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REVIEWS AND THEORETICAL ARTICLES

High-Priority Research Directions in Genetics and the Breeding of the Sugar Beet (*Beta vulgaris* L.) in the 21st Century

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Abstract—High-priority research directions for the genetics and breeding of the sugar beet in the 21st century were developed with consideration of the available scientific achievements of domestic and foreign scholars. These directions unite the classical and molecular approaches to solving the problems of increasing the effectiveness of sugar beet breeding carried out on a genetic basis, and they correspond to the contemporary level of scientific research. Seven such directions are proposed.

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INTRODUCTION

Breeding of the sugar beet (*Beta vulgaris* L.), the most important agricultural crop, is estimated to have occurred for a little over two centuries. In the first century, conventional methods for classical plant breeding were used: selection based on morphological (visible and measurable) characteristics; then, if necessary, by biochemical, physiological, anatomical or cytological features; and subsequent hybridization of forms with desirable traits. Significant success was achieved in obtaining high-yielding, stable, and high-sugar varieties based on the main achievements of genetics, in particular, those relating to the identification, study, and use of natural mutant forms and, later, the production of synthetic ones. However, further breeding work on the sugar beet was limited to the narrowness of its genetic basis because of the specifics of its origin. An opportunity to study the variability at a molecular level would greatly enhance the prospects for selection and reduce the time needed for a breeder to create varieties. And such an opportunity was provided by advances in molecular biology and genomics at the end of the 20th century, making it possible to perform classical and molecular breeding of the sugar beet in parallel via the interpenetration of their methods. The results of modern research on genetics, genomics, and sugar beet breeding, outlined in a number of monographs published in the 21st century, could serve as the reason for this [1–4]. In these works, however, high-priority directions of genomics related to research on the genetics and breeding of sugar beet, for today and for the future, were not defined clearly. In generalizing the research results carried out by foreign and domestic researchers over the past decade, we have found it necessary to do so, noting the contributions to the development of these directions from scientists of the Mazlumov All-Russia Research Institute of the Sugar Beet as a leading research institution in genetics and sugar beet breeding in Russia.

On a global scale, there are two main directions of this research: classical and molecular. However, in light of their deep interpenetration, it is better, apparently, to present them in more detail. Therefore, we formulated the following high-priority directions of genetics and sugar beet breeding, combining the techniques of classical and molecular studies:

1. Study of the genetic variability of populations and lines, varieties, and hybrids of the sugar beet using morphological, cytological, physiological, biochemical, and molecular markers.

2. Expansion of research on the genomics of the sugar beet. Obtainment and use of molecular markers for the study of its genome, the replenishment of genetic maps of chromosomes, and characterization of the initial forms, varieties, and hybrids, as well as the establishment of a link between certain types of markers and economically valuable traits.

3. Marker-assisted selection (MAS) using molecular markers that allow breeding at the molecular level.

4. Breeding for sugar beet resistance to pests, diseases, and abiotic stresses; a search for the sources of resistance genes; the mapping of resistance genes and their analogs; hybridization with wild-type species that are carriers of these genes; creating hybrids resistant to biotic and abiotic stresses using genetic engineering.

5. A purposeful search for local lesions in genomes (TILLING) as a method that combines the use of induced mutagenesis with molecular methods of

searching for mutations and provides an opportunity to obtain a complex of allelic variants of desired genes to the breeder.

6. Study of the genetic nature of complex quantitative traits of particular economic value and the mapping of loci (QTL) controlling the various stages of formation of such traits, including the use of associative mapping or linkage disequilibrium mapping, as well as the study of features of quantitative trait inheritance by hybrid offspring obtained in different systems of crossing.

7. Study of the epigenetic mechanisms of gene activity regulation during the development of organisms.

1. USING DIFFERENT TYPES OF MARKERS TO STUDY THE GENETIC VARIATION OF POPULATIONS, LINES, AND VARIETIES OF SUGAR BEET

Breeding success is largely provided by the degree of genetic species variability as an object of breeding, which is what determines the importance of its study. This is done using different methods and at different levels. Visual observations are primary; they are based on morphological traits, which serve as markers of the genes that control them, as well as on measured characteristics such as productivity. More than fifty morphological traits are known in the sugar beet [5]. Most of them are neutral, but some have also an important economic value, such as the size and shape of the root and fertility. Forms with the desired manifestation of such traits are taken as input to obtain the corresponding offspring. Thus, fertility is crucial from an economic point of view, since the cultivation of polycarpous varieties requires a significant investment of time and money on the thinning of seeds. One-seeded plants have been identified among many-seeded seeds and were used later to create one-seeded varieties. Selection based on the root form suggests a preemptive use of plants with the shape of the root, providing better cleanability of roots from the ground during harvesting. Such important economic traits as ploidy, cytoplasmic male sterility (CMS), and apomixes were revealed in studies on the cytological and cytoembryological levels. It was found that triploid sugar beet plants were characterized by larger roots and increased sugar content. The use of tetraploids that sometimes occur in seeds of diploid varieties or are created experimentally by exposing the seeds of diploid plants or their apical point to alkaloid colchicine is required to obtain them experimentally. Then tetraploids are crossed with diploids to produce triploid offspring. Triploid and anisoploid varieties, representing a mixture of triploid and diploid forms with a predominance of triploids, were used widely in Europe in the 1970s. Haploids are also of high economic value among genomic mutants, as the dihaploids derived from them are essentially analogous to the pure lines and can be used in breeding for heterosis. Hence, the development of experimental methods for obtaining haploids is important. This was particularly developed in the works of O.A. Podvigina [6, 7], in which haploids were obtained by in vitro cultivation of unfertilized ovules. She developed a method of obtaining homozygous material that enabled us to create 12 restorative lines of sugar beet, which are used in breeding at the Lgovskaya experimental breeding station in Kursk oblast. The ability to detect haploids and homozygous diploids in the offspring of gynogenetic lines was proved in the works of S.I. Maletskiy and E.I. Maletskaya [8].

Since the use of cytoplasmic male sterility (CMS) is the foundation of hybrid breeding for the sugar beet, as well as for many other crops, much attention is traditionally paid to this feature [9]. The work of Herzog and Frish [10] was dedicated to directions and problems of its use, in particular, to the conversion of seed parental lines with CMS using marker-assisted backcrossing. The search for sources of CMS is also very promising. Cytoembryological features that provide CMS in the beet reveal the nature of this phenomenon [11], the use of which in breeding has a large economic impact, avoiding the precastration of flowers during the crossing. Therefore, knowledge of characteristics of generative sphere development in the original forms is mandatory for successful breeding. Thorough research on the reproductive biology of the sugar beet was made by T.P. Zhuzhzhalova et al. [12, 13]. The effect of inbreeding on the formation of reproductive organs was also studied [14].

Sugar content is an important economic feature determined by biochemical methods. Studying variability in morphological, cytological, physiological, and biochemical characteristics, using the data obtained by hybridization of forms with desirable traits, contributed to the creation of many domestic varieties that were widely cultivated in the middle of the 20th century, not only in the Soviet Union; they gained recognition abroad as well [15, 16]. However, at present in Russia, more than 80% of sugar beet seeds are bought abroad [17]. This is not only economically very expensive but leads also to a reduction in the quality of crops, since foreign hybrids are often poorly adapted to local Russian conditions. The reasons compelling today's producers to buy seeds of foreign sugar beet hybrids are different. However, one of the main reasons is that we are behind in the use of molecular and biotechnological methods in sugar beet breeding, which could improve and intensify it. To a large extent, this is associated with the general state of Russian science in an adjustment period that is due to the lack of funding.

In this regard, it is important to know the state of research on the use of molecular techniques in sugar beet breeding abroad, in parallel to what has been done in this regard by our scientists. This issue is con-

sidered in the reviews of A.V. Kornienko et al. [18] and A.K. Butorina and A.V. Kornienko [19].

The development of molecular methods in biology contributed to the formation of a new science—genomics—that deepened our understanding of the molecular mechanisms of heredity. The genome is an assembly of all DNA in a haploid set of chromosomes of the species, in contrast to the genotype as a set of genes having phenotypic expression in a particular organism [20]. During the studying of the genome, genes are considered as a complex system of structures interacting with each other and with the cell membrane.

Jung provides a review of the fundamental information on the analysis of the genome of the sugar beet [21]. The prospects for studying genomic resources of the sugar beet and an estimation of the variability of its varieties and populations using molecular techniques for prebreeding for resistance to various stress factors are considered by Panella [22] and Li et al. [23].

2. DEVELOPMENT OF APPROACHES TO PERFORMING GENOMIC BREEDING OF THE SUGAR BEET

The obtaining of molecular markers (proteins as direct products of gene activity and fragments of the DNA molecule representing the substance of heredity) and their use for the purpose of mapping the genome played an important role in genome research. This was preceded by the definition of linkage groups and making genetic maps of chromosomes as a result of karyotypic studies, hybridological analysis, and calculation of the recombination frequency using morphological markers. However, the number of such markers is limited in contrast to molecular markers. In addition, the use of morphological markers in the breeding of some cultures, for example, the size of root in hybrids of beet and carrot, can often cause system errors, as has been shown in the work of Schaber and Goldman [24]. Protein markers represented by storage proteins and isozymes were originally derived from molecular markers. Since the late 80s, they were obtained and used in the breeding process by scientists from the Institute of Cytology and Genetics of SB of RAS [25, 26], and from 90s they were applied for the certification of sugar beet varieties in the All-Russia Research Institute of the Sugar Beet [27, 28]. Such studies were in progress at the All-Russia Research Institute of the Sugar Beet with the use of DNA molecular markers [29]. This increased the possibilities for studying variability, because they made it possible to study the polymorphism of not only the DNA coding regions but also the noncoding regions, representing the majority of the genome. Currently, different molecular markers are used to study the genome of the sugar beet: RFLP, RAPD, AFLP, SSR, ISSR, SCAR, SSCP, STS, and EST. However, SSR and SNP are considered to be the most informative molecular markers [23]. The results of studying variability using molecular markers, as noted by Eathington et al. [30], are used in the preparation of commercial breeding programs. Upon the obtaining of a sufficient number of markers evenly distributed throughout the genome, the preconditions are made for genomic breeding. Genes of certain economic features were mapped using molecular DNA markers, such as flowering in the first year of life cycle, which is controlled by a dominant gene *B* [31–33], as well as genes of resistance to diseases and their analogs. For mapping complex quantitative traits, as was shown in several studies [34–37], it is desirable to distinguish different stages of the formation of such features and then map the individual loci controlling their genes (QTL). However, beginning with the works of Schumacher et al. [38], it was not possible to make a unified genetic map of beet chromosomes, as the maps made by different scientists did not fit. A possible explanation for this is found in the work of Paesold et al. [39]: the methods used for the identification of beet chromosomes were not sufficiently correct. The small size and similarity in the morphology of the majority of chromosomes in the beet karyotype complicate their identification. It was first performed by the method of densitometry, using two sets of primary trisomics by Butterfass [40] and Romagosa et al. [41]. In contrast, Paesold et al. [39], using high-resolution fluorescence in situ hybridization (FISH), succeeded in obtaining a clear pattern of differential staining of all mitotic and pachytene beet chromosomes and thus in making appropriate adjustments to the existing nomenclature proposed by Butterfass [40].

3. MARKER-ASSISTED SUGAR BEET SELECTION

There are many publications about marker-assisted selection (MAS), which is also called molecular breeding, because of the use of molecular markers [42], since MAS has had broad application in various crops over the last decade. In this case indirect selection of a desired gene is carried out using an associated marker. According to E.E. Khavkin [43], "molecular markers are an effective tool for genetic studies and make a significant contribution to the study of the nature of genes, the mapping of genes and QTLs, and their transfer at transgenesis." Once mapped, a gene for the trait of interest to the breeder and a marker closely linked to it allow the screening of a large number of samples for the rapid identification of sources with the desired trait. The article by Xu and Crouch [44], in which marker-assisted selection using molecular markers in crop breeding was presented from scientific and practical points of view, is of substantial interest. Choudhary et al. [45] consider MAS to be a new approach to improving the yield of crop plants. Hospital et al. [46] note the difficulty in ensuring the effectiveness of MAS. MAS applied to the sugar beet is cov-

ered by the article of McGrath [42]. This author believes that MAS is ancillary to the classical methods of breeding, but Camerton [47] sees the future of sugar beet breeding in the selection of genes (using molecular markers). In our view, it is impossible not to agree with McGrath [42] on this subject, which is generally supported by both Biancardi et al. [1] and Draycott [2]. With all of the positive value of molecular methods, they can maximize the effectiveness of breeding only in combination with other methods of selection and the evaluation of breeding material. Theoretical and practical aspects of molecular sugar beet breeding at the present stage were observed in the article of Kornienko and Butorina [48].

Specification of the molecular markers of the original forms for hybridization and obtained hybrids based on molecular markers [29, 49, 50] was carried out in All-Russia Research Institute of Sugar Beet as one of the main stages of MAS, according to the scheme shown in Figs. 1–3.

Authors [29, 49, 50] compiled for the first time genetic formulas on the basis of RAPD profiles of genomic DNA obtained with single primers PAWS 5, PAWS 6, PAWS 16, PAWS 17, thus making possible molecular and genetic identification of the breeding material of the sugar beet. Using these primers genetic distances were identified, and clusterization for 33 combinations of crosses was performed, which enabled the most reasonable selection of parent components of sugar beet hybrids.

4. BREEDING OF SUGAR BEET FOR RESISTANCE TO ABIOTIC AND BIOTIC STRESSES

It is necessary to point out the special importance of sugar beet breeding for resistance to biotic and abiotic stresses at the present time. The critical importance of a comprehensive study of genomic resources for breeding crop plants for resistance to abiotic stress in the context of global climate change is noted in the review of Banzal et al. [51]. Different approaches are used in breeding for resistance, and in this case it is very important to identify resistance genes and their sources. A number of resistance genes were identified in the beet, for example, resistance to rhizomania, one of the most dangerous sugar beet diseases, and also to powdery mildew, cercosporosis, and root rot (caused by *Aphanomyces root rot*) [52]. In this case very interesting and valuable data were obtained; they show that the major genes of resistance to diseases in the sugar beet are clustered on chromosome III. A search for sources of resistance and use of the potential of wild ancestors to improve it are conducted widely abroad [53], where genes of resistance to various diseases were also mapped [54–57]. It was noted that the identification of molecular markers flanking the genes of resistance to pathogens, located at a distance of less than 5 cM, will help to speed up the transfer of these genes during closely related and remote crossings and transgenesis, as well as to provide an opportunity to conduct breeding for several genes of resistance to the same pathogen.

Genetic approaches to the long-term pest resistance in the sugar beet based on the use of molecular markers were developed by Zhang et al. [58] on the example of the most common and harmful insects.

In Russia, M.A. Bogomolov [59, 60], using irradiated pollen, carried out a series of works on interspecific hybridization of the sugar beet with the wild species of *B. corolliflora* and *B. trigyna*, which are carriers of resistance genes, in order to create breeding material resistant to biotic stresses. Homozygous apomictic lines were obtained and embryological features of their formation (diplospory) were identified. It was proved experimentally that the apomictic method of seed reproduction, in combination with hybridization, selection, and molecular marking, is an effective way to accelerate the creation of stable sugar beet hybrids on a fundamentally new basis. This made it possible initially to develop a method of homozygous line creation (see Fig. 4) [61] and to build on this basis original technological schemes for using apomictic (AP) lines in the breeding process.

In one case, apomictic gamma-lines with sterile pollen are used as the parent component in hybridization according to the scheme: $AP_{mm}\gamma$-MC × HPP (heterosis polyspermous pollinator) ⟶ $F_1AP_{mm}MS$ ⟶ $F_2AP_{mm}MS$.

In another case, self-fertile (Sf) apomictic lines are used as fixers of sterility with simultaneous transfer of apomixis genes to MS-lines according to the scheme: γ-MS_{mm} × $AP_{mm}Sf$ ⟶ $F_1AP_{mm}MS$ × HPP ⟶ $F_1AP_{mm}MS$ etc., thereby creating highly productive hybrids of sugar beet PMC-90, Vityaz, etc.

When we use apomictic lines as MS components in the cycle of hybrid creation, we exclude steps associated with the stabilization of lines on morphological features, the analysis of general and specific combining abilities, and the need to fix sterility in MS forms.

Transgenic resistant forms of the sugar beet [62] were obtained also at the All-Russia Research Institute of the Sugar Beet by agrobacterium-mediated transformation with mf_2 and mf_3 genes, which control the resistance to pathogens. The product of the used mf_2 gene is a thermostable low-molecular protein (CSP) isolated from cellular extract of *Bacillus thuringensis*. The mf_3 gene encodes a thermostable low-molecular protein—microbial factor (MF3), which isolated from a cellular extract of *Pseudomonas fluorescens*. It has a high degree of homology with peptidyl-propyl cis-trans isomerases of FKBP-type [63]. The action of mf_2 and mf_3 genes lies in the induction of protective mechanisms of a plant rather than in the direct inhibition of phytopathogens. Transgenesis of target mf_2 and mf_3 genes, carried out on the sugar beet [64], allowed the selection of seven transgenic plants with the mf_2

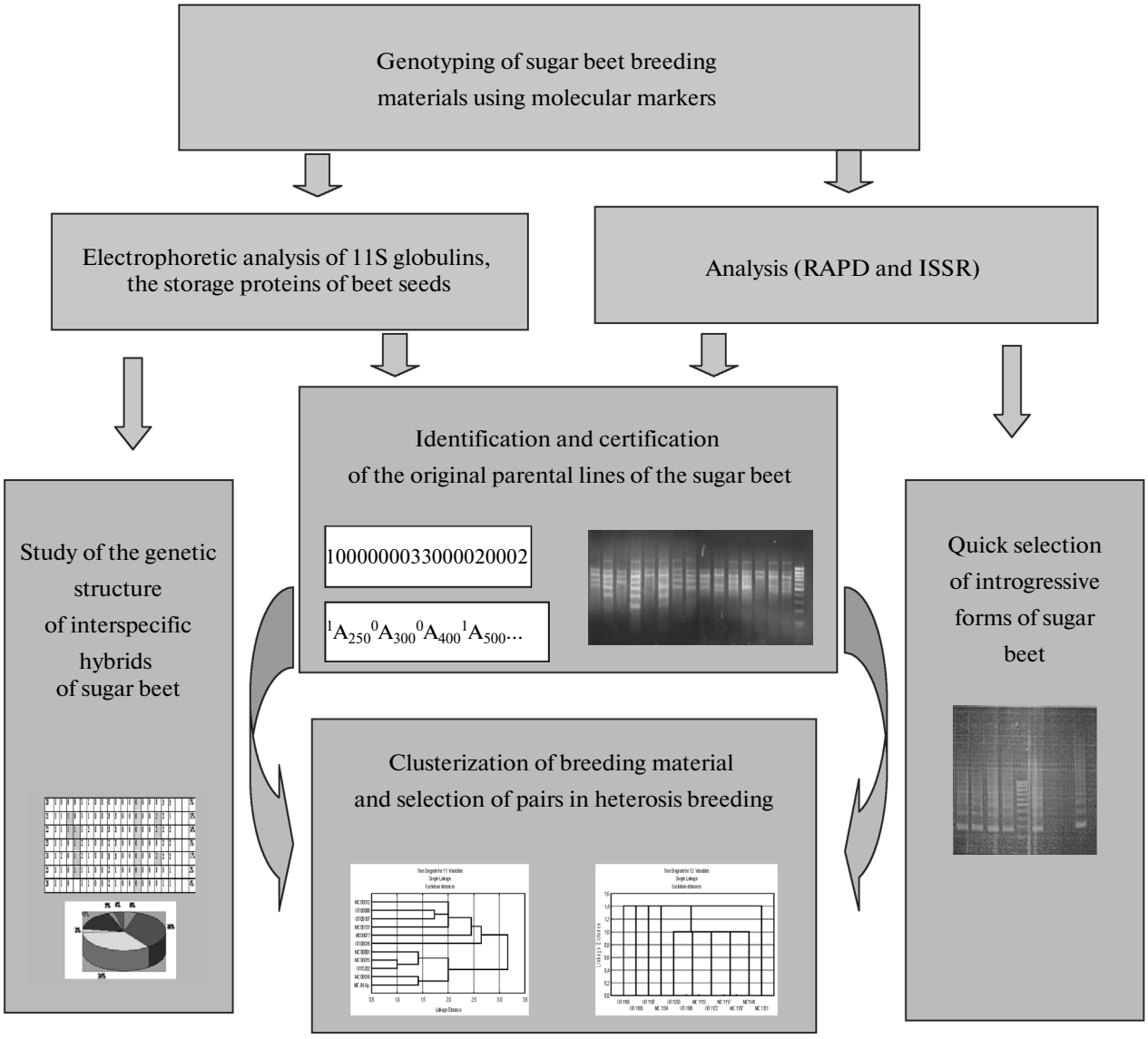

Fig. 1. Use of molecular marking in the breeding process of the sugar beet.

gene, in which a fragment of a corresponding size of 20 bp was amplified, as well as eight plant transformants with the mf_3 gene and a DNA amplicon of 400 bp. PCR analysis of the created transgenic plants with primers PAWS 5, PAWS 6, PAWS 16, and PAWS 17 showed significant differences between control and test plants, which were manifested in the form of specific additional bands in samples of their DNA. Identified structural changes in the genomic DNA spectra of transgenic sugar beet plants indicate the heterogeneity of genetic material, which is likely due to the different integration of mf_2 and mf_3 genes in the genome of experimental samples. Phytopathologic evaluation of transformants by treatment with a spore suspension of *Fusarium solani* + *Fusarium oxysporum* did not find any violations in their development, while the growth and development of control plants was retarded by 2–2.5 times.

5. INCREASE IN ALLELIC DIVERSITY OF GENES FOR SELECTABLE TRAITS IN THE SUGAR BEET

The presence of allelic diversity for traits on which selection is conducted plays a crucial role in plant breeding. In this regard, the method of targeting induced local lesions in genomes (TILLING) acquired a particular value; it was developed in the early 20th century and is based on the use of traditional mutagenesis in conjunction with the method of evaluating obtained molecular mutant forms. This implies, according to the creators of the method McCallum et al. [65], the determination of point mutations in

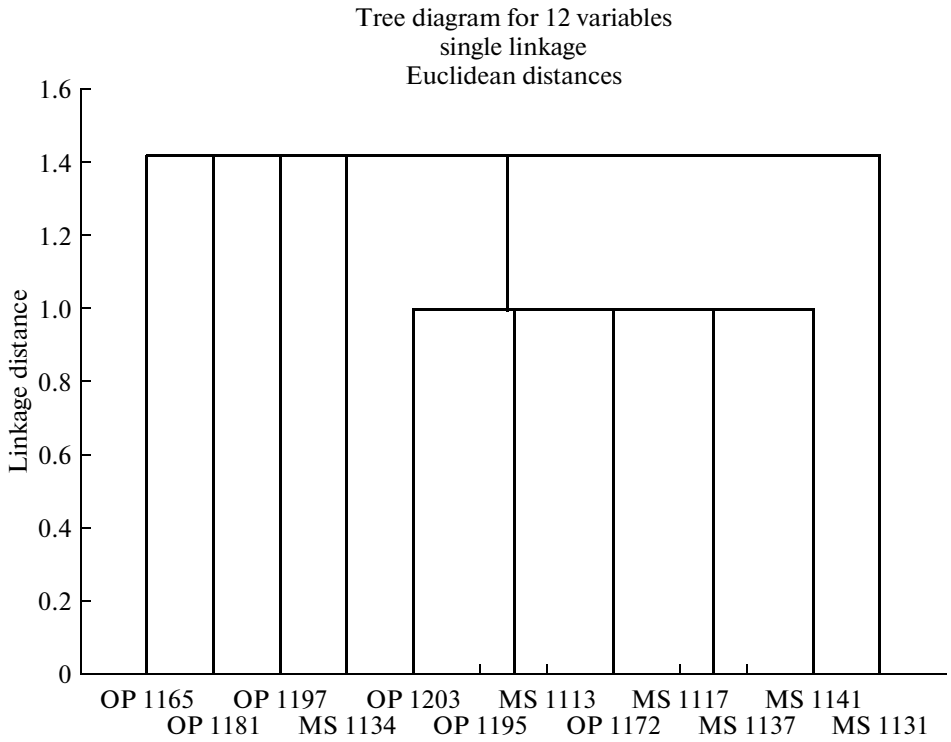

Fig. 2. Dendrogram of genetic distance between the original lines of sugar beet by protein markers.

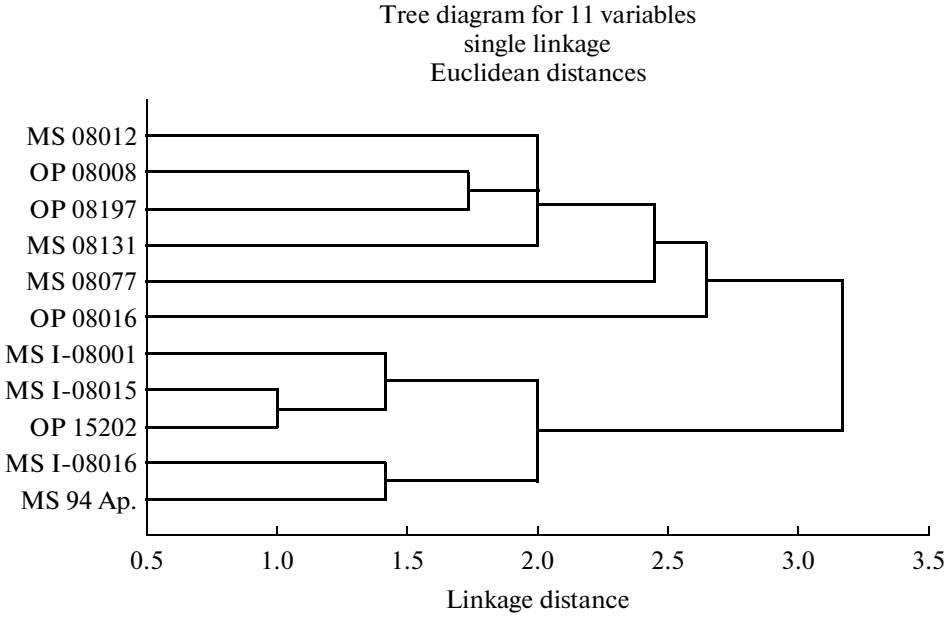

Fig. 3. Dendrogram of genetic distance between the original lines of sugar beet by DNA markers.

specific genes within large populations. Beginning with the works of McCallum et al. [65], which were successfully continued by Comai and Henikoff [66], the TILLING-method as a tool for reverse genetics is used to identify single nucleotide polymorphisms (SNPs) in the target loci of DNA sequences, leading to the emergence of new alleles. In this regard, it became widespread in the breeding of many crops [67], including the sugar beet [68–71]. Mutagen ethyl methane sulfonate (EMS) has been applied most successfully to obtain M0 mutant populations, and a collection of EMS-induced mutants was created, partic-

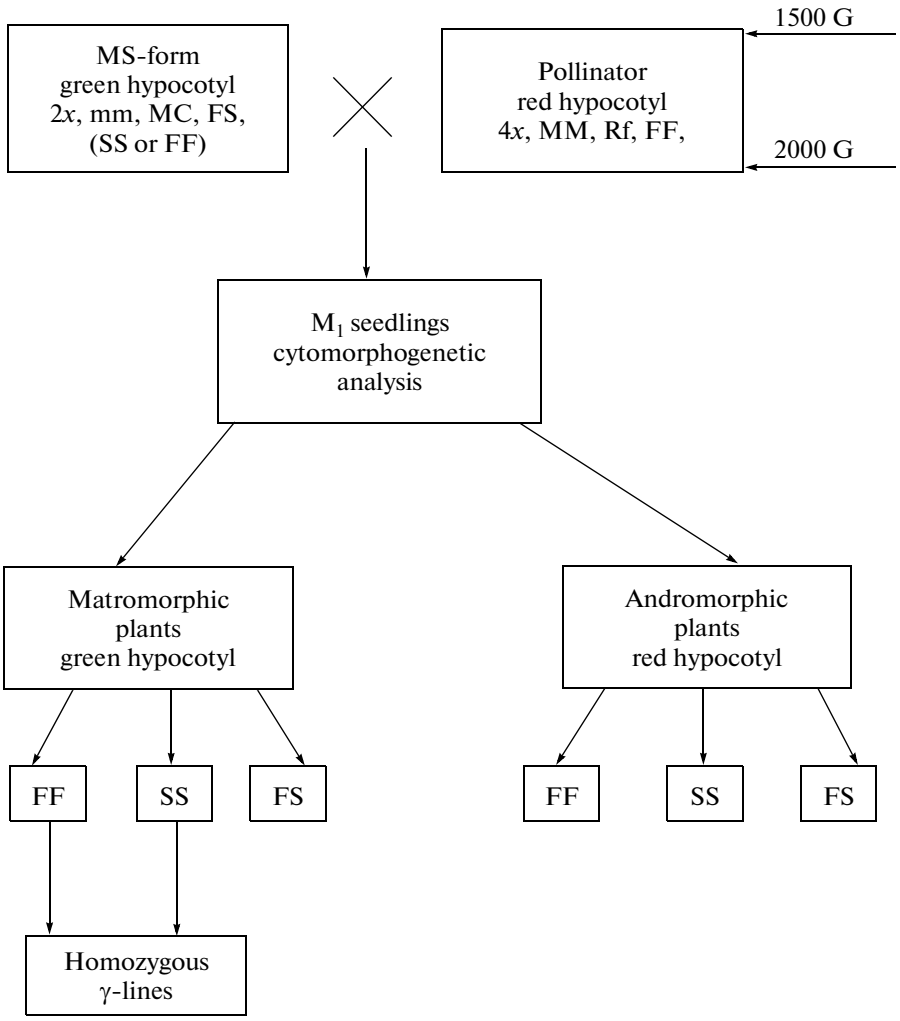

Fig. 4. Scheme of obtaining homozygous γ-lines of sugar beet 2*x*, 4*x*—diploid, tetraploid; mm—dioecious form (one-seeded), MM—multifetal form (polyspermous); MS—male sterility, Rf—fertility; FF, SS—homozygous state of *Me1* marker gene, controlling NADP-dependent malate dehydrogenase enzyme; FS—heterozygous (hybrid) state of *Me1* gene.

ularly for gene *B*, which controls the release of flowering shoots in the first years of life. It allowed the establishment of the varying activity of gene *B*, which is associated with different mutational events, and new loci that are responsible for this trait but not linked to gene *B*.

The necessary preconditions for applying this method were created at the All-Russia Research Institute of the Sugar Beet in the works of A.V. Kornienko [72] on induced mutagenesis in the sugar beet: the mutagenic activity of various physical and chemical factors that determine the optimal treatment regimes of plants was tested, and M0, M1, M2, ... Mn populations were created. The possible use of previously obtained results for the development of a TILLING-project is discussed in an article by A.B. Kornienko and A.K. Butorina [73]. Eco-TILLING, which is used to detect point mutations in the mutant populations, is an adapted technology of TILLING. Frerichmann et al. [74] used Eco-TILLING as a quick and easy method for the detection of rare SNPs and small deletions in the target genes in natural populations of the sugar beet. Endonucleases, such as CELI, are used in Eco-TILLING to cut sites with mismatches (errors of nucleotides pairing) in a DNA heteroduplex that is formed by the hybridization of different genotypes in the test panel. It is an effective technology by price, because sequencing is limited to the individual genotypes representing each different haplotype. Eco-TILLING was used for the characterization of genetic variability and for an establishment, based on candidate genes, of new alleles responsible for resistance to biotic and abiotic factors in a number of plant species. However, Frerichmann et al. [74] reported about Eco-TILLING in the sugar beet for the first time. The authors substantiate in detail the expediency of its use. The beet is currently cultivated in regions with a temperate climate; its seeds are sown in April and the roots

begin to be harvested in September. An increase in the productivity of this crop is possible by sowing seeds in the fall, i.e. using the seeds of the so-called "winter beet." However, a "winter beet" should have sufficient winter hardiness and an appropriate monitoring system for bolting (stem lengthening) for its development. Both require knowledge of genetic regularities subjected to the manifestation of these symptoms and their genetic variability. The main limiting factor for the formation of a yield of "winter beet" is the later formation of the rosette of leaves. One of the strategies to overcome this feature is the search for and obtaining of forms in which a closed rosette of leaves is developed in early spring after winter sowing.

6. STUDYING THE GENETIC NATURE OF QUANTITATIVE ECONOMICALLY VALUABLE TRAITS IN THE SUGAR BEET AND FEATURES OF THEIR INHERITANCE BY A HYBRID OFFSPRING

The great contribution of Schneider et al. [34], Setiawan et al. [35], Grimmer et al. [36], and Stevanato et al. [37] to the study of the genetic nature of complex quantitative traits in the sugar beet should be noted. Mapping quantitative trait loci, including associative mapping, has received much attention in recent years [75–79]. An important role is played by the accumulation of EST-markers, i.e. expressing the DNA sequences of genes, which are obtained by reading the cDNA from a gene's mRNA using reverse transcriptase. The catalog of expressed genes is made via the sequencing of cDNA libraries. cDNA clones are compared with the nucleotide sequences available in the database, and similar functions are attributed to investigated genes according to the high similarity of DNA sequences of expressed genes with known functions. According to Laurent et al. [80], the National Bank for Biotechnology Information (GenBank, www.ncbi.nlm.nih.gov) has over 20000 ESTsthe isolated from sugar beet; access to them provides a reserve for the identification of genes. An extremely important issue—studying the inheritance of complex quantitative traits by a hybrid offspring with different systems of crossing—was studied by Kornienko and Orlova [16], Kornienko et al. [81] Bogomolov and Fedulova [82], and Oshevnev and Gribanova [83]. It has been shown on the example of beet apozygotic offspring that an important role in the inheritance of traits, in addition to the composition of genes and their interactions, is played also by the spatial organization of the nucleus, the connection of chromosomes with the cell membrane, polyteny, and diminution of excess chromatin, which belong to the epigenetic mechanisms of inheritance [84–86].

7. STUDYING EPIGENETIC MECHANISMS OF GENE ACTIVITY REGULATION DURING THE DEVELOPMENT OF ORGANISMS

It was established in the middle of the 20th century that observed deviations from the expected results of Mendelian trait segregation in hybrid offspring may be due to epigenetic inheritance, i.e. inheritance of the functional state of gene, "which varies with the development of the individual and is not associated with a sequence of nucleotides but depends on histone modifications and DNA" [87]. The discovery of molecular mechanisms of epigenetic variability provided an opportunity to use the results of its study in breeding. One such mechanism, the methylation of a DNA area including a specific gene, was discovered by B.F. Vanyushin [88]. Methylation leads to the fact that this gene does not function. A stable and heritable modification occurs, which is reversible under the influence of demethylating agents or epimutagens [89]. Members of the Institute of Cytology and Genetics of SB of RAS, where research on the epigenetics of the sugar beet were developed for the first time in Russia, observed a change in the ratio of phenotypic classes in the hybrid offspring from that expected according to the laws of classical genetics, after treating the buds of hybrid plants with 5-azacytidine and Triton 100 epimutagens [90, 91]. E.I. Maletskaya et al. [90] studied the effect of 5-azacytidine on the morphogenesis of flowering shoots and the type of bush in the sugar beet and noted an increase among hybrid offspring in the proportion of plant phenotype with separate flowers as a result of the change in the process of plant metamerisation. Changes appearing under the influence of epimutagen are inherited via apozygotic plant reproduction. This makes it possible to regulate plant phenotypes, which is important for breeding [92]. Mechanisms controlling differential gene activity include also modification processes associated with DNA histones. The main types of modifications, in addition to histone methylation, are acetylation, phosphorylation, and ubiquitination of the N-terminal ends of the molecules of the core histones (H2A, H2B, and H4) constituting the nucleosome. This leads to changes in the nucleosome conformation and, consequently, the availability of DNA for the enzymes [87]. Such modifications are designated as histone code [93], which can also be defined as the complex of signals exposed on nucleosomes [94]. Thus, the nucleosome is the main epigenetic signaling system, and epigenetics, through the results of molecular and cytological research, is able to explain the facts that do not fit into the framework of inheritance regularities established by classical genetics. In a recent review dedicated to the role of epigenetics in the manifestation of heterosis in plant hybrids, Groszmann et al. [95] indicate that the expression of genes in hybrids is affected not only by the interaction of genomes of parental forms but by their epigenetic systems too. They also note the importance of the interaction of small RNA mole-

cules, which are capable of changing methylation patterns, in the manifestation of epigenetic variability. Thus, it can be argued that all of the factors that alter methylation patterns affect the activity of genes and cause epigenetic variability.

Problems associated with the current state and prioritized directions of the development of genetics, epigenetics, breeding, and crop seed production were discussed at the XI International Genetic and Breeding School-seminar conducted by the Siberian Institute of Plant Breeding and Agricultural Sciences in Krasnoobsk on April 9–13, 2012. Four of the presented reports were devoted to the sugar beet [96–99] and concerned the results of original research carried out in certain directions. However, as A.V. Kornienko remarks, only comprehensive studies carried out on all of the aforementioned high-priority directions using the gene pool from VIR and other institutions, with consideration of the obtained results of theoretical and methodological studies and their coordination and cooperation, can provide the most efficient development of genetics and breeding of the sugar beet in the 21nd century [100].

All of the considered high-priority directions of research in the genetics and breeding of the sugar beet demonstrate the feasibility and economic benefits of the organization of breeding works at the molecular-genetic basis. This, in particular, is reflected by the fact that there are still few works on the determination of the cost of such studies [101].

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