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EVALUATION OF THE PLANT GENETIC VARIATION AND ITS EXPERIMENTAL INCREASE

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Contents

INTRODUCTION

From the point of view of genetics the development of new commercial varieties is a multistage process beginning with the obtaining of genotypic diversity by some techniques accessible for breeders, continued by identification and selection of the best genotypes, and finished by testing the selected ones. Hence, breeding results are determined mainly by the quantity and quality of the breeding source genotypic variability, and the possibility to control this variability as well.

Genetics has a number of approaches used for evaluation and increase of genetic variability, and which on the whole form an essential component of plant breeding theory. However, the application of them is connected with many technological difficulties and not alaways it efficient.

All this fully concerns the plant quantitative traits; just quantitative variation and inheritance is typical for plant characters important for breeding purposes. Opposite to plant qualitative characters, the genetic control of which is ordinary enough and their analysis is realized by classic genetic approaches, the genetical analysis of quantitative traits is possible only by specially developed approaches, the technical aspects of which are not finally decided.

Among methods for analysing genetic variability of plant quantitative characters, a wider application have acquired those focused on phenotypical variance (genotypical, paratypical variance and others) of separate characters as well as on evaluation of combining ability in different genotypes. However, the estimation of factorial variance by the analyses of variance and correlation-regression is related with special organization of experiment and with generation changes. As a result, the obtained information on genetic variation of the corresponding plant unity is shifted time lowering its importance especially for breeding process. It is necessary to add that both the evaluation methods for estimation of variance components described above and those for estimation of combining ability are focused on independent study of separate characters. Thus, the complicated interactions caused by genotype and environment are not taken into consideration, and the obtained information is difficult to be used in breeding process as far as selection is always directed to the improvement of character unity.

According to all this mentioned above we have chosen a goal to study the application of so-called express-methods needing no generation changes for the analysis of plant genetic variation, and to use multidimensional statistical analysis based directly on simultaneous analysis of several characters.

Similar problems are related with the use of techniques for genetic variation induction. Effects of traditional mutagenes (radiation, chemical agents) on individual characters have been studied sufficiently well. However, little is known about the effect of mutagenes on trait association being of great importance both theoretically and practically. This study we have included in our programme. Additionally, we were interested in the possibility to unite plant mutagenesis with natural selection allowing to increase the variation level important for breeding.

In the recent years a principal possibility to induce a wide spectrum of inherited variability by plant tissue culture has been observed. However, the breeding perspectives of this variability are unclear. Therefore we looked for a possibility to induce favourable changes in quantitative traits important for agriculture and to obtain valuable breeding sources by plant tissue culture techniques.

Besides these general problems, it is essential to evaluate the genetic variability of plant characters in certain breeding patterns of definite species. The corresponding differences are determined by both the specific genetic determination of characters in each species and the features of breeding sources obtained in different ways. In this respect, the genetic variability of many agricultural, berry and ornamental plants, as well as deciduous and conifer trees was studied including also species with limited or no information on the character of their genetic variation. On the other hand, certain investigations were carried out on genetic variation of barley, the basic grain crop in Latvia, related to plant host resistance against one of the most damaging pathogen, Latvian population of barley powdery mildew. No such systematic investigations have been carried out in Latvia or in the Baltic area in general until recently.

Taking into account all the considerations we put forward the following aims:

1. To evaluate the applicability of genetical variation analysis methods in quantitative traits of plants.
2. To work out new ways of genetic variation in quantitative traits of plants and interrelation analysis based on multidimension methods of statistical analysis.
3. To work out new ways to increase the plant genetic variation.
4. To evaluate the genetic variation parameters in various plant species.
5. To develop new perspective initial material for breeding.

Plant quantitative trait experiments were organized by random replications. Data were calculated on different types of computers by statistical genetic methods and principal component method using conventional software or that developed by the author.

STUDY OF METHODS FOR PLANT GENETIC VARIATION ANALYSIS

Evaluation of phenotypical variation components in quantitative traits

One of the most essential character in plant quantitative traits, opposite to the qualitative ones, is the great influence of environmental factors on phenotypical establishment of traits. Therefore the genotypic diversity of the corresponding trait cannot be judged by the level of phenotypic variation. Specially developed approaches allow to evaluate the contributions of inherited and environmental factors in phenotypical variance. Information about the relations between the genotypical and paratypical variances allows to evaluate the level of inherited diversity in plant unit examined, to select the most rational breeding ways, and to determine traits on the basis of which breeding is most efficient in the given material.

Variance and correlation-regression analyses have been used most extensively for evaluation of factorial variances (Falconer, 1964). To use these methods a special experiment organization is needed allowing to register traits for plant groups of a certain relationship. For this purpose generation changes are needed prolonging the time for obtaining the indispensable information. Many of the proposed so-called express-methods, i.e. such where, generation changes are not needed, have not been tested for their significance and limitations.

Among these methods, our attention was fixed by the method developed by Shrikhande (1957) providing much possibilities including the analysis of natural populations widely applied for genetic and breeding investigations. Both special experiments and simulations by computer have been operated [8, 10, 11]. The obtained model allowed to estimate the regularities of interaction of genetic variation, soil fertility and environment heterogeneity. The executive control of limitations in Shrikhande method was not possible, and calculation results had many sampling errors even when all the preliminary limitations were in progress. Some modifications of Shrikhande method cannot give correct results (Fig. 1). It is concluded that Shrikhande method cannot be used for genetic investigations and breeding.

When other evaluation methods for genetic variations in plant quantitative traits were tested in experiments on Arabidopsis thaliana (L.) Heynh. and peas (Pisum sativum L.), it was demonstrated, that among express-methods adequate results were obtained by the so-called background trait method (Драгавцев, 1963, 1969), and among traditional ones with generation changes the analysis of variance and regression were recommended [19, 25, 29].

Evaluation of combining ability

Methods developed by Griffing (1956) have been used extensively for analysis of combining ability in many genotypes. However, in tested plants these methods enable to evaluate the genetic specifics of separate traits only, without their relations. As a result, there can be difficulties in the selection of perspective plants, especially if the same genotype has favourable estimation of combining ability for some traits, and negative for other ones. Such a situation was with gerbera [6, 7, 9] (Tab. 1). To overcome these difficulties, multidimensional statistical analysis was applied for the investigations. The possibility to use principal component methods for explanation of diallel cross data has been demonstrated [24] (Tab. 2). In order to make integrated evaluation of separate parental forms, it is required to calculate the component mean estimations of hybrids for each parent. This index is similar to the general combining ability (GCA) on the level of corresponding components; if it is compared with GCA of separate traits, it has the following advantages: 1) the number of tested indices is reduced; 2)

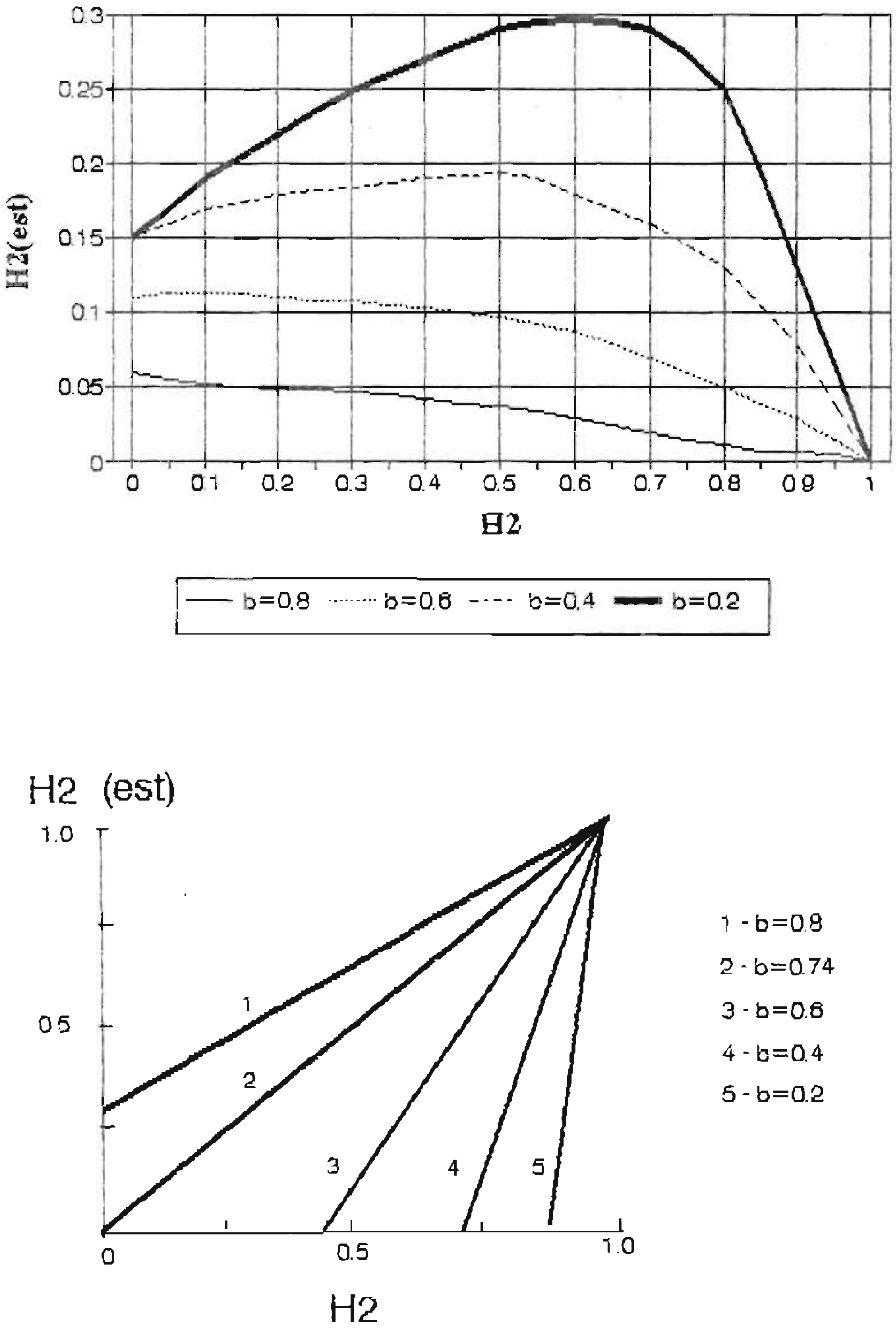

Fig. 1. Heritability estimated by Shrikhande method modified by Рашаль, 1978 (above) and Мартынов, 1977 (below) depending on true heritability.

Table 1

GCA effects of Alkemade race clones of gerbera

Clones	Traits								
	1	2	3	4	5	6	7	8	9
H-4	-2	+2		+3	+4	-5			
H-10		-2	+10	-2	-4	-5	+2	-2	-2
39		-3	-3	-3			-4	+3	
H-11			+2	+5	+4	-5	-3		
30	-4	+5	-5		+6	+8	+4	-5	-5
10		+2	-4	+5		+9	+3		
H-1	+5			-3		-4	-2		
H-17					-4	+2		+3	
24		-5	-1	-5	-4		-4		+2

The figures show how many times the absolute value of GCA effects exceeds its sampling error ("+" - positive GCA values, "-" - negative). Names of traits given in Table 2.

trait interactions are taken into consideration allowing to evaluate variations of a single trait when selection for improvement of other traits is in operation.

Evaluation of trait genetic interrelations

By a set of corresponding methods, the analysis of genetic variation was orientated to the evaluation of genetic interrelations among many traits. The importance of trait correlation levels for plant breeding has been studied [14].

Table 2

Results of principal components analysis
of genotypical correlation matrix of gerbera quantitative traits

Traits	Loadings of principal components			
	I	II	III	IV
1. Productivity	-0.612	-0.183	-0.294	0.578
2. Diameter of inflorescence	0.587	-0.291	-0.544	0.129
3. Diameter of disk flowers	0.690	-0.358	-0.340	-0.296
4. Number of marginal flowers	0.827	-0.171	-0.150	0
5. Width of marginal flowers	-0.145	0.809	-0.464	0.098
6. Length of flower stalk	0.439	-0.517	0.578	0.345
7. Diameter of flower stalk	0.587	-0.291	-0.544	0.129
8. Number of leaves (July)	-0.644	-0.591	-0.248	-0.160
9. Number of leaves (October)	-0.662	-0.547	-0.334	-0.041
% of total variation	40.0	20.7	14.7	7.5

The efficiency of multidimensional statistical analysis was demonstrated for the evaluation of trait interrelations [18-20, 24, 26]. The method of principal component analysis enables to use interrelations of different plant traits to reduce the laborious selection procedures [18]. This approach is based on relatively small but significant "learning" unit of patterns and a detailed analysis of morphological biochemical and physiological parametrs of its specimens. On the basis of these data the structure of examined traits is determined, and the most essential components are picked out. In other tested plants only relatively easy determined morphological indices are analysed on the base of which corresponding component values are calculated, and they are used as a complex trait for evaluation of separate plants. This approach is particularly important in breeding of such perennial plants of vegetative reproduction, for which competition effects at sprout stage are not significant, but early testing for improved plants is necessary.

ANALYSIS OF GENETIC VARIATION IN A EXACT BREEDING MATERIALS

By using the approaches described above, analysis of genetic variation in certain breeding material of many cereals, berry and ornamental plants as well as decidous and conifer trees has been carried out [29]. Information on genetic variation features for several plant species examined, e.g. Italian ryegrass, poplar, black currant, gerbera and others, was either limited or no at all.

In patterns of Italian ryegrass (Lolium multiflorum var. westerwoldicum Mans.), the genetic variation levels of agronomically important traits have been determined according to growing and cutting conditions [13, 20]. It was found out that the highest values of genetic variation were after the 1st cutting. But the study of correlative interrelations showed, that contribution of the 1st cutting to total yield was low, and that the selection of perspective forms had to be realized after the 2nd and the following cuttings.

Carrying out the analysis of variation and correlation in quantitative traits among poplar (Populus) and willow (Salix) interspecific hybrid heterozygous clones and their parents [16, 26], a possibility was demonstred to reduce significantly the trait number examined preliminary excluding traits of little information. In poplar, yield dependence was shown from such indices as internode weight, volume and number, but the mean number of plant shoots did not affect the yield. A possibility was stated to select productive heterozygous clones at early stages according to internode number, internode average length, 3rd internode diameter and the number of leaves. In willow similar to poplar, the highest genetic variation among the quantitative traits examined belonged to shoot and internode weights, 3rd internode length and the number of leaves. These traits can be used for selection of the best willow clones.

In perspective clones of Scotch pine (Pinus sylvestris L.) selected as valuable resin producers, several indices were pointed out at the age of 4-7 years characterizing the growth rate according to growing conditions [27]. A relatively high genetically determined resistance to Laphodermium pinastry was observed indicating to a possibility of early selection according to this trait. In pine the growth rate traits at young age are closely bound with growing conditions, hindering considerably the early genetic evaluation.

In perspective gerbera (Gerbera jamesonii H. Bolus) clones, the level of productivity was estimated as well as that of genetic variation and genotypic correlation of traits determining their ornamental character. Their combining ability was also established [6, 7, 9, 23, 24, 28]. Perspective clones have been selected on the basis of both characters and their complex.

Economical, morphological and biochemical performances of black currant interspecific hybrids Ribes nigrum L. x R. petiolare Dougl. were analysed [17, 18]. Trait correlative complexes have been established. Although a negative phenotypical correlation exists among the bunch length, density, and vitamin content in berries, it is possible to obtain such a genotype where these traits are on a sufficiently high level of expression. Criteria for hybrid early selection have been developed on the basis of trait complex.

STUDY OF GENETIC VARIATION IN PLANT RESISTANCE

Long-term and geographical studies on features of plant immunity genetic variation are very important for both practice and theory. In this respect long-term evaluations of genetic variations related with plant host resistance against one of the most damaging pathogen, barley powdery mildew, and namely, its Latvian population were carried out in barley, the most important grain crop in Latvia. Prior to this no such systematic investigations were done in Latvia or the Baltic region.

To state some race-specific genes in the tested material, and to establish their efficiency alongside with the classical hybridization techniques which is very labour consuming, a method based on hypothesis "gene-on-gene" for plant host and pathogen interactions is in use. For this purpose a special barley (Hordeum vulgare L.) test-assortment has been developed optimal for Latvian conditions and mainly consisting of race-specific resistance genes effective in Latvia and used extensively in selection against barley powdery mildew (Erysiphe graminis DC. f. sp. hordei Marchal) [39] (Tab. 3). In our work, we judged about the genetic structure of pathogen population not on the basis of pathogen race (a combination of virulent genes) structure as described in literature, but on the occurrence frequency of the given virulent gene (Tab. 4). This made it possible to modify the test-assortment excluding less effective (maximally susceptible) testers from it and adding new more perspective lines. This approach made it possibile to compare the genetic structure of pathogen populations of different regions even then if the test-assortments were not completely identical. The basic regularities of genetic variations in Latvian population of barley powdery mildew have been determined [31, 35, 37, 39]. Difference between the features of Latvian population and the populations of this pathogen in other its distribution areas have been documented [39, 40].

A particular attention was paid to the resistance expressions of barley race-nonspecific gene ml-o, as far as no isolate virulent to this gene was found during examination period in Latvia nor elsewhere in the world. However we succeeded to state the difference in agressiveness level in virulence gene of the corresponding pathogene among different isolates of natural origin. Furthermore, expressivity difference among different ml-o alleles has been shown, and some features of gene ml-o expression have been documented at early stages of its development [33, 42].

Table 3

List of test varieties used to analyse
the genetical composition of barley mildew population in Latvia

	Variety/line	Resistance gene	Sources of resistance
1.	Algerian CI 1179	Mla + Mlat	
2.	Rabat (Delta)	Mla	Algerian
3.	Ricardo	Mla3	Ricardo
4.	Gopal	Mla5	
5.	Monte Cristo	Mla9 + Mlk	Monte Cristo
6.	A 222	Mla11	
7.	Emir	Mla12	Arabische
8.	Rupal	Mla13	
9.	Akme	Mla6 + Mlg	Spontaneum
10.	ВИР пр.р. 5196	Mlg	Weihenstephan
11.	Amsel	Mla7 + Mlg	Lyallpur
12.	Klaxon	Ml(La) + Mlk + Mla7	Laevigatum
13.	M66	mlo1	
14.	ВИР пр.р. 5178	Mlp	
15.	ВИР пр.р. 5179	unknown	
16.	Atlas CI 4118	Mlat	

Special approaches of plant inoculation and analysis have been developed for quantitative evaluation of resistance againstn powdery mildew [15]. It has been shown, that the best indicator for characterization of quantitative resistance is the number of pustules on leaf surface area unit. By principal component analysis the importance of factors has been estimated which influence the number of pustules under the given method. Inheritance of race-nonspecific resistance in barley diallel hybrids has been shown as well as the effect of plant hormones on quantitative resistance of different genotypes against powdery mildew [38].

Table 4

Per cent of barley mildew isolates overcoming the corresponding resistance type in Latvia

Source of resistance	Resistance gene	1981	1986	1987			1988		1989		
		Sp	Sp	Sp	Pr	St	Sp	Pr	Sp	Pr	St
Algerian	Mla1	0	0	0	0	0	0	11	2	5	4
Arabic	Mla12	53	100	90	39	45	86	81	66	65	80
Hauters	Mlh	100	100	99	–	–	–	–	–	–	–
Kwan	Mlk	100	95	98	–	–	–	–	–	–	–
Laevigatum	Ml(La)	–	–	–	14	18	10	17	69	60	55
Lyallpur	Mla7	97	78	93	90	82	100	93	93	94	86
Monte Cristo	Mla9	97	87	82	56	85	93	75	82	66	82
Ragusa	Mlra	88	100	99	–	–	–	–	–	–	–
Ricardo	Mla3	41	18	17	17	5	49	7	12	15	10
Rupee	Mla13	–	–	–	10	11	0	9	26	25	21
Spontaneum	Mla6	60	86	93	90	98	95	93	64	74	91
Weihenstephan	Mlg	100	84	99	76	100	85	94	93	100	84

Pr – Priekuļi, Sp – Salaspils, St – Stende (location of sampled isolates).

INCREASE OF GENETIC VARIATION IN PLANTS

Induction of genetic variation in some traits

Most mutations caused by experimental mutagenesis have an unfourable influence on plant development and, therefore, frequencies of mutations perspective for breeding are very low. It is important to develop approaches enabling to increase the contribution of favourable variations. Our attention was attracted by the possibility to use of natural selection for this purpose. Special experiments demonstrated the possibility to unite effectively classical mutagenesis techniques with natural selection in populations [1-5]. In populations treated by mutagenes genetic recombination processes are occuring allowing to form favourable trait complexes and on the other hand, intensive natural selection takes place that eliminates genotypes with reduced competitive ability and vitality. It can be concluded that in such populations the artificial selection should be carried out in sowings of reduced density and no later than 3-4 generations after mutagene treatments.

In recent years the possibility to induce genetic variations in plants by tissue culture (somaclonal variation) has been shown. However, the mechanism of this variation is still unknown, the induced variation range is not clear either, and therefore, there is no consolidated opinion on the perspectiveness of somaclonal variation in breeding. Separate plant species have been studied in various level in this respect, barley somaclonal variation, particulary in field trials is not much studied, and the obtained results are contradictory. Therefore we studied the possibility to cause favorable changes in agroculturally important quantitative traits of barley by plant tissue culture and thus to obtain perspective breeding sources. It was stated that the somaclonal variation level of quantitative traits in regenerated plants obtained from barley calli (induced from both mature and immature embryos) was similar to that one induced by mutagenesis (Tab. 5). Families have been isolated with inherited changes favourable for breeding i.e. reduced vegetation period and shorter stem [41].

Table 5

Variation of plant height in R2 plants

Genotype	MS(B)	MS(E)	G	H^2
Abava families (total)	1736.29***	108.02	68.99	0.394
(imm. emb.)	1567.39***	80.36	44.66	0.381
(mat. emb.)	1613.71***	117.96	69.90	0.379
Sv 64505 families (total)	350.97***	80.98	11.51	0.125
(imm. emb.)	375.49***	57.01	22.91	0.297
(mat. emb.)	364.88***	89.51	8.80	0.090
R2 families (total)	1541.37***	90.98	60.94	0.403

Experimental change of trait interrelationship

There is little information about the influence of mutagenes on interrelationship of quantitative traits, but this is very important theoretically and practically, we have revealed the possibility how to change some correlations of plant traits by radiation and chemical mutagenes [12, 29, 30]. In self-pollinating plants a wavelike phenotypical correlation response to ionized rays has been observed. Low ray irradiation doses reduce the correlative interrelationship of traits but if ray irradiation doses are increased the interrelationship level also increases reaching and even exceeding the controls. The phenotypical correlation changes are shown to be parallel the genotypic ones. To obtain plants with the necessarry trait combination, an approach, has been developed consisting of plant treatment by mutagenes with wide range of doses and the following selection of improved plants. This methods used for hybrids of var. Maja (long stem, well developed roots) and var. Brachytic (dwarf, weakly developed roots) enabled to select lines in which short stem was combined with well developed roots [21]. It means, that we managed to break the positive correlation between stem length and root development. For this reason the described lines were applied for physiological and genetic investigations and, they were donors for short-stem barley breeding [22, 32, 34, 36].

Obtaining of breeding material

The application of perspective barley hybrids F1 and F2 has been studied for obtaining dihaploides by embryo culture techniques in order to obtain sources with recombinations of the most important characters [41]. Dihaploid induction ability was shown to be dependent on various barley genotypes, and the most effective haploproducer clones have been isolated. Dihaploid lines obtained in experiments were given to the breeding stations for further testing; the best ones after trial in 1992 have been transferred to field tests for variety probing.

CONCLUSION

The habilitation work deals with problems of breeding theory an important part of which is evaluation of genetic variation and methods for its increase.

Particular attention has been paid to methods not used previously which enable to study not only genetic variation of separate traits without specifics of other traits, but the genetic and paratypic interrelations of traits as well. The use of this method significantly extends the possibility to interpret the obtained data and allows to expand its practical applications. The use of multidimensional statistical methods, namely principal component analysis, the approaches enabling to evaluate genetically and to select best parents for crossing and improved hybrids have been developed. Working with experimental mutagenesis trait interrelationships were under analysis, and new possibilities were found. Regularities for mutagene influence on correlation changes in plant quantitative traits have been shown, and interesting forms for theoretical and practical use were obtained.

Other nontraditional approaches have also been used. Along with special experiments with plants some express-methods for evaluation of genetic variation have been examined by newly developed models realized in computer. Experimental mutagenesis was combined with natural selection in populations that enables to increase variations important for breeding. Plant tissue culture is shown to be an effective tool for increasing genetic variation. Perspective barley breeding material including dihaploid lines, which have been tested successfully in breeding stations, has been obtained by calli and embryo culture.

Simultaneously with the development of some genetic variation analyses and increase methods, the analysis of genetic variation in certain breeding material was also done. Data obtained in these investigations are important for practical and theoretical use in plant genetics. In this respect agriculturally important quantitative traits were under study in many cereals as well as trees, berry and ornamental plant species (Italian ryegrass, poplar, willow, black currant, gerbera), including such with limited and little knowledge about the genetic variation features or without it. On other hand, long-term evaluations of genetic variation related to plant host resistance against one of the most damaging diseases - barley powdery mildew, namely, its Latvian population was done in barley, the most important Latvian grain crop. No such systematic investigations have been carried out in Latvia or in the Baltic area in general until recently. For this purpose, a new approach for evaluation of genetic structure in pathogen population was in operation, and test-assortment optimal for Latvian conditions has been developed. Features of genetic variation in Latvian population of barley powdery mildew and their difference according to regions has been documented. Approaches enabling to evaluate barley quantitative resistance against powdery mildew have been developed; influence of inherited and environmental factors on the infection degree has been shown.

In habilitation work nontraditional approaches are used for data statistical calculation and induction of trait genetic variation, new methods have been developed for evaluation and increasing of plant genetic variation. By these methods, features of genetic variation have been evaluated in plants of wide range, and new barley forms are obtained used in genetic investigations and breeding.

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