWW 93/58, Shamrock and Estica (Table 4). In all examined years the affection of leaves significantly correlated with the affection of spikes by the disease (Table 3), but it is generally known that also in this case we have to reckon with differences in genetic responses. Among the cultivars listed in Table 4, Arina, Ornicar or SG-U 7068A-c with relatively low resistance to SNB on leaves showed above-average resistance on spikes. High resistance to SNB on leaves was not found to be connected with low resistance on spikes.

Tan spot (*Pyrenophora tritici-repentis* (Died.) Drechs., anamorph *Drechslera tritici-repentis* (Died.) Shoem. = *Helminthosporium tritici-repentis* (Died.) Died.)

Economic importance of tan spot caused by *Pyrenophora tritici-repentis* (PTR) has increased worldwide and great attention is paid to genetic studies of resistance on the molecular level (Friesen & Faris 2004). Both qualitative and quantitative inheritance of resistance has been observed. Predominance of additive gene action in the inheritance of resistance to tan spot was reported by Sharma et al. (2004). Multiple races of the pathogen were characterised on the basis of their ability to cause necrosis and/or chlorosis in differential wheat lines and from the aspect of production of host selective toxins (Friesen & Faris 2004).

The cultivars Frontana, Bluebird, Kavkaz and lines derived from *Agropyron distichum* were found applicable as sources of resistance in resistance breeding (Riede *et al.* 1996). Recently, responses of 22 winter wheat cultivars to artificial infection with PTR were studied in field conditions of the Czech Republic in 1999–2001 experiments (results presented by Bartoš *et al.* 2002) and also under greenhouse conditions using five isolates of the fungus (Šárová *et al.* 2002). Greenhouse experiments enabled to differentiate between the examined isolates collected in the territory of the Czech Republic. Cultivar response to four isolates (No. 98001, 98007, 98010 and 00071) correlated significantly with the field results, but specific was the response to isolate 98017. These studies were very helpful for the choice of the appropriate composition of inoculum. In the latter publication methodical details of current field tests are also available. An inoculum-containing mixture of Czech isolates is applied on experimental plots on two dates via infected oat grains.

As shown in Table 4, the highest resistance to tan spot was detected in the experiments under study in the advanced breeding line SG-U 7068A-c, which, however, like many other materials, does not possess high resistance to leaf and glume blotch. Another highly resistant cultivar Ornicar was found to suffer from susceptibility to glume blotch. Besides Senat and NSL 9257-19, the line SG-U 7029I could be classified as a valuable source of resistance to tan spot as well as to other pathogens causing brown leaf spots.

Common and dwarf bunt (*Tilletia caries* (DC.) Tul., *Tilletia laevis* Kühn, *Tilletia controversa* Kühn)

The importance of breeding for resistance to these diseases has increased especially in connection with organic farming systems and the need of lowering inputs. At least 15 *Bt* genes for bunt resistance were registered (Goates 1996) and genes in several novel sources of resistance remain to be determined and registered. Goates (1996) listed 30 races of *Tilletia caries*, 10 of *Tilletia laevis* and 17 of *Tilletia controversa*.

Sources of bunt resistance were tested in the Research Institute of Crop Production in Prague-Ruzyně (Blažková & Bartoš 1997a) and the bunt-resistant Swedish cultivars Tjelvar (T1BL.1RS) and Stava were selected for crossing with Czech cultivars (Blažková & Bartoš 1997b). Short-straw resistant lines earlier than Tjelvar and with improved bread-making quality were produced. Bunt resistance of Tjelvar was derived from PI 178383, carrying resistance genes *Bt8, Bt9* and *Bt10*. In North America this line is an important source of resistance to both common and dwarf bunt. Physiologic races *T1, L3* and *L5* were isolated from bunt samples from the Czech Republic, and analyses of bunt samples from ten other countries were carried out. The most frequent was virulence to resistance genes *Bt7, Bt2* and *Bt1,* races *L5/T5* and *L3/T3* (Blažková & Bartoš 2002).

The presence of bunt races in the Czech Republic was also demonstrated by different responses of different bunt samples on the cultivars Nela, Bussard, Euris and Tambor. Of the tested registered winter wheat cultivars Globus displayed high resistance in both experimental years (2004 and 2005), followed by the cultivars Bill and Niagara (Table 5). Percentages of infected spikes in less resistant cultivars differed according to the infection pressure (Dumalasová & Bartoš 2005).

Barley yellow dwarf virus (BYDV)

Barley yellow dwarf virus, which is transmitted by several species of aphids, causes probably the most important virus disease of cereals, widespread worldwide on wheat, barley and other cereals. It is a luteovirus with several strains, among which the PAV strain prevails in the Czech Republic. Resistance to this disease is considered as the most effective means of controlling damage caused to cereal crops. Damage to cereal crops appeared to be particularly high in conditions of double stresses (BYDV and deep frosts during winter or drought in the vegetation period) (Šíp *et al.* 2004).

Table 5. Cultivars with the lowest percentage of bunt *(Tilletia tritici)* infected spikes

Cultivar	Year-infection*	
	2004	2005
Globus	0.9	0.0
Bill	10.4	0.1
Niagara	19.3	6.3
Alana	43.0	9.6
Apache	50.2	13.5
Grandios	59.5	12.1
Complet	62.2	14.2
Average of 39 tested cultivars	52.6	28.3
Susceptible check: Batis	83.9	56.9

*percentage of infected spikes

Resistance breeding was carried out mainly within CIMMYT and ICARDA hybridisation programmes. Tolerance to BYDV in wheat is mainly based on *Bdv1* gene (Singh *et al*. 1993), which might originate from the Brazilian spring wheat cultivar Frontana (parent of the cultivar Maringá). This cultivar should be considered as a durable source because of its deployment and long-lasting effectiveness in numerous CIMMYT wheats worldwide. Great attention was also paid to interspecific or intergeneric hybridisation (especially with wheat-grass *Thinopyrum intermedium* or *T. ponticum*) as a new reservoir of BYDV resistance (Ayala *et al*. 2001) besides resistances to wheat streak mosaic virus, Fusarium head blight or leaf rust and stem rust (Fedak & Han 2005). Resistance gene *Bdv2* was detected on the *Thinopyrum intermedium* chromosome 7Ai1 and marker-assisted selection was successfully performed using SCAR markers co-segregating with BYDV resistance (Zhang *et al.* 2004). Novel germplasm with broad-spectrum BYDV resistance derived from *Thinopyrum* spp. was developed (Francki *et al.* 2001).

The materials obtained from CIMMYT/ICARDA programme, together with advanced lines and registered spring and winter wheat cultivars were tested in the Research Institute of Crop Production in Prague-Ruzyně for their resistance to the PAV strain of BYDV (Šíp *et al.* 1995; Vacke *et al.* 1996a) while the described methods have been used until now. In winter wheat the high level of resistance was not detected and crossing with resistant spring wheat materials was recommended as a promising strategy (Vacke *et al.* 1996b; Bartoš *et al.* 2002). According to the latest results (2002–2005), relatively higher, moderate resistance was detected in the winter wheat cultivars Niagara, Meritto, Rexia, Athlet, Svitava and Ebi; however, it is necessary to mention that the variation range of symptom scores was rather low in winter wheat (4.44–6.55). Average reduction of grain weight per spike due to infection was 49.6%. The effect of BYDV on a reduction of spike number per plant and consequently on grain yield may be high in winter wheat (the average grain yield reduction was 76.2% in 2004). The three-year data (2003–2005) on the tested spring wheat cultivars and lines are presented in Table 6. In accordance with the results of previous tests (Bartoš *et al.* 2002), the line WKL-91-138 and the Brazilian cultivar Maringá exhibited the highest resistance level; moderate resistance was observed in Anza, carrying *Bdv1* gene. It is encouraging that moderate resistance was also detected in Sandra and some new registered spring wheat cultivars, e.g. Leguan and Bruncka. It can be expected that the breeding of wheat for BYDV resistance will be successful if resistance genes are cumulated in crosses between moderately resistant spring and winter wheat cultivars, as reported earlier (Bartoš *et al.* 2002), and if resistance genes *Bdv1*

Table 6. Average reduction of grain weight per spike (GWS-R), visual symptom scoring (VSS: 0–9; 0 = without symptoms) and susceptibility index after infection with BYDV in spring wheat cultivars (lines) showing the relatively higher resistance level in a three-year period (Jara and Munk: susceptible checks)

Cultivar/line	GWS-R (%)	VSS	SI*	Degree of resistance**
WKL-91-138	28.8	1.6	3.54	R
Maringá	31.3	2.8	3.80	R
Anza	36.1	3.2	4.30	MR
Sandra	23.3	4.3	4.12	MR
Leguan	31.0	3.6	4.34	MR
Bruncka	26.3	4.6	4.25	MR
Zuzana	38.2	4.8	5.30	MR-MS
Vinjet	38.7	5.0	5.32	MR-MS
Jara	69.8	6.6	6.35	S
Munk	68.0	6.5	6.80	S

*Susceptibility index: 10-/4,02GWS+0,52(10-VSS)/^ 0.9 (Šíp *et al*. 1997)

**R = resistant; MR = medium resistant; MS = medium susceptible; S = susceptible and *Bdv2*, for which molecular markers are available, are used.

Prospects of obtaining combined disease resistance in wheat

Currently, molecular techniques offer new possibilities of resistance breeding intensification (pyramiding of resistance genes). However, it follows from many studies that a majority of the described resistance genes (QTL loci) have only a limited and variable (often not durable) impact on field resistance. Because multiple genes need to be transferred to achieve combined resistance, the time advantage of marker-assisted selection may be lost and breeding costs may increase. The most advantageous strategy is still to detect a germplasm possessing acceptable resistance to a majority of the most important diseases (at the best in combination with high productivity, grain quality, resistance to abiotic stresses, etc.) and to improve single characters using appropriate crossing schemes or deliberate gene transfer (backcrossing) for which molecular markers may be very helpful.

In spite of steadily increasing demands, wheat breeding achieved enormous progress in the last years and high-yielding cultivars possessing acceptable field resistance to a majority of diseases can be included in hybridisation programs. Among winter wheat cultivars registered in the Czech Republic eight cultivars (Globus, Bill, Rapsodia, Clarus, Alana, Akteur, Clever and Caphorn) could be classified by the State Variety Testing Institute (Survey of Cultivars: Cereals and Peas, Brno 2005;

Table 7. Characteristics of the selected winter wheat sources of combined resistance to diseases

Cultivar/line	*Septoria tritici*	*Stagonospora nodorum*	*Pyrenophora tritici-repentis*	Yellow rust	Leaf rust	Stem rust	Fusarium head blight	Powdery mildew
NSL 9257-19	**R**	**R**	**MR**	**R**	**MR**	**R**	MS-MR	**MR**
SG-U 7029	MS-MR	**MR (MS)**	**MR (MS)**	**R**	**MR**	**R**	**MR**	MS MR
SG-U 7029I	**MR**	**MR**	**R**	**R**	**MR**	**MR**	**MR**	MS-MR
NIC 97-4458A	MR-MS	MR-MS	MR-MS	**R**	**R**	**R**	**MS-MR**	**MR**
CH111.12772	**MR (MS)**	MR-MS	MR-MS	**R**	**R**	**R**	**MR**	MS
Reaper	**MR**	**MR**	MR	**MR**	MR-MS	**MR**	MR-MS	MS-MR
SG-U 7068A-c	MR-MS	MS-MR	R	**R**	**MR**	**MR**	MR-MS	MS-MR
Senat	**R**	**MR**	**MR (R)**	**MR**	MR-MS	S	MS-MR	**MR**
Estica	MS-MR	**R-MR**	MS	**R**	**MR**	MR-MS	MR-MS	MR-MS
Ordeal	**MR (MS)**	**MR**	**MR (MS)**	**MR**	**R**	MS		MS-MR
SG-U 2007D	MR-MS	S	**R**	**R**	**R**	**R-MR**	MR-MS	MR-MS
Ornicar	**MR**	MS-S	**R**	**R**	**R**	**R**		MR-MS
NIC 97-4135A	**R**	**MR (MS)**	MR-MS	**R**	**R**	**R**	MS	
CWW 93/58	MR-MS	**R**	S	**R**	**R**	**R**	MS-MR	MR-MS
SG-U-KM1084-9	MS-MR	**MR**	**MR**	**R**	**MR**	**MR**	MR-MS	S
SG-S 1875-01	MR-MS	S	MR-MS	**R**	**MR**	MS	**R-MR**	**MR**
Vlasta	MR-MS	MR-MS	MS-MR	MR-MS	**MR**	MS	MS-MR	**R**
Arina	**MR**	MS (S)	**MR (MS)**	MR-MS	S	MS	**MR**	S
Batis	**R (MR)**	MR-MS	MS (MR)	**R-MR**	**R-MR**	MS	MR-MS	MS-MR
SG-S 1752-01	**MR**	MS (S)	MR-MS	**R**	**R-MR**	**R-MR**		
HE 6130	**MR**	S	MR-MS	**R**	MR-MS	**MR**	MS	MR-MS
SG-S 1066-01	MR-MS	MS	S	**R**	**R**	**R**	MR-MS	MS-MR

R = resistant; MR = medium resistant; MS = medium susceptible; S = susceptible

ISBN 80-86548-65-1) as above-average resistant (scores ≥ 5) to all 10 examined diseases. According to the health value index ("Gesundheitswert" according to Spanakakis 2004) the modern winter wheat cultivar Globus showed an average score 7.6 for a disease complex in the range from 6 to 9, which indicates above-average scoring for all important diseases. Of the other cultivars Bill (6.7), Alana (6.4), Ludwig (6.2) or Batis (6.2) can be mentioned.

Based on the results of ring tests presented here it was possible to select winter wheat cultivars and lines promising for their use in wheat breeding for combined resistance. As shown in Table 7, under conditions of a high infection pressure high or moderate resistance to all examined important diseases was very difficult to find, however, it can be expected that the materials in which medium resistance (between MR and MS) was detected in trials with artificial inoculations could also provide sufficient protection under natural conditions. Among the examined winter wheat cultivars and lines especially NSL 9257-19, SG-U 7029(I), NIC 97-4458A, CH111.12772, Reaper, SG-U 7068A-c, Senat and some other materials in the front rank (Table 7) were found to be resistant or moderately resistant to most diseases and, therefore, they could play an important role in the breeding of wheat for complex resistance. Besides this, many other materials were detected that may contribute significantly from certain aspects when properly combined in crosses. Valuable are without doubt detections of combined resistance to rusts (Table 1) or resistance to different pathogens causing brown leaf spots (Table 4). Deliberate hybridisation aimed at complex disease resistance is now under progress and it is highly appreciable that wheat breeders have joined efforts to achieve this goal.

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Abstrakt

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V práci jsou shrnuty výsledky a perspektivy šlechtění pšenice na odolnost k chorobám ve světě a v České republice. Pozornost je zaměřena na rzi, padlí travní, fuzariózu klasu, braničnatku pšeničnou, braničnatku plevovou, žlutou skvrnitost listů působenou houbou *Pyrenophora tritici-repentis*, sněť mazlavou a zakrslou a virus žluté zakrslosti ječmene na pšenici. Jsou nastíněny metodické přístupy přijaté v národních infekčních testech rezistence. Na základě výsledků polních infekčních testů byly detekovány nové zdroje odolnosti k výše uvedeným chorobám a stanovena jejich charakteristika.

Klíčová slova: pšenice; *Triticum aestivum* L.; zdroje rezistence; geny rezistence; mykózy; virózy; Česká republika

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