UDC **631.528.2.23.582.28.**

TOLERANCE TO PHYTOPATHOGENS OBTAINED USING CHEMICAL MUTAGENESIS METHOD ON WINTER WHEAT

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A direction in mutation selection has been presented – chemical mutagenesis as regards the creation of material resistant to phythopathogens – mutants, mutant varieties and constant hybrids of mutants with the varieties of non-mutant origin. Various methods are analyzed in the present article as to the creation of samples and varieties resistant and full-scale resistant to various pathogens, as well as the period of resistance preservation depending on the type of the pathogen and the ways of creating the resistance.

***Keywords**: Chemical mutagenesis, resistance to phytopathogens – monogenic, polygenic, complex.*

Resistance to phytopathogens constitutes at present one of the most important factors which save the harvest and the environment, as well as agricultural produce, from pesticides, which hinder the development of epiphytoties. The resistance of the principal food culture of winter wheat is especially significant when it is widely spread. Of great value is the monogenic (vertical) resistance as well as the polygenic (horizontal) resistance. Most reliable is full-scale resistance to several types of phytopathogens [1]. One variety or sample may possess simultaneously monogenic and polygenic resistance in relation to one and the same phytopathogen, or in relation to different pathogens. Polygenic resistance can sustain itself for an indefinitely long time. Monogenic resistance subsides quickly. The duration of its persistence depends on the pathogen: the speed of emergence of new virulent races in relation to the host-plant; the viability of these races; the speed of their reproduction and spreading; the size of area occupied by the host-plant. In the case of co-existence of both types of resistance to one and the same phytopathogen within one and the same variety or sample, the loss of monogenic resistance leads to the fact that resistance becomes less pronounced, which is characteristic of the remaining polygenic resistance. The less pronounced polygenic resistance sometimes reveals itself on the level of tolerance. Monogenic resistance is often dominant. In the case of monogenic resistance the attack by a phytopathogen can be so weak that it borders on immunity, or the attack does not take place, and then the immunity is apparent. The drawback of monogenic resistance is the danger of its rapid loss as a result of the emergence of a new virulent race of a pathogen which would be complementary to the resistance gene of a host-plant. Here the danger lies in the spreading of a variety with monogenic resistance, as the loss of such resistance occurs in connection with the rapid reproduction and spreading of a new virulent race over large areas. In this case the emergence of epiphytoties is quite probable. This happened at the beginning of the 60s of the 20th century in Krasnodar territory, when the new varieties of winter wheat Aurora and Caucasus, created by P.P. Lukyanenko, with monogenic resistance to leaf rust, lost this resistance, since it was overcome by a newfangled virulent race. When these varieties quickly spread over large areas both varieties died out as a result of mass infestation – epiphytoties.

Research methodology

When using the chemical mutagenesis method of I.A. Rapoport, the highly mutable constant triticum-agropyrum hybrid (TAH) 186 was taken as the source variety. Most effective low concentrations of ethylenimine – 0.01 – 0.04% – were used when airdry seeds were soaked in a solution, with the exposure time 24 hours. Mutation-carrying plants were singled out in the second and third generations. In order to detect mutations of resistance to Ustilago and Tilletia, artificial infectuous provocative backgrounds were used; in order to detect resistance to mildew and leaf rust – artificial and natural backgrounds; resistance to snow mold, Tiphula blight, Alternaria, yellow rust – against the natural infectuous background under massive attack on winter wheat.

Research results and their discussion

It is interesting to note that the Caucasus variety in the conditions of the Central region of the Moscow Region retains its resistance to leaf rust. Apparently it can be explained by the fact that in this given region the virulent race which emerged in the Krasnodar territory is absent. This has preserved the resistance of the Caucasus variety with monogenic resistance towards the former race of leaf rust. Our chemo-mutant variety of winter wheat Bulava, created on the basis of the Caucasus variety as a result of its breeding with the chemo-mutant, which was acquired with the help of ethylenimine (EI), is also resistant to leaf rust, and not only in the Moscow Region of the Central region, but also in East Kazakhstan, where this variety is regionalized (included into the State Register of breeding achievements approved for use). Hence it can be assumed that in East Kazakhstan, too, no new virulent race came into being. That is why the Bulava variety retains its resistance to leaf rust, just as in the case of Caucasus variety, in the conditions of the Central region. In East Kazakhstan the Bulava variety came to supplant the varieties Mironovskaya 808 and Komsomolskaya 56. Here ongoing seed-production work with the Bulava variety is being conducted.

Monogenic restistance can play a positive role if the varieties in possession of it are appropriately placed and are not spread over too large a territory. It is crucial that every region growing winter wheat should be saturated with various sorts with monogenic resistance in such a manner that none of them would occupy large areas. It is desirable that the resistance-defining genes would be different with different varieties, i.e. that the varieties would not be closely related. In this case the emergence of new and various virulent races in relation to all resistance genes with different varieties is less probable. Even if a virulent race emerges in a certain variety or in a part of varieties, the rest of the varieties with monogenic resistance, in which the new virulent race has not emerged, secure the crops. Besides, the variety or varieties attacked by a phytopathogen as a result of the emergence of a new virulent race or new virulent races, will not be involved in an epiphytoty, as they do not spread over large territories.

Such placement of varieties, provided that the region is saturated with those, presupposes that among the varieties with monogenic resistance there may be varieties not resistant to a given phytopathogen. Yet there will be no epiphytoties in this region anyway, as the races attacking non-resistant varieties will hardly be virulent for all other sorts and will reproduce moderately and slowly, depending on the area occupied by each given variety.

When varieties are included into the assortment for this given region, those agriculturally valuable varieties which are not resistant to this or that phytopathogen can also be considered. The disease will ensue under natural provocative conditions, but epiphytoty will most probably not occur when there are several varieties involved if they are planted on relatively moderate areas and are not made to occupy millions of hectares, as it is unfortunately common in our country as regards the so-called hegemon varieties. Hegemon varieties not only tend to be susceptible to epiphytoties in any case, but also in the case of monogenic resistance to this or that phytopathogen and even in combination with the resistance to two or more phytopathogens – the massive attack can still take place, as resistance to all widely-spread phytopathogen races is apparently impossible, and massive attack covering large areas is possible with regard to any of those.

At present the hegemon varieties are widely spread not only in a single region, but in a number of cases cover various other regions – despite the fact that they are always adapted to growing in those regions as far as the soil and climatic conditions are concerned. Nevertheless these varieties occupy millions of hectares. Plant selection breeders who created these varieties make a big mistake when spreading them that wide, thinking that the larger the area covered by a variety, the more significance it attains. One of the more unfortunate circumstances of this misconception consists in the fact that various hegemon varieties also possess closely related genomes and were being created on the basis of one and the same variety or on the basis of few varieties taking part in the hybridization. This is what happened with the Aurora and Caucasus varieties, which were not only monogenic with one and the same resistance gene and were spread over large areas soon after being created, but also had closely related genomes, since they were created off the same basis – the Besostaja 1 variety. A new virulent race attacked both varieties simultaneously in such a manner as if it were one variety with one genome. Thus apart from the monogenic resistance and rapid race-forming, the rapid spreading of a new virulent race was sparked off also by the closely related genomes of both varieties. Everything that happened with Aurora and Caucasus varieties is an instance of how even the best varieties can make a negative impact on grain production if they are closely related and, on top of that, widely and rapidly spread. At present, on Krasnodar territory, the main supplier of grocery grain of winter wheat, there are also closely related varieties created on the basis of Krasnodar Karlik ("Krasnodar Dwarf") by means of chemical mutagenesis method with Besostaja 1 variety. These are the following varieties: Skifyanka, Smuglyanka, Polukarlikovaya 49 and others. As distinct from Aurora and Caucasus varieties, these sorts do not occupy large territories any longer and are not hegemon varieties either; they are placed mosaically or approximate the mosaic disposition. There is no existing evidence of epiphytoties in regard to these varieties. The originality of the Krasnodar Karlik genome possibly plays a role here, with various mutant genes arrived at with the help of chemical supermutagen as well as their placement, in different blends and different quantity in the above-mentioned varieties created on the basis of Krasnodar Karlik.

In midland Russia the variety Mironovskaya 808 used to be spread widely. This variety, as well as the Krasnodar Karlik sample, served as the basis for many varieties created in the 80s – 90s. Hence, closely related genomes can be evidenced also in the midland varieties. To the range of such varieties belong the varieties created in the Scientific Research Instutute of Agriculture (NIISH) of the Central regions of nonchernozem zone (TsRNChZ): Inna, In Memoriam of Fedin, Moskovskaya Nizkostebelnaya, Nemchinovskaya 24, Zarya. These closely related varieties now are beginning to fade in their significance. However, the areas occupied by them are still large. They are badly hit by snow mold, especially of the fusarial kind. On the argillaceous soils of the Central region this low-temperature saprophytic phytopathogen often massively attacks these varieties of winter wheat. There is not a single variety which would be resistant to this disease in the Central region of Russia. These varieties do not manifest sufficient regeneration capacity. Growth after the attack of disease does not always deliver the crops, decreasing them prodigiously in a number of cases. The variety Moskovskaya 39, also of the NIISH TsRNChZ (Scientific Research Instutute of Agriculture of the Central regions of nonchernozem zone) selection, created only by traditional methods of breeding without using the method of chemical mutagenesis, along with the variety of mutant origin "Named after Rapoport" and our other chemomutant varieties produced with the help of the supermutagen EI, may furnish a good example. The year 2001 was characterized by a very severe attack of fusarial snow mold. In the work-study unit Mikhailovskoye of the Podol region of the Moscow Region the attack of this pathogen reached 100%. The variety Moskovskaya 39 grew much more weakly after the attack than the variety "Named after Rapoport". As a result, the variety Moskovskaya 39 formed the crops in the amount of 8 hundreds kilograms per ha, whereas the variety "Named after Rapoport", with its high regeneration capacity and possessing tolerance in connection with that, formed the crops in the amount of 40 hundreds kilograms per ha, i.e. 5 times greater than those of the Moskovskaya 39 variety.

One more low-temperature saprophytic phytopathogen is Tifula blight, and in the case of massive attack on varieties of NIISH TsRNChZ selection created outside of the chemical mutagenesis method, it just destroys them. This pathogen develops much more rarely than snow mold, but once it has developed, it is very detrimental to the crops. In 1996 this pathogen massively afflicted closely related varieties of the NIISH TsRNChZ selection occupying large areas in Yegoriev and adjacent regions of Moskovskaya oblast. These varieties perished and were ploughed under in spring. The areas they used to occupy were sowed with spring cultures. In 1996 only the variety "Named after Rapoport" and our other chemomutant varieties, produced with the help of the chemical mutagenesis method, survived in the Yegoriev region. The variety "Named after Rapoport" occupied a smaller area of 217 ha in the

Pochinkovskoye farmstead. This farmstead in Yegoriev region was the only one to have grain thanks to the variety "Named after Rapoport" and our other chemomutant varieties. The fact that these varieties possess original genomes not related to the varietes of the NIISH TsRNChZ selection, played a role here. The variety "Named after Rapoport" and other chemomutant varieties were created on the basis of a chemomutant off the variety PPG 186, arrived at with the help of the chemical mutagen EI and the Mironovskaya 808 variety. The originaility of the genome of the variety "Named after Rapoport" stemmed from the originality of the genome of the source variety PPG 186 and those mutations which were induced in this variety as a result of the impact of the supermutagen. During this process, even that part of the genome which got to be inherited by the variety "Named after Rapoport" from the Mironovskaya 808 variety, which latter variety took part in the hybridization with a mutant, produced on the basis of the PPG 186 variety, – could not cancel out that genome's originality which had been acquired from the source variety with mutations. And all this while the genetic material passed on to the mutant from the Mironovskaya 808 variety was apparently considerable, which fact is confirmed by the phenotype of the variety "Named after Rapoport", which closely resembles the Mironovskaya 808 variety. The originality of the variety "Named after Rapoport" is confirmed by the research done by V.A. Pukhalsky, who applied a special method of using the necrosis genes [2]. In 2011 Tifula blight manifested itself to a significant extent in Snegiri of the Istrinsky region of Moskovskaya oblast. It attacked the Zarya variety and some of the hybrids of our mutants with the Caucasus variety. The bulk, however, of our collection was not affected.

Examples can also be adduced as regards the low-temperature saprophytic diseases caused by root rot pertaining to the Alternaria genus. In 1988 in the Noginsky region of the Moscow Region there was a massive attack simultaneously by Alternaria and snow mold upon the varieties having closely related genomes Mironovskaya 808 and Zarya, which are widely spread there. We observed the epiphytoties of Alternaria and snow mold in the conditions of the Kudinovo (village Mar'ino). On one field there grew the Mironovskaya 808 and three of our chemomutant varieties – "Named after Rapoport", Beseda and Belaya – created with the help of chemical mutagenesis method. Mironovskaya 808 variety was so hit by Alternaria that not only the heads turned black, but also the entire plants (100% attack by both pathogenes). The Mironovskaya 808 variety was sent to the barnyard as bedding for the animals, as this variety could not form any crops. Our 3 varieties, created by means of chemical mutagenesis method and during hybridization with the Mironovskaya 808 variety, despite the fact that the genome of our varieties contained the genetic material of that variety, were attacked by both saprophytes to a significantly lesser degree than the varieties Mironovskaya 808 and Zarya: snow mold – at 30 – 40%, Alternaria – at 3 – 10%. Against a very harsh provocative background very distinct natural selection took place. Heavily afflicted plants dropped out from the batch. Part of the plants, approximately 1/3, were little affected by the snow mold, and were not hit by root rot at all. They did not go to the barnyard. The survived plants formed the crops of 17 hundreds kilograms per ha during intensive negative selection against a harsh natural background. These 3 varieties of ours, arrived at through the mutation breeding method, have now been resistant to Alternaria year after year. Their disease rate amounts to 0 – 3% after additional individual selection. They are tolerant to snow mold and grow again well without crop losses.

Genome distinctions among varieties are highly important not only with respect to the prevention of epiphytoties and abiotic pressures. Genotypic diversity is indispensable from the point of view of breeding work intensification, because hybridization of varieties with closely related genomes is doomed to absence of diversity or deficit of diversity in the hybrid offspring. As it is, a reversal to parent forms can occur here. In other words, breeding is limited in the absence or deficit of donors of necessary features or their clusters.

Genotypic diversity secures the crops under unfavourable and extremely unfavourable climatic conditions, which recur more and more often and which not all varieties can withstand. Some of them can become rarefied or perish, which we have, time and again, witnessed in the farmsteads of various regions of the Moscow Region. In these cases the varieties with more stable genotypes can safeguard the overall crops against perishing or from diminshing.

Some time ago, abroad, two methods were used in order to retain the monogenic resistance to obligate phytopathogens. Convergent and multilinear varieties were created. The latter consisted of a number of isogenic lines. Convergent varieties were created by means of stagewise hybridization with varieties and samples possessing different oligogens which define resistance. As a result of such hybridization in one variety or in one form there accumulated the oligogens of resistance, and the latter persevered for a longer period of time. Isogenic lines for multilinear varieties were being created over longer stretches of time. It was necessary to constantly monitor each single line with regard to its possible loss of resistance and its replacement by another resistant line. Replacement lines must always be kept ready. All isogenic lines of a multilinear variety must be phenotypically identical. This complicates the task even further. Work aimed at creating convergent and multilinear varieties approximates the work of a jeweller. The shortage of multilinear varieties is also linked to such a negative as changeable grain. Such varieties were created mainly where the threat of Puccinia graminis epiphytoties was imminent.

Both ways of preserving monogenic resistance are labour-intensive and time-consuming. Besides, these methods require substantial financial expenditures and are not economical. In connection with this, we maintain that it is better to pick different varieties with monogenic resistance controlled by different gens, and place these varieties in one region or in neighbouring regions in such a way that each variety would occupy not too large a territory. In practice it can be implemented as follows: One farmstead breeds one or two varieties with different genotypes. Another adjacent farmstead breeds the same number of varieties with other genotypes. In order to implement this, it is necessary to know the origin of each variety in order not to repeat the genotypes. There are difficulties in this respect, however. They consist in the fact that the basis of many varieties is constituted by similar related genotypes, and the genotypic diversity is not present to the extent it is required. Hence the varieties with original non-recurrent genotypes are especially valuable. For instance, such a variety would be the chemomutant winter wheat variety "Named after Rapoport". Especially dangerous as regards the outbursts of epiphytoties are those varieties which host the pathogen of the corresponding new race whose virulence gene, complementary to the resistance gene of the host-plant, is characterized by frequent sexual process, high mutability, high reproduction level and rapid spreading. Such phytopathogens include, for example, mildew, the monogenic resistance to which, acquired via traditional breeding methods, is shed on average every 3 to 4 years. There have been cases of its loss even when the given resistant form had not yet dropped out of the competitive strain tests in the breeding process, or else it dropped out soon after the process was over. A quick loss of resistance to leaf rust is also to be observed, even though it is a slower process than in the case of mildew. As far as wheat bunt fungi are concerned, they reproduce at a slower pace and their mutation process is also slowed down. New virulent races emerge in them on average once every ten years, and epiphytoties are encountered more rarely than in the cases with leaf rust. In the first half of the 20th century, however, the epiphytoties of Tilletia hit a promising winter wheat variety Omar in Europe, the result of which was that the variety perished.

As regards obligate phytopathogenes, it is easier to achieve resistance here, as it is race-specific. The phytopathogens mentioned above – mildew, leaf rust, Ustilage and Tilletia belong to obligate race-specific phytopathogens.

Polygenic or non-race-specific resistance emerges more rarely, perhaps as a consequence of the fact that during backcrossing, which accompanies remote hybridization (and the latter is often used, since it is exactly the remote species and genera that are rich in resistance genes to many of the phytopathogens), the polygens which define resistance are lost. There exist cases of monogenic resistance of long duration. For instance, monogenic resistance of tobacco to the tobacco mosaic virus, passed down the line from the wild species of Nicotiana glutinosa [3], has not been lost for over 20 years, up to the moment of writing the present paper. It is probably linked to fact that in this rare case, apart from one gene (oligogene), acquired from a wild species, also concomitant resistance polygens were passed on, as a result of which the monogenic resistance, thus supported, endured for a long time. It is possible that the durable monogenic resistance is more typical of viruses than of obligate phytopathogen fungi – mildew or leaf rust. The dominant character of resistance could also have played a role here.

When using the method of chemical mutagenesis in our research, the winter wheat monogenic resistance to mildew perseveres even longer than tobacco's resistance to the tobacco mosaic virus, i.e. for more than 40 years already. Resistance to mildew under an optimum dosage of EI occurs frequently – in 12-14% of cases [1] as regards the remaining mutants of our assortment. Genetic analysis has shown that this is a dominant feature [4] and that it is defined by one and the same gene in different mutants. It is obvious that this gene is highly mutable. The hypersenstivity reaction emphasizes the monogenic dominant character of this feature. Resistance to mildew manifests itself differently with different mutants. For instance, the attack on some chemomutants amounts to 3 – 5% – close to immunity, with others it is 10 – 15%, still others – 20%, and so forth up to 35% – at the tolerance level with the affliction of the original variety PPG 186 of 50 -70%. Why is such variance in the mildew disease with different mutants – considering that the mutation emerged in one locus? Perhaps in one locus, consisting of a cluster of genes, different genes are affected by mutation, which behave themselves in a cluster as one unit as far as the indications of genetic analysis is concerned. However, as our genetic analysis showed, alongside one mutant locus with the mutants resistant to mildew, mutant polygens are still present. The following behavioral fact regarding one and the same mutant in the conditions of Podmoskovie (Moscow vicinity) and in the conditions of Stavropol territory is of interest. In the Moscow Region monogenic resistance with very low disease levels is manifest. It is dominant, with hypersensitivity reaction. Polygenic resistance, defined by genes, is not manifest in the same genome, although it is present there, as demonstrated in the genetic analysis. In the conditions of Stavropolie, polygenic resistance with disease levels of 10 – 15 – 20% without hypersensitivity reaction is manifest, whereas monogenic resistance is not manifest. This special feature of resistance to mildew is a novelty, and is a new reaction to different conditions which is inherent in chemical mutagenesis.

Polygenic resistance was detected in the mutants of our collection as regards resistance to Ustilago. A large part of mutants resistant to Ustilago possess polygenic resistance, as it happens with different number of polygens which define resistance, and with different degree of their impact [5]. For instance, in the case of our mutants which are resistant to Ustilago, there occurs a situation where a lesser number of polygens provide greater resistance if their impact strength is greater with this very mutant. Sometimes the picture looks different, and a greater number of polygens provide lesser resistance, since the impact strength of mutant polygens in this case does not amount to much. The degree of susceptibility of the original variety PPG 186 varied within the range of 35 – 45% attacked heads over the years. The attack on the Mironovskaya 808 variety was at 55 – 60%. The susceptibility of mutants with polygenic resistance is 10 – 16% on average [6]. Individual selection against artificial provocative background allowed to detect immune families not attacked in subsequent generations. As a result of this, families have been singled out with a sufficiently high concentration of polymeric mutant factors for the emergence of immunity and a possiblity of its retention down the generations. Out of those investigated in our collection, only one mutant possesses monogenic resistance to Ustilago. This was initial immunity – 0% disease rate, without selection.

A similar picture can be observed as regards Tilletia. Selections allowed to detect practically resistant families with 0.5 – 1.0% affected heads against artificial provocative background. Mutants were detected which are simultaneously resistant to Ustilago and Tilletia. Those were mutants with marker features indicating resistance and degree of resistance. For instance, mutants with heads of intensive blue-gray colour turned out to be resistant to Tilletia. Mutants with a puberulous head turned out to be resistant to Ustilago and Tilletia.

Resistance to Tilletia as a rule goes hand in hand with resistance to Ustilago. Yet resistance to Ustilago does not always entail resistance to Tilletia, and more often they do not appear in tandem. Of special value are those mutants which combine in themselves the resistance to several phytopathogens at once. For example, resistance to mildew is often combined with resistance to yellow rust; resistance to mildew and yellow rust occurs in combination with resistance to Ustilago; resistance to mildew in combination with resistance to Ustilago and Tilletia; resistance to mildew and yellow rust in combination with resistance to Alternaria; resistance to Alternaria in combination with tolerance to snow mold. Our variety Stavropolskaya Kormovaya possesses combined resistance to 5 kinds of phytopathogens: mildew, Ustilago and Tilletia, leaf rust, Septoria blight.

We also appreciate age-related resistance to mildew. For instance, the variety "Named after Rapoport" chances to be hit by mildew during the phase of tillering and the incipient stage of stem elongation. However, at a later stage of stem elongation a hypersensitivity reaction arises, which prevents the further development and spreading of the pathogen, and any further attack comes to a halt.

In the present research we focussed on obligate and certain saprophytic pathogens according to race-specific and non-race-specific resistance. Of obligate phytopathogenes in the Central region of Russia the most dangerous is Tilletia, whereas Ustilago is less dangerous. However, we also work with Ustilago, as in more southern regions it, too, is dangerous enough. Ustilago is of interest to us from the point of view of studying the mechanisms of resistance. Resistance to Tilletia comes into being under the impact of EI more rarely than resistance to Ustilago, mildew, Alternaria. Yet with a variety non-resistant to Tilletia it is also possible to avoid attacks even in the case where the seeds are infected, using some agrotechnical techniques. For instance, winter wheat is to be sowed early, the seeds are not to be buried too deeply and are to be pretreated before seeding down.

Conclusions

With respect to obligate phytopahtogenes, monogenic resistance is easier to achieve than polygenic. That is why monogenic resistance is especially attractive. Particularly difficult is the acquisition of convergent and multilinear resistance. These two kinds of monogenic resistance are the most labour-intensive and time-consuming. Varieties which possess those are not completely safeguarded against massive attacks. With the help of supermutagen EI it is easiest to acquire monogenic as well as polygenic resistance. We have arrived at multilinear resistance on the basis of mutant polygens defining resistance and contributing to it. In a number of cases, with sufficiently high concentration of mutant polygens of resistance, as a result of individual family-based selections, an immunity was obtained, which is consolidated down the generations in the offspring. Sets of mutant polygens in immune lines are different. In these lines polygenic and multilinear resistances are coupled. Such resistance is simple to arrive at under the effect of EI, – much simpler than to acquire convergent or multilinear resistance using traditional methods. Besides, it is more stable and the expenditures towards its acquisition are minimum. Multilinear resistance on polygenic basis under sufficiently high concentration of mutant polygens and sufficiently great strength of their impact with pronounced immunity will never be lost, as we imagine, however the mutant polygens would combine with one another in later generations.

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